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GREATER YELLOWSTONE PREDATORS

ECOLOGY AND CONSERVATION IN A CHANGING LANDSCAPE

PROCEEDINGS OF THE
THIRD BIENNIAL CONFERENCE ON THE GREATER YELLOWSTONE ECOSYSTEM
YELLOWSTONE NATIONAL PARK
SEPTEMBER 24-27, 1995

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Proceedings of the Third Biennial Conference on the Greater Yellowstone Ecosystem

Greater Yellowstone Predators: Ecology and Conservation in a Changing Landscape

September 24-27, 1995
Yellowstone National Park, Wyoming

Edited by
A. Peyton Curlee,
Anne-Marie Gillesberg and
Denise Casey

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PREFACE

The spectacular geology of Yellowstone country was the stimulus for the creation of our first national park; yet its bears, and more recently wolves, have played an integral part in making Yellowstone one of our best loved destinations. Now that wolves have been reintroduced, it is fitting that we look at the role of predators in the Greater Yellowstone Ecosystem. Yellowstone is one of the few areas in the lower 48 states that appears to have all the top predators that occurred prior to European settlement. The landscape is of course very different today, and the abundance and distribution of organisms are also different, undoubtedly; yet it is rare to have the opportunity to study the relationship between such a diverse array of top predators, lower trophic level consumers, and producers. Some of the most globally important large carnivore research has been conducted in Yellowstone. In his summary address at the end of the conference, Dr. Mark Boyce said that the focus on "Greater Yellowstone's Predators strikes at the very core of what Yellowstone is all about" (Boyce *this volume*). The Greater Yellowstone Ecosystem will continue to be an exciting and instructive focus of scientific query as we seek ways to balance human uses and influences with the needs of wildlife and wildlands.

These proceedings of the "Third Biennial Scientific Conference on the Greater Yellowstone Ecosystem" offer a glimpse of the rich history of Yellowstone predator research. Presentations over 2 days reflected a wide range of ecological themes, from demographics and behavior to systematics, and even included several social science studies. There was also a surprising number of predator species covered — e.g., ravens, salamanders, and spotted frogs!—though medium and large carnivores predominated, as expected. For a more comprehensive view of carnivore research in Yellowstone, *Carnivores in Ecosystems: The Yellowstone Experience* (Clark et al. 1999, Yale University Press) is based on a special symposium on the third day of the conference.

These proceedings are divided into 3 parts. Part I includes all but 1 of the keynote or invited talks from the conference (in the order in which they appeared). Paul Schullery's talk sets the stage with his look at the evolving social and political views of Yellowstone bears. Stephen Herrero's talk from the Superintendent's International Luncheon follows, in which he speaks of how "love of wild nature" keeps researchers, managers, and citizens working against difficult odds to preserve predators and other wild creatures. Next is a paper based on Steven French's talk and his research with Marilyn French and Ryk Ward, examining the potential of genetic research to help conserve Yellowstone's grizzly bears. We would have liked to include Daniel Janzen's keynote address about the role of predators in ecosystems around the world, but we were unable to translate his well-illustrated

slide presentation into an easily understood black-and-white transcript for the proceedings. Finally, Mark Boyce summarizes the many paths yet to explore as we seek a greater understanding of Yellowstone predators and become more adept at learning what they need to survive.

Following the keynote and invited talks, Part II includes 15 of the 56 papers and posters that were presented at the conference and later submitted for inclusion in the proceedings. These papers underwent peer review by numerous dedicated reviewers who have chosen to remain anonymous. Thank you for all your help. Extended abstracts that summarize various papers and posters presented at the conference appear in Part III of these proceedings.

On behalf of the 2 hosts of the conference, Yellowstone National Park and the Northern Rockies Conservation Cooperative, I would like to thank the people and organizations that made the conference and proceedings possible. The program committee (including a social sciences subcommittee) labored long hours to review submissions and put together a cohesive conference. Special thanks to Hank Harlow for his hard work as Chairman and moderator. Len Ruggiero, Mike Ivie, and Peter Gogan also went the extra mile by serving as moderators. The conference and proceedings would not have been possible without the generous assistance of the many sponsoring organizations and individuals listed in the front of these proceedings. A matching grant from the National Fish and Wildlife Foundation was especially crucial for this project.

I would like to offer special thanks and recognition to John Varley and Paul Schullery, who chose the conference theme and who, along with the staff of Yellowstone National Park's Center for Resources, work to support research and learning through programs such as the biennial Greater Yellowstone Ecosystem conferences. The following staff of Yellowstone National Park and the Northern Rockies Conservation Cooperative spent long hours helping to produce the conference and proceedings: Lisa Albert, Norm Bishop, Wayne Brewster, Sarah Broadbent, Bob Chambers, Tim Clark, Renée Evanoff, Mary Ann Franke, Carrie Gray, Bob Lindstrom, Lauryl Mack, Joy Perius, Julie Rehmer and Bo Ross. Renée Evanoff's beautiful cover art and Becky Woods' artistry with page design turned a bunch of manuscripts into appealing proceedings. Two people should receive special commendations for their work on the conference: Sarah Broadbent, for her logistical wizardry, and Paul Schullery, who was an inspired and inspiring maestro.

A. Peyton Curlee

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Part I: Keynote Presentations and Invited Talks

Yogi Lives: The Evolving Image of the Bears of Yellowstone

Invited talk given evening of the Opening Reception
September 24, 1995

PAUL SCHULLERY
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Our society has invested the bear with a multitude of personalities (Figure 1). The bear is, among many other things, a cuddly childhood friend with a heart-shaped nose, a fighter of forest fires, Wall Street excitement, the Russian people, an outdoor magazine monster, and a filcher of picnic baskets. Most cultures that have dealt with bears have done the same (Shepard and Sanders 1985, Campbell 1988). Human culture apparently finds a great deal to work with in the image or idea of the bear, and takes the symbolism of bears many directions at once.

One of the foremost textbook examples of this complex relationship is provided by the Ainu people of Northern Japan, who for centuries, and as recently as the early decades of the 1900s, maintained an elaborate ceremonial relationship with their native brown bears (*Ursus arctos*, Shepard and Sanders 1985, Campbell 1988). A newborn cub was captured and given to one of the women to nurse and raise with her own children. When it reached a certain age, it was then sacrificed in an involved ritual that concluded with the bear's remains being the guest of honor at a feast of its own meat.

Figure 1: Turn-of-the-century cartoon of Yellowstone bears (Smith 1909).

At first glance, such a ritual may seem to us either bizarre or barbarous, but in the bear literature of North America there are episodes hardly less striking, such as the account published in William Lyman Underwood's book *Wild Brother* (Underwood 1921). Underwood told the story of a Maine logger who captured a newborn cub and gave it to his wife to raise; the book features a photograph of the woman nursing the cub alongside her own infant daughter (Figure 2).

Native American relationships with bears and their images of these animals are likewise complex and individual. Though popular perception deals with these relationships in generalities, as in "Indians considered bears to be their brothers. . . ," in fact, different groups and tribes developed their own unique bear beliefs, which, though often containing some common threads, are locally distinct (Rockwell 1991). It seems safe to assume that distinct regional ecological settings were an important factor in the origination of local beliefs.

If we late 20th Century Americans have inherited or absorbed any aspect of Native American attitudes toward bears, it may be the recognition of the bear's force as a spiritual presence in wild country. Our own literature and folklore often has featured the bear as an almost mythic creature (Utley et al. 1964). By the time of the publication of Thomas Bangs Thorpe's "The Big

Figure 2: Underwood's 1921 book featured this photograph of the backwoodsman's wife nursing her own child and an orphaned black bear cub. The woman's handwritten note reads "Mr. Underwood took this picture of Ursula and Bruno and me with my consent and I am glad to have him use it in this book. Bruno's Foster Mother" (Underwood 1921).

Figure 3: A woodcut illustration from Davy Crockett's Almanack (1837), showing a woodsman with dog using an axe to fight a werewolf-type bear (Schullery 1988).

Bear of Arkansas" in 1841, the American bear story already had most of the elements it contains today: danger, humor, anthropomorphism, convoluted adventure, and a bear of near-mythic stature (Thorpe 1841). What has changed over time is not so much the various things the bear means to us as the relative emphasis we have placed on these things in our dealings with real bears.

Euro-Americans have dealt with North American bears since the beginning of our settlement of the continent, but much of what became established as our own folklore, especially relative to the grizzly bear (*Ursus arctos*), originated with early survey parties and other explorers and adventurers. Lewis and Clark's encounters with grizzly bears have been quoted and retold by generations of historians and popular writers, with the foremost emphasis on the aggressiveness of the bear. Lewis and Clark and other early writers portrayed the grizzly bear as almost invariably belligerent, attacking humans on sight. In fact, a review of the first-hand accounts of early 19th Century travelers in grizzly bear country suggests that the bears usually only displayed such aggression after having been shot, or having been surprised at short range with food or cubs. Late 19th Century writers often claimed that grizzly bears "learned" to avoid white men's rifles and became less belligerent, but it is more likely that if any change did occur in bear behavior it was the result of the most aggressive bears being selected out of each generation by hunters, resulting in more cautious animals (Schullery 1988, Herrero 1985).

The Bear as Evil Wilderness

Of the many traits of the bear that were at work in stories like Thorpe's "Big Bear of Arkansas," the one that seems to have dominated 19th-Century thinking was its ferocity, or at least its animosity toward humans. At the hands and pens of many early writers, the bear lent symbolic evidence to the view of wilderness as a place of evil: an untamed, unsafe place that only a courageous and skilled band of Crocketts and Boones could claim for society by wiping out the menace.

Published illustrations from the era when Crockett was spinning his tall tales and the frontier in question was the Mississippi Valley suggest the rich mixture of characteristics already given to the bear by our society. A woodcut from Davy Crockett's Almanack (Figure 3) captures much of this mood. While woodsmen struggle to kill a huge bear, their friend in the lower right corner engages in a standoff of overwhelming symbolism. He faces the bear with his companion, a dog—the consummate "good" domesticated animal—by his side. His weapon of choice is the great symbol of the taming of the wilderness, the axe. Perhaps even more important, what in Tennessee and other midwestern states would be a black bear (*Ursus americanus*) becomes a creature of obvious demonic personality. The elongated snout features crocodilian teeth, the eyes have lost the round neutrality of real bears' eyes, the ears are sharply pointed, and the paws

and claws are distorted into alarming and menacing proportions.

But even at this early date, the bear was not simply a devilish monster. The various memoirs published under the name of "Grizzly Adams," whose actual name was John Adams, revealed an animal susceptible to human control (Figure 4), if not entirely tamable. Adams' stories, and those published in his name and about him, excited any number of young would-be bear hunters, including William Wright, who would later become both a legendary bear hunter and one of the first serious bear naturalists (Wright 1910, Schullery 1988).

Even more convoluted was the image of the bear as portrayed in an extended article in *Harper's New Monthly* in October of 1855 (Figures 5 and 6). In these images, bears are bipedal and obviously sentient, capable of complex tasks of theft, and hold wilderness "bear dances" as part of their ursine society. Presented in one of America's leading periodicals as straight-faced natural history, such images contrast sharply with the sadder reality of what most people who lived in bear country felt about the animals: that they must be destroyed as rapidly as possible.

Destruction was the watchword for most dealings with bears throughout the 19th Century, and the war on bears, whether conducted for sport or simply to rid the countryside of a troublesome competitor, generated some remarkable figures of folklore if not history. The southern states, perhaps the leading sporting region in the United States prior to the Civil War, developed the bear hunt into an event only slightly less involved than the Ainu ritual described earlier (Figure 7). Bear hunts lasted weeks, and were supported by large numbers of slaves and other attendants in an event rather like a rough-and-ready version of the British foxhunt. The resemblance to the foxhunt was no coincidence, as many southern sportsmen felt a direct connection to their Old World forebears in matters of sporting technique and ethics. Among the many regional figures to emerge from this tradition was a former slave named Holt Collier (Figure 8), who in the closing decades of the 19th Century became one of the most famous houndsmen in the South, and who was in on the kill of more than 3,000 black bears (Schullery 1988). Collier witnessed the decline of the wilderness world of the southern black bear, attributed more perhaps to the destruction of habitat that accompanied settlement than to his sportsmanship and that of his friends.

The Yellowstone ecosystem had its own famous bear hunter, Colonel William Pickett (Figure 9), a Confederate veteran who moved to the Greybull, Wyoming, area in 1876 and hunted grizzly bears passionately and with devastating effect for more than 20 years. Pickett killed more than 70 grizzly bears in his career, including 23 in 1881 alone (Schullery 1988). We are appalled at numbers like these today, thinking as we do in modern terms of an ecosystem in which every bear is precious. But we must remember who Pickett was; he was a man of his time, doing what all of his neighbors certainly regarded as God's work. Grizzly bears were not only considered dangerous and competitors for

Figure 4: "Grizzly" Adams claimed that his tame grizzly bear defended him from a wild bear (Hittell 1860).

Figure 5: A bipedal black bear stealing vegetables (Anonymous 1855).

Figure 6: A "bear dance," offered as serious natural history (Anonymous 1855).

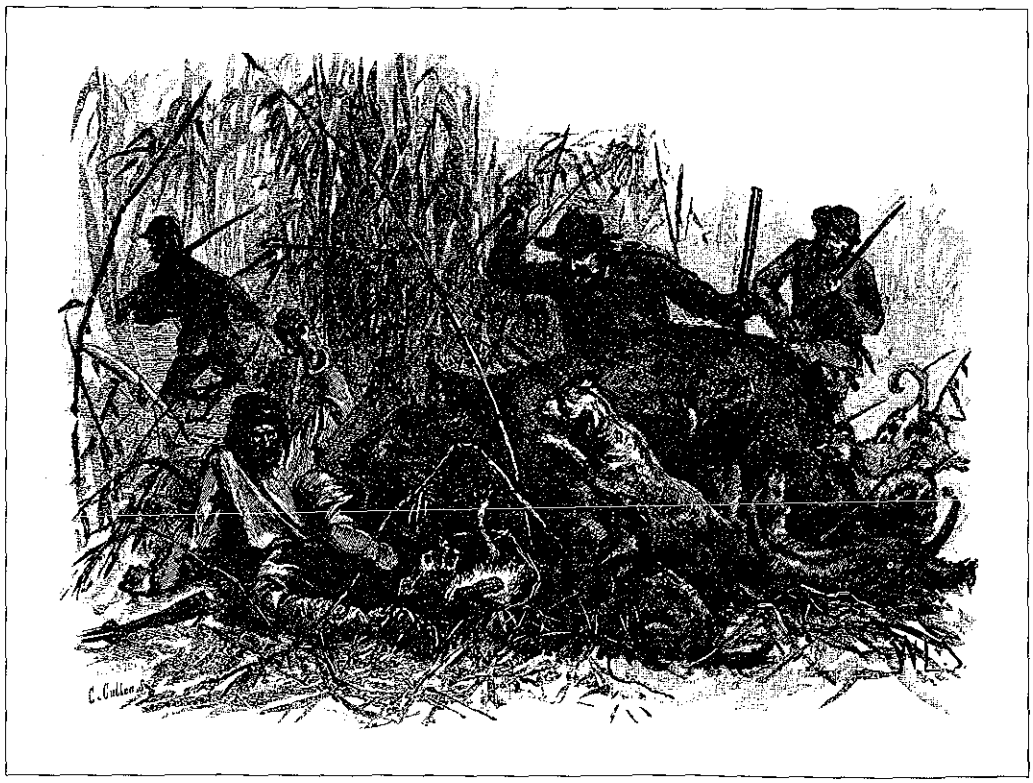


Figure 7: Bear hunting in the Old South was a rough-and-ready version of the British fox hunt with a large supporting cast of slaves and attendants and extended chases through rugged country (Meyer 1883).

wild game, they were seen as an intolerable threat to livestock (Figure 10). Pickett was greatly admired, and no less a conservationist and naturalist than George Bird Grinnell praised him as the ideal of the American sportsman (Grinnell 1913).

The Bear as a Test of Manhood

Emerging in these hunting experiences, we see a new bear with a new use. As the remaining bears became less abundant and less a threat to human society, their pursuit took on a different meaning; elements that were not previously regarded as primary became so. Hunting large carnivores has been a test of manhood for many cultures and successful bear hunts have probably always resulted in a fair amount of human male strutting in North America; sport hunting must be nearly as old as subsistence hunting and the two are probably often indistinguishable. After it was no longer an agricultural necessity to kill bears, the value of the bear hunt to the hunters changed. The veneer of killing bears for the good of society remained, but by the time Theodore Roosevelt, William Wright, and a host of lesser-known sportsmen were engaged in their various bear hunts in the closing years of the 19th Century, it was mostly a sporting proposition (Figure 11).

The Bear as Furry Person

In fact, Roosevelt's hunting career serves as a convenient benchmark in the evolution of the bear's image from that of a simple, evil, wilderness-dwelling beast to something more involved, with Roosevelt himself contributing an extraordinary new element to the American relationship with bears. As a hunter-naturalist, Roosevelt wrote a book's worth of thoughtful natural history and lively adventure material about bears (Schullery 1983), but it was one unsuccessful hunt that distinguished him as a part of bear lore. In 1902, at the invitation of the governor of Mississippi, Roosevelt participated in a bear hunt that caused him considerable public embarrassment because he did not get a bear. Toward the end of the hunt, some of the other participants managed to capture an adult bear and rope it to a tree, and then brought the President to it expecting him to shoot the bear. In their sporting tradition, the hunt, especially the chase, with hounds and horses, was the main part of bear hunting; they did not exactly understand the public furor over the President's failure to kill a bear, but they aimed to please. They were quite surprised then when Roosevelt refused to shoot the bear under what he regarded as unsporting circumstances. For him, fair chase demanded a free animal that could only be tracked and killed through good woodcraft and shooting skill.

The press loved this story and a prominent Washington, D.C., cartoonist, Clifford Berryman, produced a cartoon for the Washington Post (Figure 12) that showed the President refusing to shoot a Mickey-Mouselike bear cub. The caption read "Drawing the

Figure 8: Holt Collier about 1900 (Courtesy of Harley Metcalfe III).

Figure 9: William Pickett's portrait from the frontis to Grinnell (1913).

Figure 10: "Grizzly killing a steer" (Roosevelt 1893).

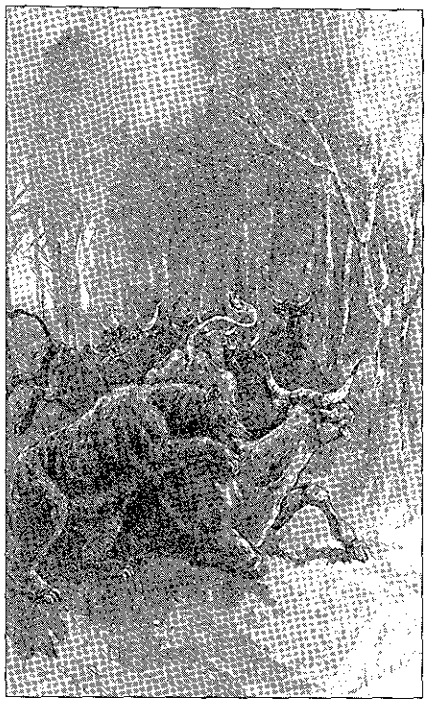
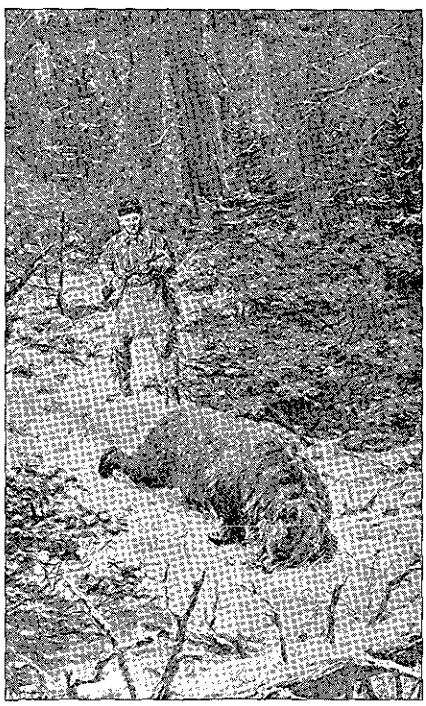


Figure 11: "The death of the grizzly" (Roosevelt 1893).



line in Mississippi." According to various historical accounts, the President was in the south dealing with Louisiana-Mississippi boundary issues ("boundary line") and race issues ("color line"), so the caption had multiple meanings besides the obvious one of drawing the line between fair and unfair sport (Wilson 1969, Schullery 1988). But the cartoon has other lessons. The actual bear in question was apparently an old one, of about 235 pounds, rather than a cute cub with absurdly large ears. Also of interest, the man holding the bear—indeed, the man who had chased it into a lake and single-handedly subdued and roped it—was none other than the legendary Holt Collier, mentioned earlier. But in the cartoon, an anonymous white man holds the rope.

Perhaps most entertaining for modern bear enthusiasts, however, is that shortly after the hunt a Brooklyn merchant introduced a new toy based on the President's adventure; that was the birth of both the Teddy bear and the Ideal Toy Company. The Teddy bear became the symbol of a dramatic new popularization and commercialization of bears as gentle childhood friends, also evident in a flood of children's books, from the "Roosevelt Bears" book series in this country to the Pooh books in England. The bear as furry person had arrived.

The Ambivalent Bear

By 1900, there were still many rural areas of the United States in which bears were a nuisance or even a threat to human safety, but for the vast majority of Americans, the bear was something remote, rarely seen outside of zoos and circuses, or in anthropomorphic children's books and sensational outdoor magazines. It was into that confused atmosphere, in which the bear was already a bit unreal, that Yellowstone introduced its bears.

Yellowstone National Park was established in 1872, primarily to protect its spectacular geological and geothermal features (Haines 1977). The Organic Act did stress the need to protect the wildlife from "wanton destruction," but foresaw no unusual role for them. Widespread market hunting and other abuses, however, resulted in eventual restrictions on public hunting in 1883 (Schullery and Whittlesey 1992). By 1886, when the U.S. Cavalry assumed responsibility for protecting the park, Yellowstone was well on its way to becoming one of the world's premier wildlife reserves (Hampton 1971, Schullery 1992).

The Bear as Cheap Entertainment

The army, with the endorsement of the Secretary of the Interior, took an active approach to park management, killing predators, fighting fires, initiating massive fish-stocking, and manipulating conditions to suit the day's best notions of what a "healthy," well-managed park should be. The bears, once protected, became regular denizens of the park's many small garbage dumps, and soon became an important tourist attraction (Figures 13 and 14).

Thousands of tourists, year after year, enjoyed the sight of several (and eventually dozens) of black or grizzly bears rummaging through a garbage pile, and the symbol of the bear took on a new twist, "from wilderness personified to wilderness enfeebled" (Schullery 1992:254). Generation after generation of visitors would learn to appreciate the bears of Yellowstone and of other parks in this way, as fuzzy garbage disposals—round, slow-moving, and apparently harmless bums.

In August 1902, Acting Superintendent John Pitcher issued a formal proclamation reminding all park visitors and residents that it was illegal for anyone to feed the bears: "The bears of the Park, while absolutely wild, are perfectly harmless, but when rendered tame by being fed—in any other way except at the regular garbage piles at the various hotels—lose all fear of human beings and will enter kitchens and camps in search of food, thereby frequently doing considerable damage to property and provisions" (Pitcher 1902). This statement reveals much of the confusion that characterized attempts to regulate bears and humans in Yellowstone through much of the 20th Century. The bears could be "perfectly wild" at the same time that they were "rendered tame." Today, we would say they were "wild but habituated" rather than tame, a distinction that Pitcher may have actually understood. His certainty that feeding bears at the garbage piles was somehow different from other feeding by humans reminds us, forcefully, of a similar conviction expressed by the Craighead research team many years later. They also believed that bears fed at dumps by humans somehow saw the food gained there as different from the human food available in park developments (Craighead 1979, Craighead et al. 1995). The distinction Pitcher made between dump food and other human food sources did not make much sense then, and it should have been equally unconvincing when the Craigheads made it many years later. It is now generally agreed among bear researchers and managers that access to any human food, regardless of its location, is inevitably bad for a bear population (Herrero 1985, Brown 1996).

Meanwhile, public attention given to Yellowstone's bears was not lost on thoughtful, creative visitors, one of whom was the popular nature writer and naturalist Ernest Thompson Seton. His *Biography of a Grizzly* (1899) was a bestseller for many years. The book was the story of the orphaned grizzly bear cub Wahb (the rancher William Pickett, mentioned earlier, was featured as the killer of Wahb's family), who roamed the country in and around the park (Figure 15). Park visitation was still small at this time, amounting to an average of less than 25,000 visitors during the period from 1906 to 1915, and so relatively few people were directly exposed to the park's bears. But books like Seton's, and a continual flow of popular articles, made the bears of Yellowstone famous very quickly.

A second Seton bear character, a small black bear named Johnny Bear, made less of a literary splash, but probably helped contribute to the growing enthusiasm for these remarkable wild-

Figure 12: "Drawing the line in Mississippi," the most famous of several cartoons by *Clifford Berryman, based on Theodore* Roosevelt's misadventure during a southern bear hunt in 1902 (Bull 1970).

Figure 13: By the 1920s, black bears were routinely fed by visitors along park roads and in park developments, such as on the porch of Roosevelt Lodge (National Park Service photo, Yellowstone National Park archives).

Figure 14: The bear show reached its most official and expansive in the 1930s, as hundreds of visitors gathered nightly at the feeding grounds near Canyon (National Park Service photo, Yellowstone National Park archives).

Figure 15: Seton's (1899) portrayal of "Wahb," a huge grizzly bear that ruled the wilderness around Yellowstone National Park at the turn of the century, may be the best-selling of all American bear books.

tame animals that anyone could watch and enjoy (Seton 1909).

A more meaningful contribution to bear knowledge, William Wright's *The Grizzly Bear* (1909), contained an extended tale of the author's experiences with flash photography in Yellowstone National Park. Wright, a skilled, self-made naturalist, took a personal interest in Yellowstone's bears, even complaining to the superintendent in 1908 about the alleged killing of bears by irresponsible soldiers (Wright 1908). His book and other writings probably added significantly to public awareness of the Yellowstone bears.

The Bear as National Mascot

By 1925, then, when Milton Skinner published his *Bears in the Yellowstone*, it was natural for him to entitle the first chapter, "Why Yellowstone Bears are Famous." The bears of Yellowstone, especially the black bears, were well on their way to being national pets, or mascots. Some time after 1900, as tourist traffic increased enough to justify a roadside presence, a few black bears began cautiously hanging out along the roads for handouts (Figure 16). After cars were allowed in the park in 1915, however, black bears became regular roadside features and continued to be so for more than half a century.

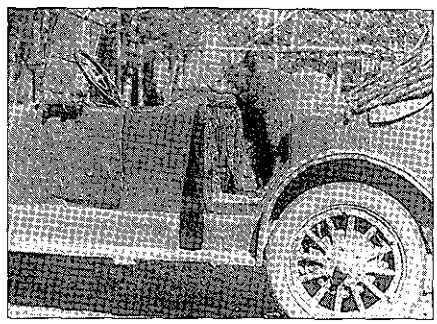
Though still only a small percentage of Americans visited Yellowstone, the bears were so often photographed (Figure 17) or written about (Allen 1925, Yeager 1933, Albright 1928, 1945) that their fame grew until they were an expected part of the Yellowstone experience, firmly ensconced in the trademarks and commercial promotion of park concessionaires and interpreted by National Park Service naturalists soon after that agency was created in 1916. The price the bears paid for this popularity was high. Between 1930 and 1970, an average of more than 24 black bears was killed each year, mostly by managers or by collisions with cars, because of the roadside bear show (Schullery 1992, Gunther 1994). Hundreds of property damage cases (Figure 18) and hundreds of injuries (most minor but some quite serious) were reported, and it can be assumed that many more were not. America's romance with the bears of Yellowstone looked great in the magazines and postcards, but was pretty rough for the participants.

The new National Park Service elevated many of the husbandry techniques and environmental manipulations initiated by the army to higher levels. For the bears, this meant the formalizing of the bear-feeding grounds, concentrating public attention especially at the Otter Creek dump site south of Canyon, where hundreds of carloads of visitors gathered nightly to watch grizzly bears in surprising numbers fight over food scraps (Figure 19). But the public was no longer uniformly pleased with this treatment of national park wildlife. Schullery (1992) and Wright (1992) reviewed the growing dissatisfaction among scientific organizations and conservation groups with this demeaning treat-

ment of wild animals. The National Park Service took advantage of the visitation hiatus of World War II to close the Otter Creek dump site to public visitation, so that, except for a few researchers and privileged gawkers, the grizzly bears of Yellowstone would enjoy their garbage in privacy (Schullery 1992). It is an interesting feature of the uneven progress of our esthetic of bear watching that we judged it inappropriate to watch park bears at garbage dumps a quarter of a century before we judged it inappropriate for park bears to eat garbage.

The roadside bear show (featuring black bears) only got more popular, however, and in the years following World War II, the "bear jams" became mile-long traffic obstacles. A survey of visitors conducted in the early 1950s revealed that 95% knew that feeding bears was illegal, but its tacit acceptance by park staff was sufficient approval for most visitors (Bock 1953).

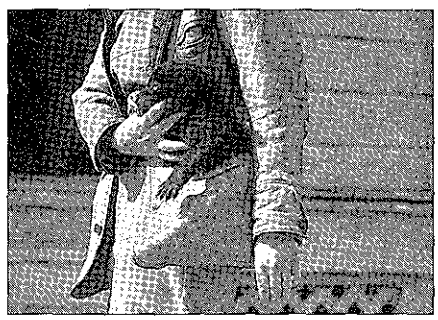
Figure 16: The habituation of black bears through roadside feeding resulted in countless "close encounters" with motorists, many amusing and some harmful to both people and bears (National Park Service photo, Yellowstone National Park archives).



The Bear as Folk Hero

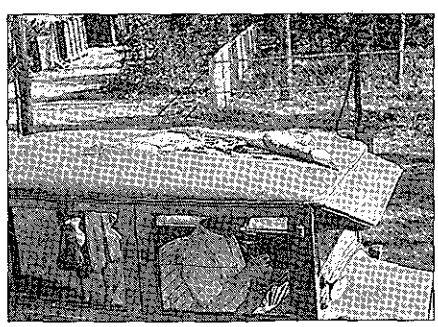
The rise of television, and especially of television cartoons, opened a whole new avenue of interpretation and celebration of the bears of Yellowstone. Of the many park bears that emerged from the cartoon world, none was as famous or as durable as Yogi, a Hanna Barbera creation of the late 1950s (Figure 20). Yogi embodied all the loveable characteristics, so enjoyed from a distance, that made the bears of Yellowstone such an unforgettable part of the park experience. He has become a part of our folklore, "as valid a part of our culture as Mother Goose or Aesop" (Schullery 1992:206). Yogi misinformed millions of people about what bear life was really like in Yellowstone, but it was hardly the fault of a cartoon, or of a cartoon's creators, that people did not understand wild animals.

Figure 17: "Barney," a black bear cub raised by Dorr Yeager and his family at Mammoth Hot Springs in 1931, became well known through published accounts of his exploits (National Park Service photo, Yellowstone National Park archives).



Meanwhile, the real bears of Yellowstone were about to be abruptly and painfully divorced from many decades of traditional use of human foods. In 1959, Drs. John and Frank Craighead and their associates began a pioneering study of the grizzly bears of Yellowstone. Though its findings have been improved upon or modified by many later studies of other grizzly bear populations, the Craighead study was perhaps the most important single grizzly bear study in history because so much of modern grizzly bear research methodology was first attempted or developed during the 11 years of their study.

Figure 18: A cloth-top sedan at Fishing Bridge in 1932 exhibits the effects of a bear's efforts to reach food locked inside (National Park Service photo, Yellowstone National Park archives).



The Craighead study may have been the only study of grizzly bears to contribute significantly to the public image of the grizzly bear. The Craigheads were excellent publicists, and the National Geographic Society portrayed them and their remarkable lives in films and publications, but that attention alone would not have given their study its reach in the American mind. Out of their study, and out of changing National Park Service policies, grew a controversy that is now well into its second generation of participants, and that greatly complicated the image of the bears of Yellowstone.

Figure 19: Ranger-naturalist talk at the Canyon feeding grounds, 1936 (National Park Service photo, Yellowstone National Park archives).

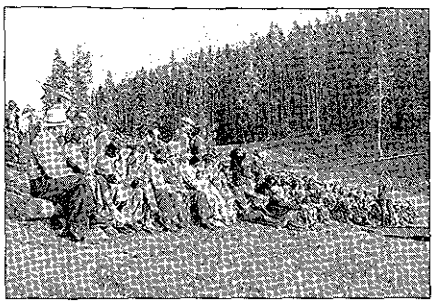


Figure 20: Smarter than the average bear (Courtesy of Hanna-Barbera).

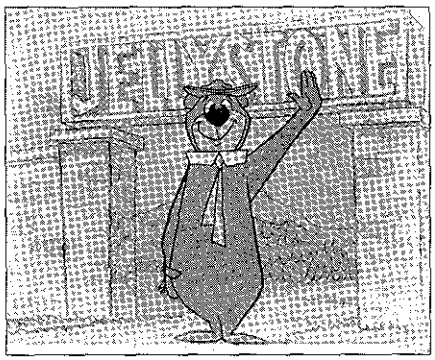
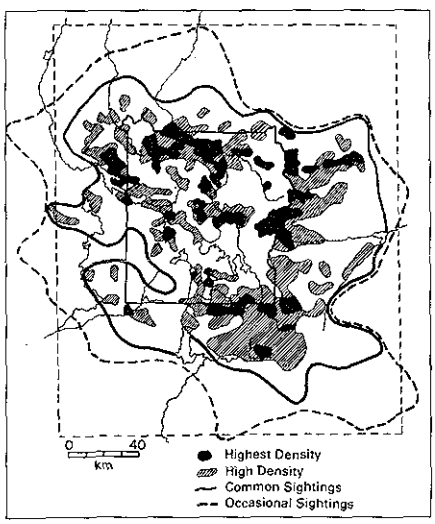


Figure 21: By the 1970s, the grizzly bear was the foremost symbol of the Greater Yellowstone Ecosystem, the boundaries of which were first tentatively defined in terms of grizzly bear habitat (Courtesy of the IGBST).



The Bear as Scientific Sore Point

In a sense, some of those who worked to save the bear became folk heroes themselves in this period; an odd twist on thousands of earlier generations of humans whose heroes were people who killed, rather than saved, bears. On the other hand, those who were perceived as opposed to grizzly bear conservation became, for the first time, villains. Unfortunately for public understanding as well as for the bears, everybody had their own set of heroes and villains. The scientific issues were complex and usually oversimplified by the media (and by some scientists), so that the public had little confidence in most information. As a result, the controversy over grizzly bear management that developed in the late 1960s did change the image of the bear. Perhaps most important, it added a new dimension to what the bear means to many people, or, perhaps, it added different elements to the image, and people chose which element they wanted. For some, the grizzly bear became a symbol of science's failure to clarify the bear's status. For many, it became a symbol of government inefficiency or mismanagement of an important resource. But perhaps the most enduring image-changing legacy of the grizzly bear controversy was that the grizzly bear became a symbol of its home; no other species has so continually driven the debates over the future of greater Yellowstone (Figure 21).

The Bear as Good Wilderness

Out of this controversy came an increasingly heightened awareness not only of the bear's plight, but also of the significant threat to its habitat. By the 1970s, for the conservation community at least, the bear was completely converted from its 19th-Century image as the symbol of evil wilderness. It became instead the symbol of something precious and threatened with destruction. That something was the Greater Yellowstone Ecosystem, one of the last great wild places in the lower 48 states and a conservation battleground of growing importance. More recently, as ecosystem management has become a byword of the environmental movement, the far-ranging grizzly bear has become a symbol of the need for better coordination of interagency management of wildlands, and the need for preservation of ecologically whole wild areas. The grizzly bear is invoked in many discussions relating to modern ecological and social thinking, whether about wildlife migration corridors, minimum population size viability, or sustainable resource use.

The Bear as Political Hammer

From this new stance, the conservation community and the grizzly bear's various defenders saw the bear as a valuable and essential tool in the struggle to save wild country. The bear, through its protection under the Endangered Species Act, became

a hammer with which to bludgeon land managers and land-use practices that were no longer as popular or easily appreciated as they once had been. It could be argued that this use of the grizzly bear as a device to address a variety of perceived problems has backfired on the bear, for the grizzly bear in modern Greater Yellowstone is surely suffering to some extent from its image as an obstacle. For example, one of the most persistent objections to wolf (*Canis lupus*) recovery was that "We don't want another grizzly bear" (see Urbigkit and Urbigkit *this volume*).

New Images of All Kinds

From this even more ambivalent image, the bears of Yellowstone have launched into all manner of unusual or surprising directions in broadening their image. The fires of 1988 challenged several decades of almost simple-minded devotion among Americans to the lessons Smokey taught us, especially the idea that all fire was bad (Morrison 1976). Suddenly, at least for most urban Americans, fire was a little more confusing and Smokey found himself symbolizing the ill-advised suppression of a natural, wilderness process. Smokey, a product of a beautifully effective U.S. Forest Service promotional campaign that even in the 1960s or 1970s seemed unimpeachably correct, was at last bound up in the power and reach of Yellowstone and its real bears.

At the same time, the bear continued its long march down the corridors of marketing history. Since early in the century, the bears of Yellowstone had been used countless times to sell everything from burgers to beer to baby slippers, and the image has had extraordinary durability as a marketing device.

Science itself contributed to the richness of the bear's image. Under the leadership of Dick Knight, the Interagency Grizzly Bear Study Team (IGBST), now with more than 20 years in the field, is probably the longest-running, most scientifically productive grizzly bear research project ever. Through many popular articles (by journalists and other writers) and several books, usually based in good part on the work of the IGBST, the wonder and complexity of the grizzly bear's world is celebrated anew. Even if the article or book is mostly about the continuing controversy, it serves to awaken some readers to the magic of bear appreciation as well. Steve and Marilyn French (see French et al. *this volume*) of The Yellowstone Grizzly Foundation (now with more than 10 years in the field) have proven to be at least as effective publicists on behalf of the bear as were the Craigheads, and have contributed enormously to this growing public sense of wonder through their many presentations, publications, and films. This may be one of the most hopeful signs for the bear, for as long as it primarily invoked images of bitter political or scientific acrimony, it might have attracted some public interest, but it had garnered little public affection. What we should learn from the Frenches, as we should have learned from the Craigheads, is that when science reaches beyond its empirical conservatism and presents a warmer, more personal view of the grizzly bear (or even of grizzly bear biologists), it brings the bear to life for a public that is ripe to learn and anxious to help.

More recently, the wolf recovery program has again affected the image of the bear. The thousands of people who have watched wolves in the park since 1995 often saw them interact with or occupy habitat with grizzly bears. Thus, the bear has been recognized, more clearly than before, as a member of a community of predators. It always shared the park with a number of highly effective carnivores. But the wolf alerted people to a new kind of relationship between the bear and its fellow wild mammals.

The Grizzly Bear as Hope

It seems improbable that we have reached any stable state in our continuing quest for understanding grizzly bears. We will continue to exercise our imaginations to express what the bear means to us, and we will continue to create new images and ideas around the real bears of Yellowstone. The bear will almost certainly become a key figure in a number of ongoing social processes in this country, as it already has been in the conservation movement for many years, and more recently in the ecosystem management debates. The Yellowstone Lake crisis, which threatens the native cutthroat trout (*Onchorhynchus clarki*) population (see Gunther et al. and Reinhart et al. *this volume*), will find the grizzly bear again occupying a starring role as a consumer of the trout. The fate of the grizzly bear will be highlighted as global warming becomes a more undeniable reality. If grizzly bear recovery should advance to the point of delisting, any state proposing a grizzly bear hunt will surely be confronted with animal rights or other anti-hunting groups that will recognize and take

advantage of the extraordinary public concern over the fate of this charismatic animal. The combination of the charisma of the grizzly bear and Yellowstone will continue to be a powerful public relations tool for any individual or group who can find a way to put it to use.

At the same time, we will draw on the traditional image of the bear for education, entertainment, and inspiration. We will continue to find enormous amusement in the antics of cubs, and rare and unfamiliar humility in the power of adult bears. The bear's entire symbolic armament will be available to us. The bear's defenders are repeatedly drawn back to earlier images, such as the bear as spiritual presence, which we mix with more recent creations, such as the bear as the symbol of good wilderness. Steve Herrero suggested that the stimulation the bear brings to our imagination—the way it seems to demand new views and new ways of seeing—should ultimately be recognized as the most important reason we should ensure the survival of bears in Yellowstone: "We should preserve grizzly bear populations, not because their ecological function is critical, but because of what they can do for human imagination, thought, and experience" (Herrero 1976:140).

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Wild Love

Invited talk given at the Superintendents' International Luncheon
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I've been asked to speak on "some global aspect of park research and management." I began this assignment by asking myself, "What is, to me, the most important international aspect of national park research and management?" My inner voice quickly answered, "the dedication and commitment of researchers, managers, and users." Even though you act as proper scientists and managers and try to justify your actions rationally, for many of you it is your love of wild nature—wild love—that has gotten you into this in the first place. It is also what keeps you going through cold, rain, snow, and the more aggressive attacks on your work, drawn out committee meetings, and other interpersonal challenges.

This love of nature is global and I believe it is widespread among researchers and managers who work to protect natural areas. I first directly experienced the international character of the love of nature in Abruzzo National Park in the Apennine Mountains of central Italy. In 1971 I was hired by the park's director, Franco Tassi, to begin ecological research on the park's remnant brown bear (*Ursus arctos*) population. My family and I arrived in the park mid-afternoon on May 1st. We had just driven across Western Europe. I was introduced to the park's only naturalist/biologist, Franco Zunino. He spoke little English, and I even less Italian. But, after gesturing and "talking" for several hours, we agreed to begin fieldwork the next day at 3:30 am so we could be in position by 4:30 or 5:00 to possibly see bears foraging in the earliest pre-dawn light. Imagine going to a new job you didn't love and voluntarily going to work in pitch dark with someone you hardly knew and with whom you could barely speak.

Zunino and I worked together productively, 6 days a week, all that spring and summer. Together we launched the first scientific study of brown bears in Abruzzo National Park. I think each of us knew from that first early morning that the other had a similar love of natural environments, and a commitment to try to understand and protect them and one of their most challenging-to-maintain components, brown bears.

Why did I so love wild nature? This is not a question I asked then, but a few years later. Not my mother, father, nor any close childhood friends shared this love, but I can look back on what I think was my earliest bonding with nature. I spent my childhood years in San Carlos, California, on the edge of San Francisco Bay. At that time, there were millions of shorebirds that wintered on the bay. On homemade wooden rafts or on foot I played in sloughs and was immersed in the myriad numbers of birds whose names I only learned later in university. I remember the sense of exploration, discovery, and absorption I felt as I pushed off on my makeshift raft, sometimes flushing a sky full of birds.

In my 20s, during the turbulent 1960s in Berkeley, California, I had an opportunity to revisit one

of the major San Francisco Bay marshes, Bay Farm Island, as a student in a zoology class. My connection with the wintering shorebirds was quickly renewed and expanded as I learned to recognize species and to understand the ecology and significance of the marsh as a wintering area.

Within 2 years of my connection with this new marsh, however, it was gone. Drained dry, every bit of it. The emergent plants, the great flocks of shorebirds, and the owls that preyed on them were gone too. The entire marsh was drained for housing developments. When I went home to San Carlos I found the same thing had happened to the marshes I loved as a child. A sea of houses replaced a bay of wild birds.

Somehow related to those and similar experiences, my love of nature became part of my core and I started to work to protect what I loved. Yes, I had excellent training as a scientist in my Ph.D. program at Berkeley, but throughout my career I have sought to apply science in the context of trying to understand and maintain wild nature.

Love of Wild Nature has been the Mainspring of Many Great Naturalists

"Nature never did betray the heart that loved her," nor did William Wordsworth ever betray nature. Wordsworth's ebullient, poetic celebrations of the beauty he found in nature led to his proposing in the 1820s that the government establish one of the world's first protected natural areas. "The author has been induced to speak...by a wish to preserve the native beauty of this delightful district" (the Lakes District of northern England). Wordsworth perceived a " sort of national property, in which every man has a right and interest who has an eye to perceive and a heart to enjoy."

No one who has read John Muir could doubt that it was his overflowing love of wild nature that made him such a successful conservationist. On the 8th of May 1871, while camped in his beloved Yosemite, his diary reflected his heart: "Nature loves man, beetles, and birds with the same love. With her storms of snow, hail, volcanic fire, and lightning, she seems to scatter firebrands, arrows, and death among her creatures, and so she does, but they are scattered as the stars are scattered in the heavens, each in its place, singing together in faithful harmony" (Wolfe 1938:66).

To many people, Charles Darwin is the most hallowed scientist and naturalist, the person who first understood the evolutionary significance of species and the environments in which they evolved. Occasionally Darwin was so awed by nature that he recorded his feelings. For example, when he first encountered tropical forest near Rio de Janeiro he wrote, "wonder, astonishment & sublime devotion, fill & elevate the mind" (Wilson 1984:27).

Nature and children are both part of a small list of things that inspire awe in adults. In the Namib Desert, one of the driest areas in the world, a highly improbable plant exists. Improbable because of its up to 2-meter spread in such an arid environment, and because it is sometimes found where few other plants exist. In 1859 or 60, when Austrian botanist Friedrich Welwitsch became the first scientist to discover *Welwitschia mirabilis* in southern Angola, he is said to have fallen onto his knees, hardly daring to touch it. He recognized how unique it was. It belongs to the cone bearing gymnosperms, but it also contains characteristics of the angiosperms. It is therefore considered to be a link between both (Craven and Marais 1986).

What is Wild Love?

Love of nature is the integration of our emotional-intuitive dimension with our rational-logical dimension into feelings, thoughts, and actions reflecting our deep connection, wonder, respect, concern, and caring for nature. Love leads to long-term commitment. I doubt if divorce is possible.

Erich Fromm (1956), in his classic work, *The Art of Loving*, says that love's basic elements are care, responsibility, respect, and knowledge. Love, as he understands it, is not something that is easily indulged in by anyone. It requires a mature, well-developed person. It requires focus, courage, faith, and discipline. When love is applied to nature the rewards can be enormous. "In the act of giving, I experience my strength, my wealth, my power. Giving means being rich" (Fromm 1956).

Love of nature can also be a celebration of the abundance of nature, of its potential for all life, including people. Paul Shepard (1995) eloquently presents the case that bears are one of the pinnacles of nature's abundance. When a bear presents itself to a hunter, the hunter is blessed with plenitude. So is a person who experiences a bear in a national park. The more one understands natural systems and what species like bears and wolves (*Canis lupus*) rep-

resent, the more one is enriched by the experience of such an animal in its natural environment.

Wild Love and Biophilia

In 1984, E. O. Wilson hypothesized that people have "an innate tendency to focus on life and life-like processes." We have a natural affinity for things living—"biophilia." Wilson believes that we distinguish life from the inanimate and move toward life "like moths to a porch light." (Wilson 1984:1).

Wilson looked at the biological evolution of our species, nearly all of which took place in natural environments over which people exerted little control. Certainly, our ancestors experienced a fabric of life, a living world that was substantially unaltered. In this context, he hypothesized that biophilia evolved because it enhanced genetic fitness. Patterns that were incorporated into our genes during our evolution, he believes, affect our feelings of awe versus aversion, peace versus fear. He grants that biophilia may exist simply as weak learning rules, but even this, he argues, is important.

Wilson sees loss of biodiversity as *the* environmental problem, robbing us of environments in which we are genetically predisposed to be relaxed and inspired. For Wilson (1993):

- Biodiversity is the creation (the source, the origin...).
- Other species are our kin.
- The biodiversity of a country is part of its national heritage.
- Biodiversity is the frontier of the future.

Wilson is a leading scientist who clearly expresses his understanding and beliefs and their implications.

Relevant to our conference theme of predators is the obvious but fundamentally important point that ecosystems that still maintain their full complement of naturally evolved predators have most of their recently evolved biodiversity. Such complex systems should have tremendous potential for expressing and developing biophilia.

I hypothesize that biophilia can function as a prebuilt genetic pathway leading to the development of love for nature. This doesn't necessarily mean that people who live close to nature will love individual animals. Jared Diamond (1993), after working for more than 30 years in New Guinea and other southwest Pacific islands, concluded that there was little evidence of love or other "tender feelings for individual wild animals." However, love of individual animals may simply be biophilia run amok in modern societies where immersion in wild nature is no longer a part of life, yet people are left with genetically predisposed attractions to living things. The overly pampered poodle may represent as much of a genetically predisposed malady as does a song sparrow raising a cowbird's parasitic offspring. A broader look at the relationship between hunter-gatherer peoples and wild animals better suggests dimensions of biophilia in this context.

In functional hunter-gatherer societies people's relationship to wild living things may be indistinguishable from their being. Peter Steinhart (as quoted in Nabhan and St. Antoine 1993:239) expressed this oneness: "Animals are far more fundamental to our thinking than we supposed. They are not just a part of the fabric of thought: they are part of the loom." Karl Luckert also captures this oneness with a statement made to him by a Navajo elder (as quoted in Nelson 1993:204): "Animals are our food. They are our thoughts." Richard Nelson (1993:205) makes an eloquent case that, among indigenous peoples, virtually all aspects of culture and tradition emanate from the natural environment. "Among hunter-gatherer peoples, the intricate weaving together of nature and culture is like the exchange between living cells and their surroundings." Many writers who love wild nature agree that by alienating ourselves from nature, we industrialized people "have created for ourselves a profound and imperiling loneliness" (Nelson 1993:223).

Wild Love and Human Well Being

A deep love of wild nature actively expressed can lead to a richly rewarding, albeit constantly threatened, life. For those who find inspiration, beauty, and joy in nature have witnessed the dismemberment of so many ecosystems—the source of their joy. The pain can be numbing, but it can also catalyze action.

To love life, the community of both living and non-living things, is to extend yourself, to commit yourself to loving something that you do not own and cannot control. If you love your dog you can treasure it, sequester it, feed it steaks or bonbons—shelter it from life's vicissitudes. But if you love wild nature and you extend yourself into wolf packs and grizzly bears, if your spirit travels across expansive wildlands with the wolverine (*Gulo gulo*), then your being shares their vulnerability. It is you, as well as

they, who lose a home to the developer's bulldozer, whose forest is flattened because "we have got to make a living."

Recently, a new field called ecopsychology has evolved to attempt to understand our attitudes, feelings and actions toward nature. Among other things, some ecopsychologists see nature as a healer. "Nature tops the list of potent tranquilizers and stress reducers," said physician Patch Adams. With the study of ecopsychology and biophilia, I see evidence that science is trying to understand the roots of the human-induced biodiversity crisis.

Joseph Sax (1980), in his book *Mountains Without Handrails*, argues that national parks offer outstanding opportunities to develop our potential as human beings. To him, a national park is a symbol of nature's pace and power, and offers outstanding opportunities to get to know nature. According to Sax, when one chooses to set his or her own agenda in nature, profound feelings of satisfaction and a very positive state of well being can result.

What is Wild Love?

Though our understanding of wild nature and of the feelings of love it evokes is as yet incomplete, we still clearly have people that love wild nature. For those of you whose business it is to manage natural systems, no doubt your jobs would be easier if more people loved wild nature. So how do we cultivate wild love? How are biophiliacs made?

The most obvious way to form a deep and profound bond between people and wild nature is to be raised as a hunter-gatherer, much like our ancestors were—directly dependent on and daily immersed in nature. But we of the industrial/technological societies are not and cannot become indigenous peoples. How then can we establish strong bonds with wild nature? How can we learn to love? David Orr (1993) suggests 8 steps that could lead individuals in this direction:

1) The capacity for love begins early in life. Therefore, intimate exposure to nature should begin early and last through the formative years of childhood. According to Orr, at age 2 Jane Goodall slept with earthworms beneath her pillow. John Muir reveled in the wonderful wildness around his Wisconsin home. Ideally, nature is viewed as a friendly place filled with excitement, discovery and adventure.

2) A love of the wild requires easily accessible, safe places where it might take root and grow. For E.O. Wilson (as quoted in Orr 1993:428) it began during his youth by exploring "woods and swamps in a languorous mood...(forming) the habit of quietude and concentration." But how many cities still offer such places for a young person to spend time in and learn to appreciate?

3) The development of the capacity to bond to wild nature requires nurturing and continued stewardship on the part of parents, relatives, teachers, and other caring adults. And, in so doing, adults may reap the benefits of rediscovery of their own sense of wonder and love of wild nature.

4) Love of the wild flourishes in coherent communities, places where the relationship between people and nature is already respectful, already nurturing. In other words, love begets love.

5) Orr thinks that based on the work of theologian James Nash, love has 6 ecological dimensions: beneficence (e.g., kindness to wild creatures), other-esteem (the rejection of the domination of nature), receptivity to nature (e.g., being capable of awe), humility (the understanding that there isn't necessarily a technofix for everything), knowledge of ecology and how nature works (e.g., Wilson argues that love of nature is greatly expanded through knowledge), and communion (the reconciliation or harmony between humankind and nature).

6) Love of nature cannot grow amidst poverty and other forms of human desperation. Nor can it easily grow in the cocooned withdrawal of the very rich.

7) Orr (1993:429) cites Erich Fromm, whom I have already mentioned, as stating that love requires "discipline, concentration, and patience throughout every phase of life." Recognizing that we must daily take from the earth to support ourselves, love tells us to do this with as little impact as possible.

8) Finally, Orr (1993:430) suggests that a mature love of nature requires something like metanoia—the transformation of one's whole being. He sees this

as constituting more than a paradigm shift (which we know is hard enough), but rather a deepening of our "loyalties and affections to life (which) in time alters the character of our entire civilization."

Wild Love for Scientists and Managers of Environmental Reserves

If you have read this far, you probably agree that love of nature is a topic worthy of scientific and humanistic study. Like most important but complex topics, scientists have avoided it, at least in their professional lives.

I can share some personal experience. Preparing this address has required me to examine the interrelationship between my feelings and my research regarding nature. At least for myself, the myth that science is value free has been rejected. The problems I choose to study and the methods I use are influenced by my love of nature. Once problem and methods are chosen, then the traditional image of science as objective and capable of producing replicable results is upheld.

Science can be the means by which some people express their love for nature. Scientific method can be applied to an infinite number of questions. As applied to knowing and protecting wild nature, it can be an act of love.

Extending the Boundaries of Our Ethics

We need guideposts and mentors to lead us in a manner that protects the living things of planet earth. Aldo Leopold (1966) wrote and lived the bible of conservation, *A Sand County Almanac*. Leopold said that we abuse land (i.e., nature) because we regard it as a commodity belonging to us. "The land relationship is still strictly economic, entailing privileges but not obligations....When we see land as a community to which we belong, we may begin to use it with love and respect....That land is a community is the basic concept of ecology, but that land is to be loved and respected is an extension of ethics."

If we believe that only people count, then we are diminished. If we shirk our stewardship responsibilities, then we limit our understanding and our ability to be a supportive part of life on earth. We, instead, choose to exploit nature for individual, short-term gain. The conservation ethic is evolving, and it is exciting and deeply rewarding to participate in this evolution of actions that emanate from respect and love of nature. What actions are appropriate toward other living entities? That is *the* ethical question. Do we have the right to extirpate an estimated 50,000 species a year (Wilson 1993)? Even if we have the right, can this rate of removal possibly be in humankind's best interests? "We must look at the very roots of our motivation and understand, why, in what circumstances, and on which occasions, we cherish and protect life. The elements from which a deep conservation ethic might be constructed include the impulses and biased forms of learning loosely classified as biophilia" (Wilson 1993).

We have options. We can become, and perhaps we already are, some of the developed world's leaders in terms of trying to live with nature and trying to restore some of what we have dismembered. We can act on our love of nature. Restoring wolves in Yellowstone then becomes not just an act of science-based ecosystem restoration, but rather an act of love for the wild.

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Using Molecular Genetics to Enhance Survival of Grizzly Bears in the Yellowstone Ecosystem: A Status Report

Paper based on invited presentation given September 26, 1995

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Abstract

The threatened Yellowstone grizzly bear (*Ursus arctos*) represents a bellwether population for many other endangered species of predators. The successful long-term conservation of this population requires 2 crucial pieces of information: managers need to know the number of grizzly bears in the ecosystem and they need an accurate assessment of the population trend over time. They also need to ensure that the population does not suffer from a loss of genetic diversity. Our project is designed to apply the techniques of molecular genetics to aid the conservation of grizzly bears in the Yellowstone Ecosystem. The primary aims of the project are to assess the degree of genetic diversity of the Yellowstone population and to use molecular techniques to develop a non-invasive system to accurately monitor the number of grizzly bears in the ecosystem. In this paper, we place the project in an evolutionary context by reviewing recent data on the genetic relationship between Yellowstone grizzly bears and other North American brown bears (*Ursus arctos*). We then outline some of the directions that we expect this project will take as we apply molecular technology to practical problems in the field. Overall, we anticipate that the techniques developed by this project will not only aid the long term survival of the Yellowstone grizzly bear population, but will also be applicable to the conservation of other threatened species.

Introduction

Recent advances in molecular genetics have provided new techniques that have revolutionized a number of areas in evolutionary biology, such as phylogeography, forensics, population genetics, and demographics (Avise et al. 1987, Avise 1989, Jeffreys and Morton 1987, Jeffrey et al. 1986). As all of these areas are fundamental to conservation biology, the application of molecular techniques to study threatened and endangered populations will help put conservation biology on a firmer scientific footing (Cohn 1990). With a primary interest in the conservation of the Yellowstone grizzly bear (*Ursus arctos*), we have begun to explore how these techniques might be applied to enhance management of this threatened species. The development of specific molecular strategies, and their successful application to the Yellowstone situation, is likely to provide some instructive data for developing molecular protocols to aid the conservation of other threatened species.

Background

The brown bear is the most widely distributed of bear species in the world, occurring from northern arctic tundra to dry desert habitats in Europe, Asia, and North America. Since the mid-1800s its range has been significantly reduced worldwide, primarily by human occupation or alteration of its habitat and coincident with the advent of modern firearms (Servheen 1989).

The brown bear in North America is commonly referred to as the grizzly bear and once occupied most of western North America from the Arctic down to the central highlands of Mexico (Trevino and Jonkel 1986) (Figure 1). In the early 1800s an estimated 50,000 to 100,000 grizzly bears were found west of the Mississippi River in the area that would soon become the United States. Increased human encroachment that began in the mid to late 1800s severely reduced the available habitat and, along with the direct killing of bears, led to a rapid decline in the grizzly population. By the early 1900s only small, scattered populations remained (Figure 2) (Merriam 1922), and most of these became extinct within the following 2 decades (Brown 1985).

In 1975 the U.S. Fish and Wildlife Service listed the grizzly as a threatened species in the lower 48 states where it was estimated that less than 1,000 bears remained. Six ecosystems were identified for recovery with 4 of these containing grizzly populations contiguous with Canadian populations: the Cascade, Selkirk, Cabinet-Yaak, and Northern Continental Divide Ecosystems (Figure 3). The Selway-Bitterroot Ecosystem had no verifiable grizzly bears at that time, but was selected for recovery because its habitat was considered suitable to sustain a viable grizzly population.

Figure 1: Historical distribution of brown bears in North America

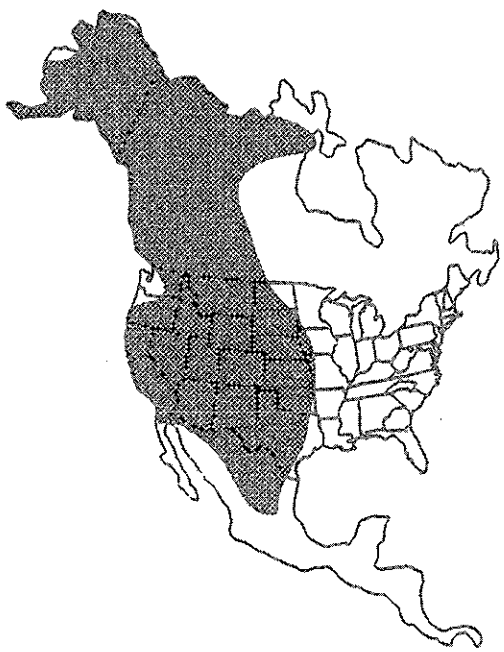
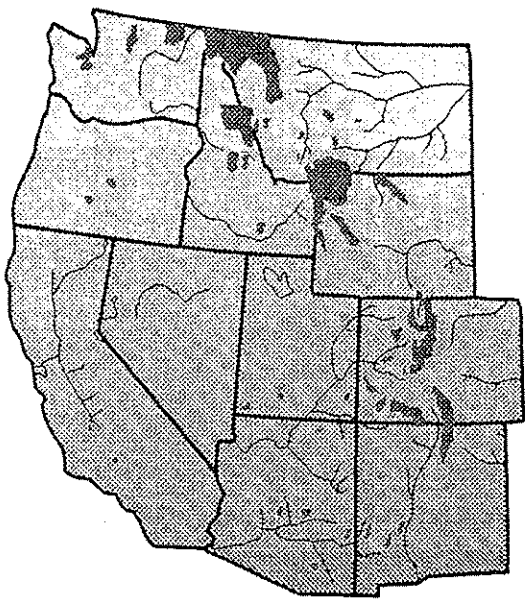


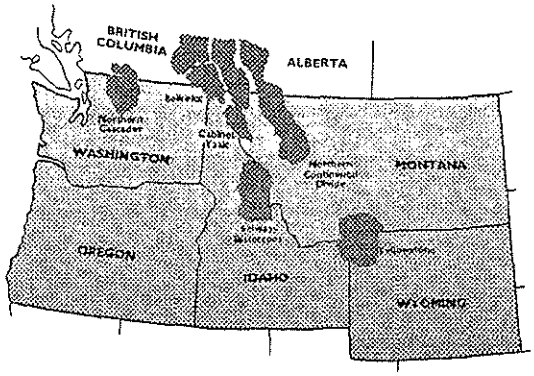
Figure 2: Distribution of brown bears in the United States, circa 1922.



Because of human encroachment and subsequent development, the grizzly population in the Greater Yellowstone Ecosystem (GYE) represents a biogeographic island population. As a result, it has probably been genetically isolated from other populations for more than 50 years. To reverse the potential loss of genetic diversity, the U.S. Fish and Wildlife Service (1993) currently recommends the introduction of grizzly bears from another ecosystem periodically.

Small wildlife populations are at risk of losing genetic diversity through a variety of mechanisms, including inbreeding and genetic drift (Frankel and Soulé 1981, Schonewald-Cox et al. 1983, Shaffer 1983). These factors potentially affect the Yellowstone grizzly population. However, the exact size of this population has never been known, and an accurate scien-

Figure 3: Distribution of brown bears in the United States, circa 1975.



tific method to determine it has remained elusive. The Yellowstone grizzly population was reported to be about 230 bears during the 1960s, based on counts of individual bears feeding at the Park's open-pit garbage dumps (Craighead et al. 1974, National Academy of Science 1974). Estimates of the minimum grizzly population during the early 1990s has varied from 200 to 250 bears based on the observations of unduplicated females with young (R.R. Knight, pers. commun. 1995). Although the exact number of bears in this ecosystem is unknown, it is probably less than 400. Another concern with this biogeographically isolated and relatively small population is the possible loss of genetic diversity due to a population bottleneck of unknown magnitude that occurred during the early 1970s. A significant portion of the Yellowstone grizzly population had fed at the Park's open-pit garbage dumps beginning in the late 1880s (Schullery 1986). When the garbage dumps were phased out during the late 1960s, bears were forced back to natural forage for survival. Some sought out foods in human developments and many were subsequently killed. From 1970 through 1972 a total of 137 grizzly bears were known to have been removed from the Yellowstone ecosystem (Craighead et al. 1988).

The small population sizes that tend to characterize the majority of endangered species can lead to a number of long-term problems, of which the most critical is the ultimate reduction of genetic diversity. In the field of conservation biology there is increasing recognition of the potential importance of measuring genetic diversity as an effective aid in managing populations of endangered species. In a very real sense, the degree of genetic diversity found in an endangered population is an important indication of its "evolutionary health."

Significant reductions in the levels of genetic diversity not only imply that the population has passed through a demographic bottleneck, but also indicates an increased probability of inbreeding with an attendant decline in fertility. Reduction of heterozygosity also increased the potential susceptibility of the entire population to decimation by epizootic pathogens, and similar environmental insults, as appears true for the cheetah *(Acinonyx jubatus)* (O'Brien et al. 1985). For this reason, when carrying out captive breeding for species with reduced diversity, such as the Speke's gazelle *(Gazella spekei)*, specially designed mating schemes are used to ensure that the negative effects of inbreeding depression are minimized (Templeton and Read 1984).

Because of these general principles it is usually presumed that reduced levels of genetic diversity in natural populations of endangered species represent a warning signal and indicate that special measures should be taken to enhance (augment) levels of genetic diversity, such as importing individuals from geographically distinct populations. However, evaluating genetic diversity in natural populations and determining the long-term implications of apparent reductions in genetic diversity are far from simple. Importing an animal from a different population may actually have a detrimental impact on the threatened population by breaking down adaptive gene complexes that developed over thousands of years in response to local environmental pressures. Therefore, it is vital that observed levels of genetic diversity, as well as specific gene types, are interpreted in the context of the evolutionary history of that population and the ecological niche in which it has evolved.

Objectives For Conservation Biology

From a genetic standpoint there are 3 basic kinds of information that need to be determined before conservation and management can be put into proper evolutionary perspective. We stress that since the evolutionary history of each species is unique, these data cannot be guessed at but must be defined in terms of properly collected scientific data. Molecular biology provides the tools to collect this information in a relatively non-invasive manner, and yet still have sufficient data to develop an adequate management strategy.

1. Identify genetic subpopulations (breeding isolates).

Virtually no species exists as a single panmictic population. Instead, species tend to be composed of a series of local populations, each tending to have a unique genetic profile that reflects evolutionary adaptations to local environmental conditions. Since this local genetic diversity (genetic microdifferentiation) is an important component of overall species diversity, it becomes important to identify local populations that are genetically distinct. Genetically distinct populations may need preservation in their own right, while genetic adaptations that characterize a local population may preclude the ability to transfer an individual from that local population to another.

Characterizing the existence of local breeding isolates requires the development of representative genetic markers that are sufficiently diverse to yield accurate estimates of genetic relationships within and between populations.

2. Define overall levels of genetic diversity.

Maintenance of adequate levels of genetic diversity is vital to the long-term survival of any population. Lacking genetic diversity, populations will have a diminished ability to respond to environmental change and are particularly likely to be susceptible to the inroads of infectious agents. Maintaining allelic diversity at a number of genetic loci helps ensure development homeostasis to buffer the population against the impact of environmental degradation. Allelic diversity also has a significant effect on the population's ability to survive infectious agents and parasites.

Populations that are monomorphic for immune response alleles have diminished capacity to respond to virulent pathogens, as exemplified by the ability of a single epizootic to virtually wipe out the Ngorongoro population of Serengeti lions (*Panthera leo)* (Packer et al. 1991).

The problem is exacerbated for most endangered species because the demographic changes that resulted in their diminished population size are frequently associated with marked loss of genetic diversity. Further, without adequate genetic management strategies, the process of genetic drift means that the reduced population size characterizing endangered species will inevitably lead to a more extensive and a more rapid loss of genetic diversity than would occur with larger populations. In order to assess the magnitude of the problem, comprehensive genetic surveys of endangered species are required. These surveys should be based on a representative set of genetic markers so that a realistic estimate can be gained of the amount of genomic diversity at the level of the entire population. These data can then be used to increase the long-term effectiveness of management strategies.

3. Identify genetically distinct individuals within populations.

Ultimately, successful management practices for endangered populations must be defined in terms of the individual organism. This requires knowledge of the distribution of ecological ranges of individuals and an assessment of how breeding patterns vary as a function of population size, population density, and existence of sub-groups within the primary population. Other sociological factors, such as breeding behavior, also come into play for many species of animals. Lastly, detailed life histories, in terms of fertility and survivorship, need to be defined for as many individuals as possible. Only by acquiring such knowledge will it be possible to develop effective management strategies that take account of the reproductive success of individuals, in conjunction with their ability to utilize portions of the ecosystem, and also to monitor the buildup of genetic kinship and mating between related individuals. While a variety of methods such as visual ear tags and radio-telemetry have been used to identify individuals, the accurate definition of reproductive success (or failure) requires genetic identification of individuals (Morin et al. 1994).

Molecular Techniques Applied To Conservation Biology

While a variety of genetic techniques are available to address the above biological issues, there is usually a need to carry out the assays as noninvasively as possible. Although direct sampling of individual animals is not always ruled out, there is also a need to obtain samples indirectly. In the case of mammals, this can most effectively be accomplished by sampling hair or scat. With the advent of the polymerase chain reaction (PCR), it has become possible to amplify polymorphic nuclear markers

from single hairs (von Beroldingen et al. 1989) and from scat (Höss et al. 1992). This strategy has been successfully used to define the biological relationships between chimpanzees *(Pan troglodytes)* in the Gombe reserve by sampling hairs from individual nests (Morin et al. 1994). It has also been used in a more limited manner to assess the distribution of endangered European brown bears (Taberlét and Bouvet 1994, Kohn et al. 1995). Hence, the utilization of PCR offers the promise of successfully carrying out an intensive genetic survey of Yellowstone grizzly bears and using this information to enhance the management of this population. However, there is still the issue of what sort of genetic markers should be developed for this strategy.

At present, there are 3 main types of genetic diversity that are amenable to amplification by PCR. Each type has distinct advantages and disadvantages. In general, a well-rounded program will utilize data from 2 or more distinct types of genetic diversity because a single type may lead to biased conclusions. Below is a brief summary of the 3 types of genetic markers.

1. Mitochondrial DNA (mtDNA) variability.

By virtue of the fact that there are many copies of mtDNA in every single cell (as opposed to a single copy of nuclear DNA), mtDNA is most highly suited for PCR amplification. Also, because it is inherited only through the maternal line, it is most ideally suited for construction of molecular phylogenies. It mutates (evolves) rapidly because it lacks error-detection and repair mechanisms. Another favorable characteristic of mtDNA is what is referred to as a built-in molecular clock (Avise et al. 1987). Each region of the mtDNA molecule evolves at different rates creating multiple levels of resolution. Therefore, when comparing mtDNA between bears, differences in the nucleotide sequences in regions that evolve more rapidly yield better information about recent evolutionary events, while differences in the nucleotide sequences in regions that evolve slowly yield better information about ancient events.

Hence, mtDNA sequence analysis can identify evolutionary clades within populations, and this in turn can be used to obtain a perspective of evolutionary affiliations between populations that stretch back hundreds, if not thousands of years. MtDNA can also be used to give perspective on the distribution of maternal lineages over broad geographic areas, and can be used to define maternal affiliation within and between populations. Even with the high resolution afforded by sequence analysis, mtDNA lineages contain insufficient variability to be used for individual identification within brown bear populations

2. Minisatellites.

These highly variable loci are well suited for defining individual affinities within populations (hence their use in forensic science). However, because relatively long stretches of nuclear DNA (nDNA) are required to properly characterize allelic variability at these loci, they are less suitable for PCR strategies. This is particularly true for attempts to amplify nDNA from scat, and similar materials, where the DNA is likely to be degraded and hence present only in small fragments. Apart from this single but important caveat, minisatellites have potential promise for bear conservation genetics, and at some stage efforts should be made to develop these markers in brown bears. Once minisatellite markers have been developed, the opportunity exists to develop the "minisatellite fingerprinting" strategy, first developed in 1985 (Jeffreys et al. 1985). This strategy has the potential to allow unambiguous identification of individual bears from a single locus, provided the problem of PCR amplification can be overcome.

3. Microsatellites.

From our point of view, microsatellites represent the most logical type of genetic marker to develop. Microsatellites are highly polymorphic, simple repeat sequences of nDNA that are ubiquitous in mammalian genomes (Tauz 1989, Stallings et al. 1991). Microsatellites reflect genetic diversity because they are evenly dispersed throughout the genome, occurring approximately every 500 kb (Weber 1990). Each microsatellite provides an independent assessment of genetic variation so examination of multiple loci increases the accuracy of genetic variation estimates. And because of their molecular structure, microsatellites are technically easier to study, making the costs of developing assays more economical. Their small size makes them ideally suited for PCR amplification (Weber and May 1989), which is essential in analyzing small amounts of tissues with degraded nDNA. Microsatellites have been used to identify genetic diversity of a variety of mammalian

species, including pilot whales *(Globicephala melas, Delphinidae)* (Amos et al 1993), chimpanzees (Morin et al. 1994), black bears *(Ursus americanus)* (Paetkau and Strobeck 1994), and ants *(Myrmica taboensis)* (Evans 1994).

The rapid mutation rate of microsatellite loci results in a high degree of allelic variability, which makes them ideal for assessing population affinities over short time depths (a few tens of generations). While a single locus is insufficient to specify individual identity, a series of about 30 independent microsatellite loci should give ample precision (Bowcok et al. 1994). Once developed, this strategy can be used to assess the distribution of genetically identified individuals (Quellar et al. 1993) and reconstruct pedigrees within the Yellowstone population, and hence assess the breeding success and subsequent dispersal of selected individuals. The ultimate application of this technology is to develop a method to accurately and non-invasively determine the number of bears in a population.

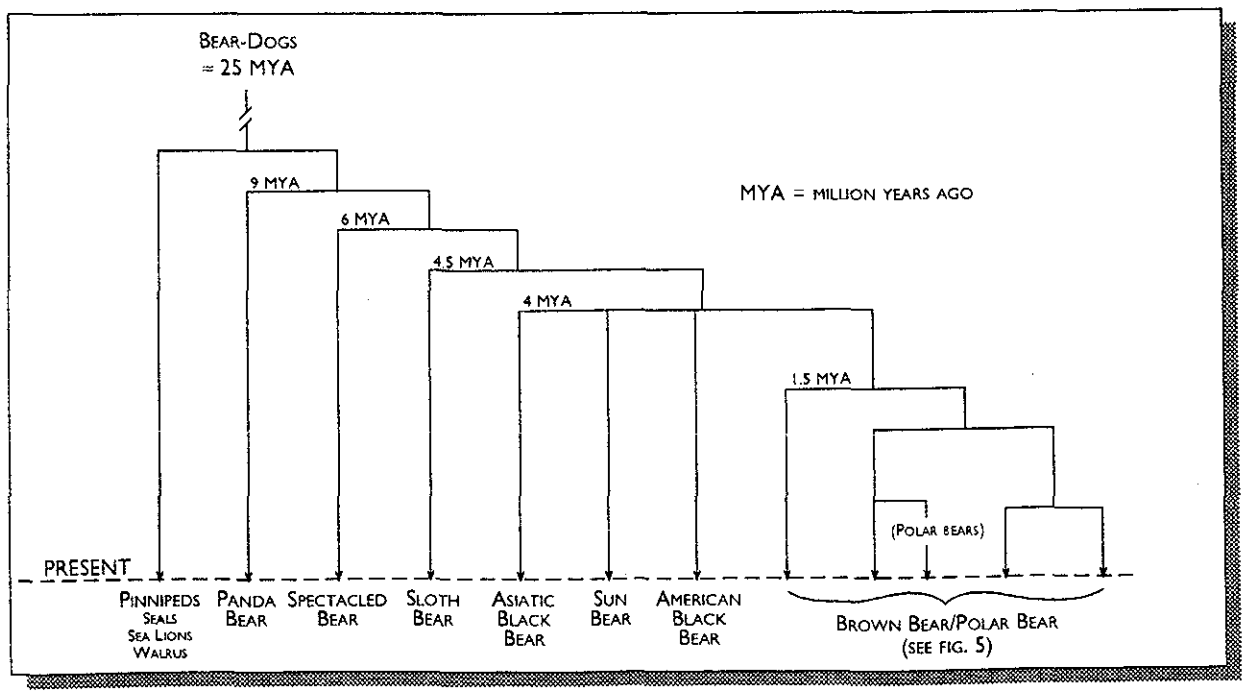
A Phylogenetic Perspective Of Grizzly Bears

To determine the phylogenetic makeup of extant bears, 6 regions of mtDNA from 2 unrelated individuals from each of the 8 bear species was sequenced. To maximize information at the root and tips of the bear tree respectively, 480 nucleotides (nt) were sequenced from the slowly evolving 16s rRNA gene and 260 nt of the rapidly evolving control region (D-loop). Parts of 4 genes with intermediate rates of evolution were also sequenced: NADH dehydrogenase subunit 5 (243 nt), NADH dehydrogenase subunit 4 (223 nt), cytochrome B (257 nt), and cytochrome oxidase II (453 nt). A consensus tree representing the phylogeny with the highest likelihood and the maximum parsimony was determined.

To examine the phylogeographic distribution of brown bears, 319 brown bears (127 from Europe, 9 from Asia, 183 from North America) and 4 polar bears (from different regions of their circumpolar distribution) were sampled comparing the mtDNA sequences from the 2 most variable genes, the control region (D-loop) and the cytochrome B gene.

To determine the distribution of maternal lineages in North America, 266 brown bears were sampled from 9 regions: 5 from Alaska, 1 from northern Canada, 1 from southern Canada, and 2 from the lower 48 states. The highly variable control region was analyzed to determine unique maternal lines. A

Figure 4: Evolution of current bears based upon recent molecular DNA analysis (Waits and Ward, 1995).



maternal line was defined as unique when there was at least a single nucleotide difference from previously sampled bears.

Interspecific Phylogeny: The Evolutionary History of Bears

The combined data set of 1,916 nucleotide sequences from 6 regions of mtDNA molecule was used to construct the evolutionary relationship among bears (molecular phylogenies) as shown in Figure 4 (Ward and Waits 1995). The group of sea carnivores called the pinnapeds, which includes sea lions, walruses, and seals, where found to be the closest living relative to the bear family. This finding was confirmed independently by another group of molecular researches who compared the mtDNA among several mammalian families (Vrana et al. 1994).

The panda bear *(Ailuropoda melanolena)* is the oldest living bear species and first emerged about 9 million years ago (MYA). The spectacled bear *(Tremarctos arnatus)* was the next species, with its divergence from the panda bear line about 6 MYA. The sloth bear *(Ursus ursinus)* diverged next, about 4.5 MYA followed by the occurrence of 3 species about 4 MYA, the American black bear *(Ursus americanus)*, the sun bear *(Ursus malayanus)*, and the asiatic black bear *(Ursus thibetanus)*. The brown bear *(Ursus arctos)* lineage occurred about 1.5 MYA with the appearance of the polar bears *(Ursus maritimus)* radiating from within the brown bear line about 0.7 MYA.

Intraspecific Phylogeny: The Evolutionary Relationship of Brown/Polar Bears

The close relationship between brown bears and polar bears was determined by comparing the mtDNA from more than 300 brown bears from around the world and 4 polar bears from different parts of their range (Watts et al. 1995). There are at least 4 major evolutionary groups (clades) of brown/polar bears, with 3 migrations into North America (Figure 5). The oldest group is currently found in western Europe and dates back to about 1.1 MYA.

The second brown bear group occurred about 0.9 MYA with descendants now living on the Admiralty, Baranof, and Chichigof (ABC) islands of Alaska. The polar bear emerged from this brown bear group about 0.7 MYA.

The third and fourth major brown bear groups emerged about the same time around 0.5 MYA. One of these groups led to current brown bears in northern Europe, Asia, and Alaska, including the brown bears on Kodiak Island, commonly referred to as

Table 1: Distribution of unique maternal lines identified in North American brown bears.

POPULATION (N)		MATERNAL LINES (n)															
		a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p
ANWR	14	9		5													
Seward Penn.	17			17													
Kodiak Island	73			73													
Katmai	21		2		19												
Kluane	14					1	2	6	3	1	1						
Banff	40											1	39				
NCDE	36											17	3	3	12		1
Yellowstone	46												42			4	

Kodiak bears. The fourth brown bear group led to the brown bears now living in southern Canada and the states of Wyoming and Montana.

This high resolution of brown bear phylogeny reveals several interesting things. First is that the brown bears of the ABC islands are more closely related to the polar bear than they are to any brown bears in the world. The second is that the brown bears in Alaska are more closely related to the brown bears in Europe and Asia than they are to the brown bears in the lower United States. This research indicates that the grizzly bears in the lower 48 states have genetically separated from brown bears in Alaska for about 500,000 years, although this separation obviously took place long before each group migrated into North America. In other words the grizzly bears in the lower 48 states represent a unique subpopulation of brown/grizzly bears. This unique genetic makeup represents their response (adaptions) to different ecological conditions for several thousands of years

Forensic Applications

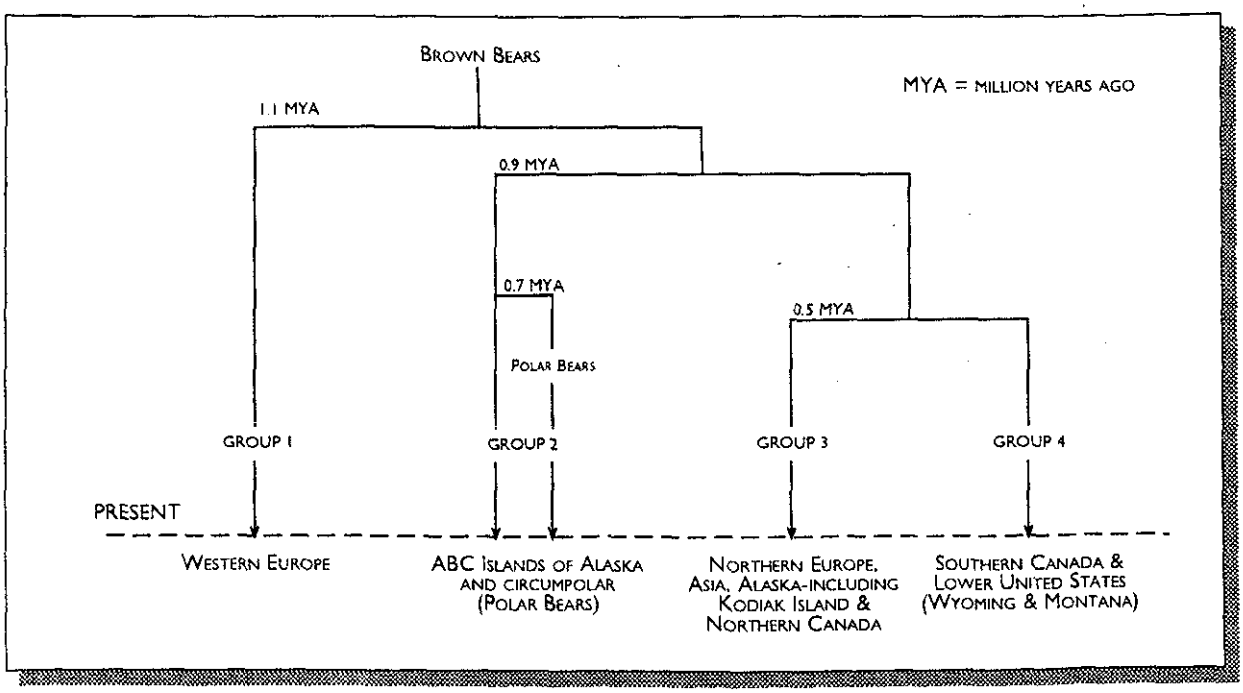
A technique for unambiguous genetic identification of bear species by unique mtDNA nucleotide sequences has been developed (Waits and Ward 1995). Each of the 8 bear species contain unique sequences that can be used to differentiate it from other species. Because this technique involves small portions of the mtDNA molecule, this test can be used to evaluate small portions of degraded DNA from a variety of bear tissues.

Phylogeography: the Location of Distinct Genetic Subpopulations

MtDNA analysis clarified the distribution of maternal lines over broad geographic areas and defined maternal affiliations within and between populations. A total of 261 bears were sampled from 8 geographic regions from Alaska down to the lower 48 states. Sixteen unique maternal lines were identified and distributed as shown in Table 1. Kluane National Park was the most diverse with 6 different maternal lines, followed by 5 in the Northern Continental Divide Ecosystem (NCDE), 2 in Katmai National Park, the Arctic National Wildlife Refuge (ANWR), and the Yellowstone Ecosystem, and only 1 maternal line was found in the bears sampled from Kodiak Island and the Seward Peninsula.

Kluane and Katmai National Parks contained maternal lines unique to their regions but a signifi-

Figure 5. Evolution of brown/polar bear genetic groups and their current distrubtion (Waits and Ward, 1995).



cant amount of overlap occurred among the other regions sampled. Kodiak Island and the Seward Peninsula each contained the same maternal line that was also found in 36% of the bears sampled in ANWR. Even more overlap occurred among the southern most regions sampled. The most common maternal line found in the Banff Ecosystem (97.5%) was also the most common one found in the Yellowstone Ecosystem (91.3%), but this maternal line was only found in 8.3% of the bears sampled from the NCDE. The most common maternal line found in the NCDE (47.2%) was also found in the Banff Ecosystem, but only represented 2.5% of the bears sampled.

Genetic Variation in Yellowstone

In the first phase of this study, we used DNA extracted from whole blood. The age, sex, geographic origin, and bear species was recorded for each blood sample collected. DNA was extracted, catalogued, and stored. A complete description of the molecular techniques and protocols involved has been reported (Ward and Waits 1995, Waits et al. 1995, Waits et al. 1995, Wooding and Ward 1995).

We have begun to assess the distribution of microsatellite variability in various populations of brown bears. At this stage the only loci available are 8 microsatellites developed from a black bear genomic library. Although these loci may not be as fully informative as loci developed from a grizzly bear genomic library, they provide an assessment of the degree of variability to be expected in grizzly bear populations.

The most diverse grizzly bear population surveyed with these black bear loci are those of the Brooks Range and the Richardson Mountains of Alaska (Waits et al. 1995). These populations have an average of 7.5 alleles per locus, and an overall heterozygosity of 74% at these 8 loci. By contrast the Northern Continental Divide population exhibits 6.7 alleles per locus with 69% heterozygosity, while the 47 Yellowstone bears exhibit 4.38 alleles per locus with a heterozygosity of 55%. The Kodiak population has the least variability of all, with only 2 alleles per locus and a heterozygosity of 26%. These figures contrast with data from black bear populations that tend to show 8.5 alleles per locus and a heterozygosity in excess of 80%.

Current Research

Molecular Techniques

These preliminary data indicate the feasibility of using microsatellites for individual identification within the Yellowstone population, but suggest that around 30 loci need to be developed to give unambiguous identification, especially since it will be necessary to distinguish between related individuals as opposed to randomly selected individuals. Developing 30 loci will also give a fail safe margin for analysis of scat samples, where a certain degree of random amplification failure is expected, resulting in increased numbers of "null" alleles (Callen et al. 1993). We also feel that these loci should be developed from a brown bear genomic library to maximize the degree of variability that will be contained within each locus. Part of the higher variability in black bears compared to brown bears is likely to be attributable to the fact that the 8 loci used were all developed from a black bear genomic library.

A genomic library will be made from DNA which was extracted from a portion of a grizzly bear liver collected from the Yellowstone population. Once the library has been created, clones will be plated out and screened for the presence of potential microsatellites by a variety of probes. All possible dimers will be probed using individual 12-mer oligonucleotide probes, as will the 8 most likely tetramers (chosen on the basis of their abundance in the human genome). We anticipate that upwards of 200,000 clones will have to be screened by all 16 oligonucleotides in order to obtain the 30 loci we desire.

Clones that give unambiguous positive results will be cultured, and each strand of the insert sequenced with standard primers. All inserts found to contain a microsatellite sequence with a minimum of 8 repeats (to maximize the possibility of polymorphoric locus) will be considered to be a potential polymorphic marker, and flanking primers will be synthesized to enable PCR amplification of the repeated region. Once primers have been developed for an insert, DNA from a pool of 10 randomly chosen Yellowstone bears will be amplified and the distribution of alleles scored in terms of band size and intensity. Loci that give a minimum of 4 alleles in this initial screen will be retained for further analy-

sis, while less informative loci will be discarded. Following this strategy, we expect to obtain 30 highly informative microsatellite loci, of which we anticipate 10 will be tetranucleotide repeats, and the remaining 20 will be dinucleotide repeats. The flanking sequence data for these loci will be deposited in the GDB international computerized data base for access by other researchers. The Yellowstone Grizzly Foundation will distribute these primers to all bear researchers free of charge.

Once the 30 loci have been developed, we will screen all Yellowstone samples in our possession, with a special emphasis on bears for which the familial relationship is known. Screening related individuals, such as mother-cub pairs, represents an independent assessment of the validity of the genetic variability that we have developed. Once all samples have been genotyped, we will attempt to determine the probability of identifying individuals in terms of the level of discrimination of each locus. The maximally informative loci for the sample will be used for the next phase of the study, which is based on obtaining genetic profiles from scat or hair roots.

In addition to determining which loci are required for individual identification, we will use the combined data on all loci to estimate the degree of genetic diversity within the Yellowstone population and assess whether distinct subpopulations exist within the Yellowstone ecosystem. These data will also provide important information about the magnitude of the reduction of genetic diversity that has occurred as a consequence of the reduced size of this population.

The greatest challenge in obtaining reliable data from scat and hair roots is in obtaining adequate amounts of high molecular weight DNA. Hence, we will experiment with a number of extraction protocols, especially those developed by Höss et al. (1992), in order to define a protocol that will maximize yield without sacrificing quality. We will then adjust PCR protocols (Innis and Gelfand 1990) so that the effect of primer mispairing and primer dimerization is minimized (Chou et al. 1992). Initially we will work with hair specimens, ideally from a bear that has already been typed. Each individual locus will then be amplified in order to gain a perspective about the probability of "mis-amplification" and whether this problem is randomly distributed with respect to individual loci.

Once an informative and efficient set of protocols have been developed, we will begin to assay hair roots collected in the field Our initial focus will be on developing a genetic census for bears ascertained through a hair collection study such as described below. A primary focus will be on the group of bears that have been observed to prey on moths in alpine habitats during the summer, since it is currently unknown whether they form a distinct sub-population. As the knowledge base increases and more bears become genotyped by this non-invasive procedure, we envisage ultimately starting to define a genealogy for the entire Yellowstone population.

Non-Invasive Collection of Genetic Material: A Hair Sample Strategy

The most significant challenge once the microsatellites have been developed is to collect DNA non-invasively from as many grizzly bears as possible. Collecting bear scat is the most readily available source of DNA, but the techniques to extract DNA from scat are currently difficult and time consuming, making its application prohibitively expensive as a routine procedure.

Consequently, our initial focus will be on a system to collect grizzly bear hair. Our preliminary field studies indicate barbed wire is very effective for this purpose. We constructed a triangular corral with a single strand of barbed wire about 2 feet from the ground wrapped around 3 trees. The objective was to attract bears into the corral where, in the process, hair was extracted from their backs by the barbs when they walked under the wire.

Not surprisingly, we found that a carcass was the most efficient attractant. An average of about 20 hair samples were collected each day the carcass was being consumed.

Since the carcasses are not always available, either in time or location, we needed to develop simple, inexpensive methods that could be used in selected, remote locations to attract bears into a hair-trap corral. The most successful method to date was to suspend a scent bag containing fish oil out of reach above the corral and painting the fish oil on the base of a tree within a corral. Other attractants, such as blood bait and turpentine, will be tried in the future.

Based upon these preliminary experiments to capture hair, we will attempt to collect hair from as many different bears as possible within a subunit of the ecosystem, such as a large valley or a single river drainage. We will then design a hair-trap system in an attempt to sample all bears within the ecosystem.

Future Research Projects

Historic Genetic Profile

Human intrusions and developments around the Yellowstone Ecosystem during the past 150 years have decreased both the numbers and distribution of bears in this area. Did this also decrease the genetic stock in this population? What was the level of genetic diversity and what maternal lines existed prior to the expansion of western civilization? These questions can be answered by genetic analysis of museum specimens since DNA can be retrieved from dental pulp from teeth in skulls and the hair roots of pelts.

If these studies indicate there is a need to genetically augment the Yellowstone grizzly population to historic levels to ensure long term viability, then the same techniques can be used to define the genetic makeup of the bear to be used for augmentation in terms of its potential genetic contribution to the population, and where such a bear is likely to be found. The same technology can also monitor the effectiveness of a genetic augmentation program

Historic Genetic Subpopulations

It is commonly assumed that grizzly bears were panmictic prior to the westward settlement of Euro-Americans. As this study has already demonstrated, we know that this assumption for brown bears in North America is wrong, particularly between brown bears in Alaska compared to those in the lower 48 states. But were there distinct subpopulations of grizzly bears that were genetically isolated 100 years ago in the lower 48 states? In other words, did habitat and topography serve to isolate bears into genetically distinct units? Was the California golden bear, the Plains grizzly, or the grizzly of the southwest genetically distinct?Again, by analyzing museum specimens we can address these questions.

Conclusions

This study demonstrates that a comprehensive project using a variety of molecular DNA techniques provides information vital to the conservation of small populations of grizzly bears, and that these same techniques can be applied to other small populations of wild animals. In all likelihood, more advanced molecular techniques will be developed in the future that will further add to our effort to conserve wildlife populations. Therefore, DNA samples should be cataloged and stored appropriately for future use.

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Greater Yellowstone Predators: A Summary

Invited talk given September 26, 1995

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My charge is to provide an overview of this conference on predators in the Greater Yellowstone Ecosystem (GYE). I have no intention of reiterating key points made by various authors during the course of the meeting. The interested reader can quickly skim the contributions of this volume. Instead, I will use this forum to suggest why I believe we are having this conference. While listening to the 2 full days of papers on predators, I found it easy to lose perspective and to become engrossed in the fascinating details of natural history. About halfway through the conference, I challenged myself to think how this meeting differed fundamentally from a garden club meeting. If one steps back to view the big picture, the reason for this meeting is obviously much more than natural history. Indeed, "Greater Yellowstone's Predators" strikes at the very core of what Yellowstone is all about.

Yellowstone is about preserving nature. This was the spirit of the original legislation that established Yellowstone National Park (YNP) as our first national park in 1872. And it has pervaded the spirit of national park management philosophy since then, even though the particulars of how to accomplish the preservation of nature have varied (e.g., Pritchard *this volume*). In the context of modern views on ecosystem management, I believe that preserving nature entails the preservation of ecological processes. Such ecological-process management has "the objective to allow ecological processes of nutrient cycling, plant succession, fire, decomposition, competition, *predation*, symbiosis, birth, and death to operate unimpeded by human intervention" (Boyce 1991:190).

We seek to preserve nature because we believe that nature has value. Wagner (1996) argues that nature does not have intrinsic value (*contra* Callicott 1989), but that values emerge from society. While Wagner's arguments appear logical, I believe that a large contingent of modern society recognizes value in maintaining areas like Yellowstone, where human influences are minimized and where natural ecological processes are allowed to run their course. This societal value attached to wildness carries over to benefit science because we need ecological baseline preserves with which to compare other areas dominated by human influences (Sinclair 1983). Granted, we do not know how to avoid all human influences such as exotic species, atmospheric changes, and contaminants encountered by migratory species outside the GYE (e.g., Harmata and Montopoli *this volume*). The best that we can do is to minimize such influences and restore natural ecological processes based on our current understanding.

The Role of Predators

Appreciating the importance of predators in the GYE requires perspective on how predators can be crucial in shaping ecosystem structure and function. Ecologists are learning that predators are often keystone species in natural ecosystems, i.e., that they have significance much greater than is indicated by

their relative abundance (Power and Mills 1996, Power et al. 1996). Many mechanisms allow predators to achieve disproportionate importance. Experiments with marine invertebrates demonstrated that predators can reduce competitive dominance, and thereby enhance species diversity (Paine 1966). In contrast, introduced predators on islands can be disruptive and cause selective extinction of prey with a net result of reduced species diversity (Schoener and Spiller 1996). Predators appear to dominate ecosystem dynamics on Isle Royale National Park where wolves (*Canis lupus*) impose top-down control of moose (*Alces alces*) populations that, in turn, has major consequences for the vegetation on which they feed (McLaren and Peterson 1974). Predators can also shape the spatial distribution of prey (Mech 1976, Nelson and Mech 1981). Increasingly, predators are recognized as agents shaping ecosystem composition, structure, and function, although their ability to do so has frequently been disrupted by human activities (Estes 1995).

Begon et al. (1996: 802-803) present the view that predators are agents that disturb community equilibriums. Such a view emerges in part because trophic-level interactions, like predator-prey or parasite-host, are often unstable. Models of such interactions can indeed be perpetually dynamic—always changing and creating disequilibriums. In this way, predators may be viewed as agents of change in ecosystems similar to fire, flooding, climatic perturbations, and other disturbances (Boyce and Payne 1997). Again, we see how predators can be fundamental to the structure and function of ecosystems.

Predators and Natural Regulation

Predators figure prominently in the ongoing discussions over Yellowstone's natural regulation management. When first proposing the notion of natural regulation management, Cole (1971) hypothesized that herbivore populations were largely limited by vegetation, and predators simply facilitated natural regulation. Cole maintained that vegetation ultimately regulated ungulate populations in Yellowstone and, following Errington's (1946, 1971) rationale, suggested that predators usually only killed animals that were predisposed to natural mortality. In other words, if predators had not killed the prey they would have died anyway from other causes.

Cole's (1983) interpretation of his study of elk (*Cervus elaphus*) in the Madison-Firehole area of YNP seemed to support Errington's view. Although about 50% of elk mortality was attributed to predators, Cole argued that many of these animals were likely to die anyway and that predators were only facilitating natural regulation, i.e., removing the annual surplus before the animals died due to starvation in late winter. Recent studies of predation on ungulates in Yellowstone substantiate Cole's observations on the levels of predation on elk prior to wolf reintroduction (Singer et al. 1997) and, like Cole, Singer et al. (1997) suggest that predation mortality may be compensatory.

Although both of these studies present results that are consistent with the possibility that predation is compensatory within a year, neither study permits rejection of the alternative hypothesis that at least part of the predation mortality is additive. Indeed, demonstrating an effect of predation requires a prey population response (Seip 1992). Even if compensation occurs within a year, ultimately this is due to density dependence, albeit seasonally distributed. The question is whether prey abundance is reduced below levels that would occur by plant-herbivore interactions.

Errington's ideas about predators only cropping the nonessential annual surplus of prey populations appear to be challenged by recent studies in Alaska demonstrating that wolves can indeed have major long-term consequences to ungulate abundance (Gasaway et al. 1992, Boertje et al. 1996). This is particularly true when confounded with human exploitation of native ungulate populations (Messier 1994, Van Ballenberghe and Ballard 1994).

Models of wolves and ungulates for Yellowstone suggest that wolves may cause significant declines in the abundance of some ungulate populations (Boyce 1992). Elk numbers are anticipated to decline by 10-30% and even larger reductions in long-term abundance can be anticipated for moose and mule deer (*Odocoileus hemionus*). Much remains to be done to reliably predict wolf-ungulate dynamics. Work reported here by Moorcroft and Crabtree (*this volume*) on spatial relationships in Yellowstone's Northern Range promises to refine these predictions. Emerging data on wolf predation in multi-prey systems like Glacier National Park (Kunkel and Pletscher *this volume*) and Yellowstone (Smith and Phillips *this volume*) afford a wonderful opportunity to evaluate alternative models for multiple-species functional responses.

Cole (1983) was explicit about how he viewed science interfacing with his natural regulation hypothesis. He articulated how he believed the system to work, presented this as a hypothesis to be tested, rejected portions of the hypothesis based on the results of his analysis, and presented a revised hypothesis as an improved statement of his view of natural regulation. This is how science works, and Cole's presentation is remarkably similar to adaptive management (Walters 1986). Cole (1971) and Houston (1976) had some details of the natural regulation hypothesis wrong, e.g., they believed that vegetation should not change appreciably as a consequence of plant-ungulate interactions. A restatement of the hypothesis was necessary as we learned more about the dynamics of plant-herbivore interactions (Boyce 1991). Developing our understanding of how natural regulation works is an ever-changing process, requiring continued monitoring (e.g. Crabtree, et al. *this volume*), research, and reevaluation.

I agree with Peek (1980) that Cole (1971) and Houston (1976) probably underestimated the role of predators in the system. The verdict on the significance of wolf predation on ungulate populations in Yellowstone is still out, but I believe that ecologists agree that wolves were an integral and crucial element of the system that needed to be replaced. Presuming that someone does the research, during the next few years we will learn much as wolves become established in the GYE (see Smith and Phillips *this volume*).

Ecosystem Management

Ensuring that predation as an ecological process is maintained and restored in the GYE is a difficult task that requires management intervention. The National Park Service's natural-regulation management has been berated as no management at all, and a laissez faire approach allowing nature to take its course. In many instances, this is as it should be, allowing natural ecological processes to prevail. However, in the case of predators, the Park Service has taken several actions that are certainly not laissez faire. Most obvious is the reintroduction of wolves into YNP in 1995. Similarly, aggressive management was implemented in 1983 under the advice of the Interagency Grizzly Bear Committee to reduce grizzly bear (*Ursus arctos*) mortalities in the GYE (Servheen 1993). Finding new and better ways to minimize bear conflicts with humans will be a continuing challenge (see Biel et al., Renkin and Gunther, Gunther et al. *this volume*). How to preserve the predator-prey interactions focused on cutthroat trout (*Oncorhyncus clarki*) in Yellowstone Lake (grizzly bears, for example, Reinhart et al. *this volume*) promises to be an enormous challenge for the National Park Service in the future; recently discovered lake trout (*Salvelinus namaycush*) in the lake threaten to decimate the cutthroat population (Gresswell et al. 1995).

Managing to maintain natural predation in portions of the GYE outside YNP will be even more difficult because large predators can come into conflict with livestock ranching and hunting. Currently, predation on elk in the Jackson elk herd is only on calves (Smith and Anderson *this volume*), and expanding wolf populations in the GYE are likely to compete with hunters for prey (Boyce 1992). Also, forest management can conflict with smaller predators, including martens (*Martes americana*), fishers (*Martes pennanti*), wolverines (*Gulo gulo*) and lynx (*Felis lynx*) (Ruggiero et al. *this volume*).

Because of conflicts with people having various priorities (e.g., livestock ranchers, hunters, loggers), managing for predators in the GYE will require strong public support from those who value nature. Public education can help. Predator ecology always captures the attention of our wildlife students and public alike. Predation somehow fascinates people. Obviously, predator management attracts political and media attention as witnessed by continuing publicity on wolves and grizzly bears. Predators indeed merit such attention because of the importance of predation as an ecological process. I believe that it is worth the effort. I believe that we need large places like Yellowstone where nature takes priority, where we have a full complement of natural predators, and where we can allow predation to run its course unimpeded. And Yellowstone is the only such place left.

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PART II:
CONFERENCE PAPERS

Bear Attractant Test of Biodiesel Fuel

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Abstract

In 1994, more than 3 million visitors toured Yellowstone National Park (YNP). These visitors, along with park concession and National Park Service administrative vehicles, burned more than 7.6 million gallons of gasoline and diesel fuel in the park. Pollution from vehicle emissions can have harmful effects on both human and plant life. YNP, in cooperation with the Montana Department of Natural Resources and Conservation and the U.S. Department of Energy, Pacific Northwest and Alaska Regional Bioenergy Program, is participating in a pilot project to explore and evaluate the use of 100% rape ethyl ester (biodiesel) as a low pollution alternative to diesel fuel in environmentally sensitive areas. Biodiesel emits fewer hydrocarbons and particulates than fossil-based fuels, is derived from renewable resources and contains negligible levels of sulfur, and reduces emissions of sulfur dioxide, one of the agents responsible for acid rain. Biodiesel is part of the natural cycle (i.e., assimilation of CO_2 by plants for growth and development), and could lead to zero net gain in oxides of carbon emissions. It is also biodegradable and will quickly break down, preventing long-term damage to soil or water in the event of a spill. YNP is an environmentally sensitive area that brings humans and wildlife, such as grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*), into close proximity. Biodiesel fuel is a vegetable oil derivative that smells similar to cooking oil. The exhaust from a diesel engine fueled by biodiesel smells similar to a french fry cooker and thus could act as a bear attractant. Having bears attracted to vehicles powered by biodiesel could draw bears into park developed areas and roadside corridors resulting in bear-human conflicts (bear-caused human injuries and property damages). This could lead to the potential removal of grizzly bears and black bears from the population. As a result of these concerns, tests were conducted to determine if the raw biodiesel fuel or its emissions were bear attractants. Captive bears were exposed to ambient air (standard) and to odor from raw biodiesel fuel, raw diesel fuel, deer meat/dog food (a known bear attractant), biodiesel exhaust, and diesel exhaust. Of 5 grizzly bears and 5 black bears tested, all displayed a significant non-attraction response to ambient air and a significant attraction and investigation response to deer meat/dog food. All bears were indifferent to biodiesel fuel and diesel fuel, but displayed a significant agitation/aggression response to biodiesel exhaust and diesel exhaust.

Introduction

Yellowstone National Park (YNP) was established March 1, 1872, and "dedicated and set apart as a public pleasuring-ground for the benefit and enjoyment of the people" and "for the preservation, from injury or spoilation, of all timber, mineral deposits, natural curiosities, or wonders...and their retention in their natural condition."

In 1994, more than 3 million visitors toured YNP. These visitors, in combination with park concession and National Park Service administrative vehicles, burned more than 7.6 million gallons of fuel within the park. Fuel consumption for automobiles and over-the-snow vehicles included 2.5 million gallons of gasoline and 57,000 gallons of diesel fuel purchased by park visitors (H. Broadhead, Yellowstone Park Service Stations, pers. commun.), 106,208 gallons of gasoline and 33,420 gallons of diesel fuel used by park concession vehicles (M. Vissage, TW Recreational Services, pers. commun.), and 186,354 gallons of unleaded fuel and 134,742 gallons of diesel fuel used by National Park Service vehicles (P. Starkweather, National Park Service, pers. commun.).

Motor vehicles powered by gasoline and diesel fuels emit pollutants into the atmosphere. The vehicle pollutants of greatest concern to human health include carbon monoxide, nitrogen dioxide, and particulate matter emissions (Environmental Protection Agency 1992). These pollutants can affect human health in several ways, including impaired lung function, lung damage, increased respiratory illness, cancer, and birth defects (Environmental Protection Agency 1992). In addition, vehicle emissions contribute to the greenhouse effect and can be injurious to plant life, and reduce yields of agricultural crops and native plants and forests (Environmental Protection Agency 1992).

YNP, in cooperation with the Montana Department of Natural Resources and Conservation and the U.S. Department of Energy, Pacific Northwest and Alaska Regional Bioenergy Program, is participating in a pilot project to explore and evaluate the use of 100% rape ethyl ester (biodiesel) as a low pollution alternative to diesel fuel in environmentally sensitive areas. Biodiesel emits fewer hydrocarbons and particulates than fossil-based fuels and is derived from renewable resources (Peterson and Reece 1995). Biodiesel contains negligible levels of sulfur and reduces emissions of sulfur dioxide, one of the agents responsible for acid rain (Peterson and Reece 1995). Biodiesel is part of the natural cycle (i.e., assimilation of CO_2 by plants for growth and development), and could lead to zero net gain in oxides of carbon emissions (Peterson and Reece 1995). The fuel is also biodegradable and will quickly break down (96% in 21 days), preventing long-term damage to soil or water in the event of a spill (H. Haines, Montana Department of Environmental Quality, pers. commun.). YNP is an environmentally sensitive area that brings humans and wildlife, such as grizzly bears (*Ursus arctos*) and black bears (*Ursus*

Table 1. Test materials and description of materials tested as bear attractants, biodiesel fuel bear attractant test, Washington State University, 1995.

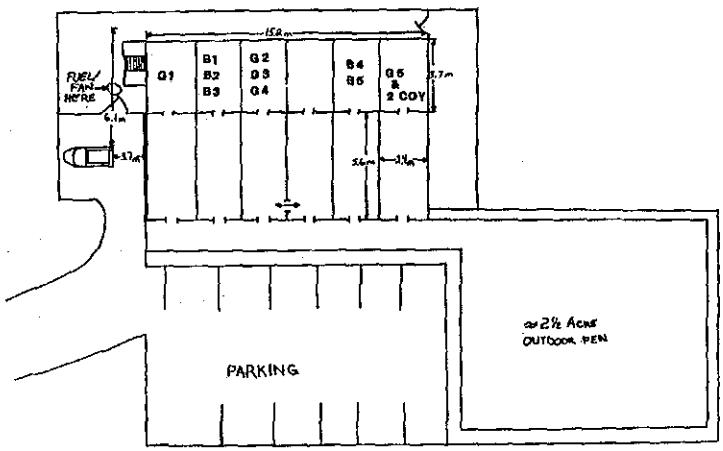
Test Material	Description
Ambient air	Fresh outside air. Not expected to be a bear attractant.
Deer meat/dog food	A mixture of deer meat and dog food, the standard foodstuff normally fed to the captive bears in the facility. The deer meat/dog food mixture is known to elicit a well defined, strong behavioral response by captive bears.
Biodiesel fuel	A bowl of raw rape ethyl ester (biodiesel) fuel placed in a bucket. The fuel smells similar to cooking oil and could act as a potential bear attractant.
Diesel fuel	A bowl of raw diesel fuel placed in a bucket. Diesel fuel has been used to power all diesel trucks in YNP for many years and is not known to elicit a response in bears in the wild.
Biodiesel exhaust	Exhaust from a biodiesel fuel-powered Dodge Cummins diesel truck. Odor from biodiesel exhaust smells similar to that of a french fry cooker and could act as a potential bear attractant.
Diesel exhaust	Exhaust from a diesel fuel-powered truck. Diesel exhaust is odorous and an eye irritant and is not known to act as a bear attractant in wild bears within YNP.

americanus), into close proximity. Biodiesel is a vegetable oil derivative that smells similar to cooking oil. The exhaust from a diesel engine fueled by biodiesel smells similar to a french fry cooker and thus could act as a bear attractant. Having bears attracted to vehicles powered by biodiesel could draw bears into park developed areas and roadside corridors, resulting in bear-human confrontations, bear-caused property damages, and/or bear-inflicted human injuries. This could lead to the potential removal of grizzly bears and black bears from the population. As a result of these concerns, tests were conducted to determine if the raw biodiesel fuel or its emissions were bear attractants.

Table 2. Species, sex, age class, and location of origin of bears tested in Bodiesel Fuel Attractant test, Washington State University, 1995.

Bear #	Species	Sex/Age Class	Location of Origin
G-1	Grizzly	Sub-adult Male	Born in Captivity
G-2	Grizzly	Adult Male	British Columbia
G-3	Grizzly	Adult Male	British Columbia
G-4	Grizzly	Adult Female	Near Glacier NP
G-5	Grizzly	Adult Female w/2 COY	Near Glacier NP
B-1	Black Bear	Adult Female	Yellowstone NP
B-2	Black Bear	Adult Female	Alaska
B-3	Black Bear	Adult Female	Ketchikan, Alaska
B-4	Black Bear	Yearling Male	Born in Captivity
B-5	Black Bear	Yearling Female	Born in Captivity

Figure 1. Diagram of bear facilities used in Biodiesel Fuel Attractant Study, Washington State University, 1995.



Methods

Ten captive bears (5 grizzly bears and 5 black bears) housed at Washington State University at Pullman were used to test biodiesel fuel and biodiesel exhaust as potential bear attractants. As part of the test, the reaction of bears to the odor of biodiesel fuel and biodiesel exhaust were compared to that of a standard (fresh air) and a known bear attractant (deer meat/dog food), as well as diesel fuel and diesel exhaust (Table 1). Diesel fuel has been used in YNP for decades and has not been known to act as a bear attractant.

The 10 bears tested consisted of both males (n = 4) and females (n = 6), as well as various age classes and locations of origin (Table 2). Tests were conducted within each bear's regular holding pen. Each pen consisted of a 2.4 m wide by 3.7 m long indoor room connected by an open door to a 2.4 m wide by 5.6 m long outdoor kennel (Figure 1). Each pen housed from 1 to 3 bears of the same species. Each outdoor portion of the kennel could be opened to allow access to a 2.5-acre (1.0-hectare) outdoor exercise area. However, during the tests access to the exercise area was closed.

Test procedures were modified from those described by Cushing (1980, 1983) for testing menstrual odor as a bear attractant. Samples of biodiesel fuel, diesel fuel, and deer meat/dog food were placed in a bowl in a 10-gallon (37.9-liter) bucket. The bucket was located approximately 6.8 m from the nearest pen and on the other side of a cinderblock wall (Figure 1). A fan was placed on top of the bucket, which forced the odor from the sample being tested through a 15-cm stovepipe into the indoor portion of each pen. For the standard test the fan was placed on an empty 10-gallon (37.9-liter) bucket and outdoor air was forced through the stovepipe. To divert biodiesel and diesel exhaust from running pickup trucks to the pens, a 10 to 15-cm stovepipe converter was placed on the truck exhaust pipe, and then a 15-cm stovepipe was hooked up to this and run to the indoor portion of each pen. The trucks were located outside and were 3.7 m from the nearest outside pen (Figure 1). Duct tape was used to

seal the seams between the sections of stovepipe for all trials to prevent odor from leaking out before reaching the pen.

Due to the small number of bears available (n = 10) and the number of stimuli being tested (n = 6), the same bears had to be used to test more than 1 stimulus. In addition, multiple bears were held in 4 of the 5 pens used (Figure 1), thus tests in these pens were conducted on multiple bears at the same time. Due to these factors, tests did not meet criteria required for being random or independent and nonparametric statistics were therefore used to test all hypotheses.

Each test was run for 15 minutes at each pen with the bears' reaction to the test stimulus recorded at the start of each minute of the 15-minute trial period. The stovepipe was flushed with ambient air between each trial. A minimum of 34 ($\bar{x}$= 358 ± 438 SD) minutes elapsed between trials of different stimuli within the same pen. From 0 to 4 ($\bar{x}$= 2.0 ± 1.4 SD) tests were conducted per bear, per day.

Each 15-minute trial was videotaped and the bears' reactions were recorded. Reactions were grouped into categories as follows:

1) no attraction to the odor piped into the bear's pen as evidenced by the bear remaining in the outdoor kennel;
2) the bear came to the door to sniff the air in the indoor pen;
3) the bear entered the indoor pen to sniff the air;
4) the bear entered the indoor pen and came up to the vent to sniff the odor emanating from the stovepipe;
5) the bear entered the indoor pen and licked the vent, walls, door, or stovepipe, indicating a strong attraction to the odor;
6) the bear became agitated and aggressive as evidenced by pacing, vocalizations, and lunging at pen-mates or bears in adjacent pens.

In summarizing analysis of the data, we use the terms no attraction, attraction/investigation, and agitation/aggression. We define "no attraction" as bears that reacted to test stimuli as described in category 1 above. "Attraction/investigation" is defined as bears that reacted to stimuli as defined in categories 2, 3, 4, and 5. "Agitation/aggression" is defined as bears that reacted to stimuli as described in category 6.

A heterogeneity G Log-likelihood test was used to test if bears' responses to the 6 stimuli were homogeneous or heterogeneous. A paired sample T-test was used to test whether bears reacted the same or differently to biodiesel fuel versus diesel fuel and to biodiesel exhaust versus diesel exhaust. An inde-

Table 3. Number of minutes grizzly bears and black bears exhibited different response behaviors to ambient air during 15-minute trial period. Biodiesel Fuel Attractant Test, Washington State University, 1995.

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	14	1	0	0	0	0
G2	15	0	0	0	0	0
G3	15	0	0	0	0	0
G4	15	0	0	0	0	0
G5	8	1	0	0	0	6[g]
B1	13	0	1	1	0	0
B2	6	9	0	0	0	0
B3	14	0	0	1	0	0
B4	15	0	0	0	0	0
B5	15	0	0	0	0	0
$\bar{x}$	13.0	1.1	0.1	0.2	0.0	0.6
SD	±3.3	±2.8	±0.3	±0.4	±0.0	±1.9

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door, but did not enter pen.
[c] Entered pen and sniffed, but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.
[g] Fan was shut off for minutes 8, 9, and 10 so sow could get 2 cubs of the year (COY) out of indoor portion of pen. Fan turned on for remainder of trial once 2 COY outside.

pendent *T*-test was used to test for differences in the agitation/aggressive response to biodiesel exhaust and diesel exhaust of grizzly bears as compared to black bears. For statistical analysis the paired sample *T*-test, independent *T*-test, and heterogeneity *G* Log-likelihood test followed procedures described by Zar (1974). $P < 0.05$ was considered to be significant. The hypotheses tested were:

H_{01} Bears' responses to the 6 stimuli presented are homogeneous.

H_{02} There is no difference in the number of minutes bears displayed agitated behavior to biodiesel exhaust as compared to diesel exhaust.

H_{03} There is no difference in bears' reactions to biodiesel fuel odor versus diesel fuel odor.

H_{04} There is no difference in bears' reactions to biodiesel exhaust versus diesel exhaust.

H_{05} There is no difference in the number of minutes grizzly bears versus black bears displayed agitated behavior to biodiesel exhaust.

H_{06} There is no difference in the number of minutes grizzly bears versus black bears display agitated behavior to diesel exhaust.

Results

Response to Ambient Air

Nine of 10 (90%) bears reacted with indifference for the majority of the 15-minute trial period that ambient air was pumped into their pens (Table 3). One bear (B2) displayed attraction/investigation behavior for more than half of the trial period and 1 bear (G5) briefly (6 min) displayed agitation/aggression behavior during the trial. In the case of bear G5, her 2 cubs of the year (COY) were in the indoor pen playing and sleeping during the trial and she was becoming agitated presumably because the fan noise was loud and she felt her cubs were threatened. The fan was shut off at the request of facility managers for minutes 8, 9, and 10 so the sow could retrieve her cubs from the inside pen and take them to the outdoor portion of the pen. The fan was then turned back on for the remainder of the 15-minute trial period.

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	5	9	1	0	0	0
G2	0	15	0	0	0	0
G3	0	14	0	0	1	0
G4	0	12	1	0	2	0
G5	0	14	1	0	0	0
B1	0	2	4	7	2	0
B2	0	7	4	4	0	0
B3	0	8	3	4	0	0
B4	0	12	0	3	0	0
B5	0	13	2	0	0	0
$\bar{x}$	0.5	10.6	1.6	1.8	0.5	0.0
SD	±1.6	±4.1	±1.6	±2.5	±0.9	±0.0

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door, but did not enter pen.
[c] Entered pen and sniffed, but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.

Table 4.
Number of minutes grizzly bears and black bears exhibited different response behaviors to deer meat/dog food during 15-minute trail period. Biodiesel Fuel Attractant Test, Washington State University, 1995.

Response to Deer Meat/Dog Food

All 10 bears (100%) displayed some level of attraction/investigation behavior when deer meat/dog food was pumped into their pens (Table 4). Three (30%) bears (G3, G4, and B1) exhibited a strong attraction as evidenced by licking the vent and walls of the indoor pen. Only 1 (10%) bear (G1) displayed no reaction for a portion of the trial period. No (0%) bears became agitated/aggressive when this stimulus was presented.

Response to Biodiesel Fuel

Eight of 10 (80%) bears displayed no reaction for the majority of the 15-minute trial with odor from biodiesel fuel pumped into their pens (Table 5). Two of the 10 (20%) bears (G1 and B3) displayed attraction/investigation behavior to this stimulus for the majority of the trial.

Response to Diesel Fuel

All 10 bears (100%) exhibited no reaction for the majority of the 15-minute trial with odor of diesel fuel pumped into their pens (Table 6). Four of 10 (40%) bears (G5, B1, B3, and B4) displayed a small degree of attraction/investigation behavior to this stimulus.

Response to Biodiesel Exhaust

Four of 10 (40%) bears (G3, B2, B4, and B5) displayed no reaction for the majority of the 15-minute trial period with biodiesel exhaust pumped into their respective pens (Table 7). Two of these 4 bears (B4 and B5) briefly licked the vent and walls of the pen at the 10-minute mark of the trial (7 minutes after the truck engine was shut off) suggesting a potential attraction to biodiesel exhaust residue. Four (40%) other bears (G1, G2, G4, and G5) exhibited agitated/aggressive behavior for the majority of the trials of this stimulus. The truck was shut off at minute 14 during the trial with bear G5. Bear G5 had 2 COY and she was exhibiting extreme agitation and vocalizations along with bears in adjacent pens. Two (20%) bears (B1 and B3) demonstrated attraction/investigation behavior to this stimulus.

At minute 3 of this trial with bears B1, B2, B3, B4, and B5 the truck was shut off due to the test bears and bears in adjoining pens exhibiting agitation/aggression behavior.

Response to Diesel Exhaust

Half (50%) of the bears (G1, B1, B2, B4, and B5) displayed no reaction for the majority of the 15-minute trial period with diesel exhaust pumped into their pens (Table 8). Four of the 10 (40%) bears (G2,

Table 5
Number of minutes grizzly bears and black bears exhibited different response behaviors to biodiesel fuel during 15-minute trial period. Biodiesel Fuel Attractant Test, Washington State University, 1995.

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	5	9	1	0	0	0
G2	15	0	0	0	0	0
G3	15	0	0	0	0	0
G4	12	3	0	0	0	0
G5	14	0	0	0	0	1
B1	11	2	0	2	0	0
B2	14	0	1	0	0	0
B3	2	0	6	7	0	0
B4	8	4	3	0	0	0
B5	8	4	2	1	0	0
$\bar{x}$	10.4	2.2	1.3	1.0	0.0	0.1
SD	±4.5	±2.9	±1.9	±2.2	±0.0	±0.3

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door but did not enter pen.
[c] Entered pen and sniffed but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.

G3, G4, and G5) exhibited agitation/aggression behavior for the majority of the trial of this stimulus, and 3 bears (B2, B4, and B5) exhibited such behavior for a brief period. The trial was stopped at the 12-minute point with bear G5 due to agitation displayed by the sow. At the request of facility managers, the truck was shut off during the trial with bears B4 and B5 at the 8-minute point due to their agitation and the agitation displayed by bear G5 and other bears in adjacent pens. One (10%) bear (B3) exhibited attraction/investigation behavior for the majority of this trial.

Statistical Analysis

The responses of the 10 bears were not homogeneous, but were significantly different between the 6 stimuli ($G = 34.19$, df = 5, $P < 0.001$) presented. Whereas bears were indifferent to biodiesel fuel odor ($G = 0.40$, df = 1, $P > 0.05$) and diesel fuel odor ($G = 1.65$, df = 1, $P > 0.05$), they displayed a significant non-attraction response to ambient air ($G = 3.85$, df = 1, $P < 0.05$), a significant attraction and investigation response to the odor of deer meat/dog food ($G = 13.86$, df = 1, $P < 0.05$), and a significant agitation response to both biodiesel exhaust ($G = 13.86$, df = 1, $P < 0.05$) and diesel exhaust ($G = 7.36$, df = 1, $P < 0.05$).

Diesel fuel has been used in YNP for decades without resulting in any known bear-human conflict situations. Therefore, we compared bears' reactions to biodiesel fuel odor versus diesel fuel odor and biodiesel exhaust versus diesel exhaust. There was no significant difference between bears' reactions to biodiesel fuel odor and diesel fuel odor ($G = 1.86$, df = 1, $P > 0.05$) or between biodiesel exhaust and diesel exhaust ($G = 1.44$, df = 1, $P > 0.05$).

Since all 10 bears displayed at least some agitation behavior due to exposure to biodiesel exhaust, and such a response could potentially lead to bear-human conflict situations, further analysis was warranted. The number of minutes bears displayed an agitation/aggressive reaction to biodiesel exhaust was compared to the number of minutes bears displayed a similar reaction to diesel exhaust. Results indicate that there was no significant difference in the number of minutes either grizzly bears ($t = 0.33$, df = 4, $P = 0.76$) or black bears ($t = -0.89$, df = 4, $P = 0.42$) displayed agitation to biodiesel exhaust as compared to diesel exhaust. Grizzly bears displayed significantly more agitation/aggression behavior to both biodiesel exhaust ($t = -5.09$, df = 8, $P = 0.001$) and to diesel exhaust ($t = -2.95$, df = 8, $P = 0.018$) than did black bears.

Discussion

Bears displayed no reaction when ambient air

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	15	0	0	0	0	0
G2	15	0	0	0	0	0
G3	15	0	0	0	0	0
G4	15	0	0	0	0	0
G5	12	3	0	0	0	0
B1	14	1	0	0	0	0
B2	15	0	0	0	0	0
B3	10	1	2	2	0	0
B4	10	4	0	1	0	0
B5	15	0	0	0	0	0
$\bar{x}$	13.6	0.9	0.2	0.3	0.0	0.0
SD	±2.1	±1.5	±0.6	±0.7	±0.0	±0.0

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door but did not enter pen.
[c] Entered pen and sniffed but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.

Table 6
Number of minutes grizzly bears and black bears exhibited different response behaviors to diesel fuel during 15-minute trial period. Biodiesel Fuel Attractant Test, Washington State University, 1995.

was pumped into their pens and a significant strong attraction/investigation response when the odor of deer meat/dog food (their standard foodstuff) was pumped into their pens. In contrast, bears did not display a significant attraction to biodiesel fuel odor, diesel fuel odor, biodiesel exhaust, or diesel exhaust. In addition, there was no significant difference in bears' reactions to biodiesel fuel odor as compared to diesel fuel odor or to biodiesel exhaust as compared to diesel exhaust. Diesel fuel has been used for decades in YNP without any known significant influence on the number of bear-human conflict situations occurring in the park. These results suggest that biodiesel fuel and biodiesel exhaust are neither more nor less of an attractant than are diesel fuel and diesel exhaust. Standard methods used to handle and store hazardous fuels make them largely unavailable to bears. If biodiesel fuel is stored, handled, and burned, and spills cleaned up in the same manner as diesel fuel currently is within YNP, then use of biodiesel fuel would not be expected to contribute to additional bear-human conflicts above existing levels.

Due to budget limitations, this study was conducted with facilities and materials available at no cost. In addition, personnel time allocated to this project was also limited by available funding (20-person days total for design, experiment, analysis, poster presentation, and final report). Due to these limitations, the study could not be designed to meet criteria required for random and independent tests. However, the 10 bears tested reacted as expected to ambient air (no response) and to deer meat/dog food (strong attraction), suggesting that the study design probably did not significantly alter each bear's reaction to the 4 test stimuli (biodiesel fuel odor, diesel fuel odor, biodiesel exhaust, diesel exhaust).

Potential study biases that may have influenced test results include:

1) Noise from the fan may have affected the bears' responses to the different stimuli.

2) Although the hose was flushed with ambient air between trials of different stimuli, the same hose was used for all trials and residue of test stimuli could have remained.

3) Due to multiple bears being held in a single pen, tests between bears and different stimuli were not random.

Table 7
Number of minutes grizzly bears and black bears exhibited different response behaviors to biodiesel exhaust during 15-minute trial period. Biodiesel Fuel Attractant Test, Washington State University, 1995.

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	1	0	0	0	0	14
G2	3	4	0	0	0	8
G3	9	1	0	0	0	5
G4	3	4	0	0	0	8
G5	2	1	0	0	0	12[g]
B1	6	0	8	0	0	1[h]
B2	12	2	0	0	0	1[h]
B3	5	1	7	1	0	1[h]
B4	9	0	1	1	3	1[h]
B5	11	0	1	0	2	1[h]
$\bar{x}$	6.1	1.3	1.7	0.2	0.5	5.2
SD	±3.9	±1.6	±3.1	±0.4	±1.1	±5.0

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door but did not enter pen.
[c] Entered pen and sniffed but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.
[g] Engine shut off at minute 14 due to agitation/vocalizations exhibited by bear #G5.
[h] Engine shut off at minute 3 due to agitation exhibited by test bears and bears in adjacent pens.

4) Because the same bears were used to test all stimuli, tests were not independent.

5) Due to multiple bears being confined to a single pen, bears' responses may have been influenced by the presence of other bears.

6) Bears confined within limited space in captivity may react differently than bears in the wild.

7) Bears in test pens were within view of bears in adjacent pens and reactions to stimuli may have been affected by their presence.

8) Bears in the test pen were within hearing distance of bears in adjacent pens and may have been influenced by vocalizations from other bears.

9) Facility managers requested that several trials with biodiesel exhaust and diesel exhaust be terminated prior to the full 15 minutes after viewing how agitated and aggressive several of the grizzly bears became.

Management Implications

Yellowstone National Park is an environmentally sensitive area and is home to several species of mammals, including grizzly bears and black bears. Each year, millions of visitors tour the park in private vehicles or tour buses and consume thousands of gallons of diesel fuel and millions of gallons of unleaded and leaded fuel. Emissions from these fuels can have potentially negative impacts on plant, animal, and human life within the park. Biodiesel fuel is an environmentally sensitive fuel that would reduce these impacts.

During these tests there was no statistical evidence that bears were attracted to biodiesel fuel or biodiesel exhaust any more or less than to diesel fuel and diesel exhaust. We recommend continued field experimentation of biodiesel fuel in YNP maintenance vehicles. Field use should be closely monitored for any indication that bears are or are not attracted to biodiesel fuel and its emissions. If monitoring of field use suggests that bears are attracted to biodiesel fuel, then methods of making it unavailable or unattractive to bears would need to be investigated and developed.

	Behavior response (minutes)					
Bear #	No Reaction[a]	At door sniffed air[b]	Entered pen sniffed air[c]	Entered pen sniffed vent[d]	Entered pen licked vent[e]	Agitated[f]
G1	15	0	0	0	0	0
G2	4	0	0	0	0	11
G3	4	0	0	0	0	11
G4	4	0	0	0	0	11
G5	6	1	0	0	0	8[g]
B1	12	2	1	0	0	0
B2	11	2	0	0	0	2
B3	6	3	6	0	0	0
B4	12	0	0	0	0	3[h]
B5	12	0	0	0	0	3[h]
$\bar{x}$	8.6	0.8	0.7	0.0	0.0	4.9
SD	±4.2	±1.1	±1.9	±0.0	±0.0	±4.8

[a] Exhibited no reaction to test stimulus.
[b] Sniffed at door but did not enter pen.
[c] Entered pen and sniffed but did not approach vent.
[d] Approached vent to sniff.
[e] Licked walls, stovepipe, or vent.
[f] Appeared agitated and exhibited intraspecies aggression.
[g] Engine shut off at minute 12 due to agitation/vocalizations exhibited by bear G5.
[h] Engine shut off at minute 3 due to aggressive behavior displayed by bears B4 and B5

Table 8
Number of minutes grizzly bears and black bears exhibited different response behaviors to biodiesel exhaust during 15-minute trial period. Biodiesel Fuel Attractrant Test, Washington State University, 1995.

Acknowledgments

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American Marten Habitat Choice: Scaled Multiple Hypotheses Provide Some Answers

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Abstract

American martens (*Martes americana*) in Yellowstone National Park (YNP) were investigated to assess the effects of the fires of 1988 on population levels and as an indicator of specific habitat types. Qualitatively, we made several important observations. First, martens do not appear to cross open areas readily if the areas are wider than about 100 meters. This corresponds with other observations in the literature. Second, martens will cross areas of lodgepole pine (*Pinus contorta*) with surface burns, but they do so in a qualitatively different way than they cross undisturbed habitat or lodgepole stands with a canopy burn. The presence of tree boles appears to allow martens to escape from terrestrial predators when crossing surface burned stands. Third, older growth, per se, does not appear to be the proximal factor determining marten habitat selection. Rather, the characteristic sub-canopy structure of coarse woody debris appears to be crucial. Coarse woody debris (CWD) provides structure that breaks the snow surface, providing access and creating subnivean spaces. The mechanisms that determine why some access sites are used and others are not well understood. Martens may require subnivean access for at least 3 reasons: a) maintenance of homeothermy, b) predation risk, and c) increased availability of small prey.

In this paper, I detail the data from studies in Yellowstone, the Uinta Mountains in Utah, and from Newfoundland, Canada, that my students and I have conducted. I also summarize the evidence explaining marten choice of mature coniferous forest habitat and suggest that the search for any single causal factor will lead to failure.

Introduction

In 1890, T. C. Chamberlin published a paper in *Science* titled, "The method of multiple working hypotheses." In his manuscript, Chamberlin traced the ontogeny of intellectual methods from the "ruling theory," with its biased characteristic of "intellectual affection" rather than "impartial rectitude," to a single hypothesis that may still be biased because of "parentage" as well as the particular observation set from which the scientist operates (O'Neill et al. 1986). He further traced the development to the more unbiased approach of multiple working hypotheses, whereby no one hypothesis is favored, but rather

the overt characteristic is an objective search for the true state of nature. The complexity of natural phenomenon suggests that searches for unitary explanations are probably destined to fail, except at very fine scales. Larger scale ecological phenomena beg more complex explanations.

Prevailing Hypotheses

At larger landscape scales in their range in North America, martens (*Martes americana*) are dwellers of older growth coniferous forest, although results from recent studies suggest that at smaller, stand-level scales, they are less restricted in their habitat affinities than previously suspected (Harrison et al. 1995, Chapin and Harrison 1995). Reasons suggested for marten habitat affiliation include: a) homeothermic considerations, b) predation risk, and c) available prey base. Studies conducted across the North American continent have provided both quantitative and qualitative observations that shed light on each of these hypotheses and suggest that all 3 influence marten habitat choice.

Differential Spatial Use of Habitat

Openings

Several authors (Bissonette et al. 1988, Hargis and McCullough 1984) have reported that martens do not cross open areas readily. Areas greater than 150-200 meters in width appear to be avoided. Rather, martens tend to use sparse cover and scattered trees when crossing more open areas. Drew and Bissonette (unpubl. data) conducted field experiments in Newfoundland and in Yellowstone National Park (YNP). Martens were offered food resources at bait boxes placed 25, 50, and 75 meters from the habitat edge in late seral forest, defoliated forest, and new clearcuts, thus providing a range of predation risk based on physical habitat structure, while at the same time controlling for food resources. Martens used all bait boxes in forested and defoliated habitats and they showed no avoidance of any box placed at any distance. However, martens did not use bait boxes placed at 50 and 75 meters in the clearcuts, suggesting that they perceived areas lacking in woody structure as more risky. On the single occasion where a marten visited the 50-meter bait box in the clearcut, it used a clump of trees to effectively shorten its distance to cover.

Canopy-Burned, Surface-Burned, and Defoliated Forest

Sherburne and Bissonette (1994) observed that martens in YNP used canopy-burned and surface-burned lodgepole pine (*Pinus contorta*) forests in a qualitatively different way than unburned forest. They reported that marten movement dynamics in canopy-burned forest were similar to unburned forest. Martens investigated and hunted as they traveled. Harrison et al. (1995) also report that canopy cover is not required or selected by martens at the smaller-scale stand level. Drew and Bissonette (unpubl. data) reported similar foraging tactics in western Newfoundland balsam fir (*Abies balsamea*)-black spruce (*Picea mariana*) forests that had widespread defoliation. In these disturbed forests, coarse woody debris (CWD) and forest floor structure were still intact. In contrast, martens in YNP behaved in a qualitatively different manner when in surface-burned forest. Although martens traveled through surface-burned forest, they did so by moving in a straight-line direction, similar to their movements across small clearings. Their tracks showed no evidence of foraging. The destruction of forest floor structure in surface-burned forests appeared to preclude hunting, possibly through its immediate and short-term negative impact on the small mammal prey base. We hypothesize that the presence of tree boles in these stands provided martens with escape routes from terrestrial predators.

Sherburne (pers. commun.) found that coyotes in YNP preyed on martens in live traps. On 2 occasions, coyotes killed female martens in live traps and consumed part of the carcasses. Sherburne recorded an incident when he approached a live trap with a captured marten and a coyote was still near the trap. As he approached closer, the coyote was unable to escape because its jaw was caught in the cage. The female marten in the cage had been partially eaten and was dead. Bissonette et al. (1988) reported 3 marten mortalities and 1 failed attempt by predators in Newfoundland. The failed attempt involved an attack on a marten by a hawk owl (*Sulia ulula*). The owl made 3 passes at the female marten while she was in a tree. She darted down the trunk and into a hole to escape. These observations suggest strongly that marten selection of forested habitat is partly in response to predation pressure. Terrestrial predation appears to be much more important than avian predation.

Importance of Coarse Woody Debris

One characteristic of older growth coniferous forest is the accumulation of CWD. Sturtevant and Bissonette (1985) have shown the pattern of accumulation of CWD in Newfoundland forests. Immediately after cutting, CWD levels are reasonably high as a consequence of the slash left after logging operations. CWD levels then decline for about 50-60 years until tree densities begin to approach a level where natural mortality occurs. Newton and Weetman (1993) refer to this intersection of tree density and mean tree volume as the zone of imminent competition-mortality (ZICM). When Newfoundland coniferous forests reach this stage, CWD levels begin to accumulate and reach an asymptote around 80-90 years of age, depending on site quality. Bissonette et al.(1988), Snyder and Bissonette (1987), Drew and Bissonette (unpubl. data), and many others have shown that, at the landscape scale, martens select older growth. However, the preponderance of data suggests that CWD per se, and not necessarily older growth, is an important key to marten habitat selection. During winter, CWD intercepts snow, creating subnivean tunnels, openings, and interstitial spaces. Alvarez et al. (1995) found that low coniferous branches acted similarly to provide subnivean access. Our data show that martens use subnivean access points to hunt small mammals during the winter. They are almost never observed in larger snowy clearings without subnivean access. However, Harrison (pers. commun.) has noted martens hunting the subnivean zone in areas of dense regenerating conifers with snow-covered openings less than 1 meter wide. Sherburne and Bissonette (1993, 1994) showed that: a) subnivean access points were not limiting in older growth, lodgepole pine stands in YNP, and b) martens keyed in on those access points with significantly higher prey levels. Coffin et al. (1995) obtained roughly similar results in Montana just north of YNP.

Buskirk (1988) has also shown that martens gain a thermal advantage from use of relatively warm subnivean spaces during winter. Martens rested more often and for longer periods in subnivean sites associated with CWD, than in subnivean sites in rock fields or above the ground (Buskirk 1988). Zalewski (1995) found that pine martens (*Martes martes*) in Poland chose ground sites over above ground nests and cavities when temperatures were coldest. Gilbert et al. (1995) found that most resting sites were underground during winter and associated with mound topography.

Martens have a high surface-area-to-body-volume ratio and must cope with the costs of being long and thin. Brown and Lasiewski (1972) have shown that the metabolism of cold-stressed long-tailed weasels (*Mustela frenata*) is 50 to 100% greater than "normally" shaped mammals of similar size. Buskirk and Harlow (1989) have shown that martens have very limited energetic reserves and may deplete their fat reserves in less than 100 hours. Assuming a metabolic rate of 0.508 m of oxygen/g x h, and a standard value of 39.7 metabolizable kJ/g fat, Buskirk and Harlow (1989) estimated that a 1 kg marten with fat levels characteristic of those they sampled in Alaska, and resting at thermoneutrality and normothermy, would metabolize all extractable fat in 92 hours. They reported that 5 martens held in confinement sustained a 23% loss of body weight after 120 hours of fasting, but appeared to remain vigorous and active, suggesting that structural protein had not been utilized significantly. It appears that animals cannot lose more than about 30% of their structural protein without seriously compromising their ability to survive (Cahill 1970, Buskirk and Harlow 1989). Buskirk et al. (1988) have suggested that martens coordinate body temperature depression, use of protected resting sites, and duration of resting episodes as a way to regulate their thermal environment during winter. Our data (Sherburne and Bissonette 1993, 1994) suggest that the ability of martens to choose prey-rich access sites enhances their energy balance and is equally important in maintaining thermal regulation.

Conclusions

It seems clear that a single, unitary explanation for marten habitat choice is probably inappropriate. Clearly, martens closely identify with older growth coniferous forest habitats at the landscape scale. They appear less selective at the stand scale in many locations, but not in Newfoundland. During winter, access to the subnivean zone and prey is made available to martens by CWD (a correlate of older growth forest) and low coniferous branches that intercept snowfall, creating subnivean interstitial spaces and access. During this same season, and because of their elongate morphology with a high surface-area-to-body-volume ratio, martens clearly gain a thermal advantage by using subnivean

spaces. However, Drew and Bissonette (unpubl. data) have clearly shown that martens are active at night, the coldest diel period during winter. At the same time, martens are themselves vulnerable to predation from a host of terrestrial predators during winter and terrestrial and avian predators during summer. Their use of forested landscapes allows them to escape from terrestrial predators by climbing tree boles. Clearly, multiple hypotheses offer a more compelling answer than any single hypothesis for marten habitat preference. The interplay of complex habitat structure, seasonal extremes in climate, predation pressures, and a fluctuating prey base is clearly integrated by martens in their response to the environment.

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The Status of Wolverines, Lynx, and Fishers in Yellowstone National Park

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Abstract

Observation records suggest park-wide distribution of wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), and fishers (*Martes pennanti*) within Yellowstone National Park, but provide no concrete evidence. Museum records are almost non-existent. We believe that Yellowstone likely helps support a population of wolverines. Lynx may have been resident over time. There is less evidence, however, to support the existence of either historic or present fisher populations. This may be due to their occurring only rarely or a result of the lack of effort exerted to document the existence of these carnivores within the ecosystem.

Introduction

Little is known about the abundance and distribution of some mammals in Yellowstone National Park (YNP), including wolverines (*Gulo gulo*), lynx (*Lynx canadensis*), and fishers (*Martes pennanti*). These carnivore species are of particular interest because of their status as candidates for potential protection under the Endangered Species Act (Ruggiero et al. 1994). All 3 are listed by the U.S. Fish and Wildlife Service (USFWS) as "category 2" species, or taxa for which information available indicates listing may be warranted but for which further information is required to make an appropriate determination. Petitions have been submitted periodically to the USFWS proposing formal listing of each of the 3 species as either endangered or threatened. To date, however, such petitions have been denied (Ruggiero et al. 1994).

Reliable information on the abundance and distribution of wolverines, lynx, and fishers in the western United States is lacking (Ruggiero et al. 1994). General references reflect this lack of knowledge. For example, Wilson (1982), McCord and Cardoza (1982), Crowe (1986), and Clark and Stromberg (1987) indicate that wolverines and lynx range throughout Yellowstone, while Strickland et al. (1982) and Clark and Stromberg (1987) indicate that fishers do not. In comparison, Long (1965) wrote that wolverines and, possibly, lynx seemed to persist in the mountains of northwestern Wyoming, if the latter were not extirpated at the time of his writing. And he refers to several reports of fishers in Yellowstone and the adjacent Beartooth Plateau made in 1892 and in the 1920s. Leopold et al. (1981) indicate that YNP supports populations of all 3 spe-

cies. But, national forests adjoining YNP indicate a lack of conclusive evidence about the status of these carnivores (Ruggiero et al. 1994).

The lack of reliable information on these species' presence and distribution has recently prompted increased efforts to improve the information base available to land and wildlife management agencies (Ruggiero et al. 1994, Ruggiero and Buskirk *this volume*). YNP is participating in these efforts. Schullery and Whittlesey (1992) summarized wildlife reports from 168 sources between 1806 and 1882. They concluded that, historically, wolverines "almost certainly were more common" than they are now. They found reports of 12 sightings and killings, as well as 1 mention of tracks and 3 additional statements about wolverine presence in the area. Their search turned up only 1 lynx sighting and 2 general statements about lynx presence, along with a reference that "lynx were sometimes killed in the Yellowstone Park." Fishers were "rarely mentioned" in the 1800s sources.

We summarize the evidence for the presence of wolverines, lynx, and fishers within Yellowstone National Park from 1883 to the present, based on our examination of various park records.

Study Area

The study area encompasses all of Yellowstone National Park, which occupies 8992.5 km^2 in the northwest corner of Wyoming and adjacent portions of Idaho and Montana. The area is predominantly a high-elevation volcanic plateau circled by mountain ranges. Elevations range from 1605 m to approximately 3462 m. Approximately 80% of the park is covered by forested habitat types, 60% of which are in the subalpine fir series; lodgepole pine is both the dominant and the seral species (Despain 1990). Fire is an important environmental influence on the forested habitat types and on many of the habitat types dominated by sagebrush in the park's river valleys. The climate is characterized by long, cold winters and short, relatively cool summers. Annual precipitation varies with topography and elevation, but most of the park receives 75 to 127 cm annually (Despain 1990).

Methods

We searched available park records for documentation of these species' presence and distribution. Yellowstone has maintained wildlife observation records made by park staff and visitors since the 1920s; these were searched and evaluated. We also searched photograph and slide collections and records from the park's natural history collection, and, with the assistance of curatorial staff, requested records from collections at state universities in Idaho, Montana, and Wyoming, as well as from the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

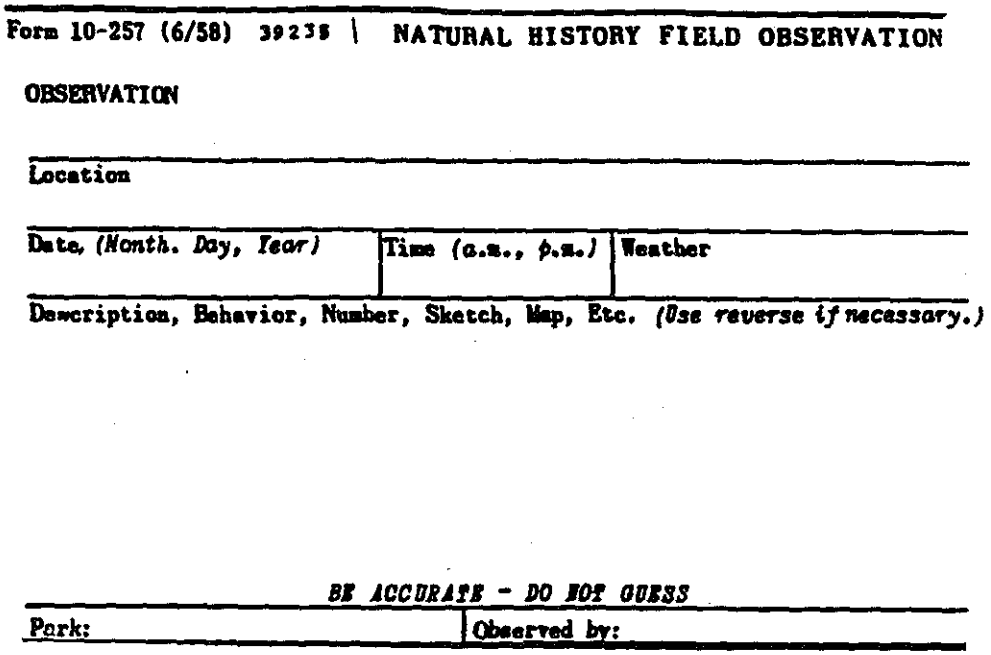
In 1992, YNP began opportunistic sampling of roadkills, natural mortalities, and wildlife handled for management or research purposes in order to build a wildlife health database; these records were also checked. No research efforts were specifically targeted toward gathering information about wolverines, lynx, and fishers until 1988-89, when Consolo Murphy initiated limited sampling for guard hairs of these rarely seen mesocarnivores (Consolo 1989). In 1992, this effort was expanded to include track surveys and sampling with remote automated photo stations (Gehman et al. 1994). A myriad of informal reports and "Yellowstone Nature Notes" from the park's early history also contain occasional references to these species. A search of the latter revealed no additional references to fishers or wolverines in YNP. Four sightings of 5 lynx not recorded in the wildlife observation files were found in the park's research library.

Results and Discussion

Reported observations of wolverines, lynx, and fishers are summarized in Table 1. Until the mid-1980s, observations were recorded on 3" x 5" cards for Natural History Field Observations (Figure 1). These records contain minimal data with which to evaluate the quality of the observation. For example, while animal sightings or observed tracks may be included, in some cases reports of "sign," without further elaboration, may be the sole information recorded. In addition, information about the experience of the observer and the conditions under which the observations were made are generally lacking. And location information is often incomplete, providing the drainage (i.e., Slough Creek), but no other specifics. Consequently, we did not attempt to plot these data on a map, although if the observations are legitimate, they do suggest park-wide distribution of all 3 species.

In 1986, park staff began to replace the wildlife

Figure 1. Form 10-257. Natural history field observation form.



Form 10-257 (6/58) 39238 | NATURAL HISTORY FIELD OBSERVATION

OBSERVATION

Location

Date, (Month, Day, Year) | Time (a.m., p.m.) | Weather

Description, Behavior, Number, Sketch, Map, Etc. (Use reverse if necessary.)

BE ACCURATE - DO NOT GUESS

Park: | Observed by:

Table 1. Summary of records in wildlife observation files, 1883-1995, Yellowstone National Park.

	SPECIES REPORTED					
	WOLVERINE		LYNX		FISHER	
RECORD	Total	In YNP	Total	In YNP	Total	In YNP
Sightings Reports	104	90	34	34	22	16
Animals Reported	113	97	39	39	24	17
Track Reports	25	23	17	17	7	6
Other Evidence	4	1	7	6	2	1
Museum Records	1		1		0	
TOTAL ON FILE	132		58		30	

Figure 2. YELL 590. Rare animal observation form.

RARE ANIMAL OBSERVATION FORM
YELLOWSTONE NATIONAL PARK

YELL 590
Revised 7/93

Please fill out all appropriate information and turn into Bear Management Office or phone 307-344-2162.

Species_____ Time_____ a.m. p.m. (circle one)
Observation Date ____/____/____ Number of Animals_____ Sex: M___ F___ Unknown___

Observer Name_____ Phone ( )_____ Visitor___ Employee___
Address_____ State_____ Zip_____
Have you seen this species before? Yes___ No___ Where?_____
(Indicate experience with this species)

Describe the Animal *(Characteristics unique to this species)*_____

Color_____ Ears_____
Weight_____ Shoulder height_____ Horns/Antlers (circle one) Describe_____
Length_____ Tail position: Up___ Down___ Straight out___ Curled___
Tags or radio collar (color, placement)_____

Describe Behavior of the Animal_____

How long did you observe the animal?_____ Distance from animal_____
Optical aid used: None___ Binoculars___ Spotting scope___ Other_____ Power of optics_____
Photos taken?_____ May we make or have copies? Yes___ No___

Exact Location_____

Drainage_____ UTM_____E_____N Elevation_____

Describe Surrounding Area (i.e. meadow, marsh, forest)_____

Describe vegetation near animal_____
Describe animal size in relation to vegetation or other animals_____
Describe weather conditions (foggy, sunny, etc.)_____

Track measurements Length_____ Width_____ # of toes____ Claw marks?____ Stride_____
In Mud?____ Dust?____ Snow?____

Scat Diameter_____ Length_____

Vocalizations Yes___ No___ (Describe in comments) How long_____ How many animals_____

Comments_____

Report taken by_____ Title_____
Date_____ Time_____ Location_____

observation cards with a more detailed "Rare Animal Sighting Form" that has been revised several times, evolving to the current form (Figure 2) now in use. These forms request more information about the observer, sighting conditions, animal behavior and characteristics, location, track measurements, and photographs (if available). A system of ranking the observations was employed, incorporating the sighting conditions, observer experience, and quantity and quality of information provided, to assess the probability of a valid wildlife report. However, in light of the change in staff responsible for maintaining the observation records during the past decade, this ranking system is not without bias.

Additional problems result because reports are frequently received in the wrong format (such as on the old 3" x 5" cards) or lack sufficient information with which to evaluate the report. Despite efforts to inform park staff and visitors about the park's interest in documenting rare animal observations, many sightings may still go unreported, though the exact number is difficult to estimate. Park staff have occasionally expressed reluctance to report rare animal sightings out of fear that park biologists will want to initiate a research project or some other management action in response. It is apparent that this type of database has not been associated with consistent observer or collection effort. And, even if complete observation records are obtained, there is no assurance that a well-documented report is associated with a legitimate sighting or that a poorly documented one necessarily reflects an inaccurate observation.

Of the 3 target species, we believe that the wolverine is most easily distinguished from other extant species in YNP. Lynx and bobcats are easily confused, especially if sightings are fleeting or made under less than ideal conditions (e.g., poor lighting and long distance). Similarly, fishers may be mistaken for the commonly occurring pine marten. We also view track reports as particularly difficult to substantiate unless accompanied by measurements, casts, or photographs.

Physical evidence of the presence of wolverines, lynx, and fishers in the park is almost nonexistent. A search of museum specimens revealed no wolverines, lynx, or fishers taken from within YNP present in the natural history collections, nor were there any reported taken from the surrounding states. The Smithsonian Institution's collections include one wolverine skin and skull received in 1895 and one lynx skull collected in 1904. Unfortunately, little other information accompanies these specimens; the only location information indicated on either specimen tag is "Yellowstone NP."

No wolverines, lynx, or fishers have been recorded during recent efforts to sample wildlife health and to record carcasses from roadkills or other sources. Results from analysis of guard-hair sampling since 1989 yielded 1 record of a wolverine from the north side of Mount Washburn, and 2 samples judged to be "either bobcat or lynx" from the Soda Butte Creek drainage. In addition, the park's photo collection lacks any documentation of the 3 species taken from within YNP. Recent photographs of wolverines (Robinson and Gehman 1998) and, possibly, fishers (Crabtree, pers. commun.) taken just outside the park's northern boundary provide the best current evidence that the park and surrounding areas may support populations of these 2 mustelids.

Conclusion

The limited quality and quantity of information about wolverines, lynx, and fishers in YNP makes it difficult to assess either their historic or present distribution. Sighting records for the 3 rarely seen carnivore species suggest a past and present park-wide distribution. However, these records exhibit considerable bias due to variability among observers and the amount and type of information provided with respect to location, animal characteristics and behavior, and sighting conditions. Substantive evidence, such as that provided by photographs and collections, both of whole animals or accurately identified parts (i.e., hairs, skins, and skulls), is almost nonexistent and dates back to the turn of the century. Despite this dearth of data, however, there have been no systematic efforts to collect museum specimens of the target species since the early 1900s. Recent efforts aimed at collecting physical evidence (i.e., guard hairs, track casts, and photographs) deserve more time and effort (see Crabtree et al. *this volume*).

We are inclined to place high reliability on well-documented observations of wolverines, given the relative ease with which this animal can be distinguished from other wildlife species found in the park. In combination with the physical evidence available, the number of wolverine observation

records leads us to believe that Yellowstone helps support a resident population. There is less evidence to convince us that a resident population of lynx exists in Yellowstone today, if it ever did historically. And we consider the evidence for a resident fisher population the least convincing. The lack of substantive evidence for these species may be the result of lynx and fishers occurring only rarely or on a transient basis, or it may be due to the lack of intensive field investigation within large expanses of the Greater Yellowstone Ecosystem. Regardless, maintenance of wildlife observation records and, where possible, efforts to augment those records with photographs, track casts, and physical evidence such as guard hairs and opportunistically-collected specimens, will help improve our knowledge of the status and distribution of wolverines, lynx, and fishers in YNP.

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The Ecological and Sociodemographic Role of the Coyote on Yellowstone's Northern Range

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Abstract

By the 1980s, Yellowstone National Park had undertaken long-term studies of all large ungulate-killing carnivores (> 10 kg), except for the coyote (*Canis latrans*). In 1989, following the 1988 fires and in expectation of gray wolf (*Canis lupus*) restoration, an intensive 6-year study of coyotes on the Northern Range (NR) was initiated to determine both real and potential impacts. The coyote is the major elk (*Cervus elaphus*) predator on the NR with an estimated 400 adult coyotes killing an estimated 1,276 elk (750 neonates) annually. In comparison, mountain lions (*Puma concolor*) kill about 600 elk (35 neonates) and grizzlies (*Ursus arctos*) kill 750 neonates and a few adults. Per capita annual kill rates for the coyote, grizzly bear, and mountain lion were 3, 13, and 36 elk, respectively.

The high density of coyotes on the NR (0.4/km^2) adds a strong numerical component to an already broad functional role as a generalist consumer. Estimates of the annual biomass consumed by coyotes of various prey species were based on independent estimates of predation rates on small mammals, carcass consumption rates, predation rates on ungulates, and seasonal estimates of the fresh weight of prey consumed from scat analysis incorporating differential digestibility corrections. Nearly 50% of the annual biomass intake came from small mammals taken mostly in summer and fall, and nearly 45% came from ungulates taken mostly in winter and spring. For example, during the 7 non-winter months, microtines, pocket gophers, ground squirrels, snowshoe hares, and elk (calves and carrion) made up 41%, 25%, 3%, 4%, and 21% of prey biomass consumed, respectively. In contrast, we estimated that 74% of the biomass intake during the winter months consisted of elk (mostly carrion) while only 26% consisted of small mammal prey. Predation rates on major prey items were 76%, 24%, 35%, and 10% for microtines, pocket gophers, ground squirrels, and neonate elk calves, respectively. During mild winters with little carrion, coyotes can lose up to 30% of their body weight. Harsh winters result in large numbers of carcasses and coyotes can gain weight late in the season.

Eighteen (of 47 known) coyotes packs on the NR were intensively examined in the Lamar Valley and Blacktail Plateau study areas. Territories were defended,

stable, contiguous, and non-overlapping areas of 8-12 km^2. Pack members constituted about 85% of the study populations with the remaining 15% (loners) occupying the periphery of, and space between, territories. Coyote packs, like those of gray wolves, consist of the dominant "alpha" breeding pair and subordinates, or "betas," which are pups born in previous years that stay and help raise their younger siblings. Some betas were not observed to help at the den and are considered "slouches." Data from 3 long-term studies of coyote populations (over 300 coyote-territory years) subjected to little or no human exploitation showed no change in the location of territories and few temporary shifts in territorial boundaries. Five of 7 denning areas located in 1946-49 were in the same location in 1990-93. Accordingly, the tenure period for an alpha pair residing in a territory averaged 6 years. These and other data suggest that the location and number of coyote territories probably stabilized shortly after wolf extirpation and have been stable ever since. Adult pack size was also stable and averaged 6.0 for 70 pack-years.

In contrast to the aforementioned spatial and pack stability, some sociodemographic characteristics varied greatly. Litter size ranged from 0 to 12 and averaged 4.44 pups observed at the den (late May through late June). High neonatal pup mortality was observed from late June through late August and averaged 65% annually. Additional pack members, or betas, were both a cost and benefit to the pack in terms of litter production. Litter size and survival were positively correlated with pack size in high food production years and were negatively correlated with pack size in low food production years. Because virtually all food consumed by pack members is extracted from within the "confines" of the territory, packs may exceed territorial carrying capacity. Subordinate betas, usually 9- to 12-month-old individuals, were often socially excluded from carcass feeding and dispersed from natal packs in winter and spring. A high proportion of betas that "stay" inherit the alpha positions in their natal pack or take over an alpha position in an adjacent territory.

With highly variable and unpredictable food resources, the NR coyote maintains consistent numbers of territories, stable pack size and pack composition, fidelity of territory and den site location, and high annual survival of adult pack members (0.91 for alphas and betas combined). This stability is maintained functionally by the coyote's broad foraging niche, and demographically at the expense of high neonatal mortality and socially mediated dispersal. Various demographic effects were not significantly affected by burn level, which varied from 0 to 52% of the territorial area. However, carcass availability, related to winter severity, was positively correlated with litter size. Vole biomass was significantly related to pack size and litter size.

Extirpation of the gray wolf by 1927 has probably resulted in high coyote densities on the NR and coyotes have, at least partially, slid into this vacant niche.

With restoration of the wolf in 1995, the ecological role of the coyote will undoubtedly change numerically, functionally, and behaviorally. These changes should generate ripple effects on their competitors and prey.

Introduction

Adolph Murie's pioneering work (Murie 1940) on the ecology of the coyote (*Canis latrans*) in Yellowstone National Park was a landmark of predator research in North America. By the late 1980s,

Yellowstone National Park had undertaken long-term studies of ungulate-killing carnivores, the grizzly bear (*Ursus arctos*) (Knight and Blanchard 1999) and mountain lion (*Puma concolor*) (Murphy 1998), but not the coyote. In response to the fires of 1988 and in expectation of gray wolf (*Canis lupus*) restoration, an intensive long-term study began in 1989 on the Northern Range (NR) of Yellowstone National Park (YNP).

Coyotes are ideal carnivores to study because of their ability to adapt and thrive in diverse environments and because of their variable social behavior (Bekoff and Wells 1986). From loose pairs (Berg and Chesness 1978) to packs of 10 adults (this study), the mid-size coyote displays many of the behavioral characteristics seen among the 35 species (Sheldon 1992) within the family Canidae. Canids themselves are instructive groups with which to examine the community structure of carnivores because of their wide distribution and variable behavioral and ecological adaptations (Johnson et al. 1996).

This paper provides an overview of the ecological role of the coyote on Yellowstone's Northern Range during the 6-year period (1990-95) prior to wolf restoration. In discussing the coyotes' functional, behavioral, and demographic role, we also provide a guide to the numerous coyote papers that were presented at the Third Biennial Scientific Conference on the Greater Yellowstone Ecosystem entitled *Greater Yellowstone Predators: Ecology and Conservation in a Changing Landscape*. The following graduate students, working on the Canid Ecology Project, gave presentations: Robert Fuhrmann, Eric Gese, Scott Grothe, Kezha Hatier, Paul Moorcroft, and Jennifer Sheldon (*all this volume*). Additional presentations were given by collaborating researchers, Mark Johnson (*this volume*), Valeda Slade (*this volume*), and Tim Stotts.

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Methods

This study was conducted on the Northern Range (NR) of Yellowstone National Park. A description of the vegetative and climatic patterns of the NR can be found in Despain (1990). Two study areas on the NR, Lamar Valley (LV) and Blacktail Plateau (BT), were chosen based on: (1) a differential pattern of burn from the 1988 fires, (2) their general topography in providing viewing for behavioral observations (LV) and, (3) fixed station radio-telemetry (BT). Our goal was to maintain 1 to 3 radio-tagged adults in all territorial packs in each study area. This provided the sample sizes necessary to investigate spatial organization, estimate social class specific demographic parameters (e.g., survival and reproduction), and enhance behavioral observations. Adult coyotes were captured with padded, offset leg-hold traps (Soft-catch, Woodstream, Inc.) with attached tranquilizer tabs (Balser 1965) and other injury-minimizing (and non-target species-avoiding) modifications developed by Crabtree (1989). No major injuries and no deaths were incurred in 121 captures of 112 individual coyotes.

Sex, weight, estimated age, condition indices (Crabtree 1989), presence of scars and unique marks were determined, and the genitalia and mammae were described for each captured coyote. We extracted the vestigial first premolar from an anaesthetized lower jaw for age analysis via cementum annuli examination. Each coyote was ear-marked and fitted with a modified (Crabtree 1989) 3-year radio collar weighing approximately 3% of the animal's body weight. Blood samples were taken for serological analysis and DNA fingerprinting. Pups were hand captured at dens when 9-12 weeks old and surgically implanted with intraperitoneal radio-transmitters. This procedure allows estimates of early pup mortality, dispersal, and social interaction, and transitions up to 2 years of age, and is described in detail in Slade et al. (*this volume*).

The above methods enable estimation of emigration (dispersal), immigration, survival, mortality factors, territorial turnover, social class transition probabilities, and population productivity. Estimates of survival and mortality factors were generated with program SURVIV (White 1984) or with the Kaplan-Meier staggered-entry models (Pollock 1989). Litter size was determined from den counts and occasional female carcasses. The proportion of females in the population that breed was estimated from activity and movement data during whelping as described by Crabtree (1989). Size of coyote populations was determined by complete census and estimates based on mark-recapture (Crabtree et al. 1989).

Both marked and unmarked coyotes were intensively observed in the Lamar study area with the aid of spotting scopes and radio-telemetry. Behavioral data (see Gese et al. 1996a) were recorded on a hand-held computer while location data were recorded on a 7.5-minute map. Behavioral time budgets were developed from systematic observations made from 10 elevated sites located throughout the Lamar Valley region. In the Blacktail study area, radio-tagged coyotes were intensively tracked, but were not readily observed due to the undulating topography. Pack size was determined by the largest count of known, yet differently marked adults during winter. Effective group size (or social cohesiveness) was determined by recording the number of adult coyotes traveling together during morning transects.

Scats were collected from predetermined transects in both the Lamar and Blacktail study areas during winter, spring, summer and fall collection periods. Estimates of the annual biomass of various prey species consumed by coyotes were based on: (1) independent estimates of predation rates (Gese et al. 1996a), (2) carcass consumption rates (S. Grothe, unpubl. data), (3) observed predation rates on ungulates (Gese and Grothe 1995, R. Crabtree, unpubl. data), and primarily, (4) seasonal estimates of the fresh weight of prey consumed from scat analysis incorporating differential digestibility corrections (Kelly 1991).

A concurrent study (1990-94) of small mammal communities on the Northern Range allowed estimates of availability and overall predation rates on small mammal prey (Johnson and Crabtree 1999). Historical data was provided by L. Whittlesey and P. Schullery, and through access to the archives at Mammoth Hot Springs.

Results and Discussion

History and Background

Based on the its pre-European distribution (Bekoff 1977), the coyote has now tripled its range and greatly increased its numbers across North America while wolves have declined (Mech 1974). These 2 canids, along with red foxes (Fuhrmann 1998), occured naturally in the GYE and the NR of Yellowstone (see also Whittlesey and Schullery, *this volume*) and coexist once again with the reintroduction of gray wolves in 1995.

The majority of the coyote's range expansion occurred during the century-long predator eradication era (1860s to 1960s), which resulted in drastic reductions in the range distributions of many carnivores. Besides its famed resiliency to predator control techniques, widespread reduction in the distribution of the gray wolf, a dominant competitor, and the clearing of forests (Sheldon 1992) contributed to the coyote's proliferation. The coyote now occupies most habitat types in North America; however, it is best adapted to the arid and open shrub-grassland areas of the West (Bekoff 1977).

What historically happened to wolves, coyotes, and red foxes across North America is similar to what has happened in Yellowstone. Schullery and Whittlesey (1992) reviewed historical sightings of canids prior to 1890 and found that sightings of wolves and foxes were common; coyote sightings were rather infrequent. Although this could be due, in part, to classifying coyotes as wolves, it is clear that several park officials were very adept at distinguishing between species, even between color morphs of red foxes (see Norris 1881). The surprising lack of frequent coyote sightings is in sharp contrast to the recorded take of predators from 1906 to 1927, when the last wolves were extirpated from the NR of Yellowstone (Murie 1940). While 127 wolves and 134 mountain lions were killed, a staggering 4,352 coyotes were taken. Even if 80% of this number represented pups killed at dens (which is doubtful), coyotes appear to have been much more abundant than wolves. Could wolves have suppressed coyote numbers and, once released from wolf pressure, could coyotes quickly rebound?

Distribution and Abundance of Coyotes

Currently, the coyote inhabits all vegetation communities below 8,000 ft in the GYE except for areas of contiguous deep snow and steep rocky areas. Based on extensive winter surveys conducted from 1992 through 1995 (Gehman et al. 1997), the coyote uses all elevations above 8,000 ft, but only on a transitory basis. The typical coyote behavior (e.g., territorial establishment, courting, pair bonding, and breeding) that takes place from December through February is completely absent above 8,000 ft. However, coyotes are commonly observed from 8,000 to 11,000 ft in meadow and mixed forest-meadow habitats from May to July. These coyotes are often seen in male-female pairs engaged in courtship and pair bonding. Non-territorial coyotes that reside below 8,000 ft during winter most likely travel to these areas in late April and May as snow melts and prey become available. These pairs vocalize, scent mark, and defend territories similar to coyotes living at lower elevation in winter, but no successful reproduction has been detected.

The estimated density of adult coyotes on the NR averages 0.45 per km^2 (Crabtree and Sheldon 1999) based on total counts and capture-recapture estimates (Crabtree et al. 1989). In the open, shrub-steppe and mesic grasslands of the GYE, coyotes can reach local densities exceeding 1.0 per km^2. However, across much of the forested habitat types of the GYE, coyote densities probably range from 0.1 to 0.4 coyotes per km^2.

Functional Role

The high density of coyotes on the NR (0.45/km^2) adds a strong numerical component to an already broad functional role as a generalist consumer. In this section, we compare historical data to current information, estimate biomass consumed of different prey species, and calculate the percent of prey species removed by coyotes in order to further define the coyote's stable, broad, and numerically large ecological role on Yellowstone's NR.

The ecological role of the coyote was defined by Murie (1940) largely from analysis of 5,086 scats. We summarized these data and compared them to a subsample of 500 scats collected in 1991 and 1992 over 50 years later (Table 1). The data sets were remarkably similar indicating stable resource use. This, combined with the apparent stability in the location of traditional den sites, suggests that prey availability and preferences have also been relatively stable. Based on these results, the observations of Murie (1940), and the similarity of den site locations during 1946-49 (Robinson and Cummings 1951) and 1990-94, we believe that the number and specific location of coyote territories on the NR have been stable since a period of rapid colonization shortly after the extirpation of the gray wolf in 1927.

Nearly 50% of the annual biomass intake came from small mammals taken mostly in summer and fall, and nearly 45% from ungulates taken mostly in winter and spring (Figure 1). In the 7 non-winter

Table 1. Coyote food habits as indicated by analysis of scats (% of biomass intake) Reprinted with permission from Yale University Press—Crabtree and Sheldon 1999.

Prey Species	Murie 1940 (5,068 scats)	This Study (1995, 500 scats)
Microtus spp	42.4	41.3
Pocket gopher	27.0	24.5
Ground squirrel	0.6	3.0
Snowshoe hare	4.3	4.4
Elk	20.3	21.2

Table 2. A comparison of estimated prey availability to that taken by coyotes in their diet on the northern range of Yellowstone, 1990-95.

	Potentially available on the northern range of Yellowstone		Coyote predation or removal of food source	
Major Prey	Number	Biomass (x1000kg)	% removed	%in diet
Microtus spp.	826,416	42	76.2	32.4
Pocket gopher	928,267	93	23.6	16.4
Ground squirrel	27,002	7	35.2	1.8
Elk calves	~7,000	140	10.0	7.5
Adult elk	~17,000	3,400[a]	2.0	36.0
Totals	~1,805,685	3,682	3.8 (139,000 kg)[b]	94.1

[a]mostly scavenging of carcasses
[b]estimate of the percentage and total biomass taken by coyotes on the northern range from the number of individuals estimated to be available

months, microtines, pocket gophers (*Thomomys talpoides*), ground squirrels (*Spermophilus spp.*), snowshoe hare (*Lepus americanus*), and elk (*Cervus elaphus*) (calves and carrion) made up 41%, 25%, 3%, 4%, and 21% of prey biomass consumed, respectively. An estimated 74% and 26% of the biomass intake during the 5 winter months came from elk (primarily carrion) and small mammal prey, respectively.

The coyotes' estimated take of small mammal prey on the NR is indicative of its high density and broad functional role (Table 2). Among 15 species of carnivores that rely on small mammal prey as their major food source, the coyote accounts for an estimated removal of 76%, 24%, and 35% of the estimated populations of microtines, pocket gophers, and ground squirrels, respectively. Nearly 3/4 of the elk biomass consumed during the 4 winter months consist of carrion and approximately 2/3 of the depredated elk are old and/or starving individuals (S. Grothe, unpubl. data).

As Murie (1940) suspected, harsh winters result in large numbers of carcasses for scavenging coyotes, and coyotes can actually gain weight during the late winter die-off. In mild winters with little carrion, coyotes can lose up to 30% of their body weight (e.g., alpha male M660 weighed 39 lbs. in October 1989 and 27 lbs. in May 1990). The fall weight and fat index of captured adult coyotes were significantly greater than those captured in the following spring ($P < 0.05$). Coyotes normally go through a 20% weight loss in the winter and a 20% weight gain from late winter through fall.

Surprisingly, the coyote is the major elk predator on the NR, killing an estimated 1,276 elk annually (Table 3). The coyote population accomplishes this not by specialization, but by sheer numbers (n = 450) along with a propensity for killing mostly young neonates (an estimated 750 annually) in June and weak or starving individuals during winter. Although coyotes are capable of killing healthy adult elk during winter, they seldom do so (Crabtree, unpubl. data, Gese and Grothe 1995). In comparison, the specialized, obligate ungulate predator, the mountain lion, kills around 600 elk (only 35 neonates) annually (Murphy 1998) and grizzlies kill an estimated 750 neonates (see Crabtree and Sheldon 1999) and a few adults (B. Blanchard, pers. commun.). Grizzlies appear to seasonally specialize only on neonate elk calves while coyotes, probably because of their size, appear not to specialize on elk at all. The estimated per capita annual kill rate (an index to specialization) for an estimated 450 coyotes, 60 grizzly bears, and 17 mountain li-

Figure 1. Seasonal biomass intake by coyotes in the Northern Range of Yellowstone National Park. Reprinted with permission from Yale University Press—Crabtree and Sheldon 1999.

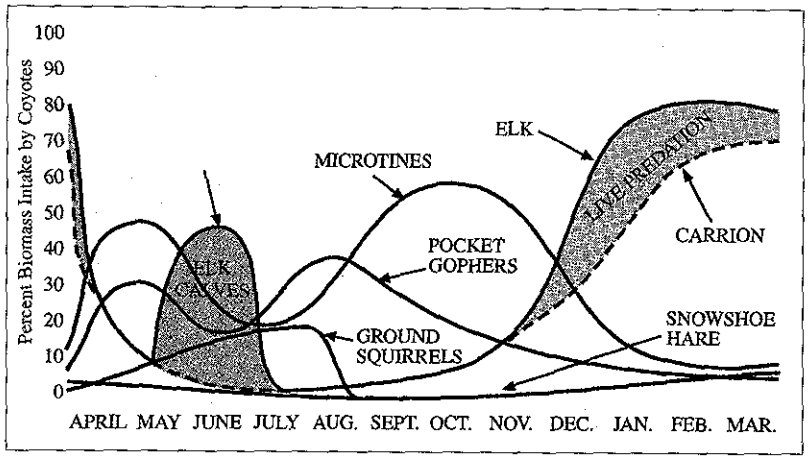


Table 3. Comparison of predation rates by large predators in Yellowstone's Northern Range. Reprinted with permission from Yale University Press—Clark et al. 1999.

Species	n	Neonate calves	Short yearling	Adult winter	Adult non-winter	Total	Elk biomass	Per capita kill rate
Mountain Lion [a]	17	35	313	70	193	611	76,150	36
Grizzly Bear [b]	60	750 [c]	0	0	Few	750+	13,500	13
Coyote [d]	400	750	360-626	20-35	0	1130-1411	66,760	3

[a] Data from Kerry Murphy, Hornocker Wildlife Research Institute
[b] Bonnie Blanchard, personal communication, estimated 60 grizzlies using the Northern Range
[c] Francis Singer, National Biological Service.
[d] This study, projected estimates

ons on the NR are 3, 13, and 36 elk, respectively.

Although coyotes commonly hunt and kill ungulate neonates (elk calves and mule deer [*Odocoileus hemionus*] / antelope fawns [*Antilocapra americana*]) from late May through early July, predation on adults is less common and rarely observed. However, 26 predation attempts were recorded in the LV study area from 1990 to 1995, and Gese and Grothe (1995) report detailed observations of 9 predation attempts by coyotes on adult and younger (>5 mos.) deer and elk in Yellowstone National Park during 2 winters (1991-92 and 1992-93). Successful attacks ($n = 5$) were related to deeper snow and nearly all attacks were led by the alpha male. Two or 3 adults took part in the attacks while the remainder of the pack (mean pack size was 6.7 adults) watched or was absent. Nonetheless, the majority of the pack feeds on both predated and winter-killed ungulates (S. Grothe, unpubl. data).

Bekoff and Wells (1986) estimated that about 90% of the coyotes' diet is mammalian flesh. Because ungulate flesh in the diet is usually carrion (Bekoff 1977, Weaver 1977, Houston 1978) and seasonal in occurrence, few studies have investigated coyote impacts on ungulate populations (but see Messier et al. 1986). Coyotes are certainly capable of killing adult ungulates, usually those that are weak, impaired, domesticated, or starving, but can kill healthy adult ungulates, even elk in Yellowstone (Gese and Grothe 1995, Crabtree, unpubl. data). Impacts of coyotes on ungulate populations are primarily the result of predation on ungulate neonates during pup rearing and secondarily attributed to predation on starving short-yearling elk during winter. We suspect that coyote predation on elk calves is largely additive mortality while predation on short-yearlings mostly substitutes for winter starvation.

We know of no study that indicates significant coyote predation on the adult segment of an ungulate population. However, predation rates on young ungulates can be high (Hamlin et al. 1984). In Yellowstone, coyotes kill more elk calves (neonates and older calves in winter) than grizzly bears and mountain lions combined (Table 3) and inflict heavy predation (> 80%) on radio-tagged antelope fawns (D. Scott 1994, pers. comm.). Given substantial neonate predation on ungulates on the NR and in many areas of the lower 48 states, attention should be paid to coyote predation on fawns as a limiting factor of mule deer (see Mackie et al. 1998), which are more abundant in areas surrounding the NR. A major impetus for coyote predation on ungulate neonates is the provisioning of large prey packages to pups during May, June, and July when coyote pups have been weaned and are larger and fast-growing. In Yellowstone, we commonly found the remains of elk calves at coyote den sites. Till and Knowlton (1983) experimentally demonstrated that coyotes kill domestic sheep to provide food for young pups.

Our research in Yellowstone intensively examined the ecology of coyote predation on small mammals populations (Gese et al. *this volume*, Gese et al. 1996a, 1996b) as did studies conducted in Wyoming (Bekoff and Wells 1981). Coyote food habit studies are numerous, but provide unreliable information because of sampling biases related to differential digestibility and inconsistent analysis methods (Kelly 1991). Nevertheless, food habit studies indicate that coyotes rely mostly upon small mammal prey. Major exceptions appear to be: (1) fruits in some southern regions when seasonally abundant, and (2) carrion in northern regions during the winter months.

Behavioral and Social Ecology

Captures

Sixty-seven adults and 62 pups were captured and radio-tagged from spring and fall capture sessions beginning in the fall of 1989 and ending the spring of 1993. Adults were monitored seasonally and constituted a total of over 200 coyote-years. An additional 37 adult coyotes not radio-collared were monitored in the Lamar Valley region due to the high visibility of the area and natural distinguishing marks of their coat pelage. Pups were intensively monitored during the summer months, the period of highest neonatal mortality.

Of the 67 adult coyotes monitored in the LV and BT study areas, 52 (78%) and 15 (22%) were classified as pack members and loners, respectively. However, because loners expressed low-fidelity to the study sites and traveled over large areas, percent composition estimates are biased. Applying the weighting factor used by Crabtree (1989) that corrects for fidelity based on resident-equivalents allowed for estimates of percent composition for the population. As such, 88% ($n = 52$) belonged to territorial packs of which 30% ($n = 22$) were alpha breeding pairs and 58% ($n = 30$) were subordinate adults or betas. Twelve percent ($n = 15$) were solitary indi-

viduals or loners that did not belong to a territorial pack. These loners occupied the periphery of established territories and the spaces between them. Similar to gray wolves, the territorial packs consisted of the dominant, or "alpha," breeding pair and subordinates, or "betas," which are pups born in previous years that stay and help raise their younger siblings. Some betas are considered "slouches" and were not observed to help at the den (Hatier 1995, Hatier and Crabtree, unpubl. data).

The average age of coyotes captured in trapping efforts (excluding pups in the fall) was 3.8 years of age, the oldest yet reported. The percentage of pups captured in the fall was very low (20%) compared to other studies (see Crabtree and Sheldon 1999), but similar to that reported by Crabtree (1989) in an unexploited population in Washington.

Figure 2. Coyote pack size. Reprinted with permission from Yellowstone Science, Vol. 7, No. 2, Spring 1999.

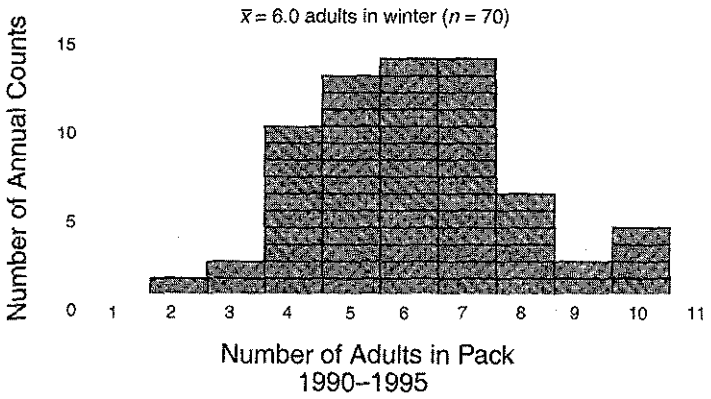
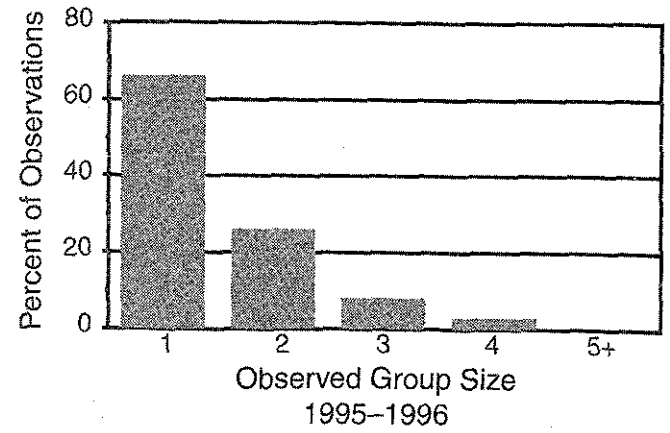


Figure 3. Pack cohesion. Reprinted with permission from Yellowstone Science, Vol. 7, No. 2, Spring 1999.



Social organization

From recent studies on unexploited populations (Crabtree 1989, this study) the contention by Camenzind (1978) that coyotes exhibit a well-defined social system similar to that of gray wolves appears correct. In "protected" areas, coyotes form territorial packs of 3 to 10 adults. On the NR of Yellowstone, coyote pack size averaged 5.9 adults per territory (Figure 2) from 1990 to 1995. During winter, packs typically consisted of the dominant (alpha) breeding pair, 2 beta adults (non-dispersing pups born in previous years), and 2 adult-sized juveniles. Smaller pack sizes tended to stay smaller and larger packs tended to stay larger over time (S. Grothe, unpubl. data). These differences appear related to the amount of available prey and prey habitat contained within defended territories (see Prey Relations below).

The belief that coyotes are more solitary than other similar-sized canids seems to be the result of cultural folklore and sampling biases in field studies. In contrast to gray wolves, coyote pack members rarely travel all together (Figure 3). However, like wolves they occupy the same territory and socialize often. Thus, winter counts of coyote pack size (standard for wolves) derived from visual counts of traveling individuals will be biased low. In addition, human exploitation lowers group size and possibly causes coyotes to become more secretive and nocturnal. Pack size in coyotes fits nicely with the behavioral and ecological relationships described by Moehlman (1986) for many canid species. Larger canids, like the coyote, are more social and tend to form packs. According to the accepted definition of a pack (three or more adults inhabiting the same territory), jackals and even red foxes commonly form packs. Many red fox territories consist of three adults—the mated pair and a yearling female helper—and are rarely seen together, but use the same territorial area (Macdonald 1977).

Coyote populations are explicit in their spatial arrangement and are spatially structured according to well-de-

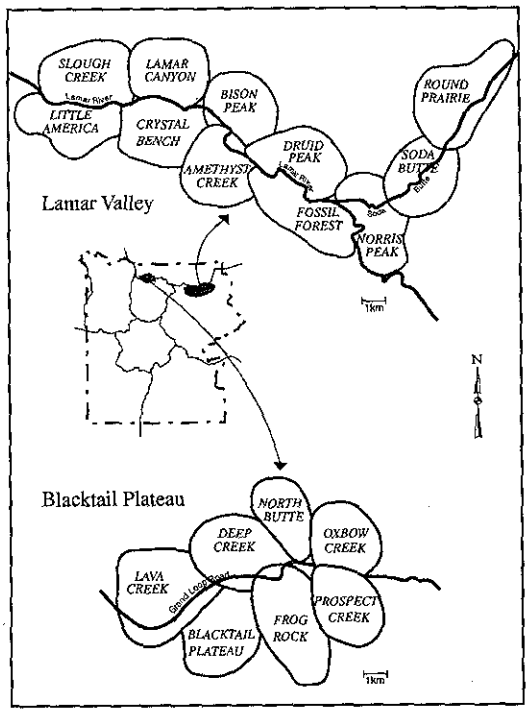
fined social classes (see Crabtree 1989). However, a review of previous studies cited in this paper indicated various discrepancies in the classification of adult coyotes into consistent social classes. We believe these inconsistencies are the result of variable human exploitation rates among the studies reviewed. Hence, we modify the classification of adult coyotes originally proposed by Bowen (1978) and adopted by Bekoff and Wells (1986) to describe two major social classes and six or seven subclasses seen in both studies of unexploited populations (Crabtree 1989, this study)

Adult coyotes captured in Yellowstone fall into two distinct social class categories: (1) either a member of a social group (territorial *pack member*) or, (2) a non-territorial *loner*. Adults in territorial packs were further divided into the dominant *alphas* or *breeding pair* and their subordinate *betas*. Beta pack members can either be *helpers* (help with pup-rearing) or *slouches*, which occupy the territorial area and socialize with the breeding pair but seldom, if ever, contribute towards pup feeding, pup rearing, and den guarding. Betas are pups born in previous years that stay in their natal territory (Crabtree 1989, Crabtree and Sheldon 1999).

Loners are subdivided into *solitary residents* and nomadic transients (*nomads*). The term transient, used in previous studies to describe non-territorial status, was inappropriate because a significant portion of non-territorial individuals expressed site fidelity and exhibited little, if any, transitory movement (e.g., solitary residents). Nomads are usually young, have low site fidelity, and range over large areas (50-300 km^2) presumably in search of a mate and a territorial vacancy (Crabtree 1989). Solitary residents have levels of site fidelity and home range sizes that vary between those of pack members and of nomads.

Solitary residents generally make up less than 15% of the population and are the most heterogeneous social class. They are divided into 2 subclasses: *floaters* and *former alphas*. Floaters tend to be younger, age 1-3 years, show weak fidelity to an area, and range over a larger area than most older solitary residents. They spend substantial amounts of time on the periphery of several territories and are suspected to be "outcasts" of one of the adjacent territories (Crabtree 1989). The characteristics of this subclass match those of individuals described by Bekoff and Wells (1986) and individuals described by Messier and Barrette (1982).

Figure 4. Location of coyote territories in the 2 study areas prior to wolf reintroduction. Reprinted with permission from Yellowstone Science, Vol. 7, No. 2, Spring 1999.



The second subclass of solitary residents, *former alphas*, consists of older adults, age 3.5-13.5 years, with a degree of site fidelity close to a territorial pack member. Evidence presented by Crabtree (1989) indicates that many of these individuals are former territorial alphas. Noticeable head and facial scars are common on breeding males as is evidence of former reproduction on females. A vocalization study by Fulmer (1990) indicated that solitary residents occasionally respond to territorial group yip-howls.

Only Bekoff and Wells (1986) describe a social category called *resident mated pairs* that do not defend a territory. We believe this category arises infrequently; however, we have observed it several times in Yellowstone as a direct result of wolf disturbance (Crabtree and Sheldon, unpubl. data), or as loose, short-term social bonds between male and female solitary residents (observed twice in southeast Washington; Crabtree 1989).

Territories

Territories were defined as defended, stable,

contiguous, and non-overlapping areas (Figure 4) of 7-12 km^2 (mean = 10.1). Territories are defended by vocalization (Sheldon et al., *this volume;* Gese and Ruff 1998), physical presence, scent marking (urine and feces), and physical defense (Allen et al. 1999). Non-overlapping areas represent further evidence of territoriality (Figure 4). Although home range analysis indicated some overlap between territories in Yellowstone and in other studies, we believe this to be an artifact of the statistical method employed. Observation of scent marking and territorial defense in Yellowstone indicates relatively little, if any, overlap between groups (Allen et al. 1999; Crabtree, unpubl. data). Statistically defined territorial "core areas" do not show any overlap.

Territory size, configuration, and intensity of use (i.e., utilization distribution) are probably functions of many factors, including prey habitat and densities, pack size, topographical features, and neighboring conspecifics. Recent work by Moorcroft et al. (1999) provided a mechanistic, spatially explicit approach to estimating carnivore home ranges using coyotes as an example. This empirically based, theoretical model examines scent marking, fidelity to an area, and neighboring conspecific territories as factors affecting the use of space by an individual pack member or an entire pack. The empirical data collected in Washington by Crabtree (1989) and in Yellowstone (unpubl. data) fit the statistical models and provided realistic utilization distributions. This work underscores the need for behavioral data as well as the need for estimation of surrounding territorial configurations.

The location of territories in LV and BT and their subsequent boundaries were extremely stable. Unexpectedly, only 4 shifts (5% rate) occurred over 93 territory-years in the BT and LV study areas. Two of 4 shifts involved a contraction of a territorial area associated with loss of an alpha individual. The new territorial area still included over 50% of the original area. The other 2 shifts appeared to be associated with access to prime vole habitat when vole numbers were high and the expanding territory had little vole habitat in its original territorial configuration. Both shifts increased the original territorial by about 20%. All 4 shifts were ephemeral and lasted no more than 1 year.

Data from 3 long-term studies of unexploited or lightly exploited coyote populations without wolves (Crabtree 1989, this study, Camenzind, unpubl. data), totaling 305 coyote territory-years, showed no change in the location and number of territories and few temporary shifts (see above) in territorial boundaries. Five of 7 denning areas located on the NR in 1946-49 during a dispersal study of coyotes (Robinson and Cummings 1951) were in the same location in 1990-93. These data, combined with the slow turnover of alpha pairs residing in a territory and the consistency of their diet over 50 years (Table 1), suggest coyotes invaded suitable habitats vacated by extirpated gray wolves and that the location (and number) of coyote territories have been stable ever since.

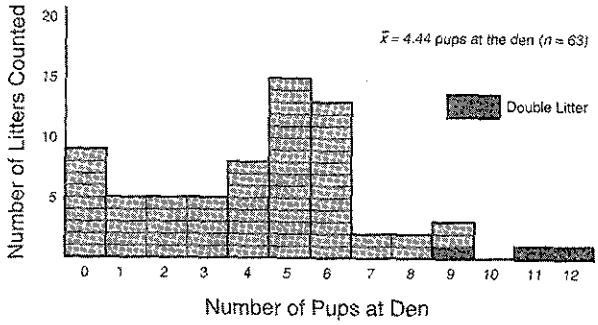
Territory size in Yellowstone is typical (e.g., 10 km^2) with latitudinal variation ranging from about 2 km^2 in southern regions (Texas; Winberg et al. 1985) to approximately 20 km^2 in northern regions (Canada; Bowen 1978). Territory size can vary inversely with prey abundance (Mares et al. 1982 for small mammals, Hixon et al. 1983 for birds), but this relationship in coyotes is not consistent (Mills and Knowlton 1991). This relationship is implied for coyotes in southeast Colorado (Gese et al. 1988), but habitat saturation of contiguous non-overlapping territories as seen in previous studies (Windberg et al. 1985, Crabtree 1989) may not allow territories to expand and contract with changing prey densities. In addition, the opportunity for a territorial pack to shift into a neighboring territorial vacancy is low. The estimated time period that alpha pairs reside in a territory in Yellowstone and Washington (Crabtree 1989, this study) was calculated at 6 years.

Population Demography

Litter size

Coyote litter size in Yellowstone, based on den emergence counts in late May, averaged 4.4 pups per territory (Figure 5). Indirect evidence from early May counts in Yellowstone, late April counts in Washington (Crabtree 1989), and other studies (Knudsen 1976) suggest that approximately 1 pup is lost in the first month after birth. This results in an estimate of litter size at birth of 5.4 pups per territory in Yellowstone. Contrary to the consistency of pack size and territorial stability (described above), litter size varies greatly (Figure 5) ranging from complete loss of litters in poor food years to

Figure 5. Litter size. Reprinted with permission from Yellowstone Science, Vol. 7, No. 2, Spring 1999.



larger litters within large packs in good food years (see Sociality and Pack Formation). Annual litter size in Yellowstone varied between a low of 2.6 pups per territory in 1994 to a high of 6.9 pups per territory in 1992. This is the greatest variation yet reported for litter sizes without the effects of human exploitation. It is possible that exploitation by humans dampens the response of litter size to fluctuations of prey.

Although productivity has been related to prey abundance (see Crabtree and Sheldon 1999 for review), it appears that litter size at birth is surprisingly invariant. Litter size averages about 6 pups per year in North America and an even sex ratio is common (Bekoff 1977). Numerous studies, spanning a variety of habitats, prey abundances, and exploitation rates, report litter sizes taken from den counts, ranging between 5 and 7 (see Crabtree and Sheldon 1999). Even with drastic 10- to 40-fold changes in jackrabbit and hare abundance, litter size only varied from 6.6 to 7.6 (unborn fetus counts, Clark 1972) and 4.3 to 6.0 (placental scar counts, Todd et al. 1981) in northern Utah and central Alberta, respectively.

Surprisingly, litter size also appears relatively invariant to level of exploitation (Crabtree and Sheldon 1999). It appears that litter survival (mortality from birth to early winter), not litter size at birth, is the major reproductive parameter that responds in a density-dependent manner, that is, compensates for density-reducing human exploitation (Crabtree and Sheldon 1999). After all, canids place relatively little energetic investment in gestation compared to lactation and provisioning of pups during the pup's maximum growth period.

Neonatal Survival

High neonatal pup mortality was observed from mid-June through mid-August each year. The summer survival rate estimated from 62 radio-tagged pups captured in June 1990, 1991, 1992, and 1993 averaged 0.30, varying from 0.15 to 0.42. The fall survival rate of pups was estimated at 0.85, which was not significantly different from the average adult survival rate ($P = 0.61$). Thus, overall population productivity was only 1.5 pups per pack per year.

Examination of 18 pups recovered shortly after death revealed enderitis, a condition associated with an active parvovirus infection. Live parvovirus was cultured from tissue samples taken from 1 pup collected just after death (see Johnson et al., *this volume*). The time of death was associated with periods of extended heat with maximum daily temperature at or above 85°F. Cause of death could not be determined for 11 pups recovered at various stages of decompostion. However, all but 1 of 11 were associated with water or a moist, shaded area. All of the 18 pups examined shortly after death were associated with water or a moist, shaded area. Commonly, pups infected with parvovirus are severely dehydrated and travel to wet areas before death.

Based on disease investigations of Johnson et al. (*this volume*) and the high transmissivity of parvovirus, we suspect that all pups in a given litter are infected. However, the weak or malnourished die and the strong (probably dominant pups) survive the infection. Examination of lactating females in Washington (Crabtree 1989) and examination of two live-captured alpha females in Yellowstone that had just lost entire litters revealed evidence of lactation. These females were in poor nutritional condition (low body weight and low fat index). This leads us to believe that some alpha females become pregnant (many have been seen courting and breeding) then lose entire litters shortly after birth (see Sayles 1984). This was first suspected by Knudsen (1976) in northern Utah.

Crabtree (1989) suggests that intraspecific strife and/or low prey abundance leads to alpha females in poor condition. Their pups are born underweight, may have inadequate food-provisioning rates, and are predisposed to disease, which becomes the proximate cause of mortality. Males always tend to be dominant over females (Sayles 1984), probably gain more access to nursing and regurgitated food, and

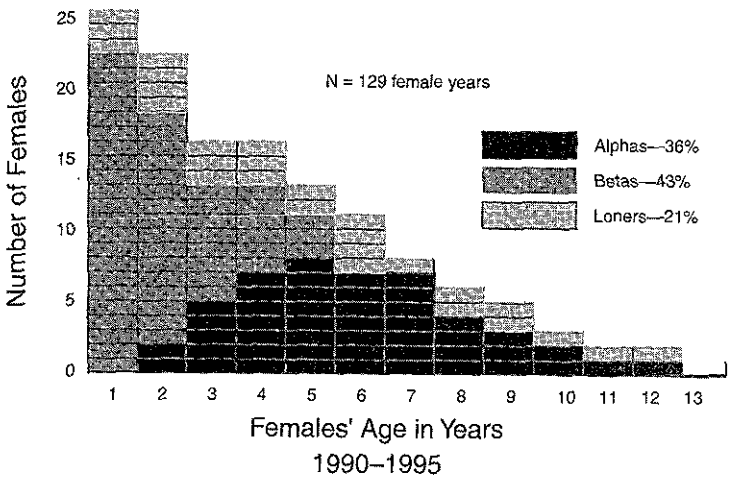
may have a higher survival rate. The sex ratio of pups in LV and BT was 34 males to 28 females.

Exclusive Breeding

With few exceptions, only the dominant alpha female successfully reproduces. Alpha females constitute 35% of the female population (Figure 6). Even then, they fail to reproduce 14% of the time while maintaining their territorial status. While likely losing entire litters shortly after birth, some older-aged alpha females still defend their territories and retain their alpha status (Crabtree 1989, Crabtree and Sheldon 1999). Reproductive suppression is common among carnivores (Creel and MacDonald 1998) and occurs among 65% of the females in Yellowstone (Figure 6). This "behavioral sterility" is socially mediated. Although 10-month old juvenile and older females are capable of breeding, nearly all subordinate females in a pack and all non-territorial females fail to breed successfully (Crabtree and Sheldon 1999).

Female coyotes are monestrous and the alpha pair mate once a year. However, similar to wolves, coyote packs occasionally produce a double litter. We have observed this 5 times in Yellowstone and estimate that double litters occur about 5% of the time. In 1 case, an 11-year-old alpha female had 7 pups together with her daughter, a 2-year-old beta female that had a litter of 5 pups. All pups were communally nursed and reared. The beta female had been a den helper the previous year and appeared closely associated with her alpha female mother.

Figure 6. Age distribution of female coyotes. Reprinted with permission from Yellowstone Science, Vol. 7, No. 2, Spring 1999.



In unexploited and lightly exploited studies, females first attain alpha status and initiate reproduction when 2-5 years of age with decreases in the probability of successful litters starting at about age 7 (Crabtree 1989, this study). Socially-sterile beta females, combined with a reservoir of loner females, provide high potential for replacement of breeding females in exploited populations. In exploited populations, many females are 10 months old when they first attain alpha status and breed. This has been clearly demonstrated in field studies (Crabtree and Sheldon 1999). However, it has been reported (Connolly and Longhurst 1975) that as many as 90% of females breed when exploited. Unless territory size significantly shrinks, these levels are inconsistent with the coyote's classic land tenure system of non-overlapping territories with 1 female breeding per territory. Unless exploitation levels are so high as to break down this system, such as that described by Berg and Chesness (1978), it is difficult to imagine levels above 66% of females breeding. All field studies examining female reproduction have reported territorial and non-territorial females that do not breed.

Dispersal

Overall dispersal rates in Yellowstone are low compared to other studies. The mean annual dispersal rate was 22% for pups and 16% for pack members (only betas dispersed). These rates are consistent with the low dispersal rates reported in Washington (Crabtree 1989) and in Idaho (Davison 1980), 2 habitat-saturated populations subjected to low levels of human exploitation.

We agree with Knowlton and Stoddart (1983) that dispersal is the primary mechanism for maintaining population densities near saturation levels. Davison (1980) documented emigration from habitat saturated areas to areas that are exploited. Dispersal also serves to reduce population density or, in the case of a food shortage, to lessen intraspecific competition (Harrison 1992). These studies also indicated lower survival rates for dispersers than for residents. Low survival of dispersers, locally abundant prey, and lack of territorial vacancies

in local and nearby areas appear to be selective conditions favoring delayed dispersal (natal philopatry).

In the case of a density reducing event, a reservoir of loner replacements colonize vacancies because only mated territorial females successfully breed and can increase their genetic fitness by reproducing themselves instead of helping raise their younger siblings. This, combined with the dispersal potential of coyotes (see Robinson and Cummings 1951), argues for immediate colonization from immigrants and resident loners and betas. Observations in southeast Washington (Crabtree 1989) and Yellowstone (this study) both suggest that a territorial vacancy is immediately filled with loners, probably competing for residency status and breeding opportunities. However, in 4 of 10 replacement events, it took 1.5 to 2 years for a new breeding pair to emerge. This delay was presumably due to intense competition between adults. In contrast to immediate immigration, increased pup survival and the subsequent recruitment of pups into the adult population proceeds at a much slower rate and can only occur once per year.

Evidence gathered in this study and in Washington (Crabtree 1989), indicates that some loners are "extended" pack members that occasionally visit their natal territory. This may indicate an adjustment of the resident pack size to provide more food for the dominant adults and survival potential for pups. This loose affiliation may also explain the high proportion of loners in some populations. Mills and Knowlton (1991) proposed that food shortages cause an increase in the proportion of non-territorial individuals (i.e., loners). This mechanistic explanation of the derivation of these loners is provided by Gese et al. (1996c), who describe the dispersal of subordinate pack members that had decreased access to food sources.

Adult Survival

During the pre-wolf period (1990-1995), if a coyote survived the high neonatal mortality rate during the first summer of its life, the chance of becoming an older, mature adult was high. The overall annual survival rate for adult coyotes on the NR was 91% and did not significantly differ between years ($P < 0.05$). Of 12 adult mortalities, 4 were attributed to mountain lions, 4 were vehicle-related, and 4 were due to unknown but natural causes.

Data from the 2 unexploited coyote populations (Crabtree 1989, this study) report a 9% and 10% annual adult mortality rate, with occasional vehicle collisions accounting for half of the total losses. These rates are far less than the 40% mortality rate assumed by Knowlton (1972) in the absence of exploitation. With Knowlton and Stoddart (1983) attributing 89% of mortalities to humans, they must have wrongly assumed that human exploitation largely substituted for natural mortality. Even some exploited populations have annual adult mortality rates less than 40% (e.g., Windberg et al. 1985). In the absence of exploitation (either from humans, predators, or lethal competitors), the major mortality period for coyotes occurs between birth and 4 months of age. At 5 months, the probability is high that a coyote will reach adulthood and survive to old age (Crabtree and Sheldon 1999).

Ecological Relationships

Prey Influence on Demography

The 2 most important food items on the LV and BT study areas are voles and carcasses (Figure 1). Voles are utilized from early spring snowmelt until early to mid-winter when dense snow prevents capture by coyotes (Gese et al. 1996a). In comparison, carcasses are utilized only from mid to late winter, except in mountain lion habitat where coyotes can usurp their ungulate kills (Murphy 1997).

Voles and carcasses fluctuated greatly during the six years of study, thus providing a natural experiment with which to test the effect of prey on population demography. In this section, we examine the influence of voles and ungulate carcasses on coyote abundance, pack size, dispersal, litter size, and territory size. In some cases, this was tested using the yearly means (n = 6, 1990-95), and in other cases, individual values were calculated for each territory for each year (n = 18-42). These data, however, were not always available.

Population Abundance: Population abundance was surprisingly invariant ($P = 0.45$) with respect to major changes in prey abundance. Despite 4-fold differences in carcass biomass (Gese et al. 1996b) and over 10-fold differences in vole biomass (Johnson and Crabtree 1999) during 1990-95, there was little corresponding change in annual coyote abundance, which varied between 42 and 58 individuals among

the 7 packs intensively monitored in LV. With the second highest recorded amount of carrion in the winter of 1992-93 and a record amount of vole numbers in 1992, the LV pack size in the spring of 1993 was the highest recorded (7.6 adults per pack), but was only a 19% increase over the mean of 6.4 ($n = 38$ pack-years, over 6 years). Although prey abundance influenced the various demographic parameters described below, its effect on overall coyote abundance was dampened by density-dependent responses (Crabtree and Sheldon 1999) and prey-switching behavior (Figure 1).

Pack size and dispersal: Neither vole ($P = 0.29$) or carcass biomass ($P = 0.79$) significantly affected mean annual pack size (overall; $r^2 = 0.38$, $F = 0.93$, $P = 0.52$). On a territorial basis, however, areas that encompass large proportions of mesic grasslands, the preferred habitat of voles, tended to harbor larger pack sizes. However, this relationship was obscured by a non-linear phenomenon. In wet years, vole biomass is very low in the extensive mesic grasslands due to flooding and the subsequent effect on reproducing adults (Pinter 1988). In dry years, vole biomass is relatively high in these floodplain habitats but low in upland grasslands. Thus, analysis on a per territory basis was conducted and vole biomass proved to be a significant predictor of pack size ($r^2 = 0.34$, $P = 0.035$, $n = 11$ for 1992-93) in LV. Although pack size was not significantly correlated with winter carcass biomass on a per territory basis, there were significant behavioral mechanisms operating (see Sociality and Pack Formation).

Litter size: Carcass biomass did not significantly affect ($P = 0.17$) mean annual litter size ($r^2 = 0.71$, $F = 3.75$, $P = 0.15$), but the influence of vole biomass on annual litter size was marginally significant ($P = 0.07$). Again, however, individual variability among territories obscured potential significant relationships. On a per territory basis, litter size in LV was positively correlated with carcass biomass ($r^2 = 0.28$, $P = 0.015$, $n = 18$). In addition, litter size was negatively correlated with the percentage of mesic/floodplain grassland habitat in the territorial area ($r^2 = -0.37$, $P = 0.022$, $n = 12$). This supports the hypothesis that, in wet years, vole biomass is very low in the extensive mesic grasslands due to the effect of flooding on reproductive adult voles (Johnson and Crabtree 1999). This, in turn, negatively affects coyote litter size. Pack size is another confounding but significant factor (see Sociality and Pack Formation). Larger pack size effectively reduces the amount of food available to pregnant females and pups, especially during low food years.

Territory size: Territory size was the most invariant parameter measured in relation to prey abundance. In fact, the number, size, configuration, and location of territories were relatively constant. The few shifts that did occur were attributable to the death of an alpha male with adjacent territorial encroachment (see Territories). In a habitat-saturated area like the NR of Yellowstone, there is little room, if any, to adjust territory size in relation to the availability and abundance of prey. Rather, adjustments made to varying prey abundance come in the form of numerical changes within the confines of stationary territories (litter size, pack size, and dispersal).

Fire impacts

The fires of 1988 had little direct effect on coyotes. Of 12 territories examined, 0% to 52% of the territorial area burned providing a gradient of burn levels with which to test burn effects. Estimates of pack size, litter size, and survival of adults and pups were not significantly affected by burn level ($P > 0.50$). However, coyotes may have benefited indirectly from the 1988 fires. Johnson and Crabtree (1999) indicate that several important small mammal species (e.g., voles and ground squirrels) utilized as prey items by the coyote are more abundant in burned habitats than in unburned habitats (Table 4). Because the number of voles and possibly ground squirrels are significantly related to litter and pack size, we can

Table 4. Short-term (4 and 5 years after) and predicted long-term effects of the 1988 fires on the abundance of small mammals on Yellowstone's Northern Range.

	BURNED SAGEBRUSH		BURNED FOREST	
Species	Short-term	Long-term	Short-term	Long-term
Ground squirrel	18x increase	increase	-	-
Pocket gopher	4x increase	increase	2x increase	increase
Microtus spp.	4x increase	increase	slight increase	unchanged
Red-backed vole	-	-	3x increase	increase
Sorex spp.	14x increase	increase	3x increase	increase
Snowshoe hare	-	-	decrease	big increase

infer that the 1988 fires indirectly, but beneficially, influenced coyote population demography by increasing the density of important prey species. However, since the coyote is a generalist and frequently switches to a variety of alternate prey species both seasonally and annually, the overall demographic effect was subtle and our sample sizes did not detect a significant effect.

Ungulate effects

We detected no effects of elk seasonal movements on coyote behavior or population demography. Mule deer occurred at such low densities that changes in their numbers were undetectable. Even then, no significant effects of mule deer would be expected because they are rarely utilized as a prey source. They were not observed in the examination of over 500 scats.

However, the effect of elk calves on coyote demography and behavior is probably significant. Coyotes were routinely seen hunting elk calves during the last week of May through June each year. In fact, we observed a total of 8 predation events in June where coyotes killed elk neonates and the remains of elk calves were commonly found at dens. Coyotes kill an estimated total of 750 elk calves annually (Table 3). Other elk killed are primarily short-yearlings (and a few adults) that are starving or severely weakened during winter. This source of food is effectively the same as carrion and probably affects coyotes in same fashion as that of carrion described above.

The role of ungulate neonates in the early summer diet of the coyote has received surprisingly little attention given its apparent impact on the demography of coyotes. Predation on neonates may also be a limiting factor for ungulate populations, especially if neonate predation is an additive form of mortality. Ungulate neonates are relatively large packages of prey available in early summer during weaning of pups that are growing at maximum rates. Substantial pup mortality due to disease and starvation occurs immediately after this period in July and August (Johnson et al., *this volume*). Central-place foragers (e.g., den-attending adults) are time constrained—in addition to being subject to the energetic demands of food provisioning—and this should result in prey specialization. According to optimal foraging theory, adult coyotes would be predicted to specialize on large food items and become energy maximizers (Pyke et al. 1984). Althoff and Gipson (1981) and Till and Knowlton (1983) suggest that provisioning of pups stimulates adults to prey on domestic ungulates.

Behavioral observations in Yellowstone and the preponderance of elk calf remains at den sites corroborate the contention of prey specialization in June. Because differential reproductive success and pup survival is apparently directly linked to the timing and availability of ungulate neonates (or other food sources), evolutionary consideration should be given to the related topics of coyote group formation, the timing of reproduction, and anti-predator behavior of both wild and domestic ungulates.

Adequate understanding of predator-prey relationships comes from the simultaneous study of both predator and prey (Errington 1935). Fortunately, the first monographical studies of coyotes did focus on prey populations, including a 24-year study in northern Utah and a 12-year study in central Alberta (Todd et al. 1981, Knowlton and Stoddart 1983). Both studies demonstrated the significant influence of coyotes on cyclic populations of snowshoe hares (*Lepus americanus*) and black-tailed jackrabbits (*Lepus californicus*). Even more profound was the effect of varying prey abundance on coyotes both functionally and numerically. Strong functional responses are expected when a classic habitat generalist/feeding generalist like the coyote (Johnson and Crabtree 1999) preys upon a relatively large, easy to handle prey source. Strong numerical responses should also occur given the behavioral plasticity and high reproductive capability of coyotes. Demographic parameters do respond to major increases or decreases in food supply, especially natality (Clark 1972, Knudsen 1976, Todd et al. 1981).

Sociality and Pack Formation

Pack size varies from year to year and from territory to territory. This natural variability allowed us to test how pack size (and a dominance hierarchy) affects the sociodemography of coyotes. We discuss these results and the results from other studies in relation to why packs form and the ecological consequences sociality has in regulated coyote populations.

Hatier (1995, unpubl. data) examined the role of helping behavior in the LV and BT study areas in 1992 and 1993. She found that larger packs, those with more betas (or associates), significantly de-

creased the amount of time that the breeding alphas spent at the den guarding. In addition, larger packs exhibited higher rates of provisioning. An increase in the number of feedings from the alphas (presumably because there were more betas) was significantly correlated with larger litter size. However, overall the size of the pack (number of betas) was not positively correlated with litter size or litter survival. These data suggest that betas were tolerated by alphas because they relieve the stress of reproduction (e.g., guarding and feeding) and because there were abundant resources to support them (Hatier 1995).

Because some of Hatier's sample sizes during the 2-year study were probably insufficient to detect significant differences, we added another 4 years of data on pack size, litter size, and survival to the analysis. Like Hatier (1995), we found no significant correlation between pack size and litter size or between pack size and pup survival to the fall period. However, because litter size is a function of prey abundance, the analysis should include prey abundance.

In the years previous to wolf colonization (1990-95) prey abundance fell into 2 fairly distinct categories: 1) years when food was abundant, namely 1991, 1992, and 1994 (only in BT because floods did not affect vole numbers), and 2) years when food was not abundant, namely, 1990, 1993, and 1994 in LV (vole flooding), and 1995. Thus, we divided the data for separate analysis. Litter size and pup survival were positively correlated with pack size in high food years ($r = 0.41$, $P = 0.05$) but were negatively correlated with pack size in low food production years ($r = 0.41$, $P = 0.04$). The same significant trends were true for litter survival. Because virtually all food consumed by pack members is extracted from within the "confines" of the territory, packs may exceed territorial carrying capacity in low food years. In good food years, carrying capacity within the territory exceeded pack size and extra beta adults contributed directly to litter size and pup survival.

The formation of packs, or sociality, in coyotes has been attributed to increased foraging efficiency (see Bekoff and Wells 1986), but this relationship remains unclear and has received significant attention. Messier and Barrette (1982) provide an excellent discussion of the subject. Bowen (1981) concludes that group formation in coyotes is an adaptation to efficiently capture ungulates and/or economic defense and consumption of carcasses. This hypothesis appears to be supported by other fieldwork (Camenzind 1978, Bekoff and Wells 1986, Bowyer 1987; and for gray wolves, Packard and Mech 1980). Sheldon (1992) questions whether successful hunting is a secondary effect as is implied by Gese et al. (1988), while Messier and Barrette (1982) provide criticism and compelling alternative hypotheses.

We agree with Messier and Barrette (1982) and find no empirical evidence to demonstrate that larger social groups lead to a *per capita* increase in food intake in coyotes (or wolves), thus improving fitness. In fact, single individuals and groups of 2 coyotes commonly take down and kill both deer and elk in Yellowstone, but larger groups can also be involved (Gese and Grothe, 1995, Crabtree, unpubl. data). Furthermore, dominant individuals tend to monopolize feeding time on both predated and winter-killed ungulate carcasses (Gese et al. 1996c). This results in the exclusion of subordinates that may or may not be involved in the predation attempt, or in defense of the carcass. Defense of the carcass appears to be a role primarily performed by the dominant alpha male (see Gese et al. 1996c, S. Grothe and R. Crabtree, unpubl. data).

The controversy of pack formation in coyotes illustrates one of the major problems in evolutionary ecology: are the observations an effect or an evolutionary cause? Messier and Barrette (1982) propose that group formation in coyotes is the result of delayed dispersal and that exploitation of ungulate prey is a secondary effect. Juveniles that forego dispersal accrue a variety of benefits, such as secure foraging, increased survival, continued learning, and the attainment of alpha status within or adjacent to their own territory. In addition, delayed dispersal may also be the result of habitat saturation—no vacancies for dispersing juveniles (Davison 1980). Movement of radio-tagged juveniles in Yellowstone and southeast Washington (Crabtree, unpubl. data) indicate that some juveniles disperse in fall or early winter but return to their natal territories later in the winter or spring before whelping. The additional contention by some authors (Bekoff 1977, Messier and Barrette 1982) that delayed dispersal may also be related to delayed sexual maturity appears weak. Data from unexploited populations (see Crabtree and Sheldon 1999) and from Texas (Knowlton et al. 1986) suggest that all females are capable of breeding at 10 months of age, and that variation in reproductive statistics (e.g., age at breeding, percent of yearling females reproducing) is caused by socially-

mediated breeding suppression (i.e., only dominant alphas breed) and exploitation effects (Crabtree and Sheldon 1999).

We suspect that delayed dispersal, along with cooperative foraging, is an effect and not the cause of sociality. Crabtree and Sheldon (1999) provide alternative hypotheses related to that proposed by Messier and Barrette (1982) and similar to that described by Packer and Pusey (1990) for African lions. These hypotheses suggest that genetic fitness (and thus a beta's inclusive fitness) is increased if "helping" actually increases pup survival. Selection pressure comes in the form of enemies—conspecifics (e.g., neighboring packs), predators (e.g., golden eagles and bears) and competitors (e.g., wolves and mountain lions).

Synthesis and Conclusions

Ecological Role

The extirpation of the gray wolf on the NR by 1927 probably resulted in high coyote population densities. This numerical increase adds a strong component to an already broad functional role as a generalist consumer. NR coyotes prey primarily on small mammals, but ungulate prey (mostly carrion) is the main food source in winter when adult coyotes are energetically stressed, highly territorial, pair-bonding, breeding, and females are becoming pregnant. The results of this study from 1990-95 (pre-wolf) regarding the coyotes' foraging niche (functional role) was surprising on two counts: (1) the coyote is the major ungulate predator, and (2) the coyote consumes a high percentage of the available small mammal prey probably to the detriment of other small mammal predators.

With highly variable and unpredictable food resources, the NR coyote populations maintain surprising stability: consistent numbers of territories, stable pack size and pack composition, fidelity of territory and den site location, and a high annual survival of adult pack members. These characteristics are maintained functionally by the coyote's broad foraging niche and ability to prey switch both seasonally and yearly. Ultimately, however, this stability is demographically maintained by a variable rate of: (1) neonatal mortality and (2) socially-mediated dispersal in saturated habitats. These 2 factors are, in turn, a function of prey availability and pack size prior to and during the reproduction and pup-rearing period.

The NR population has characteristics similar to the natural, unexploited population in south-central Washington studied by Crabtree (1989): low productivity, a highly structured social system, a contiguous distribution of non-overlapping, year-round territories, and an old age structure. Adult mortality is very low and primarily due to mountain lions and occasional vehicle collisions. Like gray wolves, 85 to 90% of NR coyote population exists in packs and average pack size is high. Wolf extirpation has probably resulted in high coyote population densities and coyotes have, at least partially, slid into this vacant niche. With the restoration of the gray wolf in 1995, the ecological role of the coyote will significantly change numerically, functionally, and behaviorally. These changes could have major ripple effects on the competitors and prey species of the coyote.

Population Regulation

Until recently (see Crabtree and Sheldon 1999), numerous studies of coyote population demographics had only prompted Knowlton (1972) and Knowlton and Stoddart (1983) to attempt a synthetic review regarding the regulation and limitation of coyote populations. In addition to the population "mechanics" they describe, it is clear that incorporation of coyote social behavior is needed. Social class dynamics, behavior, human exploitation, and competition is essential before any accurate synthesis is achieved. In addition, Crabtree and Sheldon (1999) concluded that long-term studies of coyotes in unexploited and lightly exploited areas, especially when combined with systematic visual observations, have proven irreplaceable in their contribution to a general understanding of coyote ecology.

Various sociodemographic factors that can regulate coyote populations have been identified: territoriality, exclusive breeding by dominant adults (dominance hierarchy), shortened breeding longevity, subordinate dispersal, delayed dispersal, reproductive failure, double-littering, and early and late summer pup mortality. Most studies reviewed indicate direct or indirect evidence of intraspecific competition. Unexploited and habitat-saturated populations indicate intraspecific strife (Crabtree 1989) and a higher level of intraspecific competition: low pup weights, scarring, reproductive failure, frequent territorial disputes, and high pup mortality,

including the probable loss of entire litters shortly after birth.

The abundance and availability of prey is certainly a major limiting factor, but the extent to which it is involved in population regulation remains uncertain. Prey has been strongly suggested or directly linked to every major social and demographic event (Crabtree and Sheldon 1999). Crabtree (1989) reported that the unit of the population that natality and mortality acts upon is, not age, but social class. We agree with Knowlton and Stoddart (1983) that social intolerances, mediated by the abundance and availability of food is the primary determinant of coyote density. However, recent research indicates that: (1) the role played by social/behavioral access to prey has been previously underestimated, and (2) human exploitation common in most field studies has severely confounded our understanding of coyote populations.

The most significant factor with review of studies of coyote ecology (see Knowlton 1972, Knowlton and Stoddart 1983, and Bekoff 1977) is the role played by human exploitation. Unfortunately, it has greatly biased, and even misled, our basic understanding of coyote populations. Frank (1979) called for studies of unexploited coyote populations in order to understand the evolutionarily significant situation. Unfortunately, only a few studies, like Camenzind (1978), have been conducted on lightly exploited populations and only 2 studies (Crabtree 1989, this study) have documented unexploited populations. Nearly all field studies of coyotes have been conducted on populations subjected to substantial levels of exploitation. Thus, the results of these studies simply describe a highly disruptive, unnatural situation. For example, coyotes are reported to show flexibility in their social system (Lott 1984), but could such social flexibility be the result of human exploitation and, to a lesser extent, unnatural and human-disturbance conditions? Various studies of coyote populations, all subjected to various levels of exploitation, report significant variation in both social and spatial organization (Berg and Chesness 1978, Camenzind 1978, Danner and Smith 1980, Bowen 1981, Messier and Barrette 1982, Andelt 1985, Bekoff and Wells 1986).

Like the effects of human exploitation, we know very little about the effects of interspecific competition on limitation of coyote populations (e.g., wolves). This factor has been largely ignored in coyote research agendas (but see Keith et al. 1977, Pacquet 1989, Harrison et al. 1989). Caution must be taken when inferring evolutionary mechanisms from studies without the competitive pressure of gray wolves, which coexisted with coyotes and red foxes over much of their pre-European distribution. This subject was recently examined by Crabtree and Sheldon (1999). An example of how important interspecific competition may be in limiting coyote populations comes from recent data in Yellowstone. Wolf-killed coyotes in Yellowstone's Lamar Valley during the last 3 winters have resulted in a 50% sustained reduction in coyote numbers. This is the result of significantly reduced pack size and the failure of new coyotes packs to colonize the traditional coyote territories usurped by wolves in the core-use areas of wolf packs.

Interference competition, including fighting, killing, direct displacement, and relegation to inferior habitats, has been clearly demonstrated in previous studies, yet wolves, coyotes, and red foxes coexist. Wolves are able to exclude coyotes (Peterson 1996) and coyotes are able to exclude red foxes (Harrison et al. 1989, Sargeant et al. 1987) at various scales, from individual encounters and territories, to entire regions, yet they coexist in many regions of North America. In order to better understand the role of interspecific competition in coyote and canid communities in Yellowstone, Crabtree and Sheldon (1999) provide a brief review of sympatric canid studies. They then make generalizations regarding sympatric canid studies and synthesize them into a theoretical framework applicable to the three canid species in Yellowstone.

Conservation and Management Issues

Due to the tripling of the coyote's distribution across North America during the last century, it is clear that the coyote as a species does not represent a small-population conservation problem. Nevertheless, restoration of coyotes to some areas may serve a functional role in the conservation of other species. Installing the functional role of ungulate predation, for example, where deer are over-abundant, or decreasing red fox populations that inflict heavy predation on nesting hens are possibilities. However, in an overwhelming number of situations, coyotes are considered a problem and are managed. We believe that conservation science can learn important lessons from understanding a successful and ubiquitous species like the coyote, in addition to the les-

sons learned from species experiencing declines in abundance and distribution.

Because of the numerous socio-demographic and density-dependent processes that take place in response to widespread population reductions and indiscriminate killing, federal programs to limit coyote numbers have proven ineffective and costly. Field experiments that examine the effectiveness of control programs are needed to better understand how coyote populations respond to exploitation. To our knowledge, this research has yet to be conducted. We believe that the coyote's famed behavioral plasticity and demographic resiliency to exploitation is an evolutionary product of its coexistence with competing species, mainly the gray wolf. Long-term studies of coyotes in unexploited and lightly exploited areas, especially when combined with systematic observations, have proven irreplaceable in their contribution to a general understanding of coyote ecology. The proposed 15-year study in Yellowstone (pre- and post-wolf) will provide additional understanding. So far, gray wolves have inflicted heavy losses on coyotes (Crabtree and Sheldon 1996) during winter in wolf core-use areas, and the sex and age structure of 34 wolf-killed coyotes appears to be relatively indiscriminate with a possible bias toward younger individuals (much like human trapping efforts).

Coyotes and Carnivore Communities

It is clear that interspecific relationships between canid species competing for limited resources can have significant impacts. This has major implications with regard to conservation and management efforts. Medium- and smaller-sized canids have shown a "release" (Soule 1988) following reduction or extirpation of the larger canid (Hersteinsson et al. 1989, Lewis et al. 1993, Peterson 1996). Thus, future reintroduction efforts should consider these and other community effects before implementation. Canid hybridization has occurred repeatedly (Boitani 1982, Lehman et al. 1991, Wayne and Jenks 1991, Gottelli and Sillero-Zubiri 1992) and can hamper or complicate expensive reintroduction efforts (Gittleman and Pimm 1991).

We agree with Johnson et al. (1996) that monitoring the effects of canid reintroduction programs provides a splendid opportunity to examine canid community structure and competition experimentally. Furthermore, it will provide a unique opportunity to understand community-wide effects such as functional and numerical responses by other mammalian predators (e.g., red foxes, weasels [*Mustela spp.*]) to significant reductions in coyote populations. Initial estimates of wolf numbers in northern Yellowstone made by Garton et al. (1990) equate to a tripling of the amount of potential carrion available to scavengers which could have significant impacts on, for example, threatened Yellowstone grizzly bear populations. Changes in elk behavior and distribution followed by subsequent changes in vegetation are yet other possible responses.

Canids, especially coyotes, display wide-ranging variability in their behavioral ecology and population demography and thus serve as excellent candidates for understanding carnivore communities and their relationship to prey populations. Long-term study, combined with systematic behavioral observation and experimental (and natural) manipulation is required in order to craft successful conservation strategies for communities in dire need of restoration. Such efforts are difficult and pose challenges to agencies, universities, and private organizations that must cooperate in order to plan, fund, and execute these invaluable studies.

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Changing Problems in Yellowstone Bear Management, 23 Years after the Dumps

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Abstract

Bear management policy in Yellowstone National Park (YNP) has progressively intensified efforts to reduce bear-caused human injuries and property damage and to maintain natural populations of grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) in the park. New bear management programs were implemented in 1960, 1970, and 1983. Gunther (1994) evaluated the effects of the 1960 bear management program and reported a slight increase in the number of bear-human conflicts occurring within the park during the first 8 years of the program. Cole (1976) evaluated the first 6 years of the 1970 bear management program and reported that it was successful in reducing bear-caused human injuries, the frequency of bears entering developed areas, and the number of bear management control actions (i.e., bears captured and relocated or removed) within the park. Meagher and Phillips (1983) reviewed bear management within YNP for the 10-year period 1970-79. They concluded that the bear management program during the 1970s had achieved the goal of restoring populations of grizzly and black bears to subsistence on natural forage and had concurrently reduced bear-caused injuries to humans in developed areas. We reviewed bear management within YNP during the 15-year period 1980-94. During this period, bear-caused property damage and human injuries continued to decline from previous levels and bear management control actions remained at low levels. Recent trends in bear management as well as future management considerations are also addressed.

Introduction

Yellowstone National Park (YNP) was established in 1872. As early as 1891, the acting Park Superintendent reported that bears had become very troublesome at all hotels, camps, slaughter houses, and other places in the park where human food could be found, and that it might be necessary to kill bears occasionally, if they became too destructive (Schullery 1992). As park visitation and the number of bear-human conflicts increased, park managers became increasingly concerned with, and, in

1931, began keeping more detailed records of, bear-caused human injuries, property damage, and subsequent nuisance bear control actions (Schullery 1992, see also Schullery *this volume*).

From 1931 to 1959, bears within YNP injured an average of 48 people per year (Cole 1976, Meagher and Phillips 1983). There was also an average of 98 incidents of bear-caused property damage reported per year during the same time period. During this period, an average of 3 grizzly bears and 22 black bears per year were removed from the population as a result of nuisance bear control actions.

In 1960, YNP implemented a National Park Service (NPS) bear management program (NPS 1960). This program was designed to reduce the number of bear-caused human injuries and property damage events in the park and to re-establish bears in a "natural" state. The 1960 program included the following management guidelines: 1) expanded efforts to educate visitors about bear behavior, methods for reducing bear-human conflicts, and the proper storage of food, garbage, and other bear attractants; 2) more prompt and efficient scheduled removal of garbage from developed areas to reduce the availability of garbage to bears and make bears less garbage dependent; 3) stricter enforcement of regulations prohibiting the feeding of bears; 4) the use of garbage cans designed to prevent tipping by bears and the proposed development of new types of bear-proof garbage cans; and 5) the removal of potentially hazardous bears, habitual beggar bears, and those bears that damaged property in search of human foods. These guidelines were directed primarily at the management of black bears and were largely in response to public complaints of personal injury and property damage caused by roadside and campground bears (Craighead and Craighead 1967).

From 1960 to 1969, while operating under the 1960 Bear Management Program, the average number of bear-caused human injuries within the park decreased slightly to an average of 45 per year (Gunther 1994). However, during the same time period the number of bear-caused property damage incidents within the park increased to an average of 253 per year. In addition, the number of nuisance bears removed from the park also increased, to an average of 4 grizzly bears and 33 black bears per year.

In 1970, YNP initiated a new, more intensive bear management program (Leopold et al. 1969) with greater emphasis on restoring the grizzly bear and black bear populations to subsistence on natural forage and reducing bear-caused injuries to humans (Cole 1976, Meagher and Phillips 1983). As part of the management program implemented in 1970, regulations prohibiting the feeding of bears were strictly enforced, as were regulations requiring that human foods be kept secure from bears. In addition, all garbage cans park-wide were converted to a bear-proof design and garbage dumps within and adjacent to the park were closed. The park also intensified efforts to inform park visitors of proper food handling and storage procedures in bear country and the consequences of feeding bears (i.e., increased injuries to humans and the need to destroy habituated bears). Cole (1976) hypothesized that the 1970 management program would: 1) reduce bear-caused injuries to humans in developed areas, 2) restore more natural conditions as evidenced by bears being well distributed and foraging on natural foods in summer and by declines in the number of bears visiting developed areas or being controlled, and 3) not prevent the park's grizzly and black bear populations from maintaining or reestablishing their numbers at natural carrying capacity levels.

In 1975, the grizzly bear was listed as a threatened species in the lower 48 states under the authority of the Endangered Species Act. A primary goal of the Endangered Species Act is to recover populations of threatened or endangered species to self-sustaining, viable populations that no longer need protection under the act.

In 1983, the park modified the 1970 Bear Management Program (NPS 1983). The 1983 program was similar to the 1970 program with regard to sanitation, but added greater emphasis on habitat protection in backcountry areas. As part of the 1983 Bear Management Plan, the park implemented a Bear Management Area program that restricted recreational use in areas with known seasonal concentrations of grizzly bears. The goals behind these restrictions were to: 1) minimize bear/human interactions that may lead to habituation of bears to people and subsequent removal of the bears from the population due to human safety concerns; 2) prevent human-caused displacement of bears from prime food sources; and 3) decrease the risk of bear-caused human injuries in areas with high levels of bear activity.

Further details of the history and evolution of bear management within YNP have been described in Craighead and Craighead (1971), Cole (1971, 1972,

1974, 1976), Craighead (1979), Meagher and Phillips (1983), Schullery (1992, *this volume*), Gunther (1994) and Craighead et al. (1995).

Cole (1976) evaluated the effects of the park's 1970 Bear Management Program for the years 1970-75. He concluded that the 1970 Bear Management Program appeared to be meeting its objectives because: 1) human injuries from bears had declined from previous levels, 2) the numbers of bears frequenting developed areas and being trapped and translocated had decreased through the early to mid-1970s, and 3) removals of nuisance bears did not appear to be preventing the park's grizzly bear and black bear subpopulations from maintaining or reestablishing their numbers at natural carrying capacity levels.

Meagher and Phillips (1983) reviewed the 1970 Bear Management Program for the 10-year period 1970-79. They concluded that the bear management program implemented within YNP during the 1970s had achieved the goal of restoring populations of grizzly bears and black bears to subsistence on natural forage and reducing the numbers of bear-caused human injuries occurring within the park. In addition, they concluded that the natural carrying capacities for the subpopulations of grizzly bears and black bears living within the park were not known. They also concluded that the number of bears being removed during control actions from 1970 through 1972 was high but that the number of removals after 1972 did not appear to be a cause of long lasting depression of numbers from those which would be dictated by natural conditions.

Cole (1976) and Meagher and Phillips (1983) described the implementation and effectiveness of YNP's 1970 Bear Management Program through 1979. In this report we update their work. We review the changes in bear management, bear-human conflicts, and nuisance bear control actions that have occurred within YNP over the 15-year period 1980-94. Recent trends in bear management problems as well as management considerations for the future are also addressed. Our primary objective is to identify current trends (if evident) in the types and locations of bear-human conflicts and subsequent nuisance bear management actions occurring in the park so that preventive rather than reactive management actions can be taken. We also retest Cole's (1976) hypotheses on the effects of the 1970 Bear Management Program for the 1970 through 1994 period.

Study Area and Methods

YNP encompasses approximately 899,139 ha in the states of Wyoming, Montana, and Idaho. The park was originally established to protect the area's thermal features and scenic wonders; however, bears and other wildlife quickly became one of its primary attractions (Schullery 1992, Schullery *this volume*). During the 15-year study period (1980-1994), visitation to the park gradually increased from an average of slightly more than 2 million visitors/year from 1980 to 1984 to almost 3 million visitors/year from 1990 through 1994. Most (> 80%) visitation occurs during the 4-month period from June through September. During the peak season (July through mid-August), visitation averages more than 24,000 people/day.

Approximately 1% of YNP is developed, including 2,170 overnight lodging units (accommodating approximately 7,100 people per night), 12 campgrounds (containing 2,219 campsites), 531 km of paved roads, and 117 km of gravel roads that run through the park (Figure 1).

Most of the park is considered pristine backcountry. The backcountry contains more than 1,600 km of designated trails and 301 backcountry campsites (Figure 2). The backcountry campsites have a combined total capacity of 2,620 people and 1,791 stock/night. Backcountry use nights gradually declined from 55,060 use nights in 1981 to a low of 25,188 use nights in 1988. Backcountry use nights then began to increase each year through the early to mid-1990s, increasing to 45,460 use nights in 1994.

Detailed descriptions of the geology (Keefer 1972, U.S. Geological Survey 1972), climate (Dirks and Martner 1978), vegetative characteristics (Despain 1990), and fauna (Streubel 1989, U.S. Fish and Wildlife Service 1994) of YNP have been previously reported.

The distribution (Blanchard et al. 1992), home range sizes and movements (Blanchard and Knight 1991), activity patterns (Schleyer 1983, Harting 1985, Gunther 1991), food habits (Gunther and Renkin 1990, Reinhart and Mattson 1990, Mattson and Jonkel 1990, Mattson et al. 1991, French et al. 1994, Green 1994), habitat use (Blanchard 1983, Knight et al. 1984) and population trends (Eberhardt et al. 1994, Craighead et al. 1995, Pease and Mattson in prep.) of grizzly bears in the Yellowstone ecosystem have been extensively studied and reported. The movements, food habits, habitat utilization, activity pat-

Figure 1. Locations of primary roads, secondary roads, and developed areas in Yellowstone National Park, 1994.

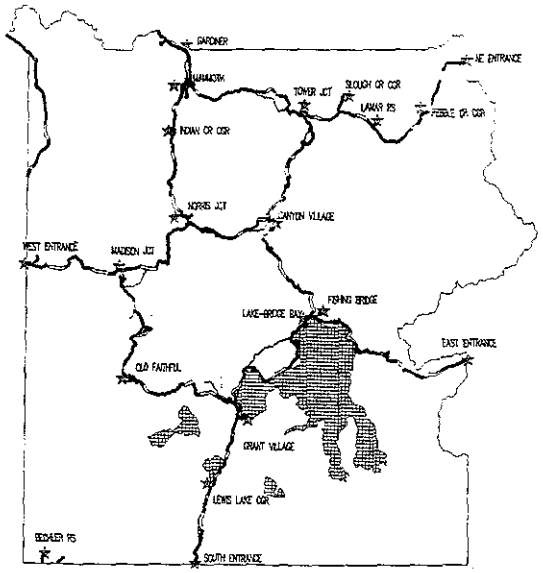
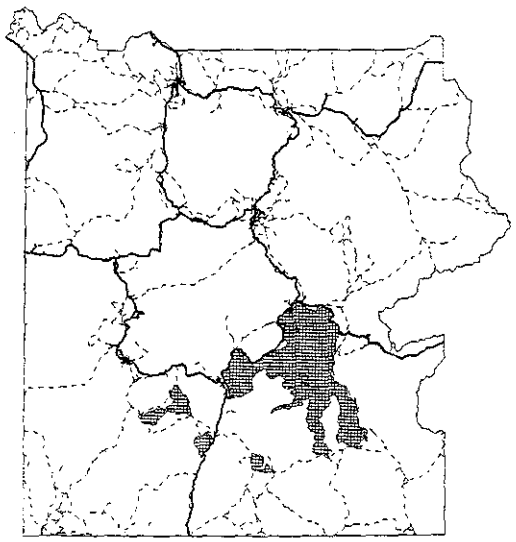


Figure 2. Locations of roads and backcountry trails in Yellowstone National Park, 1994.



terns, and population density estimates for black bears in YNP have been described by Barnes and Bray (1967).

Grizzly and black bears in YNP are a subunit of the bear populations that inhabit the Yellowstone ecosystem. In this paper, we analyze grizzly bear and black bear management data from the YNP grizzly bear and black bear subpopulations. We define the YNP grizzly bear and black bear subpopulations as those bears with home ranges either entirely within YNP or those with home ranges partially within and partially outside of YNP.

Data were collected from bear sighting reports, case incident reports, and management summary reports from park files. Information contained in these reports included bear-human confrontations, bear-inflicted human injuries and fatalities, bear-caused property damage, incidents of bears obtaining human foods, management hazing of bears, nuisance bears captured and translocated, and nuisance bears removed from the park subpopulation.

Throughout this paper, the term "bear-human conflict" is defined as any incident in which bears injured people, damaged property, obtained human foods, or were considered to pose a threat to human safety in developed areas, along roadsides, and in backcountry areas. "Nuisance bears" are defined as any bear involved in bear-human conflict situations. "Hazing" of bears is defined as the use of Thumper Gun projectiles, rubber bullets, cracker shells, or sling shots to move bears out of visitor use areas due to concern for human safety. The term "translocation" is defined as any incident in which a bear involved in a bear-human conflict situation was trapped and translocated, usually by helicopter, truck, or boat, to a remote area away from human activities. A "removal" is defined as any incident in which bears involved in bear-human conflicts were removed from the YNP grizzly bear or black bear subpopulations. Removals include bears sent to zoos, bears intentionally destroyed for management reasons, and bears killed unintentionally during management actions. "Habituated bears" are defined as bears that have learned to tolerate people, vehicles, and human structures at close distances to gain access to high quality natural foods. "Food-conditioned bears" are defined as bears that have learned to identify humans or human developments as a source of food due to prior food reward. "Confrontation" is defined as any incident in which bears bluff charged, acted aggressively toward people, approached people, or entered occupied backcountry campsites. The term "minor injury" is defined as bear-inflicted human injuries requiring less than 1 day of hospitalization or less than 35 sutures. The term "severe injury" is defined as bear-inflicted human injuries requiring more than 1 day of hospital-

ization or 35 or more sutures. "Developed area" is defined as the area within or immediately adjacent to campgrounds, hotels, lodges, cabins, restaurants, stores, or employee housing areas. "Roadside" is defined as the area within or immediately adjacent to the road corridor. The term "frontcountry" is used to describe areas within or immediately adjacent to roadside corridors or human developments. The term "backcountry" is used to describe all areas located outside frontcountry areas. "Campground" is defined as any designated roadside camping area with vehicle access. The term "campsite" is defined as any designated backcountry campsite with access to people on horseback, foot, or boat only. "On-trail" is defined as all travel on maintained trails with designated trailheads. "Off-trail" is defined as all backcountry areas other than designated trails or campsites. "Backcountry use night" is defined as the total number of people in an overnight party multiplied by the number of nights spent in the backcountry.

Our evaluation of whether or not the 1970 and 1983 Bear Management Plans accomplished stated objectives for the period 1970 through 1994 were made by testing Cole's (1976) hypotheses as to the effects of the 1970 bear management plan on grizzly and black bear behavior in the park. Cole's (1976) hypotheses are stated below.

The management initiated during the 1970s (and modified in 1983) will:

H_1: Reduce bear injuries to humans in developed areas from previous levels.

H_2: Restore more natural conditions as evidenced by bears occurring in spaced distributions on natural foods in summer and declines in the number of bears visiting developed areas or being controlled.

H_3: Not prevent the park's grizzly and black bear populations from maintaining or reestablishng their numbers at natural carrying capacity levels.

We tested Cole's (1976) first hypothesis by comparing the number of human injuries caused by grizzly bears in developed areas during the 25-year period (1945-69) prior to implementation of the 1970 Bear Management Plan to the number that occurred during the 25-year period (1970-94) after implementation of the plan. We further tested this hypothesis by comparing the number of black bear-caused human injuries that occurred in developments and along roadsides from 1945-69 to the number that occurred from 1970-94. A Mann-Whitney *U* test was used for both comparisons.

Cole's (1974) second hypothesis can be separated into 4 parts: a) bears will occur in spaced distributions in summer; b) bears will feed on natural foods in summer; c) there will be declines in the number of bears visiting developed areas; and d) there will be declines in the number of bears being controlled. Hypothesis 2, parts a and b as stated, cannot be tested using statistical methods because data on bear distribution and food habits were not collected in a comparable manner during the pre- and post-1970 Bear Management Plan periods. Hypothesis 2, part c also cannot be tested statistically because, although a common occurrence, the park did not start keeping statistics on the frequency of bears entering developed areas until after implementation of the 1970 plan. Thus, there is no pre-1970 data to compare with the post-1970 period. Due to these factors, hypotheses could only be analyzed qualitatively and the hypotheses rejected or accepted based on obviously inconsistent data. Hypothesis 2 part d was tested by comparing the number of grizzly bears removed by park managers in management actions during the 25-year period (1945-69) prior to implementation of the 1970 management plan to the number removed during the 25-year period (1970-94) after the plan was implemented. We also compared the number of black bears removed by park managers in management actions from 1945-69 to the number removed from 1970-94. A Mann-Whitney *U* test was used for statistical comparison.

Cole's (1976) third hypothesis also cannot be tested statistically. To our knowledge, an accurate estimate of the park's carrying capacity for grizzly bears and black bears has not been calculated. We review current literature on bear population estimates and trends to analyze this hypothesis.

For statistical analysis, Mann-Whitney *U* tests followed procedures described by Zar (1974) and $P < 0.05$ was considered to be significant.

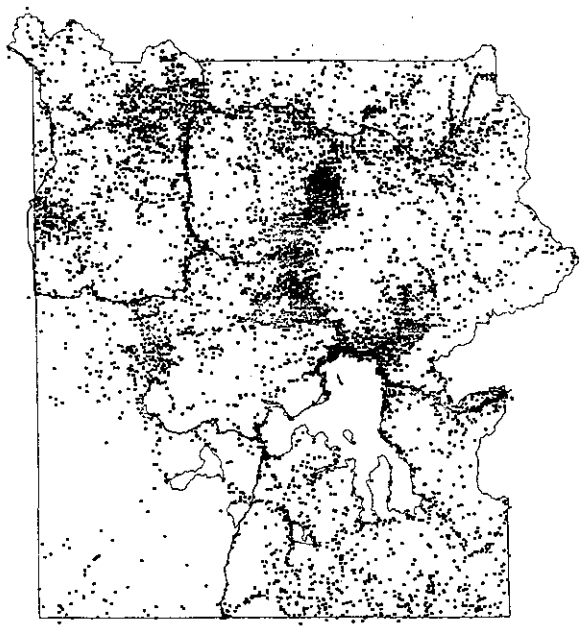
Results

Bear Observations

The number of reports of bear activity within developed areas was highly variable between years

(Table 1). Reports of grizzly bear activity in developed areas ranged from a low of 7 reports in 1980 to a high of 80 reports in 1986. Reports of black bear activity in developed areas ranged from 12 reports in 1983 to 72 reports in 1988 and 1993. The amount of bear activity observed in developed areas appeared to be related to both natural and human-caused factors.

Figure 3. *Locations of grizzly bear activity and observations reported in Yellowstone National Park, 1980-1994.*



During some years, there were natural shortages of seasonally important bear foods such as winter-killed ungulate carrion (mostly elk, *Cervus elaphus* and bison, *Bison bison*) in spring and whitebark pine (*Pinus albicaulis*) seeds and / or army cutworm moths (*Euxoa auxillaris*) in late summer and fall. During years with shortages of these foods, bears sometimes sought alternative foods (human foods and garbage) in association with park developed areas. During other years, a seasonal abundance of natural foods within developed areas attracted bears to park developments. Most notable of these foods were an abundance of chokecherries (*Prunus virginiana*) within the Mammoth developed area in 1988 and an abundance of spawning cutthroat trout (*Oncorhynchus clarki bouveri*) in the Lake / Bridge Bay and Grant Village developed areas from 1986-91. The relative abundances of these bear foods within developed areas were highly variable from year to year. In addition, the occasional presence of unsecured human food or garbage in developed areas sometimes attracted bears to park developments. These types of sanitation problems were generally quickly corrected and did not act as long-term attractants. They did, however, often lead to bear-human conflicts and subsequent bear management actions or removals.

Numbers of observations of bear activity in the wild were also highly variable from year to year (Table 1). These sightings were probably dependent on many factors, including park visitation, observer effort, the number of active field research projects,

Table 1. Numbers of grizzly bears, black bears, and unknown species of bears or their sign observed (total of unduplicated daily counts) in developed areas and in the backcountry within Yellowstone National Park, 1980-1994.

	Grizzly Bears		Black Bears		Unknown Species	
Year	Developed Areas	Backcountry	Developed Areas	Backcountry	Developed Areas	Backcountry
1980	7	277	18	322	12	106
1981	28	363	30	422	11	122
1982	39	321	30	486	22	99
1983	13	347	12	472	24	140
1984	47	710	21	439	22	177
1985	22	729	41	465	25	203
1986	80	870	48	740	21	243
1987	27	732	24	699	13	243
1988	40	752	72	726	10	202
1989	23	661	22	591	9	150
1990	31	536	46	524	9	125
1991	69	408	56	465	17	107
1992	38	502	41	528	6	118
1993	47	597	72	629	20	168
1994	52	747	59	752	12	207

climate, and the natural variations in the availability of preferred bear foods. The number of bear sightings reported is not considered to be an indicator of population numbers or trends. However, the distribution of these sightings indicates that grizzly bears are distributed throughout the northwest, northeast, and southeast sections of the park, but are relatively rare in the Bechler area and on the Madison and Pitchstone Plateaus in the southwest section of the park (Figure 3). Observations indicate that black bears are most common throughout the Northern Range of the park (i.e., the approximately northernmost 1/3 of the park), along roadside corridors throughout the park, as well as in the Mount Washburn, Canyon, Heart Lake, Shoshone Lake, and Bechler areas of the park (Figure 4). Black bears were rarely observed in the large nonforested areas of the park, such as the Hayden and Pelican Valley areas, that had high densities of grizzly bear sightings.

Bear-Caused Property Damage

There were 133 incidents where bears damaged property (without obtaining a food reward) reported in YNP from 1980 to 1994, an average of 9 (SD = 6) bear-caused property damage incidents/year (Table 2). Grizzly bears were involved in 31% ($\bar{x}$ = 3/yr, SD = 3, n = 41) of the incidents and black bears in 20% ($\bar{x}$ = 2/yr, SD = 1, n = 27). The species of bear could not be determined for 49% ($\bar{x}$ = 4/yr, SD = 3, n = 65) of the incidents. Bear-caused property damage occurred in developed areas (43%, n = 57), along roadsides (8%, n = 11), and in the backcountry (49%, n = 65).

Fifty-seven of the bear-caused property damage incidents occurred in developed areas, an average of 4/year (SD = 4). Grizzly bears and black bears were involved in 40% ($\bar{x}$ = 2/yr, SD = 2, n = 23) and 25% ($\bar{x}$ = 1/yr, SD = 1, n = 14) of the property damage incidents in developed areas, respectively. The

Figure 4. Locations of black bear activity and observations in Yellowstone National Park, 1980-1994.

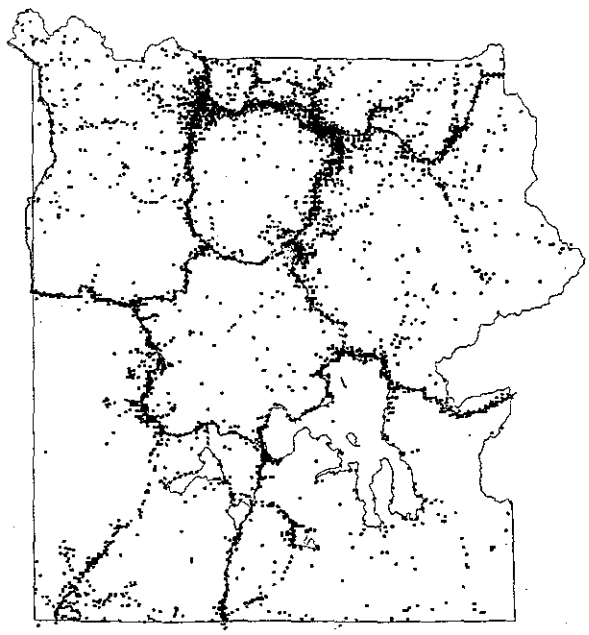


Table 2. Number of incidents of bear-caused property damage in Yellowstone National Park, 1980-1994.

	Developed Area			Roadside Corridor			Backcountry Area			Total		
Year	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk
1980	0	0	0	0	0	1	1	1	0	1	1	1
1981	1	0	1	0	0	1	0	1	2	1	1	4
1982	5	3	5	1	0	1	1	0	2	7	3	8
1983	3	2	1	0	0	1	0	0	0	3	2	2
1984	4	0	6	0	0	0	5	1	4	9	1	10
1985	1	0	1	0	0	0	1	1	5	2	1	6
1986	6	2	2	2	0	0	1	1	6	9	3	8
1987	0	0	1	0	0	0	2	0	4	2	0	5
1988	2	3	0	0	0	1	0	1	3	2	4	4
1989	0	0	1	1	0	1	0	0	0	1	0	2
1990	0	0	1	0	0	0	2	1	4	2	1	5
1991	1	2	0	0	0	0	0	1	2	1	3	2
1992	0	0	1	0	0	0	1	2	2	1	2	3
1993	0	0	0	0	0	0	1	2	1	1	2	1
1994	0	2	0	0	1	0	0	0	3	0	3	3
Total	23	14	20	4	1	6	15	12	38	42	27	64

species of bear could not be determined for 35% ($\bar{x}$ = 1/yr, SD = 2, n = 20) of the property damage incidents. Most (65%) grizzly bear-caused property damage incidents in developed areas occurred in the Lake-Bridge Bay (39%, n = 9), Fishing Bridge (13%, n = 3), and Canyon (13%, n = 3) developments (Table 3). Black bear-caused property damage incidents in developed areas occurred primarily in the Slough Creek Campground (14%, n = 2), Fishing Bridge Developed Area (14%, n = 2), Tower-Roosevelt (14%, n = 2), and the Madison Developed Area (14%, n = 2) (Table 3).

Eleven of the bear-caused property damage incidents occurred along park roads, an average of 1/year (SD = 1). Grizzly bears and black bears were involved in 36% ($\bar{x}$ = 0.3/yr, SD = 0.6, n = 4) and 9% ($\bar{x}$ = 0.1/yr, SD = 0.3, n = 1) of the roadside property damage incidents, respectively. The species of bear could not be determined for 55% ($\bar{x}$ = 0.4/yr, SD = 0.5, n = 6) of the property damage incidents that occurred along park roads. Bear-caused property damage incidents along roadsides occurred primarily along the Fishing Bridge to East Entrance (27%, n = 3), Tower to Canyon (18%, n = 2), and U.S. Highway 191 (18%, n = 2) road segments (Table 4).

Sixty-five of the bear-caused property damage incidents occurred in backcountry areas, an average of 4/year (SD = 3). Grizzly bears and black bears were involved in 23% ($\bar{x}$ =1/yr, SD = 1, n = 15) and 19% ($\bar{x}$ = 1, SD = 1, n = 12) of the property damage incidents respectively. The species of bear involved could not be determined for 59% ($\bar{x}$ = 3/yr, SD = 2, n = 38) of the property damage incidents that occurred in backcountry areas. Almost half (46%, n = 30) of the bear-caused property damage incidents in the backcountry involved bears unsuccessfully attempting to break into unoccupied backcountry patrol cabins. Bear-caused property damage incidents occurred throughout the backcountry of the park. No areas of concentrated property damage incidents were evident in backcountry areas.

Table 3. Number of incidents of bear-caused property damage in different developed areas in Yellowstone National Park, 1980-1994.

	Number of Damage Incidents			
Developed Area	Grizzly	Black	Unknown	Total
Canyon	3	0	5	8
East Entrance	1	1	1	3
Fishing Bridge	3	2	3	8
Grant Village	1	1	2	4
Indian Creek	1	0	0	1
Indian Pond CG	1	0	1	2
Lake-Bridge Bay	9	1	3	13
Mammoth	2	1	1	4
Madison	1	2	2	5
Northeast Entrance	0	1	0	1
Pebble Creek CG	0	1	1	2
Slough Creek CG	0	2	0	2
Tower-Roosevelt	0	2	0	2
Yancey's Hole	1	0	1	2
Total	23	14	20	57

Table 4. Number of incidents of bear-caused property damage within roadside corridors in Yellowstone National Park, 1980-1994.

	Number of Damage Incidents			
Road Segment	Grizzly	Black	Unknown	Total
Mammoth Jct - Tower Jct	1	0	0	1
Tower Jct - Northeast Entrance	0	1	0	1
Tower Jct - Canyon Jct	0	0	2	2
Canyon Jct - Fishing Bridge Jct	1	0	0	1
Fishing Bridge Jct - East Entrance	1	0	2	3
Old Faithful - Madison Jct	0	0	1	1
U.S. Highway #191	1	0	1	2
Total	4	1	6	11

Incidents Of Bears Obtaining Human Foods

From 1980 to 1994, 188 incidents were reported in which bears obtained human foods, an average of 13 (SD = 7) such incidents/year (Table 5). Grizzly bears were involved in 39% ($\bar{x}$ = 5/yr, SD = 4, n = 73) of the incidents and black bears in 34% ($\bar{x}$ =4/yr, SD = 3, n = 63). The species of bear could not be determined for 28% ($\bar{x}$ = 4/yr, SD = 4, n = 52) of the incidents. Bears obtained human foods in developed areas (64%, n = 121), along roadsides (13%, n = 25), and in backcountry areas (22%, n = 42).

During the study period, 121 incidents in which bears obtained human foods occurred within park developments, an average of 8/year (SD = 7). Grizzly bears and black bears were involved in 43% ($\bar{x}$ = 4/yr, SD = 3, n = 52) and 33% ($\bar{x}$ = 3/yr, SD = 3, n = 40) of the incidents, respectively. The species of bear could not be determined for 24% ($\bar{x}$ = 2/yr, SD = 3, n = 29) of the incidents. Most (75%) incidents in which grizzly bears obtained human foods in developed areas occurred in the Lake-Bridge Bay (39%, n = 20), Mammoth (15%, n = 8), Fishing Bridge (12%, n = 6,) and Canyon (10%, n = 5) developments (Table 6). Most (55%) incidents where black bears obtained human foods in developed areas occurred in the Old Faithful (25%, n = 10), Mammoth (18%, n = 7), and Slough Creek Campground (13%, n = 5) developments (Table 6).

Twenty-five of the incidents in which bears obtained human foods occurred along roadsides, an average of 2/year (SD = 2). Grizzly bears and black bears were involved in 24% ($\bar{x}$ = 0.4/yr, SD = 0.8, n = 6) and 48% ($\bar{x}$ = 1/yr, SD = 1, n = 12) of the incidents, respectively. The species of bear could not be determined for 28% ($\bar{x}$ = 1/yr, SD = 1, n = 7) of the incidents. Most (67%) incidents where grizzly bears obtained human foods along roadsides occurred along the Tower to Canyon (33%, n = 2) and Canyon to Fishing Bridge (33%, n = 2) road segments (Table 7). Most (58%) incidents where black bears obtained human foods along roadsides occurred along the Mammoth to Tower (42%, n = 5)) and Tower to Northeast Entrance (17%, n = 2) road segments (Table 7).

Forty-two incidents in which bears obtained human foods in backcountry areas were reported, an average of 3/year (SD = 2). Grizzly bears and black bears were involved in 36% ($\bar{x}$ = 1/yr, SD = 1, n = 15) and 26% ($\bar{x}$ = 1/yr, SD = 1, n = 11) of the incidents, respectively. The species of bear involved could not be determined for 38% ($\bar{x}$ = 1/yr, SD = 1, n = 16) of the incidents. Incidents where bears obtained human foods in the backcountry were widely distributed throughout the park. No areas of concentrated sanitation problems in the backcountry were evident.

Bear-Human Confrontations

From 1980 to 1994, 187 confrontations between bears and humans ($\bar{x}$ = 13/yr, SD = 7) were reported (Table 8). Of these, 75% involved grizzly bears ($\bar{x}$ = 9/yr, SD = 6, n = 141), 19% involved black bears ($\bar{x}$ = 2/yr, SD = 2, n = 36), and 5% involved unidentified bear species ($\bar{x}$ = 0.7/yr, SD = 0.9, n = 10). Bear-hu-

Table 5. Number of incidents where grizzly bears, black bears, and unknown bear species obtained human foods in Yellowstone National Park, 1980-1994.

	Developed Area			Roadside Corridor			Backcountry Area			Total		
Year	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk
1980	3	4	1	0	0	0	0	0	1	3	4	2
1981	9	4	3	0	1	3	1	2	3	10	7	9
1982	9	5	13	0	1	0	0	0	1	9	6	14
1983	3	3	2	0	0	0	1	0	0	4	3	2
1984	6	0	4	1	0	0	4	0	2	11	0	6
1985	3	0	1	1	1	2	0	0	3	4	1	6
1986	7	1	0	3	0	1	1	0	0	11	1	1
1987	2	6	0	1	1	1	0	2	0	3	9	1
1988	1	9	3	0	1	0	2	0	2	3	10	5
1989	0	2	0	0	1	0	2	1	1	2	4	1
1990	1	0	0	0	3	0	1	5	2	2	8	2
1991	0	5	0	0	1	0	0	1	0	0	7	0
1992	1	0	0	0	1	0	0	0	0	1	1	0
1993	4	0	1	0	0	0	1	0	0	5	0	1
1994	3	1	1	0	1	0	2	0	1	5	2	2
Total	52	40	29	6	12	7	15	11	16	73	63	52

man confrontations occurred in developed areas (9%, $n = 17$), along roadsides (21%, $n = 39$), and in backcountry areas (70%, $n = 131$). Forty-three percent ($n = 60$) of all grizzly bear confrontations, 22% ($n = 8$) of all black bear confrontations, and 30% ($n = 3$) of all confrontations with unidentified bear species involved female bears with young (cubs-of-the-year [COY], yearlings, or two-year-olds).

Seventeen of the bear-human confrontations occurred in developed areas (Table 9), an average of 1/year (SD = 2). Grizzly bears and black bears were involved in 88% ($\bar{x} = 1$/yr, SD = 2, $n = 15$) and 6% ($\bar{x} = 0.1$/yr, SD = 0.3, $n = 1$) of the confrontations, respectively. The species of bear could not be determined for 6% ($\bar{x} = 0.1$/yr, SD = 0.3, $n = 1$) of the confrontations. Four (27%) of these grizzly bear confrontations occurred in the Lake development (3 in 1986 involving the same female with cubs), 5 (33%) in the Canyon development, 3 (20%) in the Indian Creek Campground, and 1 each (7%) in the Tower/Roosevelt area, Cascade picnic area, and Fishing Bridge developments. One black bear confrontation occurred in the Tower/Roosevelt area, and 1 confrontation involving an unidentified bear species occurred in the Madison Campground.

Thirty-nine of the confrontations occurred along roadsides (Table 10), an average of 3/year (SD = 3). Grizzly bears ($\bar{x} = 2$/yr, SD = 3, $n = 33$) and black bears ($\bar{x} = 0.3$/yr, SD = 0.7, $n = 5$) were involved in 85% and 13% of the confrontations, respectively. The species

Table 6. Number of incidents where grizzly bears, black bears, and unknown bear species obtained human foods in different developed areas in Yellowstone National Park, 1980-1994.

	Number of Incidents of Bears Obtaining Human Food			
Developed Area	Grizzly	Black	Unknown	Total
Bechler	0	2	1	3
Canyon	5	1	5	11
East Entrance	1	0	0	1
Fishing Bridge	6	1	2	9
Grant Village	2	1	2	5
Indian Creek	0	2	1	3
Lake-Bridge Bay	20	3	10	33
Lewis Lake CG	2	0	0	2
Mammoth	8	7	2	17
Madison	2	4	1	7
Norris	1	0	0	1
Northeast Entrance	0	0	1	1
Old Faithful	1	10	3	14
Otter Creek CG	0	0	1	1
Pebble Creek CG	0	1	0	1
Slough Creek CG	0	5	0	5
Tower-Roosevelt	1	2	0	3
West Entrance	0	1	0	1
Yancey's Hole	3	0	0	3
Total	52	40	29	121

Table 7. Number of incidents where grizzly bears, black bears, and unknown bear species obtained human foods along roadside corridors in Yellowstone National Park, 1980-1994.

	Number of Incidents of Bears Obtaining Human Food			
Road Segment	Grizzly	Black	Unknown	Total
Mammoth Jct - Tower Jct	0	5	0	5
Tower Jct - Northeast Entrance	0	2	0	2
Mammoth Jct - Norris Jct	1	0	0	1
Tower Jct - Canyon Jct	2	1	4	7
Canyon Jct - Fishing Bridge Jct	2	0	1	3
Fishing Bridge Jct - East Entrance	0	1	0	1
Fishing Bridge Jct - West Thumb Jct	0	0	1	1
Madison Jct - West Entrance	0	1	0	1
Old Faithful - West Thumb Jct	0	1	0	1
U.S. Highway #191	1	1	1	3
Total	6	12	7	25

of bear could not be determined for 3% ($\bar{x}$ = 0.1/yr, SD = 0.3, n = 1) of the confrontations that occurred along park roads. Roadside confrontations involving grizzly bears occurred primarily on the Tower to Canyon (21%), Canyon to Fishing Bridge (21%), and Fishing Bridge to East Entrance (18%) road segments (Table 10). Those involving black bears occurred primarily on the Norris to Canyon (40%), Fishing Bridge to West Thumb (40%), and Mammoth to Norris (20%) road segments. Confrontations along roadsides typically involved park visitors approaching bears for pictures.

One hundred thirty-one of the confrontations occurred in backcountry areas (Table 11), an average of 9/year (SD = 4). Grizzly bears ($\bar{x}$ = 6/yr, SD = 4, n = 93) and black bears ($\bar{x}$ = 2/yr, SD = 1, n = 30) were involved in 71% and 23% of the confrontations, respectively. The species of bear could not be determined for 6% ($\bar{x}$ = 0.5/yr, SD = 0.9, n = 8) of the confrontations. Confrontations in backcountry areas typically involved surprise encounters between bears and hikers. Confrontations between bears and people in backcountry areas occurred along designated trails (73%, 68 grizzly, 21 black bear, 6 unknown), in or near backcountry campsites (14%, 8 grizzly, 8 black bear, 2 unknown), in off-trail areas (13%, 16 grizzly, 1 black), and near backcountry patrol cabins (1%, 1 grizzly bear).

Bear-Inflicted Human Injuries

From 1980 to 1994, there were 21 people ($\bar{x}$ = 1/yr, SD = 2) injured by bears in 20 separate incidents in YNP (Table 12). Of these injuries, 10 (48%) were considered minor, 9 (43%) were severe, and 2 (10%) resulted in human fatalities. Grizzly bears ($\bar{x}$ = 1/yr, SD = 2) and black bears ($\bar{x}$ = 0.1/yr, SD = 0.4) were involved in 81% (n = 17) and 10% (n = 2) of the injuries, respectively. The species of bear could not be determined for 10% ($\bar{x}$ = 0.1/yr, SD = 0.4, n = 2) of the injuries. Overall, female bears with young (COY or yearlings) were known to be involved in 48% (10) of the injuries. Injuries occurred within developed areas (10%, n = 2), in the backcountry (81%, n = 17),

Table 8. Number of bear-human confrontations in Yellowstone National Park, 1980-1994.

	Developed Area			Roadside Corridor			Backcountry Area			Total		
Year	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk
1980	2	0	1	0	0	0	7	3	0	9	3	1
1981	1	1	0	2	0	1	5	4	0	8	5	1
1982	2	0	0	0	0	0	6	4	3	8	4	3
1983	0	0	0	0	0	0	2	2	0	2	2	0
1984	0	0	0	7	1	0	15	0	0	22	1	0
1985	0	0	0	2	0	0	5	1	2	7	1	2
1986	7	0	0	8	0	0	8	0	1	23	0	1
1987	0	0	0	0	0	0	5	2	0	5	2	0
1988	1	0	0	2	0	0	3	2	0	6	2	0
1989	0	0	0	3	0	0	4	2	0	7	2	0
1990	0	0	0	1	0	0	7	3	0	8	3	0
1991	0	0	0	0	0	0	1	0	0	1	0	0
1992	0	0	0	1	2	0	11	1	1	12	3	1
1993	0	0	0	2	2	0	10	4	1	12	6	1
1994	2	0	0	5	0	0	4	2	0	11	2	0
Total	15	1	1	33	5	1	93	30	8	141	36	10

Table 9. Number of bear-human confrontations in different developed areas in Yellowstone National Park, 1980-1994.

	Number of Confrontations			
Developed Area	Grizzly	Black	Unknown	Total
Cascade Picnic Area	1	0	0	1
Canyon	5	0	0	5
Fishing Bridge	1	0	0	1
Indian Creek CG	3	0	0	3
Lake-Bridge Bay	4	0	0	4
Madison	0	0	1	1
Tower-Roosevelt	1	1	0	2
Total	15	1	1	17

and during research and management handling of bears (10%, $n = 2$). There were no bear-inflicted human injuries reported along roadsides during the study period.

Two injuries occurred within developed areas, 1 inflicted by a grizzly bear and 1 by a black bear. Only 1 person was injured in each incident. The grizzly bear inflicted injury was severe and occurred in the Grant Village Campground in August at 0215 hrs. In this incident, an adult grizzly bear of unknown sex bit a child in the arm and pulled the child out of a tent. The injury inflicted by a black bear was minor and occurred near the Madison Campground in August at 0615 hrs. In this incident, a black bear bit a person sleeping outside "under the stars" in a sleeping bag. The incident occurred in an illegal camp.

Seventeen people were injured by bears in 16 separate incidents in the backcountry (Table 13), an average of 1/year (SD = 2). In 1 incident, 2 people were injured; this incident involved a surprise encounter between 2 people and a female grizzly bear with 2 COY that were feeding on a carcass. Grizzly bears were involved in 88% ($\bar{x} = 1/yr$, SD = 1, $n = 15$) of the injuries. The species of bear involved could not be determined for 12% ($\bar{x} = 0.1/yr$, SD = 0.4, $n = 2$) of the injuries. There were no injuries to humans inflicted by black bears in the backcountry during the study period.

Most (59%, $n = 10$) backcountry injuries involved female bears with COY (29%, $n = 5$) or yearlings (29%, $n = 5$). These percentages may be underestimated because young may run off as the sow charges and thus may not be seen.

Sixteen people were injured while hiking: 69% ($n = 11$) were hiking off trail and 31% ($n = 5$) were hiking on trail (Table 13). Fifteen of these 16 incidents involved surprise encounters with bears, while 1 is believed to have been caused by a photographer approaching a grizzly bear for a picture. The photographer was killed and partially consumed by the bear (NPS 1986). Only 1 of the backcountry injuries occurred in a backcountry campsite. This injury involved a grizzly bear that pulled a woman from a tent at night and killed and partially consumed her (NPS 1984).

Two injuries to humans occurred during research ($n = 1$) or management ($n = 1$) handling of bears. In 1981, a researcher received minor lacerations when an immobilized grizzly bear awoke un-

Table 10. Number of bear-human confrontations along roadside corridors in Yellowstone National Park, 1980-1994.

Road Segment	Grizzly	Black	Unknown	Total
Gardiner Jct – Mammoth Jct	0	0	0	0
Mammoth Jct - Tower Jct	1	0	0	1
Tower Jct - Northeast Entrance	0	0	0	0
Mammoth Jct - Norris Jct	2	1	1	4
Tower Jct - Canyon Jct	7	0	0	7
Norris Jct - Canyon Jct	4	2	0	6
Canyon Jct - Fishing Bridge Jct	7	0	0	7
Fishing Bridge Jct - East Entrance	6	0	0	6
Fishing Bridge Jct - West Thumb Jct	2	2	0	4
West Thumb Jct - South Entrance	0	0	0	0
Norris Jct - Madison Jct	0	0	0	0
Madison Jct - West Entrance	0	0	0	0
Madison Jct - Old Faithful	3	0	0	3
Old Faithful - West Thumb Jct	0	0	0	0
U.S. Highway #191	1	0	0	1
Total	33	5	1	39

Table 11. Location of bear-human confrontations in backcountry areas within Yellowstone National Park, 1980-1994.

Location	Grizzly Bear	Black Bear	Unknown Species	Total
On-Trail	68	21	6	95
Off-Trail	16	1	0	17
At Campsite	8	8	2	18
At Cabin	1	0	0	1
Total	93	30	8	131

usually quickly from the effects of an immobilization agent during a research trapping operation. In 1983, while a park ranger was attempting to move an unconscious black bear that had been hit by a car off of the roadside, the bear woke up and bit the ranger on the leg.

Management Hazing of Bears

In 1987, the park began keeping records of incidents where attempts were made to haze bears away from visitor use areas. Hazing was used as a management tool prior to 1987, but complete records of these incidents were not kept. From 1987 through 1994, park managers attempted to haze bears away from visitor use areas 97 times, an average of 12 (SD = 9) such incidents per year (Table 14). Twenty-nine cases (30%) involved grizzly bears ($\bar{x}$ = 4/yr, SD = 2 SD) and 67 (70%) involved black bears ($\bar{x}$ = 8/yr, SD = 8). During this period, 8 marked grizzly bears were involved in 18 hazing actions. Of these bears, 7 had to be subsequently trapped after hazing actions failed (1 marked and released on site, 6 translocated). One subadult (bear 231) that had previously become food conditioned outside the park was later removed from the ecosystem by the Montana Department of Fish, Wildlife and Parks after both hazing and translocation failed to keep the bear from attempting to obtain human foods from developed areas. Two additional marked bears were trapped at a later date due to their history of being habituated to people and frequenting roadsides and developed areas. Unconfirmed reports suggested that a subadult male bear on which hazing was attempted was later shot outside the park after being translocated. Hazing was conducted in developed areas (26%, n = 25), along roadsides (70%, n = 67), and in backcountry areas (4%, n = 4).

Park managers attempted to haze bears out of developed areas 25 times, an average of 3 (SD = 2) such incidents/year (Table 15). Grizzly bears and black bears were involved in 40% ($\bar{x}$ = 1/yr, SD = 1, n = 10) and 60% ($\bar{x}$ = 2/yr, SD = 2, n = 15) of the incidents respectively. One incident where hazing was attempted involved a grizzly bear that had obtained unnatural foods in a developed area campground. All other incidents where hazing was attempted involved habituated bears that had been frequenting developed areas while feeding on natural foods, which created a potential for bear-human

Table 12. Number of bear-inflicted human injuries in Yellowstone National Park, 1980-1994.

	Developed Area			Roadside Corridor			Backcountry Area			Handling			Total		
Year	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Unk	Gr	Bl	Un
1980	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
1981	0	1	0	0	0	0	1	0	1	1	0	0	2	1	1
1982	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1983	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0
1984	1	0	0	0	0	0	4	0	0	0	0	0	5	0	0
1985	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1986	0	0	0	0	0	0	2	0	1	0	0	0	2	0	1
1987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1989	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
1990	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1991	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1992	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0	0	0	0	4	0	0	0	0	0	4	0	0
Total	1	1	0	0	0	0	15	0	2	1	1	0	17	2	2

Table 13. Location of bear-inflicted human injuries in backcountry areas within Yellowstone National Park, 1980-1994.

Location	Grizzly Bears	Black Bears	Unknown Species	Total
On-Trail	5	0	0	5
Off-Trail	9	0	2	11
At Campsite	1	0	0	1
At Cabin	0	0	0	0
Total	15	0	2	17

conflict. Most (80%) incidents where grizzly bears were hazed out of developed areas occurred in the Lake developed area. The highest (47%) number of incidents where black bears were hazed out of developed areas occurred in the Slough Creek Campground.

Park managers attempted to haze bears away from roadsides 67 times, an average of 9 (SD = 7) such incidents/year (Table 16). Grizzly bears and black bears were involved in 25% ($\bar{x}$ = 2/yr, SD = 2, n = 17) and 75% $\bar{x}$ (= 6/yr, SD = 6, n = 50) of the incidents respectively. All incidents involving grizzly bears were performed on bears that had become habituated to people while feeding on natural foods along roadsides. These bears generally were causing large traffic jams and were being approached within close distances by park visitors. Forty-three (84%) of the incidents where black bears were hazed away from roads involved bears that had become habituated to people while feeding on natural foods. Eight of the incidents involved 1 individual black bear that had become habituated to people while feeding on natural foods along the roadside. After becoming habituated, this bear was known to have been fed along the road at least once by park visitors.

The highest number of incidents where grizzly bears (29%) and black bears (36%) had to be hazed out of roadside corridors occurred along the Tower to Canyon road segment.

There were 5 incidents in which bears were hazed in backcountry areas. One incident involved a grizzly bear frequenting a backcountry cabin, 2 incidents involved bears (1 grizzly and 1 black bear)

Table 14. Number of incidents in which grizzly bears and black bears were hazed away from visitor use areas in Yellowstone National Park, 1987-1994.

	Developed Area		Roadside Corridor		Backcountry Area		Total	
Year	Grizzly	Black	Grizzly	Black	Grizzly	Black	Grizzly	Black
1987	0	0	1	0	0	0	1	0
1988	2	1	1	4	0	0	3	5
1989	0	0	0	2	0	0	0	2
1990	3	3	2	10	1	2	6	15
1991	1	5	5	17	0	0	6	22
1992	1	3	2	9	0	0	3	12
1993	0	2	6	6	0	0	6	8
1994	3	1	0	2	1	1	4	4
Total	10	15	17	50	2	3	29	68

Table 15. Number of incidents where grizzly bears and black bears were hazed out of different developments in Yellowstone National Park, 1987-1994.

Developed Area	Grizzly Bear	Black Bear	Total
Bridge Bay	0	3	3
Indian Creek CG	0	1	1
Lake	8	1	9
Mammoth	2	1	3
Nez Perce Picnic Area	0	1	1
Slough Creek CG	0	7	7
Pebble Creek CG	0	1	1
Total	10	15	25

Table 16. Number of incidents where grizzly bears and black bears were hazed away from roadside corridors in Yellowstone National Park, 1987-1994.

Road Segment	Grizzly Bears	Black Bears	Total
Mammoth Jct - Gardiner	0	0	0
Mammoth Jct - Tower Jct	2	8	10
Tower Jct- Northeast Entrance	0	0	0
Mammoth Jct- Norris Jct	2	6	8
Tower Jct - Canyon Jct	5	18	23
Norris Jct - Canyon Jct	1	2	3
Canyon Jct - Fishing Bridge Jct	0	1	1
Fishing Bridge Jct - East Entrance	4	5	9
Fishing Bridge Jct - West Thumb Jct	3	1	4
West Thumb Jct - South Entrance	0	1	1
Norris Jct - Madison Jct	0	0	0
Madison Jct - West Entrance	0	1	1
Madison Jct - Old Faithful	0	5	5
Old Faithful - West Thumb Jct	0	0	0
U.S. Highway #191	0	2	2
Total	17	50	67

frequenting backcountry trails, and 2 incidents involved a black bear that frequented backcountry campsites and had caused property damage and obtained human foods from backcountry campers.

Management Capture and Translocation of Nuisance Bears

During the study period, 31 individual nuisance grizzly bears were captured 60 times in 49 separate management actions (11 cubs and yearlings were captured with their mothers), an average of 3 (SD = 2) management actions involving capture of nuisance grizzly bears per year. During the same time period, 16 individual black bears were captured 19 times during 15 separate management actions (4 cubs captured with their mothers), an average of 1 (SD = 1) management action involving the capture of nuisance black bears per year. Management capture of nuisance bears occurred in developed areas (84%, $n = 54$) and along roadsides (16%, $n = 10$) (Table 17). There were no grizzly bears or black bears trapped and translocated from backcountry areas during the study period. Of the 49 management actions where grizzly bears were captured, 29 (59%) involved human food conditioned bears and 20

Table 17. Number of management actions in which nuisance grizzly bears and black bears were captured and translocated in different areas of Yellowstone National Park, 1980-1994.

	Developed Area		Roadside Corridor		Backcountry Area		Total	
Year	Grizzly	Black	Grizzly	Black	Grizzly	Black	Grizzly	Black
1980	4	0	0	0	0	0	4	0
1981	8	2	0	0	0	0	8	2
1982	4	0	0	0	0	0	4	0
1983	2	2	0	1	0	0	2	3
1984	4	0	1	0	0	0	5	0
1985	0	0	2	0	0	0	2	0
1986	7	1	0	0	0	0	7	1
1987	2	2	2	0	0	0	4	2
1988	4	3	0	0	0	0	4	3
1989	1	1	0	0	0	0	1	1
1990	2	0	2	0	0	0	4	0
1991	1	3	1	0	0	0	2	3
1992	0	0	0	0	0	0	0	0
1993	0	0	1	0	0	0	1	0
1994	1	0	0	0	0	0	1	0
Total	40	14	9	1	0	0	49	15

Table 18. Number of management actions where food conditioned or habituated nuisance grizzly bears and black bears were captured and translocated in Yellowstone National Park, 1980-1994.

	Food Conditioned		Habituated		Total	
Year	Gr	Bl	Gr	Bl	Gr	Bl
1980	3	0	1	0	4	0
1981	7	2	1	0	8	2
1982	4	0	0	0	4	0
1983	2	3	0	0	2	3
1984	2	0	3	0	5	0
1985	0	0	2	0	2	0
1986	5	1	2	0	7	1
1987	1	2	3	0	4	2
1988	1	1	3	2	4	3
1989	0	1	1	0	1	1
1990	1	0	3	0	4	0
1991	2	2	0	1	2	3
1992	0	0	0	0	0	0
1993	0	0	1	0	1	0
1994	1	0	0	0	1	0
Total	29	12	20	3	49	15

Table 19. Number of management actions in which nuisance grizzly bears and black bears were captured and translocated from different developed areas of Yellowstone National Park, 1980-1994.

Developed Area	Grizzly	Black	Total
Canyon	7	0	7
East Entrance	1	0	1
Fishing Bridge	4	0	4
Grant Village	2	0	2
Indian Creek CG	0	2	2
Indian Pond CG	1	0	1
Lake-Bridge Bay	15	1	16
Madison	1	0	1
Mammoth	3	4	7
Northeast Entrance	0	1	1
Norris	1	0	1
Old Faithful	1	2	3
Slough Creek CG	0	2	2
Tower-Roosevelt	1	2	3
West Entrance	2	0	2
Yancey's Hole	1	0	1
Total	40	14	54

(41%) involved bears that were habituated to people (but not food conditioned) (Table 18). Five of the 31 (16%) individual nuisance grizzly bears captured were bears that had become human food conditioned outside of the park and had been translocated into the park in an effort to keep them out of further trouble. Of the 15 management actions where black bears were captured and translocated, 12 (80%) involved human food conditioned bears and 3 (20%) involved bears that were habituated to people (but not food conditioned).

During the study period, there were 54 management actions where grizzly bears or black bears were captured and translocated from developed areas (Table 19), an average of 4/year (SD = 3). Grizzly bears and black bears were involved in 74% ($\bar{x}$ = 3/yr, SD = 3, n = 40) and 26% ($\bar{x}$ =1/yr, SD = 1, n = 14) of the management actions respectively. Most (55%) management actions where grizzly bears were captured and translocated occurred in the Lake-Bridge Bay (38%, n = 15) and Canyon (18%, n = 7) developments. The Mammoth developed area had the highest number of management actions where black bears were captured and translocated (29%, n = 4).

Ten of the management actions where bears were captured and translocated occurred along park roads (Table 20), an average of 1/year (SD = 1). Grizzly bears and black bears were involved in 90% and 10% of the management actions, respectively. All grizzly bears trapped and translocated from roadside areas were habituated to people (but not food conditioned). These bears were captured due to human safety concerns and due to numerous, large, unmanageable bear-jams along roads. There were no grizzly bears trapped along roadsides due to sanitation problems. The only black bear captured and translocated from the roadside was a food-conditioned bear. All grizzly bear translocations from roadside areas occurred along 4 different road segments: the Fishing Bridge to East Entrance road (44%, n = 4), Tower to Canyon road (33%, n = 3), Canyon to Fishing Bridge road (11%, n = 1), and Fishing Bridge to West Thumb road (11%, n = 1). The black bear translocated from the roadside was trapped along the Mammoth to Norris road segment.

There were 4 grizzly bears and 2 black bears that were not nuisance bears that were captured and translocated for humane reasons. In 1984, a female grizzly bear and 3

Table 20. Number of management actions in which nuisance grizzly bears and black bears were captured and translocated from different road corridors in Yellowstone National Park, 1980-1994.

Road Segment	Grizzly Bears	Black Bears	Total
Mammoth Jct - Norris Jct	0	1	1
Tower Jct - Canyon Jct	3	0	3
Canyon Jct - Fishing Bridge Jct	1	0	1
Fishing Bridge Jct - East Entrance	4	0	4
Fishing Bridge Jct - West Thumb Jct	1	0	1
Total	9	1	10

Table 21. Number of management actions in which nuisance grizzly bears and black bears were captured and removed from the ecosystem in different areas of Yellowstone National Park, 1980-1994.

	Developed Area		Roadside Corridor		Backcountry Area		Total	
Year	Grizzly	Black	Grizzly	Black	Grizzly	Black	Grizzly	Black
1980	1	0	0	0	0	0	1	0
1981	0	0	0	0	0	0	0	0
1982	1	0	1	0	0	0	2	0
1983	1	0	0	0	0	0	1	0
1984	3	0	0	0	0	0	3	0
1985	0	0	0	0	0	0	0	0
1986	1	0	0	0	1	0	2	0
1987	1	0	0	0	0	0	1	0
1988	0	0	0	0	0	1	0	1
1989	0	1	0	0	0	0	0	1
1990	1	0	0	1	0	0	1	1
1991	0	1	0	0	0	0	0	1
1992	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0	0	0
1994	1	0	0	0	0	0	1	0
Total	10	2	1	1	1	1	12	4

COY were captured on Frank Island and translocated to Flat Mountain Arm. The 4 bears were apparently stranded on the island after the ice went off and were in danger of starving to death. One of the cubs was so emaciated that it died during the capture operation.

In 1994, an adult female black bear and yearling male were captured and translocated from the shoulder of U.S. Highway 191. The adult female (estimated to be 20-30 years old) was severely emaciated, weighed only 47 lbs., and was unable to move off the roadside. The 2 bears were captured and moved to a location along Wickiup Creek where there was succulent forage. The adult female died a few days later. The male yearling was healthy and survived.

Management Removals of Nuisance Bears

During the 15-year period (1980-94), 12 grizzly bears and 4 black bears were removed from the park, an average of 1 (SD = 1) grizzly and 0.3 (SD = 0.5) black bears per year (Table 21). One of the black bears was killed due to an aversive conditioning accident. Of the 12 grizzly bears removed, 10 (83%) were conditioned to human foods and 2 (17%) were habituated to humans, but not food conditioned (Table 22). Five of the 12 grizzly bears removed (42%) were bears that had become conditioned to human foods outside of the park and had been relocated into the park in an effort to keep them out of further bear-human conflicts. Of the 4 black bears removed, 3 (75%) were conditioned to human foods and 1 (25%) was habituated

Table 22. Number of management actions where food conditioned or habituated nuisance grizzly bears and black bears were captured and removed in Yellowstone National Park, 1980-1994.

	Food Conditioned		Habituated		Total	
Year	Grizzly	Black	Grizzly	Black	Grizzly	Black
1980	1	0	0	0	1	0
1981	0	0	0	0	0	0
1982	2	0	0	0	2	0
1983	1	0	0	0	1	0
1984	3	0	0	0	3	0
1985	0	0	0	0	0	0
1986	1	0	1	0	2	0
1987	1	0	0	0	1	0
1988	0	1	0	0	0	1
1989	0	1	0	0	0	1
1990	0	0	1	1	1	1
1991	0	1	0	0	0	1
1992	0	0	0	0	0	0
1993	0	0	0	0	0	0
1994	1	0	0	0	1	0
Total	10	3	2	1	12	4

Table 23. Number of management actions in which nuisance grizzly bears and black bears were captured and removed from different developed areas of Yellowstone National Park, 1980-1994.

Developed Area	Grizzly	Black	Total
Canyon	1	0	1
Fishing Bridge	1	0	1
Grant Village	1	0	1
Indian Creek CG	1	1	2
Lake-Bridge Bay	4	0	4
Lewis Lake CG	1	0	1
Madison	1	0	1
Tower Fall CG	0	1	1
Total	10	2	12

Table 24. Number of grizzly bears and black bears killed by vehicles on different road segments within Yellowstone National Park, 1980-1994.

Road Segment	Grizzly Bears	Black Bears	Total
Gardiner - Mammoth	0	0	0
Mammoth – Tower Jct	0	1	1
Tower Jct - Northeast Entrance	0	1	1
Mammoth – Norris Jct	0	2	2
Tower Jct – Canyon Jct	0	1	1
Norris Jct – Canyon Jct	0	0	0
Canyon Jct - Fishing Bridge Jct	0	0	0
Fishing Bridge Jct - East Entrance	0	0	0
Fishing Bridge Jct - West Thumb Jct	1	0	1
West Thumb Jct - South Entrance	0	0	0
Norris Jct - Madison	1	0	1
Madison Jct- West Entrance	0	0	0
U.S. Highway #191	1	4	5
Madison Jct- Old Faithful	0	2	2
Old Faithful - West Thumb Jct	0	2	2
Total	3	13	16

to people (but not food conditioned). One of the black bears became food conditioned outside of the park, was translocated by the state of Montana, and entered the park on its way back to its original home range.

Eight (50%) of the bears that were removed were euthanized (6 grizzly bears, 2 black bears), 5 (31%) were sent to zoos (all grizzly), and 2 (13%) were sent to a research laboratory (1 grizzly, 1 black bear). One nuisance black bear was accidentally killed during a management action.

Ten grizzly bears ($\bar{x}$ = 1/yr, SD = 1) and 2 black bears ($\bar{x}$ = 0.1/yr, SD = 0.4) were removed from developed areas (Table 23). The Lake-Bridge Bay development had the highest number (40%, n = 4) of grizzly bears removed in management actions.

Only 2 nuisance bears had to be removed from roadside corridors. An aggressive grizzly bear was removed from the Norris to Canyon road segment. An habituated black bear was killed accidentally during a management action along the Mammoth to Tower road corridor.

One grizzly bear was removed from the backcountry during our study period. An adult female grizzly that was habituated to people and killed and partially consumed a photographer was removed from the Otter Creek area in 1986. One food conditioned, adult female black bear was removed from the Heart Lake area because it had learned to bluff charge hikers in an effort to obtain their packs.

Changes in Types of Nuisance Bear Behavior over Time

The types of bear problems that required management capture and translocation or removal of nuisance grizzly bears has changed over time. From 1980 through 1984, 83% (n = 25) of all management captures involved food conditioned grizzly bears and 17% (n = 5) involved grizzly bears that were habituated to people but not conditioned to human foods (Tables 18 and 22). During the period 1985 through 1994, 45% (n = 14) of all management captures involved food conditioned grizzly bears and 55% (n = 17) involved habituated bears.

There was a similar change in the types of behavior of nuisance black bears captured. From 1980 through 1984, all (100%, n = 5) nuisance black bears captured were human food conditioned (Tables 18 and 22). From 1985 through 1994, 30% (n = 3) of the nuisance black bears captured in management actions were habituated to people, but not conditioned to human foods.

The proportion of habituated grizzly bears and black bears captured from 1985 through 1994 would probably have been even higher except for the use of hazing as a management tool, which was often attempted instead of capture and translocation during our study period.

Road-killed Bears

Three grizzly bears ($\bar{x}$ = 0.2/yr, SD = 0.4) and 13 black bears ($\bar{x}$ = 1/yr, SD = 1) were hit and killed by vehicles on park roads from 1980 to 1994 (Table 24). U.S. Highway 191 along the northwest boundary of the park had the highest number (31%, n = 5) of bears killed by vehicles.

Statistical Tests of Cole's (1976) Hypotheses

The number of grizzly bear-caused human injuries in developed areas decreased significantly (Mann-Whitney U-test, U = 492, $P < 0.001$) after implementation of the 1970 Bear Management Plan. During the 25-year period (1945-69) prior to implementation of the plan, 50 people ($\bar{x}$ = 2.0/yr, SD = 2.5) were injured by grizzly bears in developed areas. During the 25-year period (1970-94) following implementation of the plan, only 5 people ($\bar{x}$ = 0.2/yr, SD = 0.6) were injured by grizzly bears in developed areas. The number of black bear-caused human injuries along roadsides and in developed areas also decreased significantly after 1970 (U = 619, $P < 0.001$). During the 25-year period 1945-69, 1,108 people ($\bar{x}$ = 44.3/yr, SD = 23.5) were injured by black bears in developed areas and along roadsides. During the 25-year period 1970-94, only 37 people ($\bar{x}$ = 1.5/yr, SD = 2.6) were injured by black bears in developed areas and along roadsides.

The number of nuisance grizzly bears that had to be removed in management actions also decreased significantly (U = 421.5, $P < 0.001$) after implementation of the 1970 Bear Management Plan. During the 25-year period 1945-69, 73 nuisance grizzly bears ($\bar{x}$ = 2.9/yr, SD = 2.6) were removed in management actions. During the 25-year period after implementation of the plan (1970-1994), 53 nuisance grizzly ($\bar{x}$ = 2.1/yr, SD = 4.3) bears were removed. In addition, the number of nuisance black bears that had to be removed in management actions also decreased significantly (U = 605.5, $P < 0.001$) during

the same time period. From 1945-69, 536 nuisance black bears ($\bar{x}$ = 21.4/yr, SD = 19.7) were removed in management actions. From 1970-94, only 36 nuisance black bears ($\bar{x}$ = 1.4/yr, SD = 2.5) were removed.

Discussion

Bear Observations

Cole (1976) and Meagher and Phillips (1983) reported progressively declining observations of bears in park developed areas from 1970 to 1979. The declining rate of bear activity in developed areas was attributed to the sanitation efforts that prevented bears from obtaining human foods in park developments. In addition, bears that did enter developed areas were promptly captured and translocated or removed from the population. During our study period (1980-94), the number of reports of bear activity in developed areas were highly variable from year to year, were generally higher than the numbers reported for the mid to late 1970s, and were quite high during some years.

Whereas bear activity in developed areas from 1970 to 1979 generally involved food conditioned bears seeking human foods (M. Meagher, pers. commun.), bear activity in developments during the 1980-94 period most often involved habituated (but not food conditioned) bears seeking natural foods. The types of natural foods that attracted bears into developed areas included spawning cutthroat trout, chokecherries, rose-hips (*Rosa woodsii*), clover (*Trifolium* spp.), and lush grasses (graminoids). Park managers were less quick to capture and translocate or remove these bears and, instead, often attempted alternative management tools such as warnings, temporary area closures, or hazing bears out of developments. Hazing generally had only short-term success and had to be repeated often, especially in situations where natural foods were abundant in developed areas. The tolerance by managers of bears foraging on natural foods in developed areas contributed to the increase of bear activity in developed areas recorded during our study.

The Bear Management Program implemented in 1970 appears to have been successful in significantly reducing the number of incidents of bears entering park developed areas in search of human foods. However, a new problem has become apparent. Non-food conditioned bears are becoming habituated to people and entering developed areas to feed on natural foods. This poses concerns for human safety in developed areas and, over time, may increase the probability of bears becoming human food conditioned, being involved in bear-human conflicts, and being captured and translocated or removed.

Bear-Caused Property Damage

The number of reported bear-caused property damage incidents declined from an average of 138/year (SD = 109) from 1931 to 1969, to an average of 49/year (SD = 41) from 1970 to 1979 (calculated from Schullery 1992) after implementation of the new bear management plan in 1970. During our study period (1980-94), the number of bear-caused property damage incidents continued to decline from previous levels, to an average of 9 (SD = 6) incidents per year. The decrease in the number of property damage incidents is the result of fewer bears aggressively seeking human foods in campgrounds and developed areas. This suggests that the public education programs, sanitation regulations, and enforcement of sanitation regulations implemented under the 1970 Bear Management Plan were successful in reducing the number of bear-caused property damage incidents occurring within the park.

Incidents of Bears Obtaining Human Foods

Craighead et al. (1995) reported a declining frequency of garbage in the diet of grizzly bears in the Yellowstone ecosystem between the period 1968-71 and the period 1977-87. Mattson et al. (1991) reported that garbage did not make up a significant portion of the diet of Yellowstone ecosystem grizzly bears from 1977-87. During our study (1980-94), the number of reported incidents of grizzly, black, and unknown species of bears obtaining human food or garbage within the park was low, an average of only 13 (SD = 7) such incidents per year. The declining frequency of garbage in the diet of grizzly bears since 1971 and the low frequency of bears obtaining human foods during our study indicate that the management program initiated in 1970 has been mostly successful in its objective of restoring the YNP subpopulations of grizzly and black bears to subsistence on natural foods. Bears are now relying extensively on forbs, winter-killed carrion, spawning cutthroat trout, elk calves, army cutworm moths, and whitebark pine seeds (Mattson et al. 1991).

Bear-Human Confrontations

Most bear-human confrontations occurred in backcountry areas and along roadsides. Very few confrontations occurred in developed areas. Confrontations in backcountry areas generally involved surprise encounters between hikers and female bears with young. More confrontations occurred on designated trails (73%) than in off-trail areas (13%). This is probably due to more people hiking on trails than off-trail. Although more people had confrontations with bears while hiking on established trails, more people were injured by bears while hiking off-trail (69% of those injured) than while hiking on-trail (31% of those injured). Bears may learn to associate trails with people and react less aggressively to encounters with people on trails, where they expect to find them. Bears may be more likely to be surprised by encounters with people in off-trail areas and thus may react more aggressively to off-trail encounters.

Confrontations that occurred along roadsides generally involved habituated bears foraging along road corridors. Confrontations occurred when people approached these bears too closely in an effort to observe or photograph them. Often times in these situations groups of people surrounded bears and bears charged at the crowd in an effort to escape. Adequate staff for public education programs and for monitoring tourists and habituated bears along roadsides may be the most effective management tool for reducing bear-human confrontations that occur in roadside corridors.

Bear-Inflicted Human Injuries

The years 1970-78 were a transition period between 2 considerably different bear management programs and philosophies (Meagher and Phillips 1983). Prior to 1970, management involved food-conditioned bears that were extensively influenced by the availability of human foods and garbage in developed areas and along roadsides. Management after 1978 involved bears that were largely uninfluenced by human food and garbage. From 1970 to 1979, bear-inflicted human injuries decreased significantly from previous levels ($\bar{x}$ = 48/year, 1931-1959) to an average of 6/year (SD = 3) (calculated from Meagher and Phillips 1983). Of these injuries, an average of 4/year (SD = 3) occurred along roadsides, 2/year (SD = 1) in backcountry areas, and 1/year (SD = 1) within developments.

By 1979, most bears with prior knowledge of sources of human foods were no longer in the population (Meagher and Phillips 1983). At this time, the management emphasis changed from correction of a problem (sanitation) to awareness that a high level of preventive management must become a routine part of park operations (Meagher and Phillips 1983). From 1980 to 1994, bear-inflicted human injuries declined further from previous levels to an average of just 1/year (SD = 2). During this period, bear inflicted human injuries along roadsides ($\bar{x}$ = 0.0/yr) and within developed areas ($\bar{x}$ = 0.1/yr, SD = 0.4) became rare, while injuries in backcountry areas remained at about the same level ($\bar{x}$ = 1/yr, SD = 2) as the 1970-79 period.

The bear management program implemented in 1970 has been successful in reducing bear inflicted human injuries within YNP, especially grizzly bear-caused injuries in developed areas and those caused by black bears in developed areas and along roadsides (Gunther and Hoekstra, in prep.).

The large reduction in injuries along roadsides and in developed areas following the significant reduction in the availability of human foods from these areas supports the theory (NPS 1960, Leopold et al. 1969, Cole 1971, 1976, Meagher and Phillips 1983) that the high incidence of bear-inflicted human injuries occurring within the park prior to 1970 was due to the presence of food-conditioned bears in combination with the availability of human foods and garbage in developed areas and along roadsides.

Despite the success of the 1970 bear management program in reducing the number of bear-inflicted injuries, an average of 1 bear-inflicted human injury/year still occurs. These injuries most often involve surprise encounters between backcountry hikers and female grizzly bears with young. It will be difficult to reduce the frequency of this type of injury, especially if backcountry recreational activity in YNP continues to increase. Public education programs that inform hikers of how to avoid surprise encounters, and how to react to encounters and attacks once they occur, may be the most useful tool in further decreasing the number and severity of the types of bear-inflicted human injuries now occurring in the park.

Management Hazing of Bears

In 1986, the Wyoming Game and Fish Department began experimental aversive conditioning of

bears in the Yellowstone ecosystem (Gillin et al. 1994). One of the goals of aversive conditioning was to apply a strong negative stimulus to alter bear behavior following a conflict with humans. Results of the study indicated that aversive conditioning was very time and labor intensive with success limited to very specific situations and circumstances. In the mid-1980s, YNP began using aversive conditioning techniques but with a modified objective. Due to the mostly short-term effectiveness of aversive conditioning techniques, YNP began using the technology for temporarily hazing bears out of visitor use areas. In some cases, this may have delayed the need to capture and translocate bears long enough so that the attractant was no longer available (natural food no longer in season or human food attractant problem corrected) and the nuisance bears then left the areas of conflict on their own.

Capture and Translocation of Nuisance Bears

The number of management actions where bears had to be captured and translocated has decreased significantly from an average of 27/year (SD = 23) from 1970 to 1979 (calculated from Meagher and Phillips 1983) to an average of 4/year (SD = 3) from 1980 to 1994. The decrease in the number of translocations necessary is due to fewer bears aggressively seeking human foods in campgrounds and developed areas as a result of the sanitation efforts of the 1970 plan. The decrease in the number of translocations may also be due in part to the use of hazing and temporary area closures as alternatives to capture and translocation of bears.

Management Removal of Nuisance Bears

The number of nuisance grizzly bears and black bears removed (sent to zoos or destroyed) for management reasons has decreased from an average of 7/year (SD = 8) from 1970 to 1979 (calculated from Meagher and Phillips 1983) to an average of 1/year (SD = 1) from 1980 to 1994. The reduction in the number of bears removed is due to fewer incidents of bears aggressively seeking human foods in park campgrounds and developed areas as a result of the sanitation efforts of the 1970 plan.

Changes in Types of Nuisance Bear Behavior

Prior to 1980, all bears that had to be captured for management reasons were food-conditioned bears that aggressively sought human foods (M. Meagher, pers. commun.). From 1980 to 1984, bears that were habituated to the presence of people, but were not food conditioned, started to appear in the population and became a management concern. The proportion of habituated, non-food-conditioned bears involved in management actions increased from 17% during the period 1980-84 to 55% during the period 1985-94.

Habituated, but not food conditioned, bears are now the cause of most bear-human conflicts occurring within YNP. At McNeil River, Alaska, management of people and habituated bears in a small, highly controlled, supervised situation has been successful in allowing bears and people to co-exist without conflict within close distances of each other (Aumiller and Matt 1994). Similar management of people and habituated bears over large areas with high numbers of unsupervised visitors, such as in YNP, has not been attempted. Management strategies designed to address the human safety concerns of having habituated bears foraging along roadsides and within developed areas with large crowds of unsupervised visitors near by need to be developed to reduce the potential for bear-human conflicts and subsequent nuisance bear management actions in the park.

Trends in Locations of Nuisance Bear Behavior

Meagher and Phillips (1983) reported high numbers of nuisance bear control actions in the Fishing Bridge, Lake, Bridge Bay, Canyon, Grant, and Old Faithful developed areas during the period 1970 to 1979. Long-term implementation of the 1970 bear management plan has corrected the problems in most of those developments.

During our study period (1980-94), the rate of bear-human conflicts in the park was very low. Occasionally, visitor-bear education efforts failed, visitors or employees failed to follow sanitation regulations, violations were not noticed by park patrol personnel, and bears came into conflict with humans. For the most part, these types of incidents were infrequent and occurred randomly throughout the park. The Lake-Bridge Bay development and the Tower to Canyon road corridor were the only areas with noticeable concentrations of bear-human conflicts and subsequent nuisance bear control actions. The presence of spawning cutthroat trout at-

tracted bears into the Lake-Bridge Bay developed area and led to most of the bear-human conflicts that occurred there. A new development concept plan for the Lake-Bridge Bay development, approved in 1993, contained management actions designed to reduce the number of bear-human conflicts (NPS 1993). Similar plans implemented at Old Faithful (NPS 1982) and Fishing Bridge (NPS 1988) contributed to reductions in the number of bear-human conflicts and subsequent nuisance bear control actions in those areas.

Habituated bears digging for biscuitroot (*Lomatium spp.*) and yampa (*Perideridia gairdneri*) roots were the cause of most bear-human conflicts that occurred along the Tower to Canyon road. These situations generally involved large bear-jams with crowds of people approaching the bears within close distance. The number of habituated bears that have to be removed for human safety reasons can be minimized by ensuring sufficient budgets to provide adequate ranger and interpretation staffing levels for monitoring and managing tourists around habituated bears. In highly controlled, supervised situations, habituated bears and people can co-exist in close proximity relatively safely (Aumiller and Matt 1994).

Tests of Cole's (1976) Hypotheses

Cole (1976) hypothesized that the 1970 bear management program would reduce the number of bear-inflicted human injuries in developed areas. This hypothesis could not be rejected for the 1970-94 period because the number of bear-inflicted human injuries in developed areas decreased significantly from previous levels.

Cole (1976) also hypothesized that the management initiated during the 1970s would restore more natural conditions as evidenced by: a) bears occurring in spaced distributions; b) bears using natural foods in summer; and c) declines in the number of bears visiting developed areas; or d) declines in the number of bears being controlled. We cannot reject parts a, b, and d of this hypothesis. Grizzly bears are no longer concentrated at garbage dumps in summer as they were prior to 1970, although secondary concentrations may occur at moth aggregations (Craighead et al. 1995). The proportion of garbage in the diet of grizzly bears has declined since 1970 (Craighead et al. 1995) and it is no longer a significant component of their diet (Mattson et al. 1991). In addition, the number of both grizzly bears and black bears removed each year in management actions has declined significantly since 1970. We reject part c of this hypothesis, that the number of bears entering developed areas would decline following implementation of the 1970 plan. Although bear activity in developed areas initially declined after human food attractants were made unavailable to bears, bear activity in developments has increased again in recent years due to habituated bears seeking natural foods in developed areas.

Lastly, Cole (1976) hypothesized that the management program implemented in the 1970s would not prevent the park's grizzly bear and black bear populations from maintaining or reestablishing their numbers at natural carrying capacity levels. The management data we collected during this evaluation were not sufficient to evaluate this hypothesis. However, Eberhardt et al. (1994) estimated that the grizzly bear population in the Yellowstone ecosystem was stable to slightly increasing (0% to 9% annual growth). In addition, the average population estimate of 312 grizzly bears for the period prior to implementation of the 1970 Bear Management Plan (Craighead et al. 1995) is within the range of the most recently published population estimate of 280 to 610 grizzly bears currently in the Yellowstone ecosystem (Eberhardt and Knight 1996). In contrast, Craighead et al. (1995) argue that insufficient data is currently being collected to make a trend estimate for the Yellowstone ecosystem grizzly bear population.

The effects of the 1970 bear management plan on the YNP black bear population were also not apparent from the management data we collected. The last population estimate (Cole 1976) of 650 black bears in the park was based on data collected in the 1960s (Barnes and Bray 1967), a period when the population was still influenced by the availability of human food and garbage.

We concur with Meagher and Phillips (1983) that the exact carrying capacities for grizzly bears and black bears within YNP are not known at this time. Although, new techniques for estimating and modeling habitat quality and effectiveness (i.e. Geographic Information Systems, Cumulative Effects Modeling, Resource Selection Modeling) may make bear carrying capacity estimates for YNP possible in the near future.

Management Implications

Public education efforts and effective enforcement of bear attractant sanitation regulations has significantly reduced the number of bear-caused property damage incidents and bear-inflicted human injuries occurring within YNP. Consequently, the number of nuisance bears captured and translocated or removed has also declined significantly. Public education programs and sanitation programs designed to prevent bears from obtaining human foods and garbage must remain a permanent component of future bear management programs within YNP.

Most incidents of bear-human conflict, bears obtaining human foods, and translocation and removal of nuisance bears now occur outside of YNP (Gunther et al. 1993, 1994, 1995, and 1996). In an effort to reduce bear-human conflict and promote grizzly bear recovery throughout the Yellowstone ecosystem, public education programs and the bear proofing of food, grain, and garbage storage facilities as well as gardens, orchards, and bee hives must also become a management priority in areas outside YNP. This will be especially critical if grizzly bears continue to expand their occupied range beyond the current designated recovery zone.

Bears that are habituated to people but not conditioned to human foods are increasingly becoming the cause of most bear-human conflicts occurring within YNP. This poses a new challenge to park managers. The spatial and temporal overlap between human recreational activity and bear activity predisposes bears to habituation to people. Habituation increases the possibility of bears becoming food conditioned, being involved in bear-human conflicts, and being involved in potentially dangerous bear-human encounters. Management strategies designed either to prevent habituation or more effectively provide for human safety in situations where habituated bears are foraging along roadsides and within developed areas need to be developed to reduce the number of bear-human conflicts and subsequent management actions occurring within the park.

As the grizzly bear population increases and recovery goals are met, the potential for habituated bears foraging in developments and along roadsides is likely to increase and expand to other areas outside of the park throughout the Yellowstone ecosystem. Innovative new strategies for managing habituated bears would also be of benefit for this potential problem and would help ensure the continued survival/viability of the grizzly bear population within the Yellowstone ecosystem.

The Future

The low number of bear-human conflicts now occurring in YNP does not necessarily ensure the long-term survival of the grizzly bear in the Yellowstone ecosystem. Several threats to the population are evident and pose new challenges to bear managers. Loss of bear habitat has accelerated in recent years due to extensive development of private land throughout the Yellowstone ecosystem (Gunther et al. 1995, 1996). Increasing development has also added more point sources where bears can come into conflict with people. Bear-human conflicts often result in bears being removed from the population due to concern for human safety and property. In addition, 2 seasonally important food sources for bears in the Yellowstone ecosystem are now threatened by the introduction of exotic organisms.

Whitebark pine trees throughout the west have been extensively depleted by infestations of white pine blister rust (*Cronartium ribicola*). Whitebark pine seeds are an important fall food for bears because of their high fat content and their potential abundance as a prehibernation food source (Mattson and Jonkel 1990). Some whitebark pine trees in the Yellowstone ecosystem are infested with blister rust (K. Kendall, pers. commun.). Whitebark pine mortality due to blister rust exceeds 90% in much of the northwestern portion of its range (Kendall and Arno 1990). Mortality rates are generally lower in drier climates such as YNP (Kendall 1994). The extent of the blister rust infestations in the Yellowstone ecosystem and the effects it will have on whitebark pine trees in the Yellowstone ecosystem are not known at this time but are currently being studied (K. Kendall, pers. commun.).

In addition, native cutthroat trout in Yellowstone Lake are threatened by the introduction of non-native lake trout (*Salvelinus namacush*) (NPS 1995). Cutthroat trout are an important late spring and early summer food for grizzly bears that have home ranges adjacent to Yellowstone Lake (Reinhart and Mattson 1990). Due to their high digestibility and protein and lipid content, spawning cutthroat trout are one of the highest sources of net digestible en-

ergy for grizzly bears in the Yellowstone ecosystem (Mealey 1975, Pritchard and Robbins 1990). Introduced lake trout have extensively reduced or eliminated some native trout species in other areas (Ellis 1914, Dean and Varley 1974, Gerstung 1988, Donald and Alger 1993). Lake trout compete with cutthroat trout for the same macroinvertebrate food sources (Elrod 1983, Elrod and O'Gorman 1991) and adult lake trout prey extensively upon cutthroat trout (Keading 1995). Unlike cutthroat trout, lake trout do not move up tributary streams to spawn. Lake trout spawn within the lake, which makes them unavailable to terrestrial predators such as bears. If the nonnative lake trout population in Yellowstone Lake is not suppressed, the native cutthroat trout population may be reduced by 80 to 90% of present abundance (McIntyre 1995). Such a large decline in cutthroat trout numbers could have a significant negative impact on the food supply of grizzly bears and black bears with home ranges adjacent to the lake (Schullery and Varley 1996). YNP is currently designing a management strategy with the objective of suppressing the lake trout population in an effort to reduce the impacts of non-native lake trout on native cutthroat trout and the subsequent impacts on species such as grizzly bears that depend on cutthroat trout as a food source.

Bears are highly adaptable animals and currently make use of several seasonal, high quality food sources (i.e. winter-killed carrion, cutthroat trout, army cutworm moths, and whitebark pine seeds) that have a high degree of natural variation in availability from year to year. Bears in the Yellowstone ecosystem are known to switch to other foods when one or more of these high quality foods are unavailable. The relationship between the use of alternate foods during years of low carrion, cutthroat trout, moth, or pine nut availability and the potential effects on grizzly bear and black bear reproduction and survivorship resulting from the quality and distribution of alternate foods is not completely understood (Servheen et al. 1986). Bear-human conflicts and bear mortality often increase during years of poor food availability (Gunther et al. 1995, 1996). What cumulative effects the potential simultaneous loss of both cutthroat trout and whitebark pine seeds, in combination with the continual loss of bear habitat due to private land development, will have on bears is unknown. We recommend monitoring of cutthroat trout, whitebark pine, and habitat loss in the Yellowstone ecosystem to determine how changes in the availability of these resources will affect bear populations.

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Wolves in Yellowstone: Records Since 1967

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Abstract

Central to wolf (*Canis lupus*) reintroduction in the Yellowstone Ecosystem is the question: Were wolves present either occasionally or in some continuous fashion prior to reintroduction? Since the extermination of wolves in the Yellowstone area in the 1930s, there have been continued reports of visual observations of large canids identified as wolves. However, such visual sightings are difficult to verify. Seven reports since 1967 deserve detailed analysis because the presence of physical evidence goes beyond the capabilities and credibility of individual observers. Photographs, movie film, track casts, or carcass material show that both male and female wolves have been present in the Yellowstone area. The potential presence of both male and female wolves in Yellowstone suggests at least the possibility of residency and breeding.

Introduction

Central to the issue of wolf (*Canis lupus*) reintroduction into the Yellowstone Ecosystem is the question of the presence of wolves before the reintroduction (Fish and Wildlife Service 1994a, 1994b).The presence of wolves would have direct bearing on reintroduction under the portions of the Endangered Species Act dealing with breeding populations and geographic separations between populations. Since the extermination of wolves in the Yellowstone area in the 1930s, there have been continued reports of visual observations of large canids identified as wolves (C. and J. Urbigkit, pers. commun.; see also Urbigkit and Urbigkit *this volume*). However, visual sightings are difficult to verify. Seven reports since 1967 (and prior to wolf reintroduction in 1995) are of special note because they include physical evidence in the form of carcasses, photographs, or track casts. These reports deserve detailed analysis because the presence of physical evidence goes beyond the capabilities and credibility of individual observers.

Methods

Reports of wolf occurrences in the Yellowstone area were solicited from state and federal agencies and private individuals. To be included in this analysis, physical supporting evidence had to have been examined or had to be available for examination. Physical evidence was considered to be photographs, movie film, video tape, track casts, or carcass material. When possible, those originating the reports were interviewed. Only 7 reports were available that met these criteria.

I compared unknown samples of track photographs and casts to my database of wolf and dog tracks using comparative morphologic techniques and discriminant analysis. My database includes tracks from about 200 known dogs and 150 known wolves. Known wolf track samples were collected from 15 locations in North America and China. Information on gender, age, and weight were available for many animals. Dog track samples were obtained by visiting dog shows to make plaster casts of dogs of known breed, age, gender, and weight. To assure consistent measurements, minimum out-

line methods were used (Fjelline and Mansfield 1989, Halfpenny 1995, Halfpenny et al. 1995). Discriminant analysis was based on my databases and those of Harris and Ream (1983).

For the purposes of this paper, 3 reliability categories were assigned to reports: positive, probable, and possible. Positive reports are those reports supported by irrefutable evidence of a carcass that was examined through DNA or morphological testing. Probable reports are those that include quality supporting evidence (film or track casts) and achieve the agreement of at least 2 wolf experts. Possible reports are those that include physical evidence (film or track casts), but are less clear as to the species of origin.

The strength of the methods used is in differentiating between tracks of dogs and wolves. While less rigorous, anecdotal and observational information was used to infer whether evidence suggested a wild or captive wolf, since track analysis cannot distinguish between the 2. Determination of wolves versus wolf-dog hybrids from tracks, like physical, behavioral, and other evidence, can only suggest not prove the likelihood of one or the other.

Results

Seven reports of potential wolves in the Yellowstone Area were accepted for analysis (Table 1). Two were classified as positive, 4 as probable, and 1 as possible. The approximate locations of the reports are shown in Figure 1. These reports span the period from 1967 to 1993. Of the 7 reports, 4 had been previously examined and classified as wolves based on carcasses (Kysar, Newman) or film and photographs (Gates, Paunovich). Further examination was not attempted on these animals, although I do report lesser known or not readily available details. Three sets of previously unidentified tracks were located and analyzed.

Footprints reported in this paper were judged to have originated from wolves, not from dogs or wolf-dog hybrids. Discriminant analysis scores were beyond the range of known dogs and wolf-dog hybrids. For the carcasses, gender was based on necropsy results. Gender was not assigned to the animal that was only represented by a photograph, but the animal represented by film was believed to be a male based on size and behavior. Two sets of tracks were judged to have been made by females based on size and, for one animal, supplemental evidence of visual reports of accompanying tracks made by pups. One set of tracks was judged to have been made by a male based on size.

Table 1. Reports of wolves located in the Yellowstone area since 1967. The type of supporting evidence and suggested sex of each animal is listed.

#	Date	Location	Source	Evidence	Sex
1	1967	Hayden Valley	Marshal Gates	8 mm film	?
2	Oct. 25, 1968	Slough Creek	L. Hendrickson	Cast	F?
3	May 21, 1988	Chico	Jeff Newman	Carcass	M
4	Aug. 7, 1992	Hayden Valley	Ray Paunovich, Kevin Sanders	16 mm film 35 mm slides	M?
5	Aug. 19, 1992	Woodard Creek	Ralph Hudelson, Ron Kent, Steve Yekel, Steve Pudroski	35 mm print	F
6	Sep. 30, 1992	Fox Park	Jerry Kysar	Carcass	M
7	May 23, 1993	Otter Creek	Jim Halfpenny, Dixie Finley, Larry & Melinda Jones	Casts	M

Jeff Newman's Report

On May 21, 1988, Jeff Newman (Perkins 1988) struck and killed an adult male wolf on the East River road near Chico, Montana (about 30 miles north of Yellowstone National Park). The wolf weighed 65 lbs. There were no ear tags, tattoos, or other identifying marks. Dr. R. Nowak (1988) determined the skull was from a gray wolf and estimated the age was 3 years. He also reported the skull was "notably smaller than those of other male wolves taken in the northwestern conterminous U.S."

With regard to the wolf's origin, Dr. Nowak stated, "your specimen looks more like a member of this original U.S. population." The original U.S. population referred to by Nowak was that thought to be exterminated in Yellowstone. He also noted that the specimen "was in good condition, with none of the deterioration or mal-

formation that sometimes is associated with captive life." I accept this as a positive wolf report.

Dan Palmisciano (1988) suggested the wolf might be "a domestic wolf escapee," citing as his reasons long claws, soft foot pads, no parasites, scars on the front legs (digging under fence!!) and bunched premolars." It was suggested that the wolf had escaped from the large, captive pack maintained by Jack Lynch (pers. commun.) on Dry Creek, approximately 20 km away. Mr. Lynch denied that this was one of his animals. Dr. Nowak supports this contention by stating that he has examined some of Lynch's wolves and they do not match the tooth characteristics shown by the dead wolf. Nowak also suggests that it might have been a wandering wolf from Minnesota because of the similarity of tooth characteristics. It would be interesting to use new genetic techniques to examine this wolf, but the University of Montana, the National Park Service and the U.S. Fish and Wildlife Service have been unable to extract usable samples since the hide was tanned.

Figure 1. Approximate locations of wolf reports in the Yellowstone area. Numbers at locations refer to Table 1.

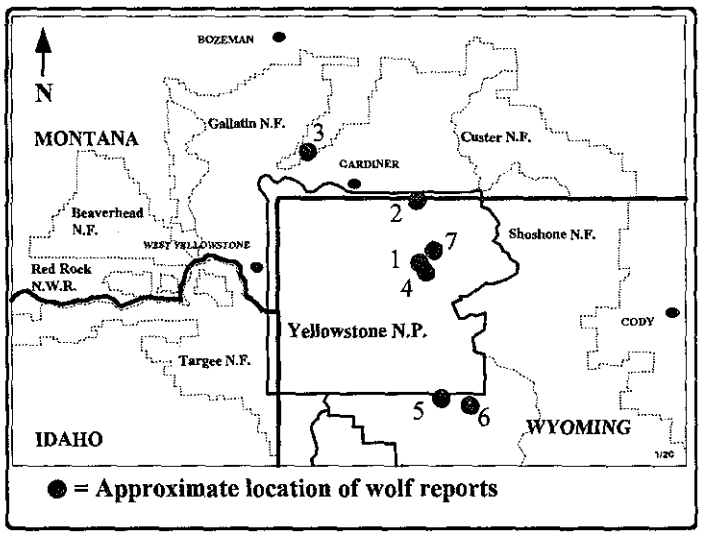
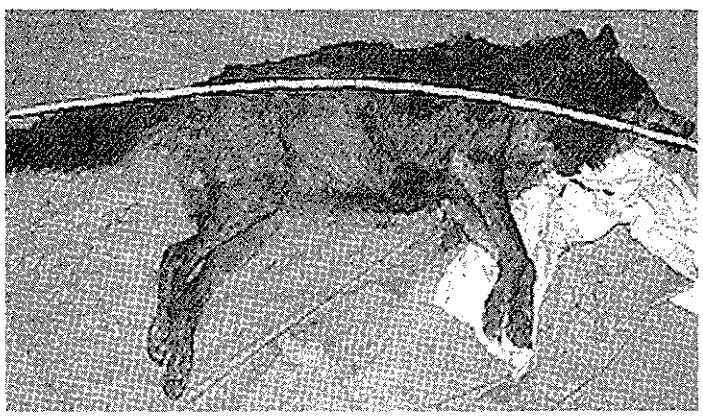


Figure 2. Wolf that was killed by Jerry Kysar in Fox Park, south of Yellowstone (photograph by John Mack).



Jerry Kysar's Report

On September 30, 1992, Jerry Kysar shot a 93 lb. male canid in Fox Park, Wyoming, just south of Yellowstone National Park (Figure 2). In my interview with Mr. Kysar (pers. commun.), he said the animal he shot "was traveling with 4 or 5 other animals of the same color, maybe one of the others was darker." The animal he shot "stood out from the rest, he was blackest." Kysar said "the others could have been pups, but he was not sure what to call [the] others." He also reported, "I could hear them first, [they] sounded like coyotes [(*Canis latrans*)], they sounded like dogs—no [they] sounded like young dogs."

Many do not believe the story told by Kysar because interviews by various researchers and enforcement personnel are conflicting, but the morphologic and genetic evidence is clear. According to Sharon Rose of the U.S. Fish and Wildlife Service, (1993), skull measurements taken by Dr. R. Nowak were "considerably smaller" than most Montana wolves and the skull was closer in size to historic skulls of native Yellowstone wolves and within the range of current Montana wolf skulls. Scientists at the Fish and Wildlife forensic laboratories in Ashland, Oregon, determined from initial tests of mitochondrial DNA that the animal was related to the wolf pack located in Ninemile Valley, near Missoula, Montana. However, further analysis showed a much smaller degree of relatedness to Montana wolves.

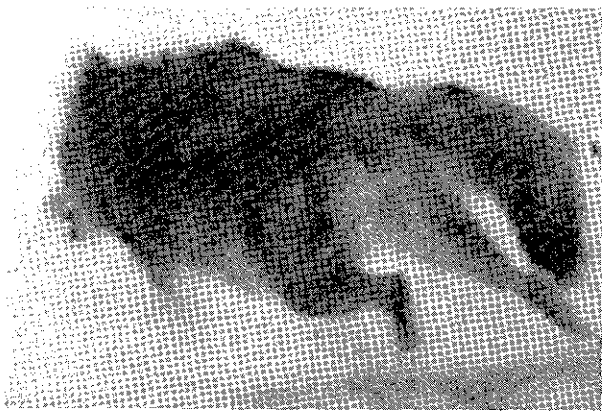
For cross reference, photographs of the feet of the wolf killed by Kysar were tested against morphologic databases and using discriminant analysis. The front feet scored high on discriminant analysis tests indicating it was a wolf. Track size indicated

it was a male. I accepted this as a positive wolf report.

Marshal Gates' Report

Two films have been made of canids believed to be wolves. The first, an 8 mm film, was made by Marshal Gates, a seasonal summer employee in Yellowstone. Gates filmed a large canid during his ski trip into Hayden Valley during the winter of 1967. I have been unable to locate either copies or the original film, and I have been unable to interview Marshal Gates. However, in 1971, I made copies of prints made from his film (Figure 3). At that time, research biologists from the Park told me that they believed the animal was a wolf. This identification is open to debate, especially based on the existing evidence. For this study, I am accepting the animal as a possible wolf. I could not ascertain any information as to gender or age from the photographs.

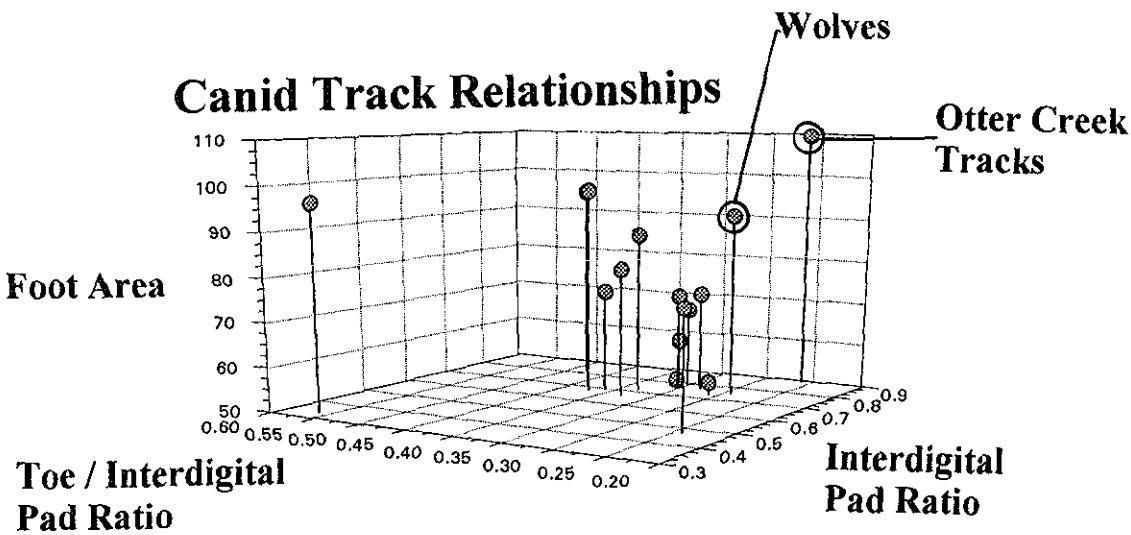
Figure 3. Suspected canid from Marshal Gate's (1967) film. In 1971, picture frames were printed from the original 8mm, and transferred to 35 mm slide film. In 1994, computer processing was used to produce this print.



Ray Paunovich and Kevin Sanders' Reports

The second film, 16 mm, was made by Ray Paunovich in Hayden Valley on August 7 and 8, 1992. Kevin Sanders took 35 mm photographs concurrently. These materials are available in the Yellowstone Park archives. Experts have not been able to agree on species in the films, but there is enough agreement to merit its consideration as a probable wolf. After viewing his film and studying the animal's behavior, I suggest that it may have been a male.

Figure 4: Canine track relationships. Relationships are depicted among several dog breeds, the average for wolves, and the suspected tracks found at Otter Creek. The 3 measures used to indicate front foot shape are the area (cm^2) of the entire foot, the ratio between toe and interdigital pad length, and the ratio of the length to the width of the interdigital pad.



Reports by Hendrickson, Hudelson et al., and Halfpenny et al.

In addition to the above carcass and photographic evidence, 3 sets of tracks were identified and included as wolf tracks. Measurements from tracks are presented in Table 2. All 3 sets of tracks had high discriminant analysis scores indicative of wolves, and all scores were well above the mean for wolves. All 3 track samples are accepted as probable wolf tracks.

The first set was an imprint preserved in mud and collected in the Slough Creek drainage in December of 1968. The cast bears the name L. Hendrickson and is archived in the Yellowstone Center For Resources. The relatively small size of this print suggests that it may have been made by a female or a juvenile wolf.

The second set of tracks were photographed and reported by Ralph Hudelson and other Wyoming Game and Fish personnel in the Woodard Creek drainage, south of Yellowstone National Park on August 21, 1992. Tracks were first observed on August 19. Their report and photographs are archived with the Yellowstone Center for Resources and copies are in my files.

In his written report, Hudelson said, "all of the observers concurred on the probability these were wolf tracks." One, Steve Pudroski, had worked with wolves in Alaska and "knew it was a wolf." Based on the apparent small size of the prints in the photograph, the animal may have been a female wolf. Additional evidence reported below also suggests a female.

When I questioned Hudelson (1993) about his original report, in which he wrote "there appeared to be at least 1 set of pup tracks with the adult," he indicated that the pup tracks were different from coyote tracks that were on the trail (pers. commun.). The "wolf pup" tracks were "smaller than the tracks photographed but there were no hind feet" (pers. commun.). The "pup tracks" were about the size of an adult coyote but differed from coyote because "this pup walked on heels." The interdigital or heel pads therefore appeared large for a coyote. In the interview, Hudelson also described the "pup" tracks as "more rounded than adult wolf tracks, with outer toe pads especially more rounded and too wide spread [for a coyote]." Measurements were not taken of the "pup" tracks.

The third set of tracks was located by a group I led in the Otter Creek drainage of Yellowstone National Park on May 23, 1993. Over several days, plaster casts were made of 6 different footprints. I have archived 3 casts. Based on the casts, Diane Boyd (pers. commun.) also identified the tracks as made by a wolf.

Discriminant analysis identified the tracks as wolf tracks and the magnitude of their dissimilarity to dog tracks can be seen through morphometric analysis (Figure 4). The tracks of the Otter Creek wolf exceed the mean for all wolves and their great separation from domestic dogs is obvious when using 3 criteria: area of the foot, ratio of the second area to the interdigital pad, and the ratio of the length to the width of the interdigital pad. The relatively large size of the footprints suggests the maker was a male wolf.

Table 2: Selected measurements from wolf prints accepted in this paper. Measurements were defined by Harris and Ream (1983). For sources, refer to Table 1.

Source	Sex	Foot	Total Length	Length Claw	Total Width	Pad Width	Pad Length	Gap Length	Toe Length	Toe Width	Inner Toe Width	Outer Claw Width	Inner Claw Width
Hendrickson	F	F	109	92	100	57	43	16	36	22	57	89	24
Hudelson	F	F	148	108	54	41	67	36	25	25	60	89	34
Kysar	M	F	118	75	50		54	25	21	21	44	62	8
Kysar	M	F	117	73	51		53	23	21	21	43	62	8
Halfpenny	M	F	110	101	105	67	49	25			60	104	41
Halfpenny	M	F	120	104	104	60	54	18	33	24	55	96	37
Halfpenny	M	F	114	104	102	64	50	15	39	21	54	107	42
Hudelson	F	H		79	39	36	60	32	24	24	43		
Kysar	M	H	102	66	37		51	23	18	18	42	51	7
Kysar	M	H	104	67	38		52	23	19	19	42	52	7
Halfpenny	M	H	110	95	108	61	46	22	30	22	58	110	45

F = female, M = Male, F (under foot column) = front foot, H = hind foot

Discussion

Wolves in Yellowstone

Physical evidence suggests that individual wolves of unknown origin were at least intermittently present in the Yellowstone area prior to reintroduction in 1995. The evidence raises several interesting questions that need to be listed even though we are not able to answer them at the present time. That wolves were present in Yellowstone is not too surprising given that wolves may migrate 886 km from their birth place (Fritts 1983). The Yellowstone area is less than 800 km from potential source populations in Canada. Wolves from Canada have moved south into Montana and have established themselves (Ream et al. 1989). Established populations in Montana are closer to Yellowstone than Canadian ones. The presence of wolves in Yellowstone also raises the question of whether or not the Yellowstone population is completely separate from populations farther to the north.

Analysis suggests that both male and female wolves may have been present in the Yellowstone area. The presence of male wolves fits well with our knowledge of their biology, in that young males often leave the pack and migrate farthest (Carbyn 1987). The wolf Newman killed was of prime age for a migrating male. Traditionally, females were thought to migrate only short distances, in which case the potential existence of female wolves in Yellowstone is less easily explained by immigration. However, new evidence in Montana indicates that females do sometimes move very long distances. If the female wolves reported in this study did not migrate to Yellowstone, their presence raises the possibility that they represent a remnant Yellowstone population. Genetic analysis also does not remove the possibility that the wolf shot by Kysar is a remnant of historic populations.

Temporal Clustering of Evidence

It is interesting to note that most reports presented here clustered at 2 points in time: 1967-68 and 1992-93. The 1967-68 evidence corresponds with several visual sightings of wolves received by the author for that same period of time. In August and September of 1992, Yellowstone National Park staff received 18 additional reports of dark colored canids. Does the temporal clustering of reports lend support to the presence, even temporary, of wolves? Or is it simply coincidence? It is of note that females may have been present during both time periods.

Breeding in Yellowstone

The potential presence of both male and female wolves in Yellowstone suggests wolves may have bred in Yellowstone after the government-sanctioned extermination program earlier in the century and prior to reintroduction in 1995. Additional support for this hypothesis was provided by Hudelson and Wyoming Game and Fish personnel, who found the later-verified wolf tracks and who reported the possible presence of wolf pups.

Also consider the time line of events in 1992-93. On August 21, 1992, an adult, possibly a female wolf, and possibly with pups, was present south of the Park. September 30, 1992, south of the Park and less than 20 miles from the August incident, Jerry Kysar shot a male wolf. Mr. Kysar reported that he shot the most obvious (darker and larger) animal traveling with 4 or 5 other smaller canids. Kysar said "the others could have been pups, but he was not sure what to call [the] others." Is Kysar's report the results of a breeding pack? Subsequent attempts to locate wolves in Fox Park during October 1992 did not yield signs of additional wolves (John Mack, pers. commun.). After being present when a pack member was shot, would the pack have stayed searching for a pack mate or would the pack have left the area? While a pack with 5-month old pups (assuming a birth date of late April) might be restricted in its ability to travel great distances, heavy rain and snow at the time (John Mack, pers. commun.) would have hindered locating tracks. On the other hand, the wolf Kysar shot was a 2-year old male, which is the prime age for dispersal in wild wolves and its age might suggest it was migrating through the area.

Whatever the case, the wolf filmed by Mr. Paunovich in Hayden Valley in August 1992 was definitely a different animal than the 1 killed by Mr. Kysar. Thus, it would appear that at least 3 adult wolves were present during late 1992, and there may have been pups. At least 10 reports of large, dark-colored canids originated from the Hayden Valley area around the time when Paunovich filmed the "wolf." At least 1 animal, probably a male and per-

haps the same animal as was filmed by Mr. Paunovich, was present in May 1993 when I tracked it in the Otter Creek drainage.

The only other wild card explanation for some of the reported wolves is the possible intentional or unintentional release of captive wolves or hybrid wolves. There were strong political reasons for intentional releases early in the 1990s, at the height of the EIS process for reintroduction. Of course, my study can not determine whether reports represent captive releases, but it is not likely that all reports can be explained by such a hypothesis.

Future Research Directions

Evidence suggests the occasional presence of wolves, perhaps even breeding wolves, in the Yellowstone area, although my study did not ascertain length of periods when wolves were present nor their possible areas of origin. While my search was not exhaustive, it is doubtful that many new records with supporting physical evidence will be found. Therefore, the best method for testing questions suggested here will be through genetic analysis of existing and new evidence of suspected wolves in the reintroduction zone. Old specimens (skulls or skins) may be tested with evolving genetic techniques. Many ranchers and outfitters have wolf skins on the walls of their homes. An effort should be made to find these skins and determine their genetic history.

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Movements, Contaminants, and Survival of Bald Eagles in Greater Yellowstone

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Abstract

Between May 1979 and August 1994, 339 bald eagles (*Haliaeetus leucocephalus*) were banded with U.S. Fish and Wildlife Service leg bands in the Greater Yellowstone Ecosystem (GYE) of northwestern Wyoming, southwestern Montana, and eastern Idaho, including Yellowstone National Park (YNP). Most were color-banded and 45 were radio-tagged. Locals (nestlings or fledglings) comprised 90% of those banded and 49% of those radio-tagged (12% and 4% in YNP, respectively). Band encounter rate was 15%. Band encounters and sightings occurred in 7 western states and British Columbia. Radio-tagged eagles were located in 6 western states. All eagles radio-tagged as nestlings spent time in YNP. Local eagles left natal areas in autumn and moved west and south to the Pacific coast states, returning to the GYE the following spring. Eagles produced in the GYE pioneered new breeding areas outside of the ecosystem and banded adults occupied at least 11 breeding areas within the GYE. Lead was detected in the blood of 27% (n =135) of eagles resident in the GYE and at low levels (> 0.06 ppm), but 91% of migrants (n = 11) had elevated levels ($\bar{x}$ = 0.75 ppm). Blood of all eagles sampled (n = 146) had selenium ($\bar{x}$ > 1.12 ppm) and 94% had mercury ($\bar{x}$ > 0.19 ppm). Mean levels in adults and migrants were 1.3 ppm. Highest mean annual levels of all metals occurred after the Yellowstone fires of 1988. DDE was the only 1 of 16 organochlorine compounds detected in plasma and it occurred in only 11% of locals (n = 9). No adults were tested. One of 9 nestlings tested may have been exposed to anticholinergic pesticides. Mortality resulted from a variety of anthropogenic and natural causes but survival of radio-tagged nestlings was >86% the first year. The oldest eagle was encountered 12 years after banding as a nestling in YNP. Despite the high incidence of potentially toxic levels of some contaminants, bald eagle populations in the GYE continue to grow rapidly and reproduce well. YNP is important as an area that enhances survival of bald eagles produced throughout the GYE and the western U.S. (e.g., Arizona and Texas).

Introduction

DDT-induced population declines of bald eagles (*Haliaeetus leucocephalus*) in the 1960s and 1970s resulted in classification of the species as endangered in Idaho, Montana, and Wyoming in 1978. Concern in the Greater Yellowstone Ecosystem (GYE) (Figure 1) focused initially on the status of bald eagles in Yellowstone National Park (YNP). Although the number of nesting pairs had been stable for many years, existing population models indicated production of young eagles in YNP was not adequate for long-term maintenance of the nesting population (Sprunt et al.1973). Among assumptions included in the model was that population maintenance would be exclusively from recruits produced only within YNP. In June 1979, we, along with our colleague Kurt Alt (now employed by the Montana Department of Fish, Wildlife, and Parks), initiated a banding program to test this hypothesis and generate other information about basic population dynamics that would be useful in conservation and management of the species within the GYE. The study was expanded in 1985 and funding increased, which enabled more intensive research with an ecosystem emphasis. The goal of the study was to obtain information that would allow for a better understanding of the population dynamics of bald eagles in the GYE. Specific objectives included:

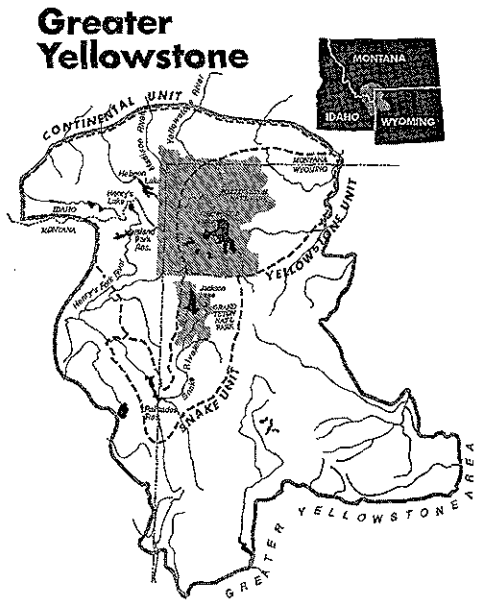
1. Determination of movements, habitat use, and mortality of fledgling, immature, and subadult bald eagles; and
2. Evaluation of the incidence and severity of environmental contaminants, especially lead (Pb) in blood of bald eagles throughout the GYE.

These objectives are mandated with high priority in GYE bald eagle management plans (GYEBEWT 1983, 1996) and the Pacific Bald Eagle Recovery Plan (USFWS 1986).

Study Area

Alt (1980) delineated 3 population units within the GYE for the purposes of describing bald eagle population dynamics (Figure 1). The Snake Unit (SU) included bald eagle breeding areas associated with the Snake River watershed in northwestern Wyoming to 8 km southwest of Idaho Falls, Idaho. The Continental Unit (CU) included portions of southwestern Montana and northeastern Idaho, and the Firehole and Madison rivers in YNP. The Yellowstone Unit (YU) includes most of YNP.

Figure 1: Bald eagle management and population units in the Greater Yellowstone ecosystem.



The GYEBEWT (1983, 1995) further divided GYE population units into management units (Figure 1). The SU was divided into the Snake Teton (ST), Snake Wyoming (SW) and Snake Idaho (SI) management units. ST included the Snake River watershed in Grand Teton National Park (GTNP). SW included the Snake River watershed in Wyoming outside of GTNP. The SI included the Snake River watershed from the Wyoming State line downstream to Idaho Falls. Two management units were delineated in the CU, Continental Montana (CM) and Continental Idaho (CI). Unit boundaries at all levels were based on similarities or differences in bald eagle nesting phenology, nest substrates, productivity, and food habits in addition to climatic variables, topography, and administrative jurisdictions (see Swenson et al. 1986 for descriptions).

Methods

Bald eagles were banded with U.S. Fish and Wildlife Service (USFWS) "pop-rivet" aluminum leg bands from 1979 to 1994. In 1980, plastic color-bands indicating natal origin either in or outside YNP were added. In 1985, color combinations were increased to include all management units and colored aluminum "pop-rivet" bands were used from 1987 to

1994 (Table 1). Eagles were banded as nestlings at least 8 weeks old. Fledglings and older eagles were captured by padded leg-hold traps (Harmata 1985) and a radio-controlled bow net (Jackman et al. 1993).

Nestlings at least 10 weeks of age were radio-tagged with solar powered transmitters approximately 100 to 110 g in weight. Attachment was via backpack harness constructed of flaccid teflon tubing. Backpack straps were secured with a veterinary suture material to insure permanent retention.

Movements of eagles were evaluated by analysis of band encounter data provided by the USFWS Bird Banding Laboratory (BBL), Patuxent, Maryland, and locations of radio-tagged individuals. An encounter was defined as any number of experiences that permitted the USFWS band number to be read. Banded eagles may have been found dead or alive, captured, or observed and identified at a distance. Only encounters of eagles banded or radio-tagged as nestlings were included in analysis of regional (extra GYE) movements.

Blood for contaminant analysis was collected from the brachial vein and deposited in sodium heparinized vacutainers. Three cc's of whole blood per eagle were sequestered for heavy metal and Se analysis. If available, an additional 2-5 cc's of whole blood per eagle were centrifuged to separate plasma, which was pipetted off and separated into 2 equal samples. Whole blood and plasma were frozen and stored at -22° C. Whole blood was analyzed for Pb, Hg, and Se at Montana State University (MSU) Chemical Analytical Laboratory. Samples for Pb analysis were digested with nitric acid and concentrations determined by Graphic Furnace Additions (GFAAS). Samples for Hg analysis were digested by nitric acid in closed vessels and analyzed by Cold Vapor Generation using $SnCl_2$ reductant Atomic Absorption Spectroscopy. Samples for Se analysis were digested with nitric acid and concentrations determined using Palladium Matrix Modifier and GFAAS. Recovery of all 3 elements from spiked samples was >90%. One plasma sample (0.5 to 2 cc) from each bald eagle was analyzed for 16 organochlorine compounds at MSU Chemical Analytical Laboratory using methods recommended by the U.S. Environmental Protection Agency (EPA)(see Thompson 1974). All results are reported on a wet weight basis. Detection limits of Pb, Hg, and Se, were 0.06, 0.03, and 0.10 ppm respectively. Detection limits of organochlorine compounds were between 0.001 and 0.009 ppm (DDE = 0.005 ppm).

Remaining plasma samples (0.5-2 cc) were analyzed for acetylcholinesterase (AChE) activity at the EPA Environmental Research Laboratory in Corvallis, Oregon. Not all samples, however, were frozen or analyzed at equal intervals from collection. Some thawed briefly and were refrozen, while some were stored at different temperatures. Thus, reactivity of AChE in some samples may been affected (Fairbrother et al. 1991). Because of chronic lack of funds, duplicate samples were not analyzed for any constituent.

Eagles were grouped by age class and residency status for comparisons of mean contaminant concentrations. Distributions of concentrations for all contaminants were skewed; therefore, data were log transformed and geometric means computed for comparisons. Means tests were performed among groups only when ≥50% of samples from all groups exhibited detectable concentrations of a contaminant. Samples below detection limits were assigned values equal to 1/2 the detection limit for the respective contaminant (Wiemeyer et al. 1989). Chi-square analysis was used to compare frequency of occurrence among groups when >50% of samples in 1 group were below the detection limit. Arithmetic means were used for AChE comparisons and analyses were performed on non-transformed data. Years with <4 samples (1990) were not included in analysis of annual differences in contaminants. SOLO, a statistical software package for personal computers (BMDP, 1440 Sepulveda, Los Angeles, CA 90025), was used for chi-square and analysis of variance (*ANOVA*) tests. Statistical significance was assigned at $P \leq 0.05$, but P values >0.05 were presented when differences were considered biologically significant. BMDP Neuman-Keuls Range tests identified differences detected by ANOVA. Contaminant concentrations are reported in parts per million (ppm) wet weight. AChE activity is expressed in μmoles of

Table 1. Colorbanding scheme for bald eagles in Greater Yellowstone.

Management Unit	Band Color (position)	Leg
Snake Wyoming (SW)	Green with White midline strip	Right
Snake Teton (ST)	White (over) Green	Right
Snake Idaho (SI)	White (over) Green	Left
Continental Montana (CM)	Green (over) White	Right
Continental Idaho (CI)	Green (over) White	Left
Yellowstone Unit (YU)	Green with White midline strip	Left

Figure 2: Extra-regional encounters of bald eagles in Greater Yellowstone.

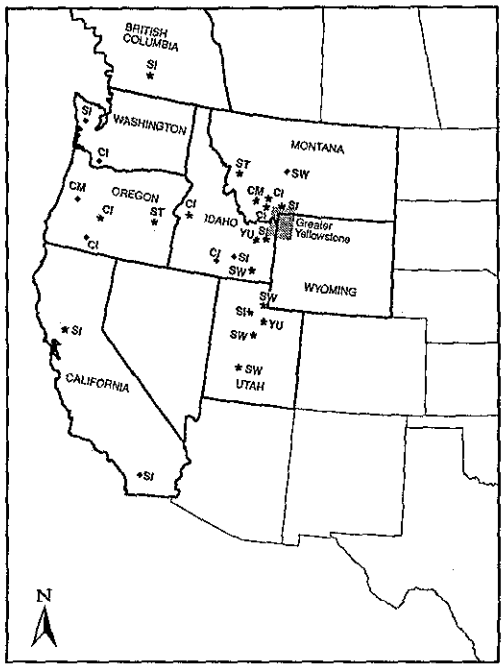
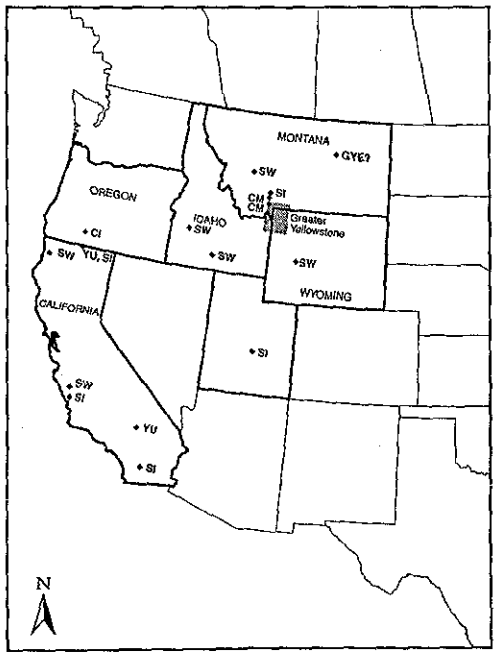


Figure 3: Sightings of bald eagles color-banded in Greater Yellowstone.



acetylthiocholine iodide substrate hydrolized/min/L of plasma (μmoles/min/L).

Survival of bald eagles was evaluated by analyzing detection of bald eagles radio-tagged as nestlings only. Mortality and longevity were evaluated by analysis of band encounter information provided by the BBL.

Results

Banding and Encounters

Between June 1979 and January 1994, 339 bald eagles were banded with USFWS bands; 306 nestlings, 6 fledglings, 3 resident immatures, 14 resident adults, and 10 migrants (i.e., winter residents) were color-banded. Through June 1995, 51 USFWS bands were encountered (15%). Encounters of eagles banded as nestlings or fledglings (also known as locals) totaled 46 (15% of all locals banded). Four (28.6%) eagles banded as adults and 1 (10%) banded as a migrant were also encountered.

Movements

Numbers of encounters did not differ significantly among Management Units of origin ($\chi^2 = 1.5$, 0.35; $P = 0.9$, df = 5) nor did number of encounters inside or outside the GYE ($\chi^2 = 7.4$, $P = 0.68$, df = 10) differ among Management Units (Table 2). Bald eagles banded in the GYE were encountered in 7 western states and 1 Canadian Province (Figure 2). Color-banded eagles were observed in 5 western states and mirrored USFWS band encounters (Figure 3). Ninety-five percent of encounters and all observations of color-banded eagles outside of the GYE were between September and April, indicating migration or wintering locations. Autumn movements of a radio-tagged juvenile bald eagle from ST spanned 8 days and 5 states, terminating in northern California (Bath 1987), which is indicative of first fall migration of bald eagles produced in the GYE.

Nine of 15 bald eagles radio-tagged as nestlings were tracked sufficiently to record summer movements within the GYE at least 1 year after fledging. Movements of 2, identified by kilohertz portion of the 148 mHz frequency, illustrate typical local movements of immature bald eagles produced in the GYE.

BAEA 700: On 11 June 1985, a nestling female bald eagle produced at the Butler Creek site on the Snake River, southwest of Jackson, Wyoming, was

radio-tagged with a solar powered transmitter. She exhibited a previously unrecorded plumage coloration of bald eagles (Harmata and Montopoli 1998). From the time 700 fledged on 26 June until she left the GYE on her first autumnal migration in mid-September, she remained within 800 m of her natal nest. She was absent from the GYE in winter and periodic aerial searches for all radio-tagged eagles throughout the GYE failed to locate 700.

Next located on 30 April 1986, 700 was on Palisades Reservoir in eastern Idaho and stayed on the reservoir until late May. Bird 700 was next detected on Yellowstone Lake and triangulation located her at the Eagle Bay area, a minimum of 132 km from her last location. Over the next 4 years, 700 was often located in Yellowstone, mostly in association with Yellowstone Lake. In spring 1987, she was at the South Arm and again at Eagle Bay. In summer 1988, she was on the Flat Mountain Arm and Heart Lake. And in 1989, an adult bald eagle wearing a transmitter and color-band was seen near LeHardy Rapids on the Yellowstone River, which may have been 700.

BAEA 923: On 15 July 1987, the male of 2 siblings produced at the Eagle Bay nest site on Yellowstone Lake was banded and radio-tagged. The eagle was intermittently monitored during summer from Lake Butte, 15.5 km northeast of the nest. Distance and intervening lake prevented determination of fledging date and immediate post-fledging movements, but by early August bearings indicated 923 was moving as much as 9 km from the nest, possibly as far as Flat Mountain Arm and the Promontory. On 7 September, 923 was still on Yellowstone Lake near the nest site but on 10 October he was located near Soda Springs in eastern Idaho. Obviously, he was beginning his first autumnal migration.

On the first aerial survey in the spring of 1988, 923 was located on Upper Red Rocks Lake in southwestern Montana. By 6 May he had moved to Henry's Lake Idaho and by mid-June he was back in Yellowstone. When first located on Yellowstone Lake, he was in the company of *BAEA 944*, an eagle radio-tagged in 1987 in a nest on the Promontory between the South and Southeast Arms. Along a small stream known for spawning cutthroat trout (*Oncorhynchus clarki*), a grizzly bear (*Ursus arctos*) sow was snagging spawning trout, lacerating the gut and selecting the row. She then discarded the carcass. When the bear moved off about 3 m, both eagles scavenged the carcasses. The bear and eagles remained in the vicinity about 1 week. The grizzly then moved to Pelican Valley, again visiting streams full of spawning cutthroat. Within 1 day, the eagles were also located there.

During subsequent aerial and ground surveys, 923 was located mostly in the Southeast and South Arms of Yellowstone Lake. He was last located in the GYE in 1988 on the west shore of the West Thumb

Table 2. Distribution of encounters of bald eagles banded as nestlings in Greater Yellowstone management units, 1979-1994.

		No. Encountered		
Origin	No. Banded	In GY	Outside GY	Total
Yellowstone Unit (YU)	37	4	1	5
Snake Wyoming (SW)	75	8	3	11
Snake Teton (ST)	47	3	4	7
Snake Idaho (SI)	78	8	7	15
Continental Idaho (CI)	30	1	4	5
Continental Montana (CM)	33	1	2	3
	306	25	21	46

Table 3. Heavy metal and selenium concentrations (ppm wet weight) in blood of bald eagles in Greater Yellowstone by age and residency status.

	Pb			Hg			Se		
Status (n)	$\bar{x}$[1]	Range	%[2]	$\bar{x}$	Range	%	$\bar{x}$	Range	%
Breeding Adults (11)	0.06	ND[3]-0.21	46	2.16	0.90-4.00	100	2.43	0.60-7.00	100
Nestlings (124)	0.05	ND-0.80	30	0.19	ND-1.20	93	1.09	0.10-3.70	100
Migrants (11)	0.75	ND-5.00	91	1.33	0.40-3.40	100	1.12	0.30-3.50	100

[1]Geometric mean.
[2]Percent (of n) detected.
[3]None detected.

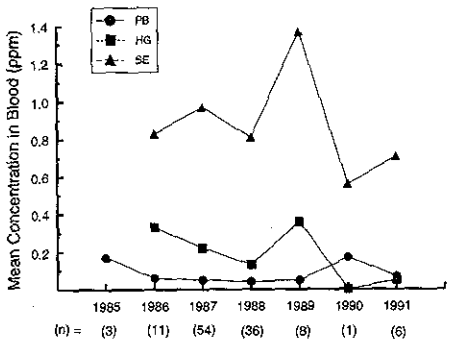
of Yellowstone Lake on 21 October. In November, 923 was located on Tule and Klamath Lakes in northern California and southern Oregon along with another GYE eagle. He remained in the Klamath Basin until mid-December and was not located again in 1988.

On 30 March 1989, 923 was located near Fishing Bridge on the Yellowstone River in the Park. On 14 April, he was seen (color-band and transmitter "backpack" were observed) farther downstream on the Yellowstone River near LeHardy Rapids. Cutthroat trout are abundant in this section of the Yellowstone River. By 24 April, 923 was on the south shore of Yellowstone Lake near Breeze Point. On 12 May, 923 was located and observed on Holmes Point on the southeast corner of Mary Bay. Proximity allowed close inspection of plumage, bands, and transmitter. All were in excellent condition. As in 1988, 923 spent most of the summer in the South and Southeast Arms of Yellowstone Lake. Periodic aerial and ground checks located him mostly at the mouth of the Yellowstone River on the Southeast Arm and Outlet Creek on the South Arm. On 5 October, 923 was located on West Thumb, indicating he may have been in the initial stages of his second autumnal migration. Subsequent ground checks around Yellowstone Lake failed to detect 923.

On 25 February 1990, 923 was located in Bear Valley National Wildlife Refuge, roosting 3.2 km southeast of Worden in southern Oregon. He was located on 2 successive days until 28 February. Monitoring ceased on 29 February through 3 March and when resumed on 4 March no signals were detected. Timing of locations suggests 923 may not have wintered in the Klamath Basin but visited only during migration.

923 was found dead on 17 January 1994 in central Utah. Cause of death was unknown. The eagle was mounted and currently resides in Fishing Bridge Visitor Center in YNP.

Figure 4. Annual mean (geometric) heavy metal and selenium concentrations of nestling eagles in Greater Yellowstone.



Contaminants

Frequency of occurrence of detectable concentrations of Pb differed significantly among locals, resident adults, and migrant bald eagles tested in the GYE ($\chi^2 = 6.1$, $P = 0.049$, df = 2). Migrant eagles exhibited the highest concentrations (Table 3). ANOVA detected differences in Hg concentrations among age and residency classes ($F = 10.89$, $P < 0.05$) with resident adults higher than locals but not different than migrants ($\propto = 0.05$, $P > 0.05$, Duncans Range Test). Se concentrations were not different among age/residency classes ($P > 0.05$) (Table 3).

Table 4. Heavy metal and selenium concentrations (ppm wet weight) in blood of nestling bald eagles in management units (see text) of Greater Yellowstone.

	Pb			Hg			Se		
Management Unit (n)	Mean[1]	Range	%[2]	Mean	Range	%	Mean	Range	%
YU (18)	0.04	ND[3]-0.14	22	0.29	0.30-1.20	100	0.59	0.30-1.10	100
ST (21)	0.06	ND-0.30	48	0.19	ND-0.60	90	1.00	0.37-2.30	100
SW (22)	0.08	ND-0.40	45	0.37	0.20-0.60	100	1.67	1.00-2.20	100
SI (40)	0.05	ND-0.80	26	0.21	0.10-0.50	100	1.22	0.10-3.70	100
CM (7)	0.05	ND-0.17	29	0.08	ND-0.50	57	0.98	0.50-1.10	100
CI (16)	0.03	ND-0.20	6	0.06	ND-0.50	56	1.02	0.20-3.50	100

[1]Geometric mean.
[2]Percent (of n) detected.
[3]None detected.

Frequency of occurrence of detectable Pb was not different among Management Units ($\chi^2 = 3.2$, $P = 0.66$, df = 5) (Table 4). ANOVA indicated differences in Hg ($F = 6.26$, $P < 0.001$) and Se ($F = 3.74$, $P = 0.0036$) concentrations in eagles among Management Units. YU had the highest mean (arithmetic) concentrations and detection rate of Hg but the lowest mean and detection rate of all Management Units for Se.

Frequency of occurrence of detectable Pb was not different among years ($\chi^2 = 4.4$, $P = 0.49$, df = 5) (Figure 4). However, concentrations of both Hg and Se among years was different ($F = 2.47$, $P = 0.037$ and $F = 7.74$, $P < 0.001$, respectively), with highest concentrations of both in 1989, one year after the Yellowstone fires of 1988.

Productivity per Management Unit from 1982 to 1993 was negatively correlated with both Pb ($r = 0.30$) and Hg ($r = 0.003$), but positively correlated with Se (1985-1991) ($r = 0.63$). Stepwise regression revealed only Se, and Pb added significantly to the model ($R^2 = 0.93$, $P = 0.019$).

DDE was the only organochlorine compound detected in nestling bald eagles and found in only 1 of 9 tested. It was present in a concentration of 0.004 ppm.

The mean AChE concentration of nestling bald eagles was 192.4 µmoles/min/L ($SD = \pm 45.3$, $n = 9$). An eaglet from CM contained 57 µmoles/min/L AChE in plasma suggesting exposure to anticholinergic compounds. The nest site was close to large ground squirrel (*Spermophilus* spp.) populations managed with organophosphate rodenticides.

Survival

Circumstances of encounters of bald eagles banded in the GYE varied with the majority of encounters involving eagles dead of unknown causes (Table 5). Research activities (captures and bands read) accounted for 15.4% of encounters, the second largest proportion of encounters. Band encounter distribution by age suggests that only 50% of bald eagles banded in the GYE live beyond 3.25 years and less than 10% live beyond 7.5 years (Figure 5).

More than 86% of bald eagles radio-tagged in the nest survived their first winter (Figure 6). Survival remained relatively stable after the first year, averaging 78.3% annually. By age 7, 20% of the original cohort was still alive.

Figure 5. Cumulative percent of band encounters by age of bald eagles banded in Greater Yellowstone.

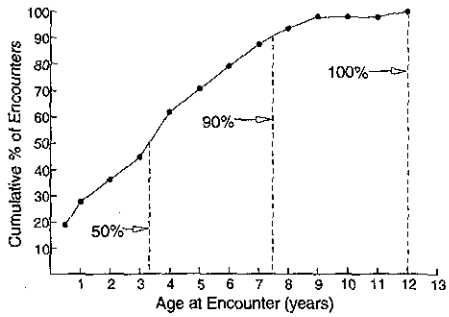


Figure 6. Survival of bald eagles in Greater Yellowstone.

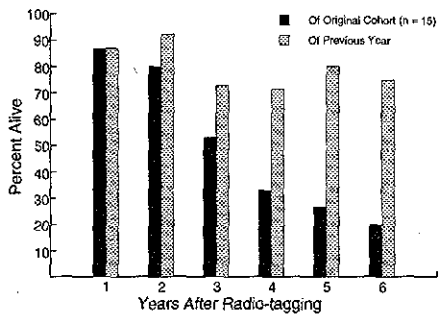


Table 5. Circumstances of 51 encounters of bald eagles banded in Greater Yellowstone.

Agent	Number of Encounters	Percent of Encounters
Unknown	21	40
Electrocution	6	12
Captured for Research	6	12
Gunshot	4	8
Poison	4	8
Trap	4	8
Vehicle Impact	2	4
Territorial Dispute	2	4
Band Read	2	4

Discussion

Movements

Movements of radio-tagged juvenile and immature bald eagles and distribution and timing of band encounters reveal certain trends. Juvenile and immature bald eagles produced in the GYE indicate virtually all leave the ecosystem the first autumn post-fledging. Ostensibly, juveniles need not leave the GYE. Juvenile eagles originating in Canada winter within the GYE, indicating requisites for survival of at least some juveniles were present. Regardless, survival of immature eagles leaving the GYE during winter has probably been higher than those that did not, resulting in a population with a genetic propensity to migrate as immatures. Once initiated, both deterministic and stochastic components may have dictated timing, direction, rate of movement and destination of initial migration. Unlike juvenile migrants from Canada, which may also be affected by proximate ecological factors (Harmata et al. 1985), genetically-induced responsiveness to photoperiodic cues may be primarily responsible for the initiations of migration of GYE eagles. GYE eagles left their natal areas well before food resources dwindled or became unavailable due to snow cover or ice. In fact, waterfowl numbers in the GYE actually may have been at peak when young eagles departed. Once initiated, orientation was primarily southwest to the Snake River plain in Idaho and northern Utah, then west to the coastal states of the Pacific Northwest.

After initial compass direction was determined, responses of GYE eagles to stochastic events most likely dictated the exact route and timing of migration since parental guidance was obviously lacking and migration was solitary. Physiography and meteorology probably modified orientation and migration, while rate was dictated by chance encounters with locally abundant food, adequate roost sites, and optimal flying conditions. Presence of 2 immature GYE eagles for 2 subsequent years in the Klamath Basin of Oregon and California coincident with large die-offs of waterfowl supports this theory. Apparently both birds encountered the area, either by watching other eagles (McClelland et al. 1982) or by chance, and returned the following year with the guidance of memory. The somewhat unusual longitudinal migration pattern (as opposed to the more common latitudinal avian migration pattern) and eventual destination of GYE eagles was consistent with the theory of genetic memory; eagles were homing to regions of historical abundant salmon runs in the Pacific Northwest (Hunt et al. 1992). Close genetic relationships among eagles within the GYE and with eagles produced in the Pacific Northwest lends strong support to the theory.

Considering a genetically-based propensity for GYE eagles to migrate longitudinally and westward, care should be taken when selecting donor populations for reintroduction (hacking) efforts. Donor populations chosen should exhibit migration patterns most consistent with those of recipient populations. At least availability of adequate winter habitat at appropriate distance and direction, as dictated by donor population movements, should be considered. It may be ill advised, for instance, to use GYE eaglets for reintroduction efforts in coastal California; they may end up in Hawaii.

Upon arriving on the West Coast, timing of available encounters suggest juvenile eagles wandered the coast, ranging from Los Angeles in the south to Puget Sound in the north, possibly "looking" for extinct salmon runs. Homing immature eagles from the GYE may have been searching for vacant nest sites or incomplete pairs as virtually all returned to their natal nest areas in the spring. Subsequent to investigating natal nests, juveniles then dispersed throughout the ecosystem, essentially defining its limits. Young eagles radio-tagged in all population units were detected in all other population units at least once, seasonally exploiting mostly lentic habitats and associated spawning runs or waterfowl concentrations. Immature eagles apparently moved freely among nesting and non-nesting habitat of adult bald eagles throughout the ecosystem. As autumn approached, immature eagles moved gradually back towards their parent's territories, often as close as a few hundred meters from their natal nest. Such movements again may represent investigations of occupancy of territories for potential future nesting, indicating recruitment and pioneering occur primarily in spring and fall.

During summer, radio-tagged juveniles and immatures were regularly located throughout the GYE but rarely located on waters considered bordering or outside of the GYE. Few surveys were conducted outside of the GYE, but the majority of radio-tagged eagles were in fact located within the ecosystem, indicating surveys outside would have a low probability of success in locating missing eagles.

Thus, movements and habitats used by these eagles may indicate real boundaries of the GYE and reinforce the importance of maintaining a large, continuous, intact ecosystem.

Immature eagles were found primarily on lakes within the GYE, although the Snake River and smaller rivers and creeks received periodic use by concentrations of immatures. Young eagles seemed to quickly key on temporal concentrations of prey and carrion and were found regularly along water bodies where fish were spawning (i.e., cutthroat trout in YNP and Henry's Lake, Idaho, in spring; whitefish *(Prosopium williamsonii)* in Cottonwood creek in GTNP in autumn) or areas where ungulate viscera piles left by hunters were available (i.e., early elk *(Cervus elaphus)* hunts in Jackson Hole and late elk hunts in GTNP and near Gardiner, Montana). Some areas previously overlooked as important bald eagle habitat because of lack of breeding adults may be of critical importance to floating immatures that move great distances from one temporal food source to another.

As eagles aged, the tendency was to leave the GYE later in the fall and return earlier in the spring. Juveniles almost all left the GYE in mid September, returning from mid-April to early May, as reflected by annual early and late detection times. Two-year-olds and older tended to leave in mid- to late October, returning from mid- to late March. Some eagles, notably the 2 fledged from a nest in Grand Teton National Park in successive years, may have remained in the GYE as late as late mid-January, leaving for only 1 month. Decreasing time away from the GYE is probably facilitated by increasing knowledge of routes and terrain as eagles grew older.

Data on movements during the second fall migration post-fledging are more sparse. However, initial directions of eagles leaving the GYE appeared more directly south. Implications of those direction changes are unknown but may have been influenced by increasing knowledge of geography and locations of seasonal food resources. The juvenile eagle followed west on its first migration did not visit the Great Salt Lake area, but band encounters suggest that many older birds visit the area on both vernal and autumnal migration. Waterfowl are abundant and dispersed throughout the region and eagles are probably more likely to encounter concentrations as age increases.

As radio-tagged eagles aged, basic movement patterns remained but variability in both extent and frequency of long-range movements increased. Movements of older immatures suggests increased wandering outside of the GYE in summer, especially north into Montana. In fact, an adult bald eagle that was a member of a productive pair on the Madison River in southwestern Montana from 1989 through 1992 had been banded as a nestling in the GYE (color-band sighting). A new breeding area initiated on the Missouri River, Montana, in 1991 was occupied by an adult bald eagle produced in the eastern Idaho portion of the GYE. Clearly, the highly productive GYE population has provided recruits to expanding populations outside the ecosystem.

Although no data exist for seasonal movements of adult bald eagles in YNP, movements of the Third Creek pair may provide clues. Yellowstone Lake is essentially ice covered until late May, and adults associated with lake territories probably leave their primary breeding range in winter. Populations of wintering bald eagles along the Yellowstone River in Montana vary considerably, but numbers always account for the number of adults nesting in YNP.

Contaminants

Redig (1984) considered blood Pb concentrations of 0.2-1.00 ppm in eagles indicative of toxic, chronic, sublethal exposure. Hg in blood of bald eagles suggests eagles fed on a moderately contaminated food supply (Eisler 1987) that was most likely aquatically associated (Wiemeyer 1991). Frenzel and Anthony (1989) found very low Hg concentrations in waterfowl but very high concentrations in bald eagles in Oregon. Although they did not analyze Hg in fish, other studies show fish often contain high concentrations of Hg (Eisler 1987). The source of Hg in aquatic ecosystems is generally unknown but is often related to leaching Hg from hard rock mine tailings treated with the "Washoe Process" (Martin 1992). Mines with tailings piles thus treated are present throughout the northern Rocky Mountains and western Canada. Portions of the western U.S. and Canada cover mercuriferous rock (Jonasson and Boyle 1971 in Wiemeyer et al. 1989) and natural leaching also may be a source of Hg in watersheds. Once in aquatic ecosystems, Hg is bioaccumulated as methyl-mercury through micro-organisms (Colwell et al.1975) to invertebrates (Hildebrand et al. 1980) to fishes or, directly into fish through gill surfaces from water (Phillips and Bubler 1980). Tissue Hg in some fishes increases exponentially with

size (Phillips et al. 1987) and the contaminant is further biomagnified in predators.

Dietary Hg affects raptorial species neurologically (Fimreite and Karstad 1971) and reproductively (Fimreite and Karstad 1971, Wiemeyer et al. 1984). Neurological effects appear to be manifested in a threshold effect resulting in overall weakness and wasting. None of the eagles sampled in this study displayed symptoms of Hg poisoning and we are unaware of any published accounts of toxic concentrations of Hg in blood of bald or golden eagles (*Aquila chrysaetos*).

Incidence of Se residues in bald eagles was high, with mean concentrations higher than those considered toxic in bovines (≥0.50 ppm in blood: R. Eisler, Patuxent Wildlife Research Center, pers. commun.). However, applicability of this toxic concentration to birds is tenuous. Se-induced mortality has been documented in waterfowl, but the effects are primarily teratogenic or manifested in reduced natality or productivity (Eisler 1985, Ohlendorf et al. 1988, Heinz et al. 1989, Hoffman et al. 1990). Although congenital mandibular deformities have been observed in bald eagles in the Great Lakes Region, Bowerman et al. (1994) stated Se was an unlikely causative agent and similar effects have not been recorded for eagles elsewhere. None of the eagles from our study exhibited symptoms of Se poisoning.

DDE (a metabolite of DDT) was the primary contaminant reducing reproductive success of bald eagles in North America with the majority of exposure from the avian portion of the diet (Wiemeyer 1991). Although DDE is less toxic to birds than most organochlorines, it can elicit abnormal behavior, eggshell thinning, and adult and embryonic mortality (Risebrough 1986). Low concentrations found in our study reflect the ban on DDT and subsequent decline in use, but continued presence (i.e., detection frequency) indicates persistence of the chemical.

Survival

Band encounter rate was high (15%) relative to most eagle studies (e.g., approx. 3% for Bird Banding Laboratory data), but did not necessarily indicate higher mortality in the GYE eagle population. GYE eagles are associated with lentic and lotic environments situated in areas of North America where human and eagle populations are most proximate and in regions well known for recreational fisheries. This probably increases the potential for encounters. Although the rate was high in this study, causative agent proportions of GYE eagles were similar to those of eagles in other areas of North America. Most eagle mortalities in North America were from anthropogenic causes with gunshot deaths the primary agent (USFWS, National Wildlife Health Laboratory, Madison, Wisconsin). Gunshot deaths were also high in the GYE but just may indicate the percent of human-induced mortalities rather than overall mortality. Eagles most likely to be shot (i.e., those near houses and roads) are also those most likely to be encountered. The highest proportion of GYE encounters were of unknown causes, most of which were probably from starvation, undetectable poisonings (e.g., organophoshates that have short half-lives), nonhuman related accidents, and interspecific aggression.

Survival of radio-tagged nestlings was high. Survival of older immatures dropped between 3 and 4 years post-fledging. Indeed, few 3-year olds were observed throughout the study. Survival of eagles from 5 to 6 years post fledging increased. Eagles in their third year may have tough times. After 1 year of age, plumage of immature eagles changes. Adult eagles, upon which juveniles are somewhat dependent up to 1 year, are much less tolerant of eagles with plumage more similar to their own. Yet foraging and hunting capabilities of older immatures may not be adequately developed for full independence, hence survival drops. Those eagles that adapted or were educated sufficiently then have a greater probability of survival as age increases.

Most likely, survival rate indicated by detection rates of radio-tagged immatures was the absolute minimum. Failure to detect eagles was probably more a function of incomplete survey coverage or transmitter life rather than eagle deaths. Some immature eagles wearing non-functioning backpack radios were observed and mal- or non-functioning transmitters were recovered from recaptured adult eagles. Considering the immensity of the GYE, the relatively small area scanned on any one survey mission, the mobility of eagles, and the propensity of returning eagles to continue to other regions makes the number of eagles actually detected truly significant. In fact, at least 3 immature eagles of GYE origin were observed alive in Montana outside the ecosystem in spring or summer.

Conclusion

Despite fairly pervasive incidence and occasionally high concentrations of potentially toxic contaminants, the GYE bald eagle population is increasing (Figure 7). Additionally, bald eagles in the continental U.S. were reclassified from endangered to threatened on 12 July 1995 (Fed. Reg. 60:36000-36010). Status of breeding populations was paramount to reclassification.

Seasonal movements of radio-tagged eagles and band encounters defined the extent of the greater ecosystem. Eagles produced in each Management Unit were located in all others, either as band encounters or locations of radio-tagged individuals. Early concern over a potential lack of long-term

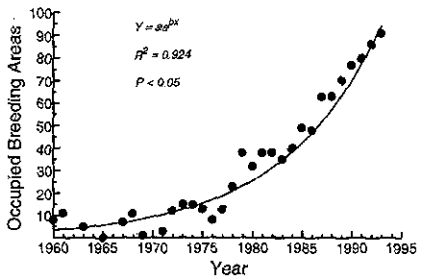


Figure 7. Population growth of bald eagles in Greater Yellowstone.

population stability in the Yellowstone Unit (YU) proved unfounded. Since 1982, breeding pairs in YNP have increased as has productivity. Recruitment to the breeding population undoubtedly is supported by eagles produced in all other Management Units. All radio-tagged eagles followed ≥1 year visited YNP, primarily Yellowstone Lake. As other Management Units support the population of nesting eagles in YU, the value of YNP to the GYE population is as an area that enhances survival of young eagles produced throughout the ecosystem.

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Migratory Chronology of Adult Tiger Salamanders and Survey of Larvae in Ice Lake Reservoir in the Northern Range of Yellowstone National Park

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Abstract

The tiger salamander, *Ambystoma tigrinum,* inhabits many lakes and ponds in Yellowstone National Park (YNP) and is a major consumer of invertebrates in these systems. The movement chronology and time required for metamorphosis of the tiger salamander were studied using a drift fence and pitfall traps at Ice Lake Reservoir, a permanent lake in YNP. Ice Lake Reservoir was sampled with minnow traps to determine whether reproductively mature (paedomorphic) larvae existed. During the period of 9 April-10 October 1993, 280 metamorphosed individuals were intercepted at the drift fence. The pattern of migratory movement was influenced by environmental factors. Of the total immigration (lake-directed movement) recorded, 96% occurred when the minimum daily air temperature was 0° Celsius (C) or greater, and 83% occurred within 24 hours after a precipitation event. All emigration (land-directed movement) occurred when the minimum daily air temperature was 0°C or greater, and 95% occurred within 24 hours after a precipitation event. Males immigrate to the lake earlier than females and males and females emigrate at approximately the same time. Migrations were nocturnal 99% of the time. Most larvae metamorphosed during their second summer in the lake. Six larvae from Ice Lake Reservoir were reproductively mature, demonstrating the presence of paedomorphosis in tiger salamanders in Yellowstone National Park.

Introduction

A study of tiger salamanders *(Ambystoma tigrinum)* in Yellowstone National Park (YNP) was initiated for 2 reasons: first, to determine whether reproductively mature (paedomorphic) *A. tigrinum* larvae exist in YNP, as anecdotal evidence suggests (Turner 1951, 1955); and second, to provide baseline data on a breeding population of salamanders against which future studies of *A. tigrinum* might be compared. Movement chronology around a breeding pond, time required for metamorphosis of larvae, and sex ratios have been studied in other regions of the United States; however, there is little information available from the region in and around YNP. This study would also provide baseline data that may be valuable in the search for explanations for recent worldwide declines in amphibian popu-

lations, including a population of *A. tigrinum* in central Colorado. Amphibians are an important part of aquatic and terrestrial food webs. They are major consumers of invertebrates and, in turn, provide a significant prey base for birds, mammals, and reptiles because their biomass converts very effectively.

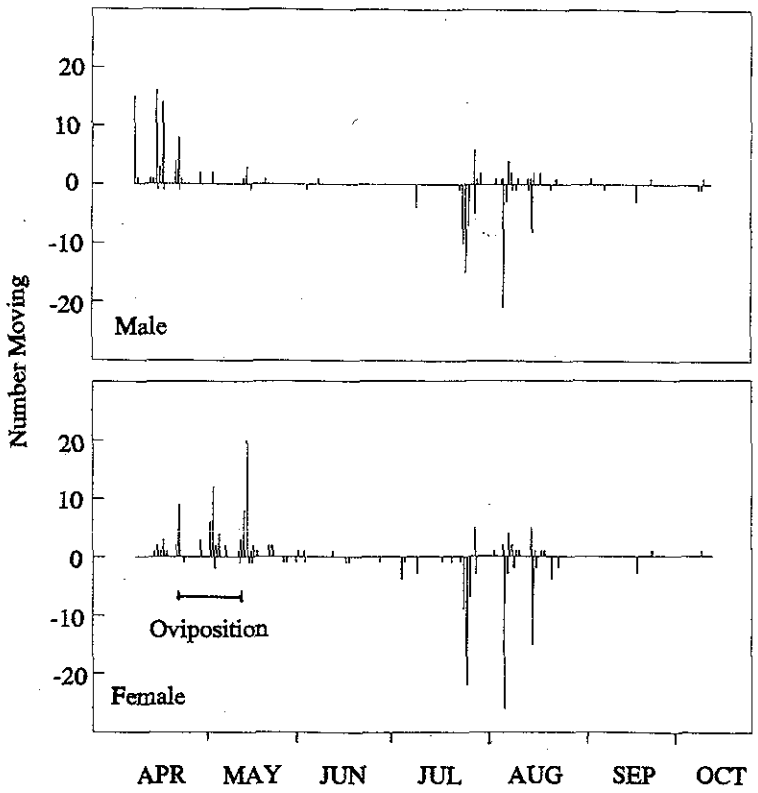
The objectives of this study were to:

1) Describe the migratory (immigration and emigration) chronology of a population of *A. tigrinum* in a permanent lake;
2) Determine the effects on migration of environmental parameters such as air and water temperature and rainfall;
3) Determine the approximate size of a population of *A. tigrinum,* its sex ratio, larval growth rates, and sizes of new metamorphs; and
4) Determine the number of years required by *A. tigrinum* to metamorphose in a permanent lake and whether or not reproductively mature (paedomorphic) larvae exist in YNP.

Methods

The primary site for this study was Ice Lake Reservoir, a permanent lake in YNP. The lake is located near Gardiner, Montana, and, at an elevation of 1,670 meters, is the lowest elevation lake in the park. A drift fence and pitfall array were constructed around the entire periphery of Ice Lake Reservoir in late March and early April, 1993 to intercept *A. tigrinum* moving to and from the lake. The time of construction coincided with the breakup of winter ice on the lake. The fence was constructed of aluminum and was buried in a trench. Fifty-one pairs of pitfall traps were buried, one on each side, with their rims touching the fence. Traps were checked daily within an hour of sunrise and, during times of peak movement, within an hour of sunset. Each captured salamander was marked, weighed, and measured, and its sex and reproductive state noted, before being released onto the opposite side of the fence. Five minnow traps were set in the lake to capture larvae and to provide information on the number of unmarked metamorphs in the lake.

Figure 1. Migratory movements. Postive bars indicate movement toward water, negative bars indicate movement toward land.



Results and Discussion

Trapping for 185 days with pitfalls and 84 days with minnow traps at Ice Lake Reservoir during the 1993 field season yielded 306 individual salamanders (280 metamorphs and 26 larvae) that were marked and released. Two hundred eleven individuals were sexually mature and presumably present in the lake during the spring breeding season of 1993. The breeding population exhibited a sex ratio of 1.00M:1.11F.

Some movement of salamanders, either in or out of the lake, was recorded during each month from April through October (Figure 1). Immigration by those individuals that were to participate in the breeding effort began 9 April and continued through 11 June. A second round of water-directed movement occurred but was coincident with the peak of emigration. Concerted emigration ef-

forts were recorded between 8 July and 14 August. Sporadic, low level emigration continued into the fall, with a few salamanders still actively emigrating as of 8 October.

Male *A. tigrinum* entered Ice Lake Reservoir significantly earlier than females in 1993 (two sided-test, $P < 0.05$). The mean arrival date for males was 21 April, while the mean arrival date for females was 10 May. The mean dates of emigration were not significantly different between the sexes. Males remained in the lake for a significantly longer period of time due to their earlier arrival. I determined the diel pattern for salamander movements and found 98.8% were nocturnal.

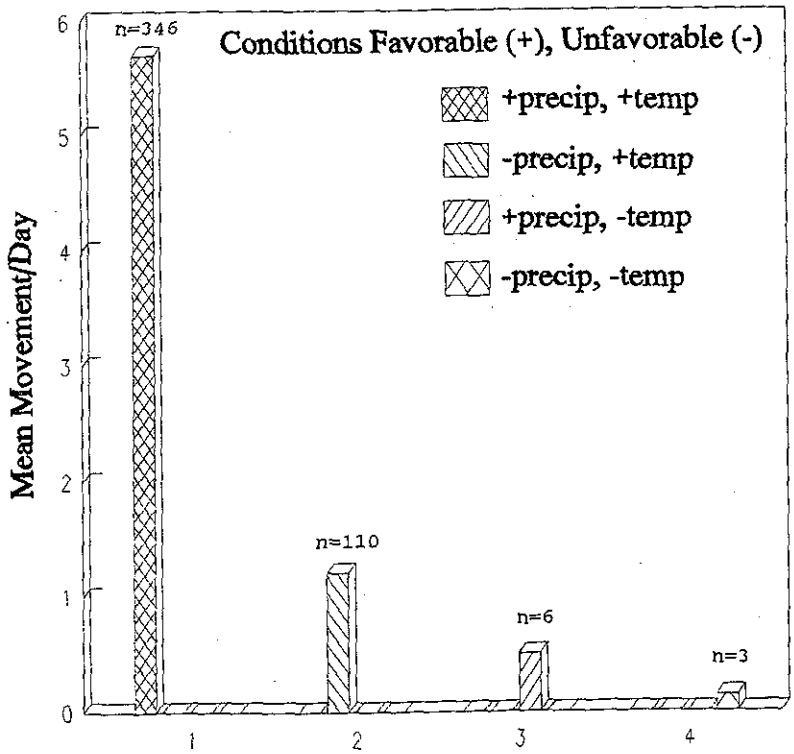
Linearly regressing the number immigrating on minimum daily air temperature, daily precipitation, and time of year was not significant ($P > 0.05$, df = 181). However, the majority of immigrations occurred on days when there were precipitation events. For example, precipitation occurred on only 64% of the days between 9 April and 11 June, yet 94% of the recorded immigrations occurred within 24 hours of these precipitation events. During the entire study, precipitation occurred on only 39.5% of the days, yet 83% of the recorded immigrations occurred within 24 hours of these precipitation events. Precipitation seems to be important as a predictor of the daily occurrence of immigration, but it was not a good predictor of the magnitude of migrations. Immigrations occurred in fresh snow on 4 occasions.

The majority of lake-directed movements occurred on days when the minimum daily temperature was greater than 0°C. Ninety-six percent of immigrations occurred on days when the minimum air temperature was between 0°C and 15.6°C. The lowest temperature recorded for a day on which immigration events occurred was –5.6°C.

Linearly regressing the number emigrating on minimum daily air temperature, daily precipitation, and time of year was not significant ($P > 0.05$, df = 181). The majority of emigrations occurred on days when there were precipitation events. Precipitation occurred on only 43% of the days between 8 July and 14 August, yet 99% of the emigrations occurred within 24 hours of these precipitation events. Furthermore, during the entire study, precipitation occurred on only 39.5% of the study days, yet 95% of the recorded emigrations occurred within 24 hours of these precipitation events. Again, while precipitation seems to be important as a predictor of the daily occurrence of emigration, it was not a good predictor of the magnitude of emigration. Emigration did not occur when the minimum daily temperature was less than 0°C. All emigration occurred on days when the minimum daily air temperature was between 0°C and 15.6°C.

Emigration from Ice Lake Reservoir did not immediately follow oviposition despite the presence of favorable temperature and precipitation events. Daily morning water temperatures of 5.6°C to 18.9°C were also not found to affect emigration (two-sided t-test, $P = 0.31$). It may be beneficial for these salamanders to remain in the breeding pond after oviposition to feed, in which case other environmental

Figure 2. Mean movement per day when precipitation and temperature are favorable and unfavorable.



or biological factors may influence emigration. Emigration was observed soon after oviposition in *A. tigrinum* (Botts 1978) and *A. macrodactylum* (Beneski et al. 1986). The onset of emigration by *A. tigrinum* in this study corresponds with the initial decrease in day length. Day length has been shown to affect migratory disposition in many species of birds (Welty and Baptista 1988) and fish (Orr 1970) by causing an increase in the activity of the thyroid gland. Day length may also influence migration in *A. tigrinum* (Wolstenholme and Knight 1970, Taylor 1972, Taylor and Adler 1978, Adler 1978, Duvall and Norris 1978, 1980, Tamarkin et al. 1985, Gern et al. 1986, Welty and Baptista 1988).

Temperature and precipitation are commonly studied variables with respect to salamander migration. Interpretations of which variable is the most important differ with location and habitat. Precipitation has been suggested to be more important in warm habitats (Semlitsch 1985), whereas temperature has been judged more important in cold habitats (Beneski et al. 1986). There is a broad overlap in this study between favorable precipitation events (> 0 mm) and favorable air temperatures (≥ 0°C) (Figure 2). At Ice Lake Reservoir, an average of 5.7 movements occurred on each day that both precipitation and daily minimum air temperature were favorable. However, when temperature was favorable but pre-

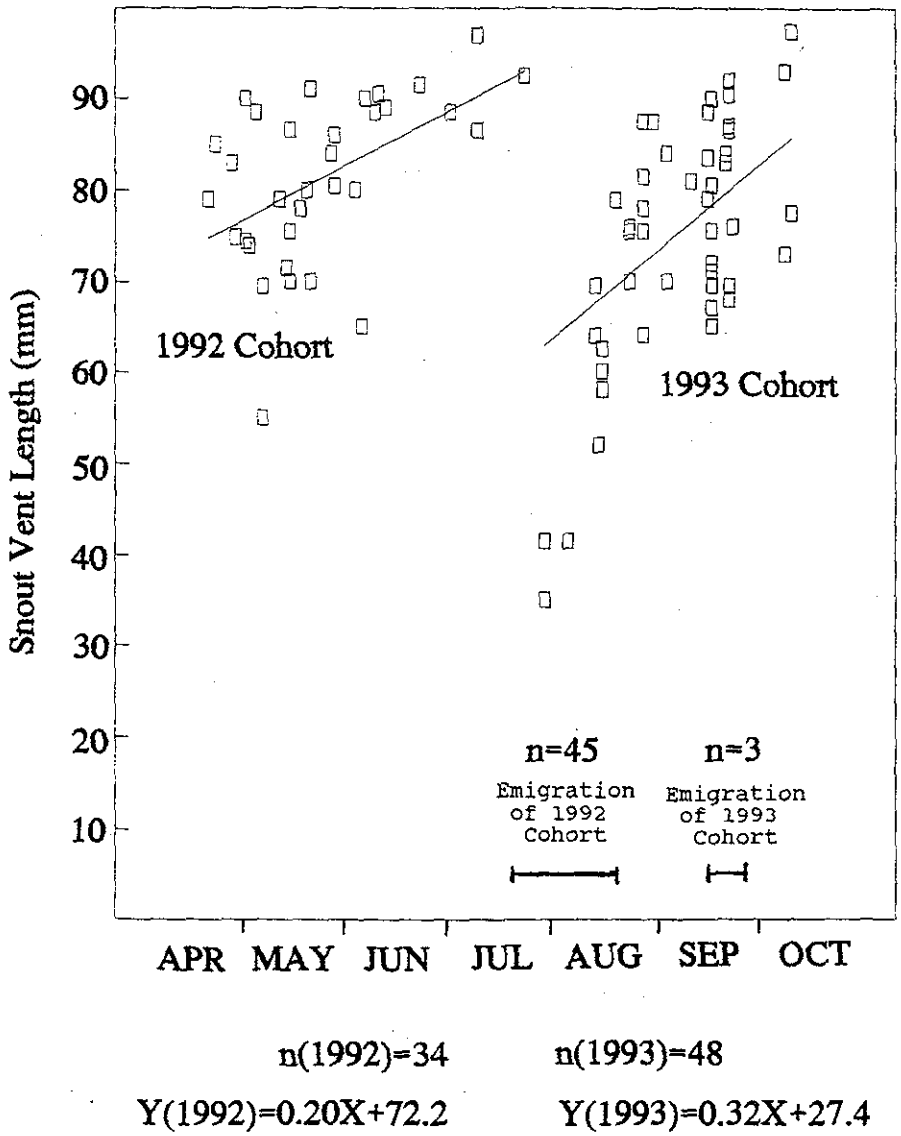


Figure 3. Growth of 1992 and 1993 larval cohorts in Ice Lake Reservoir, 1993.

cipitation was not, only 1.2 movements occurred per day. In comparison, when precipitation was favorable but temperature was not, 0.5 movements occurred per day. When neither was favorable, only 0.14 movements occurred per day. Thus, daily minimum air temperature was a better predictor of the daily occurrence of migratory movement than precipitation, indicating that this population of salamanders in Yellowstone National Park is characteristic of other populations studied in cold habitats (Beneski et al. 1986). Nevertheless, much more movement is likely to occur when both precipitation and temperature are favorable.

Two size classes of larvae, determined to belong to cohorts representing 2 different years, existed in the lake in 1993 (Figure 3). The older (1992) cohort was present in the lake at the onset of the study. During the period from 23 July to 14 August, 45 recently metamorphosed individuals from this cohort (determined by the presence of gill stubs) were intercepted while emigrating. Three of the emigrants were individuals that had been marked as larvae.

The first 2 larvae belonging to the 1993 cohort were captured on 29 July. Extrapolation using a growth rate curve for larvae in Utah (Tanner et al. 1971) suggests that the 1993 cohort hatched sometime between 4 July and 9 July. Three recently metamorphosed individuals from this cohort were intercepted while emigrating during September. Thus, it seems that most larvae in Ice Lake Reservoir postpone metamorphosis until the second summer following oviposition, but limited metamorphosis does occur during the first summer.

The 5 minnow traps placed in Ice Lake Reservoir provided information regarding the frequency of paedomorphs in that lake. Four hundred twenty minnow-trap-nights in Ice Lake Reservoir resulted in the capture of 97 larvae. Twenty-one larvae, representative of the range of size observed, were sacrificed for dissection. Six of these larvae (3 males, 3 females) were found to be reproductively mature. These larvae tended to be larger than the reproductively mature metamorphs at the site. The mean snout-vent length of the paedomorphs was 123.5 mm (112.5 mm for males, 142.0 mm for females), while the mean snout vent length of the 6 largest metamorphs captured at the site was 118.8 mm (115.5 mm for males, 122.0 mm for females). The mean weight of the 5 paedomorphs (96 g, [74 g for males, 117g for females]) for which weight data were available was significantly greater than the mean weight of the 5 heaviest metamorphs (66 g, [53 g for males, 79 g for females]) captured at the site.

This study demonstrated that paedomorphosis occurs in at least 1 site in Yellowstone National Park. Further study would be required to determine if paedomorphosis occurs in other permanent lakes in the park.

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Trust for Wolf Conservation: A Proposed Model for Funding Carnivore Conservation in the U.S. and Canada

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Abstract

We observe that support for restoring and conserving large predators within remaining wildlands is increasing and that many members of the public value large carnivores as integral parts of ecosystems. Despite this support, the cost of recovery efforts and management of large predators is increasingly difficult for federal and state agencies to meet. Hunting is declining while interest in non-consumptive wildlife activities, such as wildlife viewing, has surged. At a time of extraordinary prosperity, funds to maintain existing federal endangered species programs and support new initiatives have shrunk. State wildlife agencies are pressured to use Pittman-Robertson funds normally allocated for traditional state wildlife programs to also cover the costs of non-game wildlife interests, especially in western states. There is understandable and growing resistance by state wildlife officials and hunting constituencies to fund carnivore restoration with firearm sale proceeds that have traditionally contributed to big game research and management in western states. To enjoin public support and federal and state efforts for funding such non-consumptive interests, we propose a conservation stamp for carnivores modeled after the hunting and conservation tax for waterfowl (16 U.S.C.A. 718a et esq.) commonly referred to as the "Duck Stamp." We use wolf recovery efforts in progress across the United States (red wolf [*Canis rufus*], southeastern U.S.; gray wolf [*Canis lupus*], Minnesota, Yellowstone, and central Idaho; and Mexican wolf [*Canis mexicanus*], southwestern U.S.) to elucidate how proceeds from a Wolf Conservation Stamp could be generated and used on a continental basis.

Introduction

Support for restoring and conserving large predators within wildlands throughout the West is increasing. Even where contentious, residents of western states value the presence and role of large carnivores as integral parts of intact ecosystems (U.S. Fish and Wildlife Service 1993, Bath 1994, Duda and Young 1994, Duda and Young 1995).

Despite public support, costs for recovery efforts and management of large predators are increasingly difficult for federal and state agencies to afford. Across-the-board program cuts because of the existing federal deficit, coupled with political gerrymandering of agency budgets through the appropriations process, pose significant obstacles to conservation. Reductions of funds for endangered species programs and resistance to funding carnivore recovery efforts through firearm sales (i.e., Pittman-Robertson Fund), such as those that contribute to big game research and management in western states, is likely to continue. Hence, costs for managing large carnivore conservation and recovery in the West under the current scenario will soon exceed funds available to adequately conserve these species.

A Wolf Conservation Stamp

To garner public support and federal and state efforts for funding large carnivore conservation, we propose a conservation stamp modeled after the hunting and conservation tax for waterfowl (16 U.S.C.A. 718a et seq.) commonly referred to as the "Duck Stamp." We use wolf (*Canis* spp.) recovery efforts in progress across the United States (red wolf [*Canis rufus*], southeastern U.S.; gray wolf [*Canis lupus*], Minnesota, Yellowstone, and Central Idaho; and Mexican wolf [*Canis mexicanus*], southwestern U.S.) to elucidate how proceeds from a public conservation stamp could be used on a continental basis.

Purpose

A Wolf Conservation Trust is a means for capturing broad public interest and leveraging state, federal and non-government funds to support efforts to learn more about wolves and the predator-prey communities of which they are part. A goal of outside funding would not be to replace state and federal agency funds for conserving wolves but, rather, to add to that source. A key element of this approach, then, is linking the broad public interest in conserving wolves with agency funds to expand conservation efforts under one "umbrella." Such an effort would focus attention on the public interest without the friction that characterizes the competitive political arena in which existing conservation organizations, various public constituencies, and state and federal agencies are operating, making progress difficult. Outcomes of this collaborative effort would engage a broad yet specified interest in wolf conservation, allow wolf conservation groups and programs to retain their identity, produce tangible achievements through fiscal responsibility, and enhance public knowledge and "ownership" of wolf conservation in wildland habitats. Finally, public interest and support for wolf conservation at the community, regional, and national levels would be strengthened through a closer link between people, public and private funds, and those to whom management of wolves is entrusted.

Mechanisms

In contrast with the obligatory purchase of a "Duck Stamp" for waterfowl conservation by hunters, we propose a voluntary conservation stamp for wolves. As the program developed, we believe that other mid-sized and large carnivores could be included.

Enabling Legislation

The Partnership in Wildlife Act (1993) and the Sport Fisheries and Wildlife Restoration Act (1937) provide the primary legislative mechanisms for implementing a wolf conservation trust program. Minor amendments would be necessary. Authorizing language in new legislation, such as exists for the "Duck Stamp," would be necessary and could incorporate the appropriate legislative language necessary to implement a trust on the ground.

Generation of Funds

Competition among artists for one-time issuance of red wolf, gray wolf, and Mexican wolf

prints and accompanying postage stamps would initiate the Wolf Conservation Trust funding effort. One stamp and print of the respective species would be issued in each of the first 3 years. Members of the public could purchase a conservation stamp and print in the year they are printed, after which neither would be available. Each stamp would cost $15.00, equal to the cost of a wolf conservation decal in subsequent years. The cost of original prints would be subject, in part, to the artists' consent, but would be priced so as to be available to the general public.

For the first 3 years of issuance of the respective prints, private donations would be matched on a 2:1 basis through congressional appropriations. No funds would be expended during this time period, so the balance of funds available would accrue, drawing interest. In the fourth and fifth years, 1/3 of the total funds available could be spent. Congressionally appropriated funds would continue to match private donations on a 2:1 basis. After the fifth year, 2/3 of total funds could be spent in any given year. Each year, 1/3 of the total funds would revert to a "trust" account, intended to accrue with interest. Trust funds would be held in escrow accounts indefinitely. Annual interest would remain with the Trust account.

Congress would match the annual balance of funds in years 6 to 10 on a 1:1 basis. After year 10, Congressional appropriations designated for matching of private funds would cease, subject to congressional discretion to extend the period for matching funds beyond the first decade.

Use of Funds

Three emphases for proceeds from this public conservation stamp distinguish a wolf conservation stamp and program from the primary goal of the duck stamp, which is land acquisition. Wolf Conservation Trust funds would be used for:

1) research on wolves, their prey, and other members of the predator community;
2) management of wolves, including control where and when necessary and purchase of lands for maintaining ungulate populations; and
3) information and education including the sharing of research and management findings in public forums.

Research funding includes ecological investigations of wolves and wolf-prey relationships, prey species such as ungulates, small mammals, and rodents, other predators, policy and social issues, information and education. Funds for management activities would include monitoring of wolves, prey populations, and other predators, control of wolves exhibiting predation pressure on prey populations or population segments (e.g., herds), control of depredating wolves on livestock, translocation of problem animals or restoration efforts, and purchase of lands for conserving wolves or prey populations within wolf range.

Information and education funds could be used for actively linking public knowledge about wolves, their ecology, and management among diverse interests through collaborative education programs. Trust-sponsored regional and national conferences would be held to advise contributors and stakeholders of progress and knowledge gained, and regular newsletters would be issued to provide updates on the status of regionally important wolf populations.

Funding Distribution

Funds from the Conservation Trust would be equally available to states, federal agencies, and private entities within their appropriate roles and jurisdictions for research, management, and information and education. One-third of the total funds available in any year could be used for each respective element (e.g., research, information, and education). Sharing of funds between agencies and private entities under collaborative or cost-sharing efforts, or combining funding elements would be an outcome of proposals and need. While funding of each element is important, flexibility to share funds among elements is also an important aspect of the intended program. Presuming that recovery of wolves will follow within 6-9 years of cessation of translocations, states, in collaboration with federal agencies, will have the primary role of managing wolves in the Northern Rockies. Similar actions will likely follow in other geographic areas where wolves are to be restored.

Administration

Non-governmental and apolitical entities with a demonstrated capacity to administer coopera-

tive funding efforts, such as the National Fish and Wildlife Foundation, the Yellowstone Association, and the Wolf Research and Education Center are logical entities to be considered for administering Conservation Trust funds. A scientific panel composed of U.S., Canadian, Mexican, and conservation science representatives would review and recommend project proposals for funding approval.

A 1:1 match of Wolf Conservation Trust funds is envisioned where a project is proposed by a state, federal, non-governmental, or academic institution. Matching funds would increase to 2:1 where a project involved two cooperating entities (e.g., state and federal or state and academic institution), and 3:1 matching funds for projects that involve cooperating state, federal, and non-governmental interests (e.g., state, local community, or private donation, and federal funds).

Finally, we recommend engaging the Canadian and Mexican governments for cooperation through existing conservation programs such as those that exist for the Duck Stamp, and environmental funding provisions of existing trade agreements as appropriate. The North American Office (U.S. Fish and Wildlife Service) currently in place to assist implementation of the Duck Stamp program and coordination of habitat acquisition in Canada serves as 1 example of how wolf conservation funds in Canada and Mexico might be coordinated.

Evidence for Success of a Conservation Trust

Notwithstanding a shortage of available funds and the proposed approach described above, what evidence is there that such an approach could be successful? Public interest and support for conserving large carnivores is high (U.S. Fish and Wildlife Service 1993). Two key reasons for people's interest in supporting efforts to restore large carnivores in Yellowstone and elsewhere are that they are important members of the natural community, and they were present historically (Bath 1989, Boise State University 1992, Duda and Young 1995). Primary concerns expressed, even by the general public that was supportive of restoring wolves to Yellowstone and central Idaho, include the wide-ranging nature of wolves, wildlife impacts that may affect elk and deer hunter harvest, prompt wolf control where and when necessary, and cost (U.S. Fish and Wildlife Service 1993).

Where funding shortages exist for maintaining the public interest regarding wildlife conservation or appreciation, voluntary conservation stamps were most favored by the public as a means of raising money to conserve wildlife (Duda and Young 1994). People want to pay for programs they feel are positive.

Lack of available funds at the state and federal level to match public interest in harvestable game populations has spawned successful non-government organizations such as the Wild Turkey Federation, Rocky Mountain Elk Foundation, Trout Unlimited, and the Foundation for North American Wild Sheep. On the basis of private donations alone, these organizations have expanded operating budgets, over short time periods, from 15 to 20 million dollars. While these efforts largely track a traditional interest in harvest of game populations by members, they too have contributed significantly to conservation efforts for many species through habitat improvements on public and private lands.

An extraordinary interest in non-game wildlife during the past decade has helped to generate a national constituency for recreational wildlife viewing. The inability of state and federal agency budgets to meet public demand for these programs and legislative indifference to Americans' interest in non-commodity values has resulted in increased support from recreationists and industry for legislation that would dramatically increase non-game wildlife funds.

Public interest in non-game and watchable wildlife is exceeded only by the level of interest and intrigue with carnivores.We propose that a unifying model for broad support of wolves is needed and perhaps, at some point in the future, a similar program for carnivores in general. A Wolf Conservation Trust may serve as a place to begin such efforts.

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The Economic Value of a Predator: Yellowstone Trout

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Abstract

Tens of thousands of people fish the streams of the Greater Yellowstone Ecosystem (GYE) each year. Several GYE streams have reputations as world class fly-fishing sites. The primary purpose of this paper is to understand the economic (or dollar) value that GYE anglers attach to the resource. To estimate these values, we use the travel cost method (TCM), modified to fit the diverse and special characteristics of GYE anglers. The secondary purpose of this paper is to paint a statistical portrait of the GYE angler.

During the summer of 1993, 1,075 self-administered surveys were distributed to anglers at 5 different sites in the GYE. About half the surveys were presented to interviewees and about half were left on windshields of parked cars. Surveys were distributed every day of the week and during a wide variety of hours. The survey contained 51 questions ranging in subject matter and including the angler's socio-economic characteristics, fishing skills and methods, travel cost and time, vacation plans and vacation alternatives, and willingness to pay additionally for GYE fishing. Thirty-six percent of the surveys (387) were returned and 22% (236) contained all the information necessary for statistical analysis.

Calculation of travel costs are based on 3 sections of the survey. Section 1 collected demographic data, measures of angler satisfaction, travel cost data, and on-site cost information. All anglers were asked to complete this section. Section 2 was to be filled out by anglers making a multi-day trip, but only to the GYE. Section 3 was filled out by individuals on a multi-day trip who were also visiting sites outside of the GYE. Those making day trips only filled out Section 1. Long-distance travel costs were separated from on-site costs. Long distance travelers on their way to another destination, whose plans would not have changed if they had not stopped, were assigned a travel cost of 0.

Travel cost appears to positively influence the number of fishing days. Of the demographic variables, age, marital status, and level of education are not statistically different from 0, but those who had children spent fewer days fishing.

Outdoor recreation expenditures are positively associated with visitor days. Of the angler variables, skill and catch rate are positive determinants of visitor days. The degree of congestion on streams negatively influenced visitor days, but was only statistically significant for the linear specification. Of the location attribute variables, anglers visiting sites on the Madison River and Yellowstone River spend more days fishing than those on the referent Slough Creek. Gallatin anglers also fish more days than the referent. Our research indicates that the value of the fishing resource in the GYE is substantial. Anglers are willing to pay significantly more for the privilege of fishing in Yellowstone National Park than they are currently required to pay. Fishing costs $5.00 per week or $10.00 per year currently, and our estimates indicate the average angler would be willing to pay an additional $45.00 to $75.00 dollars per day of fishing in the GYE.

Introduction

The Greater Yellowstone Ecosystem (GYE) is one of the most popular outdoor recreation sites in the United States and, for the multitudes enjoying its wonders, fly fishing is an increasingly popular activity. Several GYE streams have reputations as world class fly-fishing sites. These and nearby waters attract tens of thousands of anglers each year. A writer in the high profile *New York Times Magazine* recently called these waters "the center of the sport" of fly fishing (Raines 1991).

Although some of this acclaim is due to the GYE's natural endowments, a large portion is the result of management decisions made by resource managers in Yellowstone National Park (YNP) and the states of Montana, Idaho, and Wyoming. GYE fisheries management is a dynamic process, responding to changes in the natural environment and to changes in the way people view and use the fisheries resources. Most, if not all, management decisions must be made with an eye toward the opinions and perceptions of GYE anglers (Carty et al. 1987). All decisions must be implemented with scarce resources that could also be used to pursue other goals. Therefore, it is important that fisheries managers understand how GYE anglers will perceive their decisions.

The primary purpose of this paper is to explore an important aspect of these perceptions, namely, the economic (or dollar) value that GYE anglers attach to the resource. To estimate these values, we use the well-established travel cost method (TCM), modified to fit the diverse, and somewhat exceptional, characteristics of GYE anglers. Specifically, the method is modified to accommodate the fact that a large percentage of GYE anglers travel long distances to get to a fishing site.

We obtained data for statistical analysis from a survey of 1,075 anglers conducted at 5 different sites in the GYE during the summer of 1993. These data are also a rich source of information on the socioeconomic characteristics of GYE anglers, their spending patterns, and their ways of vacationing. The secondary purpose of this paper is to paint a statistical portrait of the GYE angler using these data.

The next section describes the survey and uses the survey data to describe GYE anglers. The modified TCM for estimating economic values is explained in Section III; Section IV presents and discusses the statistical results. In Section V, we present and discuss the estimates of the economic value of GYE fishing for the average angler. We end with a short overview.

Surveying the Greater Yellowstone Ecosystem Angler

During the summer of 1993, 1,075 self-administered surveys were distributed to anglers at 5 different sites in the Greater Yellowstone Ecosystem (GYE). The survey sites included 2 different sites on the Madison river in Montana, 1 below and 1 above Quake Lake; and 3 different sites within YNP: Slough Creek, the Gallatin River, and the Yellowstone River above the Grand Canyon. In all cases, the survey began with a cover letter explaining the purpose of the survey and asking for the angler's cooperation.

In about half the cases, surveyors personally presented anglers with the survey instrument either at their cars or on the stream, gave them a brief de-

scription of the survey's purpose, and asked them to return the survey in the addressed, stamped envelope provided. In the remainder of the cases, the survey was left on the windshields of parked cars at popular parking locations near the stream. Surveys were distributed every day of the week and during a wide variety of hours (morning, afternoon, and evening).

The survey contained 51 questions ranging in subject matter and including the angler's socio-economic characteristics, fishing skills and methods, travel cost and time, vacation plans and vacation alternatives, and willingness to pay additionally for GYE fishing.

During the next 4 months, 387 (36%) of the surveys were returned and 236 (22%) of those contained all the required information for our statistical analysis. Thirty-two percent of the responses were from the Yellowstone; 22% from the Madison below Quake Lake; 30% from Slough Creek; 10% from the Gallatin; and 6% from the Madison above Quake Lake. These proportions correspond approximately to the proportions of surveys distributed at each site.

The responses provide an interesting picture of the GYE angler. A few variables are shown graphically in Figure 1, while descriptive statistics for all of the variables used in the statistical analysis are presented in Table 1.

Respondents were generally middle aged (average age 43.5 years), highly educated (the mode response was "graduate degree"), married males (93%). They were predominantly, and surprisingly, wealthy. The mode response to the question of household annual income was "greater than $100,000." Household income averaged slightly more than $50,000; and more than 53% of the respondents reported annual incomes of $60,000 or more.

On average, respondents spend nearly 12 days fishing the GYE during the May-October season, as well an additional 4 days in the GYE not fishing. While only 8% fish a single day, 63% fish from 2 days to 2 weeks and 8% fish from 30 days to every day of the season. There is a strong correlation between days spent fishing and total days spent in the GYE ($P = .67$).

Respondents seem to spend a large share of their incomes on recreation. The responses to a question about annual expenditures on outdoor recreation averaged $1,347, with 23% of respondents spending more than $2,000 per year. A healthy portion of this is spent locally. Respondents spent an average $26.50 on the previous night's camping or lodging and nearly $16 on tackle to enhance the day's fishing. Thus, a typical angler will spend $510 on accommodations and tackle during a summer fishing trip to the GYE.

Respondents consider themselves skilled anglers, with an average self-ranking of 7, on a 1-10 scale. The vast majority are fly fishermen; 93% reported using dry flies and 61% used nymphs. Only a trivial number used bait or lures. Respondents reported seeing an average of 19 other anglers, but there was wide variation. One-third of the respondents reported seeing 8 or fewer other anglers; 11% saw 35 or more.

With a catch rate of about 1 trout per hour, the average angler caught 5.4 trout on the day surveyed, but this statistic masks the bimodal nature of the catch, as illustrated in Figure 1. While 20% of the anglers caught no fish, 24% caught between 2 and 5 fish, 12% caught between 11 and 20 fish, and a lucky 3% reported catching more than 20 fish.

The data indicate a positive simple correlation between the angler's skill and his catch ($P = .37$) and a negative but small correlation between catch and the number of other anglers seen ($P = -.04$). Nearly 95% of the trout caught were reportedly released. The number of whitefish caught was very small compared to the number of trout.

A Travel Cost Method for the Yellowstone Angler

The simple travel cost method (TCM) for measuring the benefits of a recreational resource was first proposed by Hotelling (1949) in a letter to the Director of the National Park Service. The basic model posits that the recreationist will continue to visit a particular recreation site until the marginal benefit of the last trip is just equal to the cost of getting there. This assumption allows data on visits to a site and the costs of those visits to be used to estimate a demand curve of the form:

$$G(V) = \alpha + \delta * TC + X\gamma + Z\tau + \varepsilon \qquad (1)$$

where G(V) is a monotonic function of the number of visits to a site, V; TC is the travel cost to the site; X is a vector of recreationist's characteristics; Z is a vector of site characteristics; α, γ, and τ are conformable vectors of unknown parameters to be estimated, and ε is a random error. The X and Z vectors act as

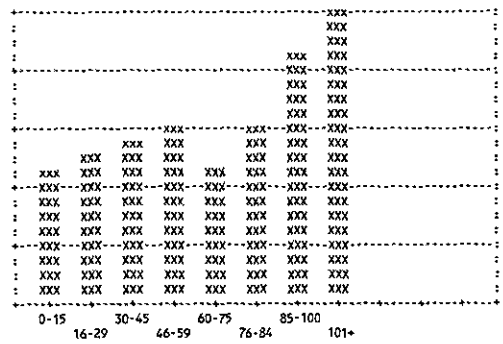
demand shifters. The area under the demand curve and above the mean TC gives an estimate of the economic value of the site.

Numerous researchers have developed and refined the basic TCM (see references in Bockstael et al., 1991) and have produced hundreds of applications. Throughout this development, however, researchers have been uncomfortable with using the simple TCM with data from long-distance travelers. For example, Smith and Kopp (1980) argue that the assumptions of the simple TCM become less tenable as travel distance increases and that a single model is unlikely to apply to both the short- and long-distance traveler. They demonstrate that the estimated coefficients may be unstable as distances traveled to the site vary widely. Shaw (1991) reports that long distance travelers were too often simply dropped from the statistical analysis.

This concern led Bell and Leeworthy (1990) to propose and apply an expanded TCM tailored to the case of long distance travelers. They propose a demand model of the form

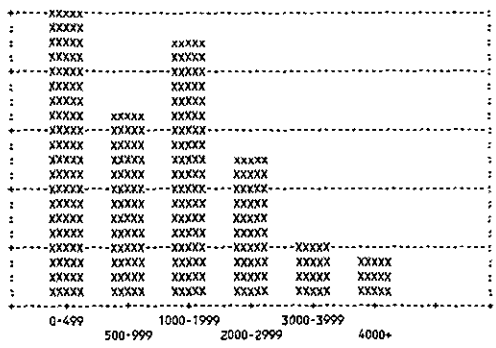
$$G(V) = \alpha + \beta*OSC + \delta*TC + X\gamma + Z\tau + \varepsilon \quad (2)$$

where OSC stands for on site cost, the cost of visiting the recreation site, the larger expenditures for travel, TC, have been made, and β is an unknown parameter to be estimated. In this formulation, TC becomes just another demand shifter, while OSC

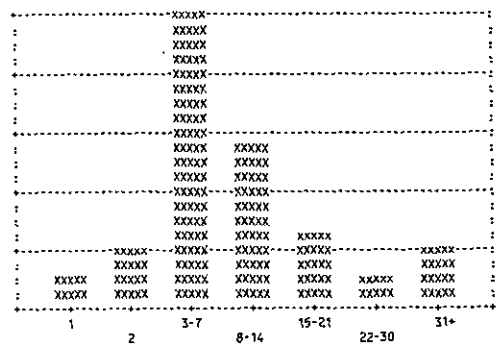


Household Income

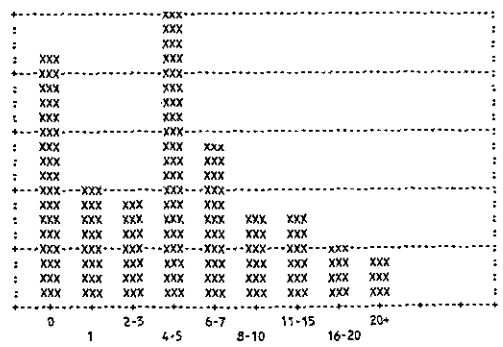
Figure 1. Survey Tables



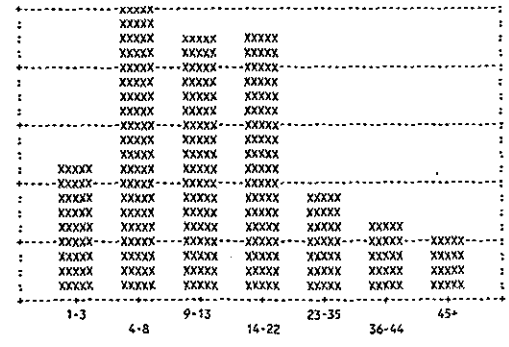
Outdoor Recreation



Days Fishing in GYE



Fish Caught



Number of Anglers Seen

takes the role of the price that rations visits. Computing the area under the demand curve and above the OSC that just eliminates visits gives an estimate of the economic value of the recreation resource.

Many visitors travel long distances to visit the GYE; more than 1/3 of our sample report traveled 1,100 or more miles to reach the GYE. Simply dropping these individuals from the analysis would undermine the generality of our results. Conversely, some GYE anglers are from nearby communities and, for others, a trip to the GYE is part of a vacation with 2 or more destinations. A visit to the GYE may add only marginally to their travel expenses. The use of a TCM requires a specification that can accommodate these heterogeneous users of the GYE. We therefore adopt the Bell and Leeworthy TCM as being especially well suited to our purpose. In this model, the short and long distance travelers' behaviors can be modeled realistically in the same equation. For the short-distance traveler TC = 0 and OSC > 0. This may also be true for the long-distance traveler stopping in the GYE on the way to another destination.

We estimate an equation corresponding to the second equation. The variable definitions and their sample means and standard deviations are given in Table 1. Explanatory variables are broken into 4 broad categories: costs, demographic characteristics, angler attributes, and location attributes. Demographic variables include age (AGE) and the square of age (AGESQ), gender (GENDER), marital status (MARRIED), the number of children (KIDS), and education level (EDU). Angler characteristics include angler's self-ranking of skill (SKILL), catch rate per hour of fishing (CATCHPH), number of anglers encountered (NUMANG), and a binary variable (PRIMP) equal to 1 if the primary purpose of the visit to the area was for fishing and 0 otherwise. As a measure of income, we use reported annual expenditures on outdoor recreation (OREXP).

The different attributes of the 5 locations surveyed are crudely measured by a set of binary or dummy variables: GALLATIN = {1,0} for the Gallatin River, MADABOVE = {1,0} for the Madison River above Quake Lake, MADBELOW = {1,0} for the Madison River below Quake Lake, and YELLOW = {1,0} for the Yellowstone River. Slough Creek is the referent site.

Our calculations of travel costs are based on 3 sections contained in the anglers' survey. Section 1 of the survey collected demographic data, measures of angler satisfaction, travel cost data, and on-site cost information. All anglers were asked to complete this section. Section 2 was to be filled out by anglers making a multi-day trip, but only to the GYE. Section 3 was filled out by individuals on a multi-day trip who were also visiting sites outside of the GYE. Those making day trips only filled out Section 1.

Long distance travel costs to the GYE were separated from on-site costs differently for the 3 classifications of visitors. Recreationists making a day trip had all costs associated with their visit allocated to on-site costs. Individuals making multi-day trips to the GYE were assigned on-site costs equal to the sum of their single day travel cost to the site, costs for the prior nights lodging, and costs for fishing equipment dedicated to the day's use. Long distance travel costs were based on the cost of getting to and from the GYE from their home.

To classify individuals visiting the GYE as part of a larger trip, we asked these individuals if their total driving distance changed due to their stop in the area. If individuals were driving through the GYE on their way to another destination and indicated that their

Table 1. *Descriptive statistics.*

Variable Name	Variable Definition	Mean	SD
FYEL	Days fishing in GYE during season	11.64	13.51
LN (FYEL)	Natural log of days	1.99	0.94
OSC	On site costs	70.27	51.63
TC	Cost of travel GYE	442.64	459.74
PRIMP	1 or 0 if fishing is primary purpose of trip	0.94	0.23
AGE	Age in years	43.55	14.47
AGESQ	Age in years squared	2104.70	1289.40
CATCHPH	Catch rate of trout per hour	0.92	1.14
SKILL	Self-ranking of fishing skill (0-10)	7.00	2.10
NUMANG	Number of fellow anglers seen	18.68	16.24
KIDS	Number of children	1.55	1.56
MARRIED	1 or 0 if married	0.68	0.46
OREXP	Expenditures on outdoor recreation	1352.00	1472.20
GENDER	1 for males, 0 for females	0.932	0.252
EDU	Level of education	5.101	1.25
GALLATIN	1 or 0 if Gallatin fishing site	0.11	0.31
MADABOVE	1 or 0 if Madison above Quake Lake site	0.06	0.22
MADBELOW	1 or 0 if Madison below Quake Lake site	0.32	0.47
YELLOW	1 or 0 if Yellowstone site	0.21	0.49

long distance travel plans would not have changed if they had not stopped in the area, we assigned them a long distance travel cost of 0. If their trip mileage did change because of coming to the GYE, we calculated their marginal increase in mileage traveled to visit the area. For example, if a family left Portland, Oregon, and visited 2 recreation areas, Glacier National Park in Montana and Yellowstone National Park in Wyoming, we calculated the additional mileage that going to Yellowstone added to their trip. Mileage was calculated from the Rand McNally Road Atlas.

Our sample included individuals who flew, drove private cars, rental cars, and motor homes. Costs per mile for private cars, car-trailer units, trucks, and vans were obtained from the U.S. Department of Transportation and adjusted for inflation. Rental car and mobile home costs were estimated from information obtained from several area rental businesses.

Airfares were estimated by collecting a sample of airfares from 60 different locations across the U.S. to Jackson, Wyoming, and Bozeman, Montana. Using these data, we estimated the following cost function for airline travelers:

$$\text{Airfare} = 280.9 - 146.28*D + .1401*\text{DIST} + .0654*(\text{DIST}*D) \quad (3)$$

where DIST is one way airline distance, and D = {1,0} depending on whether the trip distance is greater than or less than 1,500 miles. For air travel costs, we used fitted values obtained by substituting the distances traveled by respondents into the third equation.

We use ordinary least squares to estimate 2 specifications of the second equation. The first specification is a linear model, where G(V) = FYEL and FYEL is the number of days spent fishing in the GYE during the May-October season. The second specification is a semi-log model, where G(V) = LN(FYEL). The parameter estimates for both models are reported in Table 2.

The estimation results are generally as expected and qualitatively invariant across specifications. As predicted by theory and found by Bell and Leeworthy (1990) and Hof and King (1992) OSC costs are negatively related to visitor days. Using a one-tailed test, the estimates are significant at the $\alpha < .05$ level for both specifications.

TC appears to positively influence the number of fishing days in both specifications. Although theoretically the sign of this coefficient is ambiguous, the negative sign found here is consistent with the findings of Bell and Leeworthy (1990), but not Hof and King (1992). This finding implies that an increase in long distance travel costs (e.g., increased airline fares) provides an incentive to spend more days visiting the GYE per trip. Although fewer trips would be made, the net effect is more days spent fishing the GYE in a season.

Of the demographic variables, the effects of AGE, marital status, and education are not statistically different from 0. KIDS has a negative effect and the result is statistically significant ($\alpha < .05$) for the semi-log model. Outdoor recreation expenditures positively influence visitor days, and significantly so for LN(FYEL).

Of the angler attributes, SKILL and catch rate (CATCHPH) are positive and very significant determinants of visitor days for both specifications. As expected, the coefficient for the congestion variable (NUMANG) is negative, but significant only for the linear specification ($\alpha < .05$, one-tail test).

Table 2. Travel Cost Model estimates.

(Coefficient estimates and t-statistics)

Name	FYEL		LN (FYEL)	
Constant	5.26	8.27	0.476	0.900
OSC	-0.031	-1.86	-0.0024	-2.194
TC	0.004	2.17	0.0005	4.377
PRIMP	6.07	1.67	1.266	5.363
AGE	-0.37	-1.18	-0.013	-0.065
AGESQ	0.006	1.75	0.0002	1.070
CATCHPH	1.97	2.59	0.114	2.308
SKILL	1.21	2.85	0.075	2.700
NUMANG	-0.095	-1.69	-0.004	-1.116
KIDS	-0.88	-1.41	-0.080	-1.973
MARRIED	-2.42	-1.14	-0.123	-0.897
OREXP	0.0006	1.073	0.0008	2.032
GENDER	-6.36	-1.88	-0.123	-0.562
EDU	0.40	0.56	-0.2556	-0.552
GALLATIN	0.22	0.076	-0.044	-0.233
MADABOVE	1.38	0.36	0.356	1.433
MADBELOW	7.13	3.13	0.414	2.790
YELLOW	2.31	1.05	0.086	0.602
R-SQUARED	0.25	0.19 ADJ	0.34	0.29 ADJ

The location attribute variables indicate that anglers visiting sites on the Madison River and the Yellowstone River are associated with more days of fishing than are anglers of the referent Slough Creek. In the FYEL specification, Gallatin anglers fish more days than the referent, ceteris paribus, while the opposite result is found using LN(FYEL). Singly, the MADBELOW is the only significant coefficient; however, Chow tests indicate that the other location variables are statistically significant as a group.

The estimates of both equations yield respectable goodness of fit measures. The percentage of total variation explained by the FYEL and LN(FYEL) equations are .25 and .34, respectively. Likelihood ratio tests that all the coefficients except the constant are zero lead to rejection of the null hypotheses with probability values of effectively 0.

The Economic Value of Yellowstone Trout

The estimation results can be used to calculate the economic value of GYE fishing for the average angler. This value has been named consumer surplus. Consumer surplus is defined as the difference between the total amount that anglers would be willing to pay to fish for GYE fishing and the amount that they actually do pay. Given our estimates of the demand curve for fishing days from equation 3, this difference is the area underneath the demand curve and above the sample average OSC. See Bell and Leeworthy (1990) and Hof and King (1992) for details.

Our estimates of economic value per day of fishing are in Table 3. Different estimates appear for the two demand curve specifications and, because the respective intercepts differ, for each of the 5 fishing sites.

The estimates indicate that anglers obtain substantial consumer surplus from GYE fishing, even after paying long-distance travel costs and on-site costs. For the linear specification, estimated consumer surplus per day of fishing ranges from $185 to $191, depending on the site. For the semi-log specification, the estimates are considerably smaller, ranging from $47 to $75.

Both sets of estimates indicate that the streams of the GYE are valuable resources. In theory, the anglers would be willing to pay any amount less than their consumer surplus for the opportunity to use these resources. Whether anglers could or would actually be charged such amounts depends on complex factors such as political institutions, resource managers' decisions, and, of course, the quality of our estimates.

However, in assessing the quality of the estimates presented here, it is disturbing that the levels of the estimates are so sensitive to specification and vary by factors of 2.5 to 4.6. We consider 3 approaches with respect to determining which of the 2 sets of estimates is likely to be more reasonable.

The first approach is to correct the linear model estimates for possible statistical biases, following an approach outlined by Bell and Leeworthy (1990). In this approach, linear model estimates are divided by $(1+1/t^2)$, where t is the absolute value of the t-statistic for the OSC coefficient in the linear model. These corrected estimates (shown in Table 3) are 22% less than the first FYEL estimates. The linear and semi-log consumer surplus estimates now differ by factors from 3.1 to 1.9.

The second approach is to compare the present results with those in the extant literature. The only recent research on blue-ribbon Western streams that we know of is Duffield et al. (1992). These authors used an alternative method (contingent valuation) to obtain measures of economic value for high quality trout fishing in Montana's Big Hole River. Casual observation suggests that the Big Hole is similar to the waters considered in this study.

For the average non-resident Big Hole float angler, Duffield et al. (1992) estimate a consumer surplus $2,234 per trip, or $586 per day. A corresponding figure for the Montana resident angler is $194 per day. The former estimate is substantially greater than our highest consumer surplus estimate and the latter is about the same as uncorrected estimates we

Table 3. Economic value by fishing site ($/day).

	GALLATIN	MADABOVE	MADBELOW	YELLOW	SLOUGH
FYEL	191.36	187.75	184.95	187.73	191.35
FYEL (corrected)	148.06	145.54	143.37	145.53	148.33
LN (FYEL)	47.46	70.80	75.34	54.05	49.59

obtain from the linear specification.

Recognizing that their figures are at the upper end of the reported range of values for cold water fisheries, Duffield et al. (1992:2177) defend their estimates, saying, "It also appears that values for non-resident anglers on a major 'destination' trout fishery like the Big Hole may be quite high. These values may be plausible given the income level, trip length, and expenses of this group of dedicated anglers."

A third approach to examining the quality of our estimates is the econometric way of testing which of the 2 specifications more fully represents the behavior of our survey respondents. To do this, we conducted a J-test of the null hypothesis that G(V) = FYEL compared to the alternative hypothesis that G(V) = LN(FYEL) (see Green 1993:321-322 for details). Results of this test indicate rejection of the null hypothesis and provide evidence in favor of the semi-log specification. This suggests that the lower consumer surplus values reported in Table 3 are the most reliable.

Conclusion

Management of the fishing resources in Yellowstone National Park is a contentious issue. In a recent interview, John Varley, Yellowstone National Park Chief of Resources, says (La Pierre 1993:40), "A growing number of people question the practice of fishing in the parks. Their argument is simple—the harvest of fish by angling is fundamentally at odds with the mandate of the Park Service to maintain natural ecosystems in a 'unimpaired' condition."

Our research indicates that the value of the fishing resource in the GYE is substantial, and that management decisions regarding fishing regulations have a significant effect on the welfare of anglers throughout the country. Anglers are willing to pay significantly more for the privilege of fishing in YNP than they are currently required to pay. Currently, fishing fees in YNP are $5.00 per week or $10.00 per year. Our estimates indicate the average angler would be willing to pay an additional $45-$75 dollars per day of fishing in the GYE.

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The Common Raven: Field Notes on an Important Yellowstone Predator

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Abstract

The role of the common raven (*Corvus corax*) as a predator in Yellowstone has been largely overlooked. The information presented here is based on 9 years of field observations recorded by the author. Three points are discussed in detail, namely raven morphology, food habits, and anecdotal observations on behavior and predation. Morphology and behavior suggest that common ravens are quintessential Yellowstone predators that specialize in killing small- to medium-sized prey. Seasonal availability and abundance of food plays an important role in raven predation. Ravens merit systematic study to better understand their functional ecological role in the Yellowstone ecosystem.

Introduction

The life history of the common raven (*Corvus corax*) in Yellowstone has largely been ignored due to attention given to other more dramatic species of wildlife. Although this bird was undoubtedly observed in Yellowstone by native peoples and early white explorers, the first scientific documentation of the species occurred in August 1872 by C. Hart Merriam, official ornithologist for the Hayden Expedition (Hayden 1873).

Past and current information collected on the common raven has centered primarily on general observations of raven occurrence and behavior. The author's field notes, excerpted for this paper, document the common raven as an important Yellowstone predator.

Methods

Located primarily in northwestern Wyoming, but also in portions of southwestern Montana and eastern Idaho, Yellowstone National Park comprises 898,714 hectares. The information presented here is the result of 9 years of incidental observations made by the author in the park and recorded in field notebooks.

Field Notes and Discussion

Examination of raven morphology, food habits, and predatory behavior provides support for the role of the common raven as an important Yellowstone predator.

General Raven Morphology

Of the 10 species of ravens found worldwide, all are represented under 1 genus. The common raven is the largest North American passerine or perching bird. In North America, ravens are lumped into 1 family (Corvidae) along with relatives such as jays, crows, magpies, and nutcrackers (Monroe and Sibley 1993). In comparison to their paraneotropical relatives, corvids found in the far northern latitudes of North America exhibit rather drab coloration, occupy

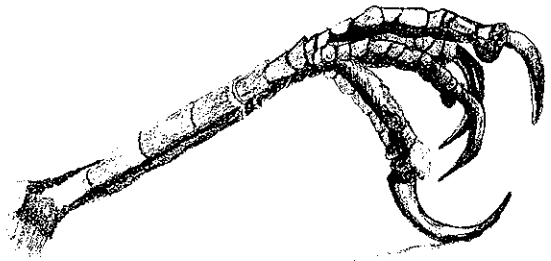
limited habitats, and number fewer species. All North American corvids produce a wide range of calls, and all have nostrils covered by narial feathers, with the exception of the pinyon jay (*Gymnorhinus cyanocephalus*) that has exposed nostrils. Corvids represent a highly advanced group of birds and are considered extremely intelligent.

The raven is represented in North America by 2 species, the Chihuahuan raven (*Corvus cryptoleucus*) and the common raven. The Chihuahuan raven may be distinguished from the common raven by its smaller size, its characteristic high-pitched voice, hidden white feather bases at the neck and breast, and narial feathers that extend farther onto the bill. It is found primarily in low elevation deserts of the southwest composed of mesquite (*Prosopis chilensis*) and yucca (*Yucca* spp.). Common ravens, in comparison, are much more general in distribution and can occupy mountains, canyons, boreal forests, and tundra in addition to desert habitats.

Ravens can produce a casting or pellet similar to those produced by other aerial predators such as raptors. The casting forms in the gizzard and is composed of hair, feathers, bone, insect exoskeletons, or similar items that are difficult to digest (Craighead and Craighead 1956). The casting is ejected in pellet form when enough decomposed material has built up in the gizzard.

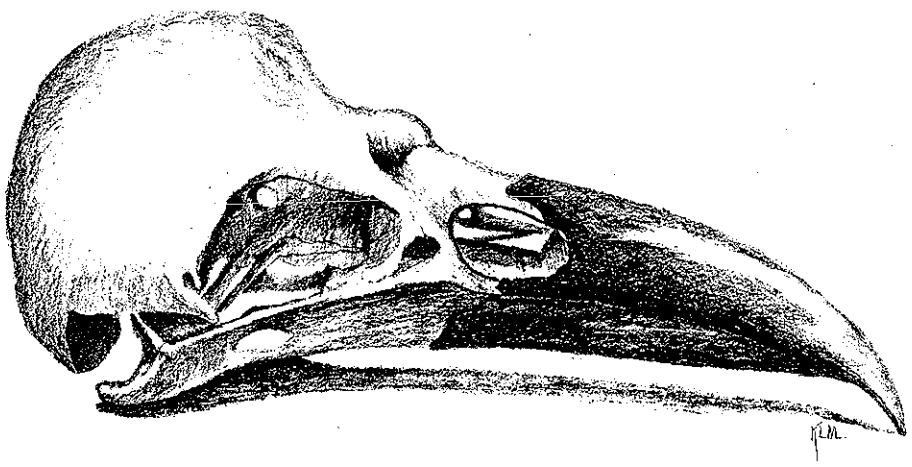
The bill of the common raven is long and laterally flattened. The nostrils are oval and are covered by narial feathers arranged posteriorly (Figure 1). The narial feathers keep the nostrils clear of debris and serve also to keep the nostrils warm during cold weather and cool during hot weather. At the posterior end of the maxilla is an important projecting point known as the dertrum. The dertrum is a key structure for ravens since it helps them secure and, more importantly, dismantle, dismember, pulverize, and kill prey. Because the bill is laterally flattened, it allows ravens to pick up food items on relatively flat surfaces with their tomium (i.e., the edge of the bill). The long beak serves other important functions such as probing, dismantling, and consuming carrion or carcasses without allowing many feathers to become bloodied or otherwise soiled.

Figure 2. The tarsus and foot of the common raven, showing the unique scutellate and booted investments on the tibiotarsus, the large hallux, and raptorial-like feet.



An examination of the raven tarsi and feet reveals some other interesting morphological adaptations. The tibiotarsal bone is moderate in length. Ravens have an ansiodactyl foot configuration, typically found in many passerines (Proctor and Lynch 1993). The ansiodactyl foot has the characteristic 3 toes pointing forward (digits 2, 3, 4) and 1 toe point-

Figure 1. The skull of the common raven showing the laterally flattened bill, oval nostrils, and the dertrum.



ing backward (digit 1). The hind toe (digit 1) is often referred to as the hallux (Figure 2).

The foot is, in essence, a modified raptorial foot used for grasping and securing prey. The scutes found on the tibiotarsus are arranged differently in each species or group of birds and are termed an investment. Anteriorly, the investment of scutes on a raven's foot has a scutellate arrangement, with the smaller individual scutes overlapping one another. Posteriorly, the scutes have a booted arrangement and thus resemble 1 long scute. This particular scute configuration is unusual in passerines and can be found in only a few species of birds, such as the gray catbird (*Dumetella carolinensis*) (Proctor and Lynch 1993).

Raven Food Habits in Yellowstone

The food habits of the common raven have been documented throughout North America (Bent 1964, Heinrich 1989, Nelson 1934). However, information on raven food habits is lacking in Yellowstone. Because of the wide variety of foods utilized in other areas, ravens are generally considered omnivorous. In Yellowstone, ravens consume a small amount of vegetative matter, particularly pocket gopher (*Thomomys talpoides*) caches in the spring, and whitebark pine (*Pinus albicaulis*) seed caches and juniper (*Juniperus spp.*) berries in the fall. Ravens also consume reptiles and amphibians during the spring,

Table 1. Live prey taken by common ravens in Yellowstone 1986-1995, based on personal field observations.

Very Small Prey
earthworms (Oligochaeta)
stoneflies (Plecoptera)
butterflies (Lepidoptera)
moths (Lepidoptera)
grasshoppers (Orthoptera)
Mormon crickets (Orthoptera)
brineflies (Diptera)
beetles (Coleoptera)
mayflies (Ephemeroptera)

Small Mammals
Uinta ground squirrel (*Spermophilus armatus*)
red squirrel (*Tamiasciurus hudsonicus*)
yellow pine chipmunk (*Tamias ameonus*)
Nuttall's cottontail (*Sylvilagus nuttallii*)
snowshoe hare (*Lepus americanus*)
white-tailed jackrabbit (*Lepus townsendii*)
northern pocket gopher (*Thomomys talpoides*)
deer mouse (*Peromyscus maniculatus*)
montane vole (*Microtus montanus*)

Fish
cutthroat trout (*Oncorhynchus clarki*)
mountain sucker (*Catostomus platyrhynchus*)

Bird Eggs
osprey (*Pandion haliaetus*)
great gray owl (*Strix nebulosa*)
trumpeter swan (*Cygnus buccinator*)
Canada goose (*Branta canadensis*)
mallard (*Anas platyrhynchos*)
gadwall (*Anas strepera*)
green-winged teal (*Anas crecca*)
lesser scaup (*Aythya affinis*)
American coot (*Fulica americana*)
killdeer (*Charadrius vociferus*)
spotted sandpiper (*Actitis macularia*)
dark-eyed junco (*Junco hyemalis*)
olive-sided flycatcher (*Contopus borealis*)
western tanager (*Piranga ludoviciana*)
American robin (*Turdus migratorius*)
yellow-headed blackbird (*Xanthocephalus xanthocephalus*)
red-winged blackbird (*Agelaius phoeniceus*)
Brewer's blackbird (*Euphagus cyanocephalus*)

Nestlings/fledglings
(same species listed under bird eggs but including)
Barrow's goldeneye (*Bucephala islandica*)
ruby-crowned kinglet (*Regulus calendula*)
mountain bluebird (*Sialia currucoides*)
yellow-rumped warbler (*Dendroica coronata*)

summer, and fall, but they represent a relatively small percentage of the overall diet. Small insects are consumed during the warmer months but are difficult to identify and quantify. Other, not so obvious and "unnatural" food items consumed by Yellowstone ravens include those obtained from garbage cans, dumpsters, sewage ponds, and from human visitors in the form of handouts. Although some of the items previously mentioned are scavenged, ravens can be predatory as evidenced by the prey species observed taken by ravens in Yellowstone (Table 1).

Ravens are a significant egg predator in Yellowstone (Table 1). They can break and eat eggs on location, transport eggs for later consumption, or carry eggs to young in the nest. Small eggs are often transported whole and can be concealed in the mouth and sublingual pouch, a sack-like extension on the floor of the mouth. Ravens commonly carry medium-sized bird eggs visibly lodged between the maxilla and the mandible. Large eggs are often eaten on location, but have been observed being transported in a skewered fashion with the bill piercing the shell.

Ravens also eat carrion, and serve an important function by acting as carrion guides, alerting other predators/scavengers and conspecifics that a carcass is nearby. Upon locating the carcass, mammalian scavengers proceed to open it, thus benefiting their raven guides as well as a myriad of other scavengers.

In general, predation by the common raven is much more seasonal and ephemeral compared to scavenging behavior and largely depends on prey availability and abundance. When food is readily available, such as in the late spring and summer, ravens take on the role of predators. In the fall and winter, however, they function more as scavengers and carrion guides.

Anecdotal Information on Raven Predation and Behavior

Ravens have keen eyesight and are quick to pick up on behavioral clues of prey or other predators. The common raven in Yellowstone specializes in hunting small- to medium-sized prey. They hunt prey by employing techniques used by other avian predators (e.g., buteos, harriers, eagles, gulls, flycatchers, and owls). The following are some first-hand accounts of ravens capturing or securing live prey in Yellowstone.

Capturing Cutthroat Trout

April 17, 1987: A pair of common ravens was standing on a sandbar on a tributary of the Yellowstone River in Hayden Valley. A bald eagle (*Haliaeetus leucocephalus*) had just left the site with a cutthroat trout (*Oncorhynchus clarki bouveri*) in its talons. The ravens employed the same capture technique used by the eagle. They waited on the sandbar until a fish ascended a riffle in the creek. Then 1 raven walked out in the water and pulled the fish by its dorsal fin until it was completely out of the water and on the sandbar. The raven proceeded to pulverize the fish with its beak until the fish was lifeless. It then broke apart the .91 kg fish, collected all it could in its mouth and sublingual pouch, and flew off low over sagebrush (*Artemisia spp.*) until it was out of sight. The other raven approached the carcass. It too filled its mouth and pouch and flew off to cache the food. The process was repeated until the entire fish was dismantled and cached. Then a second spawning fish was caught by the ravens, killed, and cached in a similar fashion. In a 3-hour period, the 2 ravens caught, killed, and cached 12 cutthroat trout.

Stealing Olive-sided Flycatcher Young

June 18, 1994: An adult olive-sided flycatcher (*Contopus borealis*) was making repeated alarm calls from a lodgepole pine (*Pinus contorta*) stand along Antelope Creek. Another adult flycatcher arrived and the noises increased. The flycatchers were in a tree about 10.7 meters off the ground. A raven was perched nearby in the top of a lodgepole pine. The raven flew and landed in the middle of the tree where the flycatchers were perched and the flycatchers became noisier. The raven hopped from branch to branch, walking the length of each branch from the bole to the branch tips, apparently searching the bark. The raven soon found the carefully concealed flycatcher nest on a horizontal branch and flew off with 3 nestlings in its mouth.

Stealing Eggs from Ospreys

May 3, 1988: A female osprey (*Pandion haliaetus*) was incubating eggs on a nest in the Grand Canyon of the Yellowstone. A common raven flew by and spotted the nest. The raven stole part of a fish that was on the nest and the female osprey pursued the

raven. A second raven flew in and stole 1 of the eggs. The male osprey chased the second raven who had the egg visibly lodged between the upper and lower mandibles.

Hunting Pocket Gophers

September 19, 1993: A great gray owl (*Strix nebulosa*) was observed hunting pocket gophers in a meadow near Canyon. A common raven flew by while the owl was on the ground with its prey. When the owl noticed the raven, it quickly swallowed the pocket gopher whole and returned to its normal hunting perch. The raven flew to the top of a lodgepole pine and watched the great gray owl. After watching the owl for awhile, the raven flew, landed on a small tree, and eyed the meadow. After about 6 minutes, the raven spotted something, flew to the ground, and came up with a pocket gopher. The raven smashed the gopher with its beak until the gopher was lifeless, swallowed the prey whole, and then headed south with a full crop.

Dismembering Large Prey

February 10, 1995: A cow bison (*Bison bison*) was observed stuck in the mud on the Madison River near Mt. Holmes. Two common ravens were observed close to the live, helpless bison. Three hours later, the ravens were even closer to the exhausted bison and continued to approach it. By this time, the head of the bison was propped on the ground in exhaustion. The large mammal was still alive, as indicated by the open eyes and steam coming out of its nostrils. The ravens proceeded to peck both eyes out of the live bison, 1 at a time. Surprisingly, the ravens succeeded in incapacitating this large mammal.

Conclusion

The morphology and behavior of the common raven suggest its functional importance as a predator in the Yellowstone ecosystem. But perhaps because ravens secure small- to medium-sized prey, predatory behavior often goes unnoticed and, therefore, is not well understood. In general, when food is plentiful, ravens function primarily as predators. When food is scarce, ravens function more as scavenger/carrion guides and feeders. Apparently, seasonal availability and abundance of food play an important role in raven predation. It is likely that ravens as predators affect prey populations in some instances, though it is not known if composition, abundance, and/or distribution of prey are significantly altered. Obviously, raven predation merits much more systematic scientific study.

Acknowledgments

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Predation on Reintroduced Beavers in Wyoming

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Abstract

Beavers (*Castor canadensis*) alter riparian landscapes through dam building and woodcutting, activities that affect terrestrial and aquatic flora and fauna. In Wyoming, beavers are absent from many areas due to past over-harvest, disease, or conflicts with man. Reintroduction programs have been implemented in many states to restore some of the lost benefits that beavers can provide. We initiated a study in 1994 to examine the feasibility of reintroducing beavers into unoccupied habitat for the purpose of riparian improvement and wetland creation. From August 1994 to August 1995 we trapped and implanted radio transmitters in 22 adult beavers. Additionally, we trapped 17 subadult beavers. Animals were transplanted to 4 locations in Wyoming; 32 km west of Cody, 48 km south of Rock Springs, 32 km north of Sundance, and 32 km east of Saratoga. As of August 31, 1995, only 4 radio-marked beavers were known to be alive. Seven telemetered beavers and 15 non-telemetered beavers have unknown fates but are presumed to be dead. The remaining 13 beavers were confirmed dead at the various study sites. Evidence from hair and bite wound samples indicate that 3 beavers were killed by grizzly bears (*Ursus arctos*), 4 were killed by coyotes (*Canis latrans*), 4 were killed by black bears (*Ursus americanus*), and the remaining 2 animals died from wounds inflicted by unknown predators. Predation on naturally dispersing beavers may influence occupancy rates and habitat modification in unoccupied areas.

Introduction

Great interest has been expressed in improving riparian areas for wildlife, livestock, and humans (Apple et al. 1985). Beavers, through their dam-building activities, can increase water storage, reduce sedimentation, and improve vegetation communities (Naiman et al. 1988). Like many western states, Wyoming has been very interested in using natural methods to improve riparian areas (Collins 1993). Beavers can be used to realize these benefits and many states have undertaken beaver translocation programs (Butler 1991, Hill 1987).

In 1994, we initiated a study to: 1) document the effects of beavers on riparian areas in Wyoming, 2) determine the best methods of trapping and translocating beavers, and 3) monitor beaver movements, survival, and habitat changes that occur as a result of beaver translocations. Montana, Colorado, Idaho, Oregon, and Wyoming have all initiated transloca-

tion programs, but definitive studies have not been done to address the above objectives. This paper will address survival and mortality of beavers introduced for the purposes of riparian enhancement and wetland creation. The findings reported herein are preliminary results from 2 field seasons of work. At least 1 field season of data remains to be collected.

Study area

Beavers were translocated into various habitats throughout Wyoming. All habitats had perennial water sources and sufficient vegetation to support beaver. Release sites are shown in Figure 1; vegetation types and elevations listed by release site are given in Table 1.

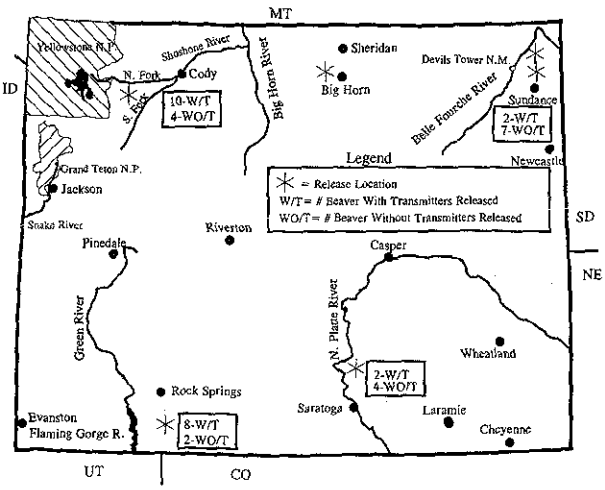
Methods

Beavers were trapped from areas where their activities were in conflict with landowner practices (e.g., irrigation). All beavers were trapped from colonies that were dam and lodge builders (creek-dwelling beaver) as opposed to bank denning, non-dam builders (river beavers). We felt that these animals would be more likely to create the desired habitat and would be more successful at avoiding predation. Snares and Hancock live-traps were used to trap all animals (Krause, no date). Animals >55 kg were implanted with Advanced Telemetry Systems (Isanti, Minnesota) model 17 internal telemetry transmitters using techniques described by Davis et al. (1984). All transmitters were equipped with 24-hour mortality sensors. Implanted beavers were monitored for a minimum of 24 hours post surgery prior to release (Davis et al. 1984). All animals were released after 1500 hours in an attempt to decrease exposure to predation during daylight hours.

We monitored beavers for movements and mortality for 2 days after release and approximately every 2 weeks thereafter. Streams were walked a minimum of 1.5 km in both directions to determine if beaver had become established. By examining the stream for evidence of tree cuttings or dam construction, we also determined if non-telemetered beavers were still active.

Causes of mortality were determined through examination of hair and scat samples found at kill sites, bite marks on beaver carcasses, and tracks present (O'Gara 1978). Lab work and necropsies were performed by Dr. Elizabeth Williams, Pathologist at the Wyoming State Veterinary Laboratory. Hair samples were examined by Tom Moore, Forensic Supervisor for the Wyoming Game and Fish Department Laboratory.

Figure 1. Beaver release sites in Wyoming



During trapping, 2 adult beavers (22.7 and 13.2 kg) caught in snares were killed by coyotes. Both animals were captured in sets made on dry land and were partially eaten. The traps were not located in the same area and the incidents occurred on different dates (6 September 1994 and 6 June 1995). A coyote was inadvertently captured in a snare set at the same beaver pond complex where a snared beaver was killed by a coyote. We also trapped several ducks (mostly mallards [*Anas platyrhynchos*], green-winged teal [*Anas creccal*] and common mergansers [*Mergus merganser*]) in snares set on dam crossovers and canal runways, suggesting that these runways are frequented by both predator and prey species.

Results

Of 22 beavers trapped, implanted with transmitters, and relocated, 13 (59%) died as a direct result of predation (Table 2). Coyotes, black bears, and grizzly bears killed 4 (18%), 4 (18%), and 3 (14%) beavers, respectively. Two (9%) other beavers were killed by undetermined predator(s). Four (18%) beavers are still alive and apparently healthy. An additional 22 beavers (7 telemetered, 15 non-telemetered) have not been relocated.

Beavers killed by predation lived for an average of 17 days; however, 6 of 13 died within just 6

days of release. With the exception of 1 animal, all documented beaver kills occurred within 0.25 km of the release site (the exception was found 0.75 km upstream of the release site). The 4 remaining animals have also stayed within 0.25 km of the release site, building dams and lodges.

Discussion

Limited range of implanted transmitters may have affected the number of animals located. The advertised range of transmitters was 0.5 km, but the effective range was usually 200 m. Animals in dens were often not located until we were within 50 m of the transmitter. Walking up and downstream of the release site allowed us to be within 20 m of the creek bed and was undoubtedly necessary to determine movements and mortality.

Although animals that were not relocated may have had higher survival rates, we feel this is improbable. It is more likely that these animals may have been killed and cached in holes and dens, or dragged out of range of the receivers. Animals moving out of the vicinity of the release area may also have experienced higher predation rates due to increased exposure and less time spent hiding in dense vegetation or constructing dens. Smith et al. (1994) found that beavers that were sympatric with black bears on islands in Lake Superior traveled less distance from water than those found on islands where bears were not present. This finding suggests that this was a direct attempt to avoid predation.

Stanley-Price (1989) reported that relocated animals would be more susceptible to predation. Beavers have many natural predators and are not capable of using direct confrontation or evasive action to avoid predation, preferring instead to use water as an escape medium (as reviewed in Smith et al. 1994). Therefore, without ponds and dens to use for escape, beavers are particularly vulnerable. Naturally dispersing beavers have been seen in upland areas > 1 km from water sources and have even been observed crossing mountain passes (Smith 1980). These animals, however, would be as vulnerable to predation as newly introduced beavers. While it is not known how natural dispersal occurs in beavers, we hypothesize that they move primarily in a linear fashion up or down established waterways. Movements across upland areas can be successful, but we question the frequency of success in areas where predators occur sympatrically.

During 1994, all of our release sites received less than 70% of the average annual precipitation (86% of annual precipitation average statewide, although

Table 1. Habitat type and elevation (m) for beaver introduction sites. Habitat types are defined by Hansen et al. (1991).

Release Site	Vegetation Type	Elevation
Cody	Quaking aspen/Western Sweet-cicely (*Populus tremuloides/Osmorhiza occidentalis*)	2000
Rock Springs	Spruce/Bluejoint Reedgrass (*Picea/Calamagrostis canadensis*)	2350
Saratoga	Narrowleaf Cottonwood/Recent Alluvial Bar (*Populus angustifolia*/Recent Alluvial Bar)	2250
Sundance	Scrub Oak/Common Chokecherry (*Quercus gambelii/Prunus virginiana*)	1150

Table 2. Fates of introduced beaver by release location.

Fate	Release Location			
	Cody	R. Springs	Saratoga	Sundance
Coyote	3		1	4
Black Bear		4		4
Grizzly Bear	3			3
Unknown Mortality	2			2
Alive	1	3		4
Unknown Fate w/ Transmitter	1	2	2	27
Unknown Fate w/o Transmitter	4	1	3	715
Total # Beaver Released	14	10	6	39
w/ Transmitters	10	8	2	22
# Beaver Released w/o Transmitters	4	2	4	17

the spring / summer precipitation in many areas was below 50%; Wyoming Water Research Center). Many authors have emphasized the value of riparian areas to wildlife (see review by Naiman et al. 1988), but predator-prey relationships and how they relate to habitat quality and availability are not well understood (Smith et al. 1994). During dry years, animals may concentrate in riparian areas along with their respective predators. These predators, while normally dependent on other species, may find beavers easy prey.

Where wolves (*Canis lupus*) and beavers are sympatric, beavers may constitute up to 75% of wolf diets (Thurber and Peterson 1993, Voight et al. 1976). Beavers are found throughout the Greater Yellowstone Ecosystem but are thought by many to be in a state of decline due to factors unrelated to predation (Chase 1987). Newly introduced wolves, along with coyotes, grizzlies, and black bears, may impede naturally dispersing beavers from colonizing new areas.

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Managing Bears and Developments on Cutthroat Spawning Streams in Yellowstone National Park

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Abstract

Grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) prey on spawning cutthroat trout (*Oncorhynchus clarki*) in tributaries of Yellowstone Lake. Bear use of front-country spawning streams in the Grant Village and Lake-Bridge Bay developments was monitored from 1989 to 1995. Average spawn ending date was consistent between 22 and 27 June; however, average onset and length of spawn varied between "early" and "late" years. Spawner abundance declined on most streams during the study period. Most recorded bear activity within park developments, especially grizzly bear activity, occurred at the Grant Village and Lake-Bridge Bay developments, with Grant Village reporting almost twice the activity of Lake-Bridge Bay. Seventy percent of all bear management actions in Yellowstone National Park occurred at the Grant Village and Lake-Bridge Bay developments. Without bear management restrictions, human facilities at developed areas opened earlier each year of the study. Results of monitoring have been implemented in park management to reduce the potential for bear-human conflicts. To further reduce or eliminate the temporal overlap between bears using front-country spawning streams and humans using these developments, we recommend opening visitor facilities at Grant Village and Lake-Bridge Bay no earlier than 22 June to 27 June.

Introduction

Grizzly bears (*Ursus arctos*) and black bears (*U. americanus*) prey on spawning cutthroat trout (*Oncorhynchus clarki*) in tributary streams of Yellowstone Lake in Yellowstone National Park (YNP) (Mealey 1980, Reinhart and Mattson 1990). Cutthroat trout are an important seasonal food source for Yellowstone grizzly bears because of their high digestibility and protein content (Pritchard and Robbins 1990).

From 1985 through 1987, all Yellowstone Lake tributaries were surveyed to collect baseline data on the timing and relative magnitude of cutthroat trout

spawning runs and associated bear activity along spawning streams. This research showed that 59 (48%) of the 124 tributaries of Yellowstone Lake supported a cutthroat trout spawning run. Ninety-three percent of these 59 spawning streams had associated bear activity and 61% had conclusive evidence of bear fishing. Thirty-five percent of all spawning streams bisected park roads while 15% of tributaries with a spawning run occurred within 1 km of park developments (Reinhart and Mattson 1990).

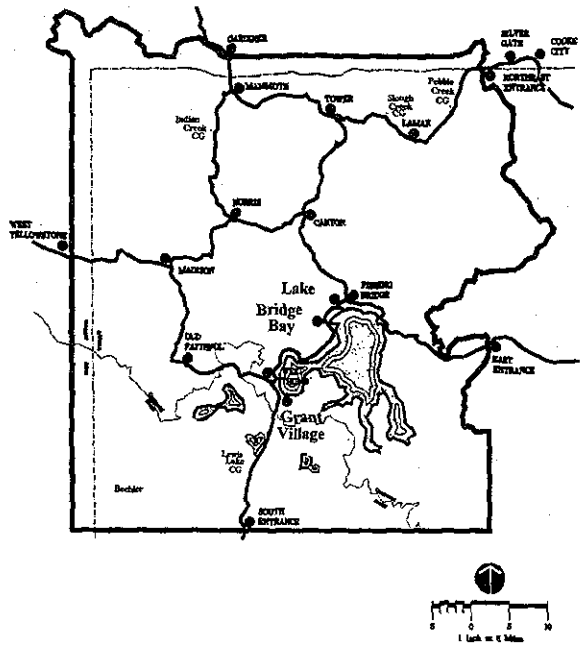
This study also showed that less bear use than expected occurred within 1 km of park developments. Moreover, when the opening of park lakeshore developments occurred during the cutthroat trout spawning-bear fishing season, more bear-human conflicts occurred, typically resulting in bear management translocation and removals (Reinhart and Mattson 1990).

The likelihood of displacing bears from a seasonally important, high-quality food source and the potential for bear-human conflicts demonstrated to park resource managers the need for continued monitoring of spawning streams near park developments. The goals of this monitoring effort were to:

1) Use the monitoring results from the current year to establish opening dates for some of the human facilities at Lake and Grant Village that are in closest proximity to spawning streams.
2) Determine the timing of bear activity in relation to fish spawning activity.
3) Determine the number of bears that routinely utilize the fish spawn in the Grant and Lake Developments and recognize any significant trends in bear use and occupancy at these developments.
4) Determine the variability in peak numbers of spawning fish and the reliability of this seasonally important, high-quality food source.
5) Use the monitoring results to generate a long-term management strategy at Lake and Grant Village that will allow human occupancy of developments yet minimize bear translocation and / or mortalities.
6) Determine whether the monitoring results can be used to predict the onset, peak, and end of spawning.

The study area included the Grant Village and Lake-Bridge Bay developments. Park lakeshore developments are defined as areas within one kilometer of hotels, campgrounds, stores, or restaurants. Three spawning streams in the Grant Village development (Sandy Creek, Stream 1167, and Sewer Creek) and 5 spawning streams in the Lake-Bridge Bay developments (Lodge Creek, Hatchery Creek, North and South Incinerator Creeks, and Bridge Creek) were monitored from 1989-1995 (Figures 1 and 2). Reinhart (1990) describes the limnology and landscape physiognomy of Yellowstone Lake and the lake drainage basin.

Figure 1. Map of Yellowstone National Park developments.



Methods

Spawning streams near Grant Village and Lake-Bridge Bay developed areas were checked from 1 May until spawn onset from 1989 through 1995. After spawn onset, streams were monitored weekly to determine cutthroat spawner abundance and extent of bear fishing activity. Cutthroat trout spawner abundance was recorded by counting adult spawners while walking from the mouth to the upstream extent of spawning activity. Presence or absence of bears and bear fishing activity were determined by recording bear tracks, scats, and fish carcasses. Bear tracks were measured to establish the number and

species of bears on each stream for each visit. Tracks that varied by greater than 2 cm in width, were different species, or were associated (e.g., adult with young) were determined to be different bears. To maximize comparability among observations, stream surveys were made between 1030 and 1600 hours and in the same order during the course of the study.

Bear activity reports and bear management translocations and removals were recorded for Yellowstone Park developed areas. The opening dates of human use facilities, including the campground, lodge, and store at Grant, the hotel and lodge at Lake, and the campground at Bridge Bay were recorded for each of the study years.

The trends in the number of fish at peak spawn and the Recorded Bear Visits (the yearly sum of the number of bears recorded on each weekly monitoring trip on each stream) were tested for each stream over the course of the study using the Mann-Kendall test for trend (Gilbert 1987). Streams were clustered into "early" and "late" groups based on onset date using a K-Means cluster analysis. A repeated-measures two-way ANOVA was used to determine whether significant differences in mean length and mean end of spawn existed between groups ("early" versus "late") (Kachigan 1982, Zar 1984). All statistical analyses were performed using SYSTAT software (Wilkinson 1988).

Results

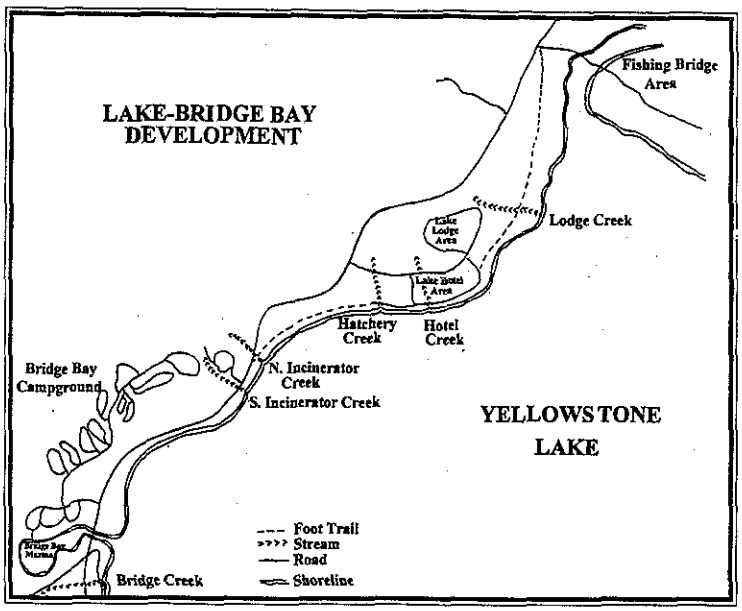
Timing of Spawner and Bear Activity

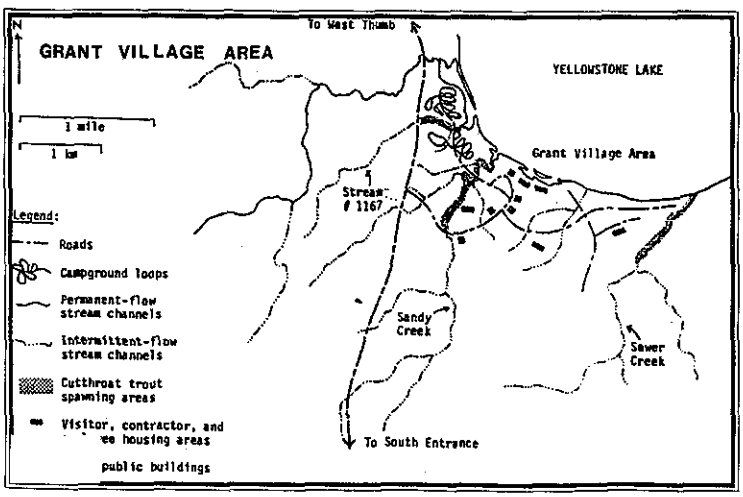
The timing of cutthroat trout spawning varied among study years. Average yearly onset ranged from 7 May through 6 June. Peak spawn ranged from 21 May through 16 June. End of spawn ranged from 12 June through 6 July.

Streams were clustered into 2 groups ("early" versus "late") based on mean onset date. Mean onset date differed between the "early" group ($\bar{x}$ = 14 May, SD = 6 days, n = 29) and the "late" group ($\bar{x}$ = 4 June, SD = 6 days, n = 27) (F = 169.054, P = 0). The 2 groups separated predominantly into "early" or "late" years, with 3 exceptions out of 56 total occurrences. The years 1989 (except Sewer Creek at Grant Village), 1990, 1992, and 1994 (except North and South Incinerator Creeks at Lake-Bridge Bay) were classified as "early" years. The remaining years, 1991, 1993, and 1995 were "late" years.

The spawn length, but not the ending date, varied between the "early" and "late" groups. The spawn was shorter in the "late" group ($\bar{x}$ = 23 days, SD = 12) compared to the "early" group ($\bar{x}$ = 39 days,

Figure 2. Map of the Grant Village and Lake-Bridge Bay developments and spawning streams.





SD = 8) ($F = 29.851$, $P = 0$). There was no significant difference in the spawn ending date between the "late" group ($\bar{x}$ = 27 June, SD = 10 days) and the "early" group ($\bar{x}$ = 22 June, SD = 9 days) ($F = 3.27$, $P = .077$).

Bear fishing activity at Grant and Lake area streams was apparently related to fish migration. Out of a total of 215 Recorded Bear Visits during the course of the study, 190 (88%) occurred at or after peak spawner abundance. This total included 138 (64%) Recorded Bear Visits at Grant Village and 77 (36%) at Lake-Bridge Bay.

Trends in Spawner Abundance and Bear Use

Peak spawner counts (the number of fish counted during the peak week each year) on most streams declined during the study (Figure 3). Sandy Creek ($S = -19$, $P < .05$), Stream 1167 ($S = -17$, $P < .05$), Sewer Creek ($S = -13$, $P < .05$), Lodge Creek ($S = -17$, $P < .05$), South Incinerator Creek ($S = -13$, $P < .05$), and Bridge Creek ($S = -15$, $P < .05$) declined significantly. Peak spawner count declined on Hatchery Creek, but the trend was not as significant as other creeks ($S = -9$, $P = .119$). Peak spawner count did not decline significantly on North Incinerator Creek ($S = -3$, $P = .386$).

Bear use of spawning streams in the study area, measured by the number of Recorded Bear Visits, apparently declined from 1989 through 1995 (Figure 4). Although the Mann-Kendall S values for each stream were negative, only Stream 1167 ($S = -15$, $P < .05$) and Bridge Creek ($S = -15$, $P < .05$) showed significant downward trends.

Bear Management

Most recorded bear activity within park developments, especially grizzly bear activity, occurred at the Grant Village and Lake-Bridge Bay develop-

Figure 3. Number of spawners during the peak week for Grant Village and Lake-Bridge Bay streams, 1989-1995.

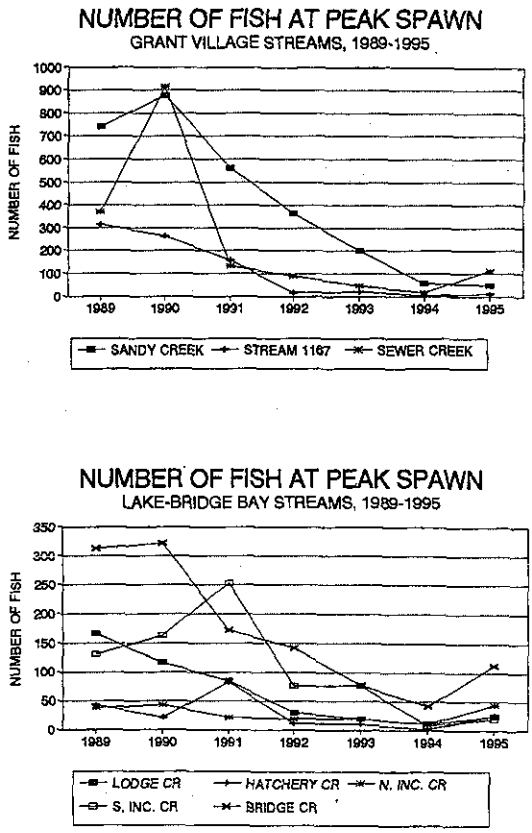
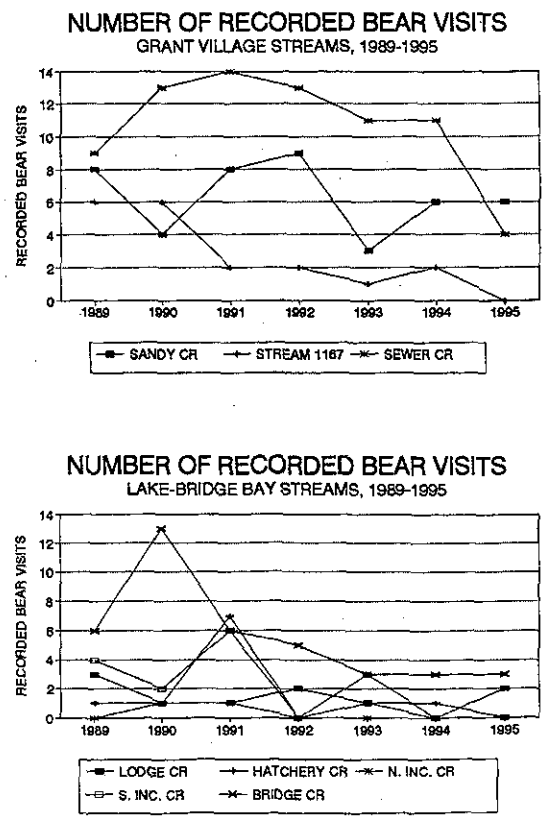


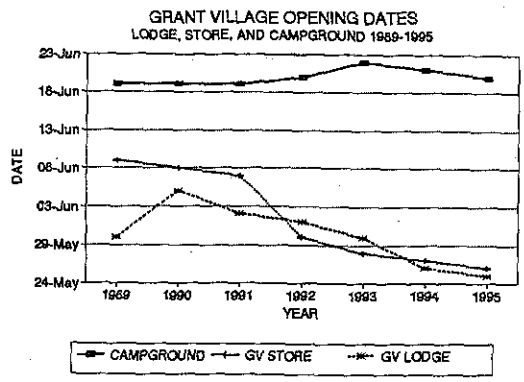
Figure 4. Number of recorded bear visits for Grant Village and Lake-Bridge Bay streams, 1989-1995.

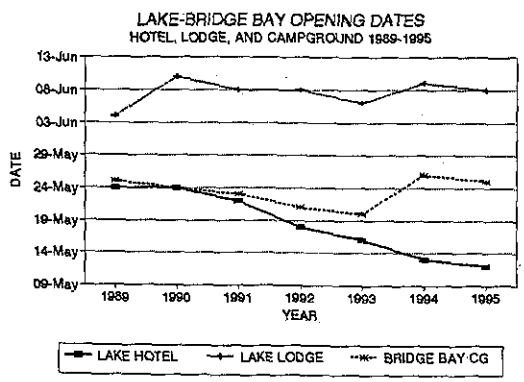


ments (Table 1). This included 42% of all bear activity reports and 58% of all grizzly bear activity reports that were recorded in Yellowstone National Park developments during the study period. Grant Village accounted for 27% of total reported bear activity and 35% of reported grizzly bear activity while Lake-Bridge Bay accounted for 14% and 23% of total and grizzly bear activity, respectively.

The Grant Village and Lake-Bridge Bay developments have been the site of the majority (70%, n = 10) of bear translocations in Yellowstone National Park since 1989. All grizzly bear management removals from 1989 through 1995 have occurred at either Grant Village or the Lake-Bridge Bay Development (1 at each location, n = 2). Related grizzly mortalities included 1 grizzly bear hit by a car near a Grant spawning stream and 2 individual grizzly bears habituated to people while frequenting Lake-Bridge Bay spawning streams but later killed outside of Yellowstone National Park.

Figure 5. Opening dates of the Grant Village Lodge, Hamilton's Store, and Campground, the Lake Hotel and Lodge, and the Bridge Bay Campground, 1989-1995.





Human Use Management

During the 7 years of this study, Grant Village opening dates for the Lodge, Store, and Campground varied from 26 May to 6 June, 27 May to 10 June, and 20 June to 23 June, respectively (Figure 5). In 1995, the Grant Village Lodge and the Grant Village Hamilton's Store opened 5 days earlier and 14 days earlier, respectively, than in 1989. The Grant Village Campground opened 1 day later in 1995 compared to 1989.

Opening dates for the Lake Hotel, Lake Lodge, and Bridge Bay Campground varied from 13 May to 24 May, 5 June to 11 June, and 22 May to 27 May, respectively. In 1995, the Lake Hotel opened 12 days earlier compared to 1989. There was no change in the opening date of the Bridge Bay Campground from 1989 through 1995. The Lake Lodge opened 4 days later in 1995 compared to 1989.

Discussion

Cutthroat Trout Spawn and Bear Activity

Spawn ending date did not vary significantly among study years, regardless of spawn onset and length. Spawn onset varied considerably among study years, probably related to winter snowpack and spring snowmelt conditions within the drainage basin (Reinhart 1990). When spawn onset occurred after 24 May, the spawn length was considerably shorter than during years when onset occurred earlier.

Classifying a year as "early" or "late" is possible based on average onset date. However, the onset date is less relevant to managers than the ending date, since the temporal overlap between bear and human use typically occurs closer to the end of spawn. Since the end of spawn is relatively consistent among years, regardless of spawn onset, this information can be used to establish opening dates for human use facilities in close proximity to spawning streams.

The majority of bear activity occurred at or after the peak of spawner abundance. Reinhart and Mattson (1990) found similar trends during a survey of all Yellowstone Lake tributaries. The timing of bear use was likely related to increased prey vulnerability from post spawner fatigue and lower stream depths and bear use of riparian vegetation (Reinhart 1990).

Cutthroat trout spawner abundance declined on streams in the Grant and Lake-Bridge Bay areas during the course of the study. This trend was also reported in another large Yellowstone Lake tributary (Kaeding et al. 1995a). However, spawner abundance increased slightly on most streams in 1995, and pre-study data (Reinhart 1990) showed spawner numbers on study area streams were lower than peak numbers during the early years of the current study. Declines in cutthroat trout abundance during the 1960s in Yellowstone Lake have been previously documented (Gresswell and Varley 1988, Gresswell et al. 1994). However, changes in angling restrictions implemented in the 1970s have reversed this downward trend (Gresswell and Varley 1988). Recent evidence of declines in spawning cutthroat trout found in this study might best be explained by natural variation in spawner abundance due to annual climatic conditions. This variation is probably related to poor age class recruitment during extreme water years (Bulkley and Benson 1959), varying weather conditions during the spawning season, piscivorous predator influences, and human caused perturbations (Gresswell et al. 1994).

The long-term health of the Yellowstone Lake cutthroat trout population may be in jeopardy. In 1994, illegally introduced lake trout (*Salvelinus namacush*) were discovered in Yellowstone Lake. In 1995, 195 lake trout were taken from the lake (153 from experimental gill netting efforts and 42 from angler catches). The data suggest that tens of thousands of lake trout may now inhabit Yellowstone Lake (Kaeding et al. 1995b). The effects of introduced lake trout on the native cutthroat trout population and the wildlife that depend on cutthroat trout are not completely understood. The presence of lake trout in Yellowstone Lake may not be the cause of the documented declines in cutthroat trout spawner abundance during the study period. However, lake trout have reduced and even eliminated native cutthroat trout populations in other lakes in the United States (Gerstung 1988, Dean and Varley 1974). The advent of lake trout in Yellowstone Lake has the potential to greatly reduce the cutthroat trout population (McIntyre 1995) and adversely affect the grizzly bear population that depends on spawning trout.

Table 1. Number of reports of grizzly bear, black bear, or unknown species of bear activity recorded within different developed areas in Yellowstone National Park, 1989-1994.

Developed Area	Grizzly Bear	Black Bear	Unk. Spp.	Total
Grant Village	83	67	19	169
Lake-Bridge Bay	54	13	20	87
Roosevelt	8	46	1	55
Canyon	21	26	8	55
Mammoth	8	30	9	47
Slough Creek	23	18	3	44
East Entrance	21	3	0	24
Indian Creek	5	15	1	21
Tower Falls	0	18	1	19
Pebble Creek	2	14	1	17
Gardiner[a]	3	9	4	16
Northeast Entr.	1	14	0	15
Norris	5	5	3	13
Fishing Bridge	9	1	1	11
Madison	0	5	6	11
Old Faithful	6	2	2	10
Snake River	1	4	0	5
Bechler	1	3	0	4
Lewis Lake	0	0	1	1
West Entrance	0	0	0	0
Lamar	0	0	0	0

[a] Areas within Yellowstone National Park boundary only.

Bear and Human Use Management

Spawning cutthroat trout and Yellowstone Lake spawning streams are an important component of Yellowstone grizzly bear food habits and habitat use. Cutthroat trout were used by grizzly bears occupying 30-45% of the Yellowstone Grizzly Bear Recovery Area. More than 80% of all grizzly bears located within 2 km of spawning streams during the spawning season foraged on cutthroat trout (Mattson and Reinhart, 1996). Reinhart and Mattson (1990) estimated that a minimum of 44 autonomous bears used Yellowstone Lake spawning streams in 1987 when all streams were surveyed.

Understanding the relationship between spawning cutthroat trout and Yellowstone grizzly bears is essential for managers. The highest incidence of Yell-

owstone National Park grizzly bear activity reports and management actions in developed areas have occurred in recent years near the Grant and Lake-Bridge Bay developments. However, not all bear sightings and management actions occurred at the time of bear fishing activity or resulted directly from bear use of front country spawning streams. Bear use of the Grant Village and Lake-Bridge Bay developments was likely a result of a number of complex factors. These include grizzly bear population dynamics and behavioral responses, overall grizzly bear habitat quality including the protein component of spawning trout, and the extent that human use overlapped bear use in these developed areas (Mattson 1990, Mattson et al. 1992). Some bears that use front country spawning streams may not be involved in bear-human conflicts for a number of years. However, these bears, given the opportunity to forage near human facilities, may eventually become habituated, which often leads to bear-human conflicts, especially during poor food years (Mattson et al. 1992, Meagher and Fowler 1989).

Overall bear activity on spawning streams was lower at Lake-Bridge Bay compared to Grant Village. Reasons for this difference may include:

1) Three grizzly bears that used Lake area streams were removed during the study period.An adult female that persistently returned to front-country spawning streams after being translocated was sent to a zoo. An adult and subadult male that became habituated to humans while frequenting Lake-Bridge Bay spawning streams were later illegally shot outside YNP. Only 1 grizzly bear, a subadult male, was trapped and removed from the Grant area during this period.
2) Bear use of habitat may vary between the Lake-Bridge Bay and the Grant Village areas. Overall habitat complexity and perhaps quality may be higher near the Lake area compared to the Grant area (National Park Service 1984). Bears at Lake-Bridge Bay appear to have other foraging options, such as ungulate carcasses and elk calves, during poor spawner years. Overall bear foraging options appear less near the Grant Village area where streams run through lodgepole forests. Bears may use spawning streams and associated riparian vegetation at Grant even during years of poor spawner abundance (Reinhart 1990).
3) The opening date of the major overnight facility in close proximity to spawning streams at Grant Village, Grant Campground, has been regulated through a Bear Management Area since 1986 (National Park Service 1986, Sholly 1989), ensuring a consistent, later opening. In contrast, the Lake Hotel, the largest Lake facility near spawning streams, has consistently opened earlier each year of the study. It is likely that the high level of human activity associated with the earlier opening of Lake Hotel has displaced some bear use of Lake-Bridge Bay spawning streams (Mattson et. al. 1987, Reinhart and Mattson 1990). At Lake, only the Lake Lodge opening date has been controlled in recent years due to grizzly bear mitigation from the Lake-Bridge Bay Development Concept Plan (National Park Service 1993).

Bear use of spawning streams overlapped with the opening of most lakeshore visitor facilities. While spawning runs and associated bear use typically did not end until 22 through 27 June, visitor facility opening dates occurred from 13 May through 21 June. While some facilities near spawning streams have opened on consistent dates because of management decisions to protect bear use of spawning streams, others continued to open earlier each year. This increasing temporal overlap between bear use of spawning streams and opening of visitor facilities increases the likelihood of bear-human conflicts and may lead to more bear management actions and removals.

The following management actions were implemented before or during the study period based on the results of the spawning stream surveys:

1) Closing specific areas near spawning streams to park visitors during spawning runs.

2) Regulating the opening dates of some human-use facilities near spawning streams.

3) Developing a public and employee education program on bear use of cutthroat trout.

4) Incorporating information about trout spawning and bear activity into park planning efforts to reduce the temporal overlap of bear and human use.

While these actions have helped reduce the frequency of bear-human conflicts in Yellowstone National Park, more effort is needed to ensure greater protection for bears using spawning streams near developments and to reduce the risk of future bear-human confrontations. Because bear populations appear to be vulnerable to human caused mortality (Mattson and Reid 1990), and the proximity of human and bear aggregations is considered detrimental to the grizzly bear population (U.S. Fish and Wildlife Service 1993), management of park developments near spawning streams should include eliminating or further reducing the temporal overlap between bears and humans in the Lake and Grant developments.

Recommendations

Management measures that we recommend to ensure further protection of both people and bears using front-country areas near spawning streams include:

1) Open visitor facilities no earlier than 22 June to 27 June at Grant Village and Lake-Bridge Bay to reduce or eliminate the temporal overlap between bears using front country spawning streams and humans using these developments. A more consistent opening date will allow bears to utilize a valuable food resource and reduce the risk of bear-human conflicts (Jope 1985, McLellan and Shackleton 1989, Mattson 1990).

2) Protect the Yellowstone Lake cutthroat trout population. Conduct more research and monitoring to determine the overall health of the cutthroat trout population. This includes better explanations for the recent declines in spawner abundance as well as potential risks from and possible management strategies to control a growing lake trout population in Yellowstone Lake.

3) Continue monitoring spawning streams. Front country streams should be surveyed on an annual basis to maintain a long-term database for cutthroat trout spawning activity and bear use. Data from yearly monitoring can be used by park managers to determine the opening of areas near spawning streams in the Lake-Bridge Bay and Grant developments.

4) Initiate long-term monitoring on other Yellowstone Lake spawning streams. Monitoring results can be used to further understand the influence of developments on bear use of spawning streams and to detect changes in bear use of spawning fish resulting from changes in the cutthroat trout population.

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Predicting Grizzly Bear Mortality in Developed Areas of Yellowstone Park

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Abstract

In 1986, a grizzly bear (*Ursus arctos*) mortality risk model was developed as part of the Environmental Impact Statement (EIS) for the Development Concept Plan (DCP) of the Fishing Bridge developed area. The model provided an estimate of the number of management transfers and, ultimately, bear mortalities that could be attributed to each of the 16 developed areas in the park for the subsequent 10-year period, 1987-96. Given that bear mortalities in relation to developed areas actually declined during the following decade, the model overestimated the number of transfers and mortalities that occurred across all developments from 1987-96. The model, however, accurately accounted for the 15 transfers and 3 mortalities that occurred at the 5 developments requiring bear management actions. Although restricted in utility to identifying point sources of continued mortality and the incremental risk associated with the placement of new facilities or the expansion of existing facilities within the park, the empirical model could supplement other efforts in quantifying mortality risk as part of a cumulative effects assessment for grizzly bears in the Greater Yellowstone Ecosystem (GYE).

Introduction

Attempts to model human-caused grizzly bear (*Ursus arctos*) mortality across the Greater Yellowstone Ecosystem (GYE) have theoretically focused on the type and intensity of human recreational activities across the landscape (e.g., Weaver et al. 1987). It was assumed that the density, concentration, or frequency of the various activities could be correlated with bear deaths. For subsequent modeling, activity types could then be assigned a mortality coefficient to reflect the relative risk of causing or contributing to grizzly bear mortality. But in assessing ecosystem-wide mortalities, several authors (Povilitis 1987, Knight et al. 1988) demonstrated that major causes differed among administrative units within the GYE. Generally, human-caused grizzly bear mortalities in Yellowstone National Park (YNP) were attributed to management actions associated with front country developed areas whereas other activities like hunting (both legal and illegal) and the management of livestock depredating bears accounted for a majority of bear deaths beyond park boundaries.

Recognizing such limitations, the National Park Service (NPS) introduced a grizzly bear mortality risk assessment in 1986 as part of the Final Environmental Impact Statement (EIS) of the Development

Concept Plan (DCP) for the Fishing Bridge Developed Area (National Park Service 1988). The development of an empirical "mortality model" was described whereby the number of bear management trappings and transfers (and ultimately bear mortalities) was attributed to each of 16 front country developed areas in YNP over a 10-year period. For purposes of the EIS, the mortality model was used to estimate the number of bear management transfers and mortalities attributable to each of the 16 developed areas under various management alternatives for the 10-year period 1987-96.

Here we compare known grizzly bear management transfers and mortalities that occurred in relation to the 16 developed areas during 1987-96, with those estimated by the model in 1986. We further compare known bear management transfers and mortalities at the 16 developed areas between 2 time periods: the 10-year period 1977-86, from which the model was constructed, to the subsequent 10-year period 1987-96, in which the model was applied. The purpose of these comparisons is to evaluate the utility and application of the mortality model, as well as to provide insight into trends in grizzly bear mortality in relation to developed areas in YNP.

Methods

Initial Derivation and Application of the Model, 1977-86

Data used to derive the empirical mortality model were obtained for the 10-year period 1977-86 relative to bear management actions, conditions that existed at each of the 16 developed areas within YNP, and local measures of bear habitat quality and population density indices (National Park Service 1988). The model was developed using the statistical techniques and assumptions of simple- and multiple-correlation analysis followed by least squares analysis. The resulting equation explained 90% (R^2 = .903) of the variation in bear management actions as related to all developments:

$$TRAN = e^{(-2.305 + .00251*CAP + .141*WALL + .05532*MALE)}$$

Where:

TRAN = the estimated number of bear trappings and transfers over a 10-year period;

e = 2.718281828 (natural logarithm, base e);

CAP = the number of campsites and lodging units at each developed area;

WALL = the presence (1) or absence (0) of a physical barrier (i.e., large lake or canyon) that would channel bear movements into a development;

MALE = the percent of adult males in the local bear population.

The final step in estimating bear mortalities required the extrapolation of mortalities as a function of bear management trappings and transfers (National Park Service 1988). From 1977-86, 34 management trappings resulted in 10 bear mortalities and 24 bear transfers to other backcountry localities within the park (Table 1). The corresponding relationship of 1 bear mortality for every 3.4 management trappings (34/10 = 3.4) was then applied to the estimated number of trappings and transfers to derive the estimated number of bear mortalities for each of the 16 developed areas. Mortality used here includes management kills, or bears otherwise removed from the population and sent to zoos or research facilities.

Estimating bear mortalities in relation to developed areas therefore becomes a two-step process. First, estimate the number of trappings and transfers relative to each development and then extrapolate mortalities as a function of management trappings and transfers. This process was used to evaluate a wide range of administrative alternatives on grizzly bear trappings and mortalities in relation to removal, reduction, and/or relocation of visitor facilities to various existing and proposed locations throughout YNP (National Park Service 1988). While the number of bear mortalities is the underlying management concern, the number of trappings and transfers (TRAN) is the variable or index used to evaluate the power of the regression equation and, ultimately, the utility of the model.

Application of the Model, 1987-96

The estimated number of grizzly bear management trappings and transfers and related mortalities for each of the 16 developed areas as earlier reported (National Park Service 1988) for the 10-year period 1987-96 were compared to known trappings and transfers and mortalities that actually occurred from 1987-96. Input data were relative to Alternative A in the DCP, which called for removal of the 310-site Fishing Bridge Campground beginning in 1988.

Grizzly bear management trappings and transfers and subsequent mortality information were derived from records archived in the YNP Bear Management Office. By maintaining detailed records and compiling a management history of problem bears, it is possible to determine at which location a given bear initially developed problem behavior. In this way, problem bear behavior and subsequent bear management actions can be attributed to a particular development even when many developments are in close proximity, as in the case of the Fishing Bridge, Lake, and Bridge Bay developed areas. Only successful attempts at capturing problem bears are included here.

Chi-square analysis (Zar 1984) was employed to compare observed vs. estimated bear trappings and transfers (TRAN) across all 16 developments as well as only those developments ($n = 5$) where trappings and transfers actually occurred. Ninety-five percent confidence limits (Zar 1984) were also calculated for estimated trappings and transfers at each development and used for presentation purposes only.

Results

Estimated versus Observed Bear Management Trappings and Transfers

Table 1 lists the model input variables used to derive the estimated number of bear management trappings and transfers (TRAN) for the 10-year time period 1987-96 at each development. The model significantly overestimated the number of trappings and transfers across all 16 developments ($\chi^2 = 10.14$, df = 1, $P < .05$). While 33.4 transfers were estimated, only 15 (44.9%) occurred. Eleven developed areas, including Fishing Bridge and Old Faithful, did not experience any bear transfers, even though 16.3 were estimated. Bridge Bay, Grant Village, and Mammoth all experienced transfers in proportion to those estimated. Only Lake Village experienced more transfers than estimated (6 vs. 3.9); Canyon Village experienced fewer transfers (3 vs. 7.0) than expected.

On the other hand, 88% of the estimated number of transfers actually occurred at the 5 developed areas requiring bear transfers (Table 1). The 15 trans-

Table 1. Model input variables, the estimated number of grizzly bear management transfers (±95% confidence limits), and extrapolated estimates of bear mortality attributable to the 16 front country developed areas of YNP. Estimated mortalities were obtained from the relationship of 3.4 transfers resulting in 1 bear mortality (see text). The observed number of bear management transfers and mortalities for 2 time periods (1977-86 and 1987-96) is also shown. "Other" reflects the pooled data for 7 developments (Indian Creek, Lewis Lake, Roosevelt, Tower, Slough Creek, Pebble Creek, and West Thumb) where CAP ≤100. Here, the range of input variables is given. The empirical model and variable definitions are described in the text.

	INPUT VARIABLES			OBSERVED TRANSFERS			OBSERVED MORTALITIES	MORTALITIES	
	Cap	Wall	Male	Tran. (95% CL)	'77-'86	'87-'96	per 10-year period	'77-'86	'87-'96
DEVELOPMENT									
Canyon Village	868	1	35	7.0 (3-16)	7	3	2.1	1	0
Old Faithful	705	0	36	4.3 (1-13)	5	0	1.3	1	0
Grant Village	536	1	36	2.5 (0-10)	1	3	0.7	0	1c
Lake Village	475	1	42	3.9 (1-12)	6	6	1.1	1	2d
Bridge Bay	438	1	36	2.5 (0-10)	3	2	0.7	3	0
Fishing Bridge	351	1	50	4.4 (1-13)	9	0	1.3	1	0
Mammoth	309	0	31	1.2 (0-8)	0	1	0.4	0	0
Madison Jct	292	0	36	1.5 (0-9)	1	0	0.4	1	0
Norris Jct	116	0	35	0.9 (0-8)	1	0	0.3	0	0
Other	0-100	0-1	31-36	5.2 (0-58)	1a	0	1.5	2b	0
TOTALS:				33.4 (6-157)	34	15	9.8	10	3

[a]transfer occurred at Roosevelt; [b]mortalities occurred at Lewis Lake and Indian Creek Campgrounds; [c]bear 223, subadult male, removed 8/94; [d]bear 134, adult female, removed 4/90; bear 83, adult female, removed 10/87.

fers that occurred did not significantly differ from the 17.1 estimated by the model ($\chi^2 = 0.26$, df = 1, $P > .05$). The empirical model adequately accounted for management trappings in those developed areas requiring bear management actions.

Estimated and Observed Bear Mortalities

Table 1 shows the estimated and observed bear mortalities attributed to the 16 developed areas. Although 9.8 were estimated, only 3 (30.6%) occurred. Two bear mortalities were attributed to Lake Village and 1 to Grant Village. The pooled estimate of bear mortalities for these two developed areas was 1.8.

Differences in Transfers and Related Mortalities between 1977-86 and 1987-96

An overall decrease in bear transfers was observed between the 10-year period 1977-86 and the 10-year period1987-95. Fishing Bridge, Canyon Village, and Lake Village experienced the greatest proportion of transfers (22/34 = 64.7%) during the former period, whereas Lake, Canyon, and Grant Villages experienced the greatest proportion (12/15 = 80%) during the latter period. Collectively, Fishing Bridge and Old Faithful experienced a dramatic decrease in bear transfers between the 2 periods (14 vs. 0). All other developed areas experienced transfers that were proportional (20 vs. 15) between the two periods ($\chi^2 = 1.67$, df = 1, $P > .05$). Bear transfers at Lake Village, however, remained relatively high (6 vs. 6), and transfers at Grant Village may be increasing (1 vs. 3).

Similar trends were observed with bear mortalities between the 2 periods. The rate of mortality decreased from an average of 1 bear per year during the former period to 1 bear per 3 years recently. No mortalities occurred during either period at 7 developed areas in the park, while 7 other developments experienced a mortality decrease. Only Lake (1 vs. 2) and Grant (0 vs. 1) Villages experienced increased mortalities during the latter period.

Discussion

Model Utility and Application

Use of the empirical model is predicated on independent variables that appear static but, realistically, may be quite dynamic. Only the presence or absence of a physical barrier (WALL) will remain constant over time. Changes in the percent of adult males in the local population (MALE) require continual modification based on bear population monitoring data and are subject to the inherent difficulties of quantifying bear population numbers. This input could be expected to change in response to landscape-level bear population trends or habitat disturbances such as the fires of 1988. Furthermore, annual variation in food availability can affect the seasonal distribution of bears (Mattson et al. 1991), but this variation is assumed to average out over the 10-year period. As such, the number of campsites and lodging units at each developed area (CAP) is the only independent variable easily manipulated or justified for analysis of administrative alternatives. Application of the mortality model is therefore limited to anticipated or proposed changes in the number of campsites and lodging units (CAP). There is no opportunity to allow for independent variables to co-vary within a given development without a rigorous reevaluation of bear density trends.

The empirical model is further constrained by 3 underlying assumptions, all of which are expected to remain constant over time: 1) bear behavior; 2) management actions in response to bear behavior; and 3) human behavior within developed areas. Enforcement of sanitation within developments will most likely ensure consistency of human behavior with regard to providing little or no human food opportunities for bears over the long term. However, increased bear use of spawning streams resulting from changes in the management of cutthroat trout in Yellowstone Lake (Reinhart and Mattson 1990, Reinhart et al. *this volume*) and the suspected increase in bear predation on elk calves following the cessation of elk population controls (Gunther and Renkin 1990) could potentially violate the former assumption. Additionally, as problem bear behavior has evolved from a human-food-conditioned to a habituated (but not human-food-conditioned) situation in developed areas, managers have become increasingly tolerant of bear activity in developed areas (Gunther et al. *this volume*). However, the increasing practice of relocating problem bears throughout the ecosystem may decrease the tolerance for a given bear, even if the bear has no previous management action history in relation to a given development.

These described limitations and the inherently

small sample size and concomitant high degree of variation in transfers among developments probably account for the overestimation of transfers across all park developments. Still, the model appears sufficiently robust to account for management transfers and subsequent bear mortalities where repeated problems do exist. It appears the greatest utility of the empirical mortality model is that it allows for the identification of specific developments as "mortality sinks" where managers should focus efforts to mitigate bear problems.

Other applications may include analyses of where to situate a proposed new development in the park, or the predicted consequences of expanding an already existing facility. Such applications may be valid provided the independent variables (particularly CAP) fall within the range of values presented here. Caution should be exercised, however, when attempting to apply the model outside park boundaries where other causes of mortality may predominate or when evaluating the mortality contribution of gateway communities. If such applications were desired, it would be beneficial to reexamine independent-dependent variable relationships by including relevant data for the gateway communities. Alternately, developing a mortality risk index similar to Povilitis (1987) may be preferred. A more inclusive analysis would allow for quantitative comparisons between park developments, gateway communities, and, perhaps, other mortality sources. Such an approach would contribute substantially to modeling population viability by way of a cumulative effects analysis. Regardless of the intended application, the mortality model will predict an increase in management actions and, ultimately, bear deaths whenever recreational developments are situated or expanded in occupied grizzly bear habitat.

Comparisons between 1977-86 and 1987-96

A reduction in both management transfers and mortalities within the park was observed during the last decade. As a result, the ratio of mortality to trappings and transfers decreased from 1:3.4 to 1:5. These trends parallel the decrease in ecosystem-wide, human-caused bear mortalities where an average of 9.1 per year ($n = 91$) were observed during 1977-86 compared to 7.9 per year ($n = 79$) from 1987-96 (Knight and Blanchard 1995, Gunther et al. 1996, K. Gunther, pers. commun.). The reduction of visitor recreational facilities at Fishing Bridge undoubtedly contributed to this decrease. The observed declines can also be attributed to the continual emphasis on sanitation, visitor education, and elimination of human foods within park developments.

Contemporary management removals not only involve habituated, human-food-conditioned bears, but also may include habituated bears seeking natural foods within developments, representing a particularly challenging problem. Of the mortalities presented here during 1987-96, 1 involved a bear (#134, an adult female) with a known history of utilizing spawning cutthroat trout within the confines of the Lake Village developed area. Given that sanitation and visitor education will remain a vital component of the bear management program, innovative strategies to deal with habituated bears seeking natural foods will be required to avoid unnecessary bear deaths in relation to front country developed areas (see also Reinhart et al. *this volume*).

Potential Refinement of Model Constants

Although the model provided reasonable estimates of transfers and bear mortalities, it may be desirable to refine model constants in the future. For instance, projecting mortality using the 1:5 ratio of mortalities to management trappings would result in a more conservative estimate of 6.7 mortalities per 10-year period rather than the 9.8 originally derived. Such an estimate would be more commensurate with the 3 observed mortalities from 1987-95. In addition, it may be desirable to express outputs over a 20-year period if both transfers and mortalities continue to decline across all 16 developments by at least 50% over the next 10-year estimation period (1997-2006). Model refinement may be premature at this point, however, considering that observed transfers and mortalities were within the range of 95% confidence limits calculated for the dependent variable (see Table 1).

Conclusions

The grizzly bear mortality model as presented here appears to be a useful tool for both scientists and managers and could be refined to reflect changing relationships between management actions and subsequent bear mortalities over time. Management utility and application is related to the identification of developed areas where continual problems

exist or are increasing. The model could similarly be used to evaluate the effectiveness of localized management strategies designed to reduce problems within specific developments. While the model appears to satisfy its intended use by managers to evaluate the consequences of removal, reduction, or relocation of visitor facilities within the park, it also provides scientists with a quantitative means to evaluate the contribution of park developments relative to other ecosystem-wide sources of bear mortality. The model further provides a promising framework to explore similar relationships with other non-park point sources of mortality.

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A History of Wyoming Wolf Bounties: Transitions in Public Attitudes

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Abstract

This paper examines the activities of the Wyoming legislature with regard to wolf (*Canis lupus*) bounties. A brief overview of wolf bounty legislation and results dating back to 1875 is provided, along with selected quotations from explorers and residents to give insight into the prevailing social context. Review of some historic and current references to wolves indicates that majority attitudes of Greater Yellowstone residents toward the wolf may have gradually undergone a transition from annoyance, to fear and hatred, and eventually, to respect. We suggest that a generally negative attitude toward government is the basis for much of the opposition to wolf reintroduction, rather than a fear and hatred of the species itself, which may pose serious problems for wildlife managers. More than 100 years of history is reviewed, concluding with the activities of the 1995 legislature.

Introduction

Local opposition to wolf reintroduction into Yellowstone National Park was reflected in the actions of the 1995 Wyoming Legislature when it passed a $1,000 bounty on wolves, although the state hadn't paid a wolf bounty for many years. We wondered whether wolf bounty legislation was generally indicative of public attitudes toward wolves at the time of enactment. To answer this question, we conducted a review of historic and current references to wolves in the Greater Yellowstone Ecosystem (GYE) and determined the bounties offered and the number of wolves killed as a result.

Trapper/Explorer Era

To understand how transitions in public attitudes toward wolves have influenced Wyoming wolf bounties, we need to step back in time to the days before bounty laws were enacted. We start by reviewing the accounts of trappers and explorers, the first white men to become familiar with the wolf in the Rocky Mountain West. Journals of explorers to Wyoming in the early to mid-1800s contain few references to wolves beyond presence or abundance. Fur trappers were mainly interested in beavers (*Castor canadensis*); wolves were considered of little or no value. Brigadier General Hiram Martin Chittenden, in his *American Fur Trade of the Far West*, described the wolf as a source of extreme annoyance: "Such was the wolf, an animal of little value to man, yet one that he had to take account of because of its troublesome habits" (Chittenden 1954:829). The wolf was known to sneak into camp at night and kill tethered livestock and to steal articles from camps while the occupants slept. "They were thus always a source of extreme annoyance" (Chittenden 1954:830). Trapper Osborne Russell probably would have agreed when, after carefully caching a supply of meat by burying it deep in a snow drift and topping it with stones and burning gunpowder as a deterrent, he "found the wolves had dug it up and taken the best of it notwithstanding our precautions" (Russell 1965:110). George Ruxton, who traveled through the Rockies in the 1840s, complained that wolves would come into camp and chew up saddle leather, ropes, and buffalo hides (Porter 1950). Durward Allen noted: "Yet knowledgeable travelers had no fear of wolves and usually did not waste ammunition shooting them. The animals lurked about waiting to share the spoils of a hunt, and at worst they were a nuisance" (Allen 1979:402-403).

We found no accounts of wolves being killed in the Yellowstone area during the fur trade era of the early 1800s. Russell was once surrounded by a pack of howling wolves, which he quickly dispersed with a "flashing" of his pistol (Russell 1965:35). Yet Russell stated that "they are not ferocious towards man and will run at sight of him" (Russell 1965:129). Chittenden agreed. "The animal was rarely, if ever, known to attack man, even when impelled by extreme hunger" (Chittenden 1954:830). Perhaps Russell even felt some sympathy for the wolf, as suggested in his description of an incident that occurred when, upon catching the scent of Russell's dinner, a wolf sat upon a nearby rock and bewailed "his calamities in piteous moans" (Russell 1965:46). When describing the howl of the wolf, other trappers and explorers in the area in the late 1860s through the 1870s did not describe the blood-curdling howls of an evil beast, but instead used words such as "mournful," "dismal," "plaintive," and "doleful" (Schullery and Whittlesey 1992). These words are all associated with sadness, so regardless of whether these men actually held any compassion for the animal, perhaps they at least felt some slight empathy. Ruxton most certainly did. After a large gray wolf had followed him for several days of travel he noted: "I had him twenty times a day within reach of my rifle, but he became such an old friend that I never dreamed of molesting him" (Porter 1950:204). Later, while spending a cold and miserable night in a storm near Pike's Peak, Colorado, Ruxton observed that his "old friend the wolf [however] was still a companion, and sat all night within sight of the fire, howling piteously from cold and hunger" (Porter 1950:205). These words are not descriptive of an animal these mountain men feared. Ruxton also described an interesting incident while camping in a heavy snowstorm on the Platte River:

> In the middle of the night I was awakened by the excessive cold, and turning towards the fire, which was burning bright and cheerfully, what was my astonishment to see a large grey wolf sitting quietly before it, his eyes closed, and his head nodding in sheer drowsiness! Although I had frequently seen wolves evince their disregard to fires, by coming within a few feet of them to seize upon any scraps of meat which might be left exposed, I had never seen or heard of one approaching so close as to warm his body, and for that purpose alone. However, I looked at him for some moments without disturbing the beast, and closed my eyes and went to sleep, leaving him to the quiet enjoyment of the blaze (Porter 1950:261).

By the 1850s, the beaver population had been decimated in the Rocky Mountain West and atten-

tion turned to wolves and bison (*Bison bison*). Wolves were easily taken by lacing bison carcasses with strychnine poison. George Bird Grinnell described that "often while this is being done, the wolfer would be surrounded by a circle of ten or a dozen or more wolves, waiting patiently for him to complete his operations and go away, so that their meal might begin. In those days wolves had no fear of man. They were seldom shot at, and knew of the gun chiefly as an implement to call them to a feast" (Grinnell 1897:161). Stanley Young summarized similar accounts such as the following made by John Townsend:

> I have often been surprised at the perseverance and tenacity with which these animals will sometimes follow the hunter for a whole day, to feed upon the carcass he may leave behind him. When an animal is killed, they seem to mark the operation, and stand still at a most respectful distance with drooping tail and ears, as though perfectly indifferent to the matter in progress. Thus will they stand until the same is butchered, the meat placed upon the saddle, and the hunter is mounted and on his way; then, if he glances behind him, he will see the wily forager stealthily crawling and prowling along towards the smoking remains and pouncing upon it, and tearing it with tooth and nail, immediately he gets out of reach (Young 1944:125-126).

Horace Greeley commented on wolves after his 1859 trip across the country, stating, "It is very common for these wolves to follow at night a man traveling the road on a mule, not making any belligerent demonstration, but waiting for whatever may turn up" (Young 1944:126). These men did not fear the wolf, even given the close association they had in sharing a hunter's harvest. To these early residents of and visitors to the West, the wolves were neither feared nor hated, but were merely another interesting member of the natural wildlife community.

Western Settlement

The early fur trappers and explorers had told of the richness and diversity of nature to be found to the west. By 1845, at least 5,000 emigrants had followed the Oregon Trail, crossing the Rocky Mountains at South Pass, Wyoming, to settle the Willamette Valley of Oregon, known as the Garden of Eden for its free virgin land. In 1847, Brigham Young, the new leader of the Mormon Church, began settlement of the Salt Lake Basin, organizing a huge migration to the new Zion. And, in 1849, the gold rush to California began. Freighters became wolfers during the winter. Thousands of dollars worth of wolf hides (at only 50 cents a hide) were shipped from the Upper Missouri as a result of the popularity of strychnine by the 1860s. In 1862, Congress passed the Homestead Act, furthering the cause of western settlement. The "long drives" of cattle began in 1866, and a year later Horace Greeley urged easterners to "Go west, young man." This great westward movement may have led to the era of fear and hatred of the wolf. While explorers and trappers in the uninhabited Rockies were adventuresome, self-reliant outdoorsmen who had no real reason to fear the wolf, later emigrants experienced an entirely different reality. The emigrants faced a 2,000-mile trek from the Missouri River to the Pacific Coast, leaving the Missouri early in May. "More often than not, men made the decision to make the crossing. Wives either went with their husbands or faced being left behind. Four out of five men on the overland trail had picked up stakes and moved before, some of them several times. Most had little cash, but they needed only strong legs, a few staples, and a willingness to tighten the belt when game was scarce. The majority of people traveled in family groups, including in-laws, grandchildren, aunts, and uncles" (Divine et al. 1984:495).

The first leg of the journey, following the North Platte River to Fort Kearney, was fairly pleasant and was usually completed by late May. But the second leg, into the Wyoming Territory and the Great American Desert to Fort Laramie, was much more difficult for the emigrants. There was no wood for campfires and the blazing sun burned the grass. Indian wars raged. In a hurry to beat the snowfall, travelers rushed on to South Pass, a barren land with cold nights even in mid-July. The emigrants were lonely and exhausted. Still, more than a month of travel was ahead of them if they were to get as far as Fort Hall, Idaho, before winter set in. Wyoming was a land of desolation to these travelers. After months of hardship on the trail and many miles still

to go, the wolves appeared to be the physical manifestation of everything that had gone wrong on the trail or that could go wrong. They were always there, in view, watching and waiting for the next misfortune to befall the travelers. General Chittenden observed:

> The wolf was the most ignoble of the inhabitants of the plains. It personified cowardice, beggary, craftiness, deceit, mercilessness, and all the group of evil qualities that are comprised in the term wolfishness. It was the shark of the plains, and it followed the caravans for whatever it might find along the route, such as the refuse of camps, or the remains of buffalo and other game slain by the hunters. It delighted to disinter the bodies of persons who died on the way, and only the most thorough protection could save the graves of the dead from this desecration.... In the night it filled the air with its unearthly and hideous howlings, and gave an impression of power out of all proportion to what it really possessed (Chittenden 1954:829).

Young wrote:

> During the earlier days of western settlement, the eating of dead humans by wolves seems to have occurred whenever bodies were available. During the outbreak of cholera among the traveling emigrants in 1849-50-51, accounts of the epidemic state that more than 500 fresh graves on the south side of the Platte between the Missouri and Fort Laramie were visible along the trail. Brigham Young admonished the migrating Mormons to avoid this part of the road while traveling west for fear of the epidemic. Narrators of the Mormon trek at the time state: 'Scarcely a grave that had not been robbed of its contents by wolves, and the bones of its occupants lay bleaching on the prairie. At the same time those who perished on the trail while trekking to try their fortunes at gold digging in California were reported disinterred by wolves' (Young 1944:216-217).

For the emigrants, to experience the hardships of travel followed by the trauma of sickness and eventual death of beloved members of the family and to bury these loved ones in hastily dug graves along the trail, only to witness this 'shark of the plains' quickly excavating the gravesites and consuming the remains, made the wolf an animal to fear and hate. The wolf had become the personification of evil, the physical manifestation of death and hardship.

Cattle Depredations

Hatred of wolves was further reinforced in the early settlers by the wolves' acceptance of domestic livestock as a food source. With the 1871 discovery that buffalo hides made quality leather, bison hunting mounted. Six years later, however, bison hunting began to decline and by 1884 only a few hundred bison remained. As bison were eliminated and the range was stocked with herds of cattle, wolves began to change their prey base. Young wrote:

> The wolf was thus brought into direct competition with the livestock producer and provoked continued warfare. Every known means such as guards, guns, traps, poisons, bounties, and wolf-proof enclosures were sooner or later employed to obtain relief from wolf depredations.... Although disease might decimate his flocks and herds, or drought or severe winters might result in starvation or extreme cold losses, none of these factors seemed to arouse such outstanding resentment and determination of the stockman-farmer to adopt every means of elimination, as when the wolves killed on the open prairie or mountain range, or maimed and mutilated his range cattle and entered corrals to prey upon domestic stock. The cowman of the Old West wrought special vengeance on the wolf. Combating the wolf was not, however, a matter of mere revenge. Losses caused by this animal were often the chief factor in determining whether a season's range operations were to produce a profit or the reverse, to the individual stockman, particularly the small producer (Young 1944:378).

In 1875 the Wyoming Territorial Legislature enacted legislation authorizing a 50-cent bounty to be

paid on wolves, increasing it to $1 in 1879 and to $1.50 in 1884. The 1875 and 1879 laws were entitled "for the protection of sheep" and wolves were the only predators bountied. Only later were the laws expanded to include the destruction of other predators. The year 1886 brought a summer of drought in which the grass on the range burned and cattle went into the winter in poor condition. That winter of 1886-1887 became known as the Great Die Up because of the death of thousands of head of livestock. Wyoming became a state in 1890, and by 1893, the bounty on wolves was up to $8 per wolf. Ranchers and stock associations offered rewards of up to $1,000 for the killing of individual renegade wolves, which were responsible for the killing of thousands of dollars worth of livestock.

By 1896, it was claimed that wolves were causing almost a million dollars worth of damage to the Wyoming livestock industry every year. Wyoming's United States Senator Thomas B. Kendrick testified before a congressional committee that wolves had sometimes destroyed as much as 50% of the year's calf crop. From 1895 to 1907, 24,113 wolves were bountied by the State of Wyoming for $3-5 per pelt (see Table 1). When the Wyoming Legislature lowered the wolf bounty from $5 to $3 in early 1905, the citizenry was outraged as evident by the following, taken from the *Pinedale Roundup* at the time:

> Sights now to be witnessed on the range are such as to take all the heart away from the sturdy ranchman who has worked for the upbuilding of this country. The damnable terrorists of the timber—the wolves—are sweeping down on the range and playing havoc with the cattle. Riders coming in every day tell of the damage being done. Animals have been found hamstrung, and with portions of the carcass eaten away, while others have been found in a crippled form, but had managed to get away from the beasts. The shame should be pointed in the face of every member of our late legislature who opposed the bounty appropriation or had any part in the reduction of the bounty on predatory wild animals. A little hamstringing of some of them one year from next fall might prove compulsively that the voice of the people must be respected (*Pinedale Roundup*, May 24, 1905).

The depredations continued. The Wyoming Legislature appealed to the United States Congress for assistance, which wasn't provided until several years later. Problems were reported in 1906 in the area from Jackson to Pinedale. The killing had started with the appearance of the wolves in the lower country in mid-January of that year. It was reported:

> Ranchers are using up good horse flesh every day in riding after them but to no avail. Nearly a score of cattle have been reported killed by the varmits which sweep down at night. The sight is heart rendering to the rancher who must ride among his cattle and note the work of destruction. Many that were not killed have been badly bitten, chunks being taken out, leaving them badly crippled (*Pinedale Roundup*, February 7, 1906).

Locals formed bounty associations in an attempt to provide some relief. It seemed the wolf population was growing. In 1906, Charles Budd near

Table 1. Wolf bounties paid by the state of Wyoming.

Year	Number	Price ($/wolf)	Source
1895	1699	3.00	Bailey 1907
1896	3458	3.00	Day & Nelson 1928
1897	897	4.00 Adult .75 Pup	Bailey 1907
1898	3384	4.00	Day & Nelson 1928
1899/1900	4908	3.00	Bailey 1907
1901/1902	4480	3.00	Bailey 1907
1903/1904	2256	5.00	Bailey 1907
1905/1906	3214	3.00	Bailey 1907
1907	447	3.00	WY Auditor
1908	2928	5.00	WY Auditor
1909/1910	3419	5.00	WY Auditor
1911/1912	313	5.00	WY Auditor
1913/1914	1559	5.00	WY Auditor
1915	100	5.00	WY Auditor
1916	113	7.50 Ad. Male 12.00 Ad. Female 5.00 Pup	Hampton 1995
1917/1918	71 241	15.00 Adult 10.00 Pup	WY Auditor

Big Piney had yearling calves and 4 colts killed in his pasture over a 6-week period centering on March. In one area near Pinedale, 22 head of cattle were killed by wolves between January and April. These were significant numbers for individual stock producers. Eva Hayes of Lander grew up in the Split Rock area of central Wyoming in the early 1900s. She told us of the wolves that had come in and killed the family's turkeys. The family had invested all of their life-savings in these turkeys, and the wolves had effectively cleaned out the family accounts in 1 night. The family was heartbroken, angry, and destitute.

By 1908, Wyoming was again paying a $5 bounty on wolves. From 1908 to 1910, the State of Wyoming paid a $5 bounty on more than 6,000 wolves. A 1911 report on the legislative bounty appropriation noted that "the last appropriation (1909) made under this act was sixty thousand dollars, but it was all spent on bounties long before the meeting of the next legislature, when another appropriation might be made" (Hebard 1911:200). In 1911, then Governor Carey, believing the bounty program wasn't working, vetoed the bounty legislation. The citizens felt this unjust: "The stopping of bounty payments was a mistake of the present administration and a poor economy plan, for the man who owns a ranch and a small bunch of cattle has as much right to protection from predatory animals as the citizen of any town has in having police protection" (*Pinedale Roundup*, April 25, 1912). Governor Carey again vetoed a bounty bill in 1913, but before the end of the legislative session he relented.

Table 2. Wolves taken in Wyoming by the U.S. Biological Survey and its cooperators, 1917-1926.

Year	Number	Source
1917	98	Hampton 1995
1918	55	Young 1944
1919	88	Young 1944
1920	26	Young 1944
1921	104	Young 1944
1922	116	Young 1944
1923	52	Hampton 1995
1924	14	Hampton 1995
1925	1	Hampton 1995
1926	12	Roop 1971

U.S. Government Begins Predator Eradication

In 1914, the United States Congress passed legislation calling for the elimination of predators from all public lands and in 1915, the U.S. Biological Survey took over predator control efforts in Wyoming. Hundreds of wolves were killed in the following years. Wolves were reportedly abundant in Yellowstone National Park at the time and did much damage to the wildlife in the park. The local wolf bounty associations in northwestern Wyoming were paying $20 for a wolf pup, and $50-60 for an adult wolf. In 1916, the National Park Service was created and the new agency took over management of Yellowstone, becoming active participants in the predator eradication program. In the next 10 years, more than 100 wolves were killed or taken alive from the park.

In 1922, after a pack of wolves had killed and partially consumed 5 elk calves, Park Ranger Harry Anderson killed 3 members of the pack. According to the *Livingston Enterprise*, "The others escaped, but the park ranger has vowed to avenge the death of the tiny elk and is determined to clean out all wolves in Wonderland" (*Livingston Enterprise*, July 13, 1922). By 1926, only a few wolves remained in western Wyoming. Several wolf hunters in the region outside of Yellowstone National Park live-captured a few dozen wolf pups for the purposes of sale to eastern zoological parks and local exhibitions; a few were kept as pets by locals. The U.S. Biological Survey and its cooperators had killed 566 wolves in Wyoming in the 10 years prior to 1927 (see Table 2). By 1928, the Biological Survey estimated that there were no more than 5 adult wolves left ranging in Wyoming outside of Yellowstone National Park (Day and Nelson 1928:4).

The last of the lobos, the renegade wolves known by the physical characteristics unique to each individual and some of the worst livestock killers of all time, prompted a change in public attitude. These wolves were wary, clever animals that seemed almost impossible to stop, regardless of the enormous capture efforts. These wolves gained the respect of their observers, though it may have been only a grudging respect. Even the wolf hunters that in time dispatched the last of these legendary stock killers expressed some hesitancy about their work. H.P. Williams, after finally catching up to and kill-

ing the famous Custer Wolf in 1920, stated, "I tell you I'd built up such respect for the old devil that, if he hadn't had a trap on one foot, I might not have killed him. I really think I might have let him go" (Roop 1971:37). Ernest Thompson Seton also popularized these wolves in his widely read stories, such as "Lobo, the King of the Currumpaw", and "Badlands Billy: The wolf that won" (Seton 1985).

The 1927 Wyoming legislature reenacted the wolf bounty at $5 for each wolf, but lowered it to $3 2 years later. With few wolves left, bounty hunting became an unprofitable business. By 1939, the Forest Service estimated that only 6 wolves remained on the national forests in Wyoming (Young 1944:54-55). In 1940, Wyoming Game and Fish Department game warden H.B. Sanderson shot a large male wolf on the north rim of Shell Canyon in the Bighorn Mountains. Three years later, a sheep rancher on the Wind River Indian Reservation killed a male wolf, later stating: "But it was kind of sad to think that he was the only one that I'd ever seen and I killed him. Of course, at the time I was thinking there was nothing else I could do. But at the time he was endangering my sheep herd" (Cottenoir 1993:12). In 1944, Young noted:

> In many parts of the West ranchmen are still to be found who vividly recall the depredations and the costliness of these renegade wolves. It is probable that never did more intelligent wolves exist. Rarely have more dramatic hunts been planned and carried out, nor greater ingenuity employed, then the efforts put forth by the hunters who trailed these wolves and finally killed them. These animals had become wise beyond all other wolves through constant experience with the devices employed for capturing them. At times they seemed to be possessed of uncanny intelligence in avoiding steel traps, and in detecting various poisons, despite the variety of methods used in attempting to give the drugs to them. They likewise seemed to know when a man was weaponless. With every hand turned against them, their wisdom was respected by the stockmen upon whose cattle they depredated, as well as by the wolf trappers who finally eliminated them at the cost of much time, money, and patience (Young 1944:285).

The short era of the lobos produced a startling effect. Despite the recent memory of the monetary damage wolves could cause to livestock, these last wolves instilled a very different attitude in at least a few people. They were seen as worthy adversaries—cunning, intelligent, and bold animals that could strike back with vengeance. Wolves had won respect.

The bounty for wolves in Wyoming remained on the books at $2-3 through the late 1950s, even though control of predators was mainly accomplished by designated predatory animal control districts and other government programs. Government predator control agents were unable to receive the bounties. In 1949, a federal predator control agent accidentally killed a white wolf near Lander using a cyanide poison set which had been placed to kill what was believed to have been a depredating dog. Government predator control efforts were not aimed at controlling individual problem animals, but instead were geared toward complete eradication of all predatory animals and rodents, mainly through the use of Compound 1080 poison baits. In the 1960s, poison baits were dropped from airplanes throughout western Wyoming, until a ban on this practice went into effect in 1972.

Wolves were seen periodically by locals, but there were so few wolves that they were not viewed as a threat and instead were viewed with pleasure. Even the old timers who remembered past damage were not inclined to kill a wolf, unless it caused trouble. One rancher, Snook Moore, whose stepfather hunted wolves for the Fish Creek Wolf Association in the early 1900s, has seen a few wolves (as many as 4 together) on his ranch in the Gros Ventre periodically over the last 50 years and has never shot at one. When asked whether he was tempted to shoot the wolf he had spotted out his kitchen window 3 years ago, Snook (pers. commun.) replied: "No, I didn't want to shoot it. I could have, but I didn't want to." But Snook also cautioned, "If the wolves get thick, they'll bother." The few wolves living in the wilds of Wyoming offered opportunities for rare wildlife encounters that residents enjoyed (see Halfpenny *this volume* re sightings in GYE post government eradication). Snook explained that there were always a few wolves around until the government use of 1080, but then "that poison situation, they really destroyed the wolves, there's no doubt about it." According to Snook, the public, in-

cluding many ranchers "felt pretty bad about that poison 'cause it killed so damned much stuff than what they was putting it out for."

Federal Protection Begins

Wolves were finally given federal protection in 1973. It seemed that the rarer the wolf became, the higher the regard it received. One Carbon County, Montana, rancher stated: "The last time I saw a gray wolf was the winter of 1978 on my ranch in Carbon County. This wolf hung around for days and watched us feed. We had no reason to shoot this wolf; he didn't bother the cattle" (Strickler 1993). A Wyoming woman who saw a wolf while hunting described the experience: "His broad head, beautiful gray coat, and his dignity as he stood watching us, made a lasting impression. It was an experience I shall never forget" (Barthell 1988). Other residents of the Greater Yellowstone Ecosystem became somewhat protective of the few remaining wolves. For instance, 3 Sublette County ranchers whom we contacted about their wolf observations initially denied that they had ever seen a wolf. Eventually they shared their experiences, which included taking their wives to a remote lake to catch a glimpse of a mother wolf and her pups. They explained their earlier denial of wolf sightings by stating that they simply wanted the wolves to be left alone.

Wyoming residents have been hesitant to report wolf sightings. We've heard several reasons for this, including 2 based on the old "if it ain't broke, don't fix it" philosophy: 1) some residents don't approve of the hands-on, aggressive approach to wildlife management practiced today—the thought of biologists capturing these wolves and putting radio collars on them to "save" them is very unappealing; and 2) some residents also believe that public awareness of these wolves could lead to their demise. However, the primary reason seems based on a dislike and mistrust of government agencies. Many people believe that if government agencies discover the presence of an endangered species, hunting seasons, grazing leases, etc., will be closed or revoked in the area where the species occurs. This reasoning featured prominently in the debate over wolf reintroduction into Yellowstone National Park. Perhaps Wyoming's U.S. Senator Malcolm Wallop summarized it best when he stated, "I think most people in the West have had a belly full of the U.S. government and its ability to keep its word." Wallop continued: "The wolf isn't as much the problem as are the regulations under the Endangered Species Act that come with him. The wolf takes over the management of everything—of recreation, wildlife, timber operations, and other kinds of things" (Senator Malcolm Wallop, July 13, 1993).

Exactly 1 week after the first wolves were reintroduced into Yellowstone National Park from Canada, the Wyoming House of Representatives Agriculture Committee passed a measure to put a $500 bounty on wolves that strayed outside the park. This would require the State Attorney General to legally defend any hunter who attempted to collect the bounty if the federal government were to prosecute. The bill was sponsored by Republican businessman Roger Huckfeldt of Torrington. When asked why he sponsored the bill, Huckfeldt (pers. commun.) explained: "The federal government is forever imposing unfunded mandates on states and communities. We want the federal government to be more responsible for the actions they take." Huckfeldt, who collects wolf artwork, said, "I am not a wolf hater, but the federal government is wasting our money. We have a truly endangered species, one unique to Wyoming—the black-footed ferret. Wyoming can't get enough money to save this endangered species from extinction, yet the federal government spends millions on a species that really isn't even endangered. We are sick of the waste and the bureaucracy." Huckfeldt reported he had watched 2 wolves cross a meadow in front of him while elk hunting south of Yellowstone Park 3 years prior. He said of this encounter: "I was angry. I was angry because the Fish and Wildlife Service had lied to us for years and years, saying that there were no wolves." After weeks of debate and negotiation, Huckfeldt's bounty bill, revised to a $1,000 bounty on wolves and requiring the state to file a friend of the court brief on behalf of anyone prosecuted, was approved by the 1995 Wyoming Legislature. Just hours before the bill was to become law, Governor Jim Geringer vetoed it.

Conclusion: Dislike of Government and its Impact on Wildlife Management

Public dislike for government has become a heavy burden for resource managers to bear. Many residents of the West believe the United States gov-

ernment is a government out of control. Many are involved in the "local control" movement, an attempt to bring decision making to the local level, rather than through the Federal Register. Items such as the Nye County, Nevada, road controversy, reflect citizens' mistrust and dislike of the federal government. Closer to home, we have the case of the killing of the wolf reintroduced into Central Idaho and the local sheriff, citizens, and legislators condemning federal wildlife agents for what they viewed as "heavy-handed actions" in dealing with the rancher on whose land the wolf was found.

It is evident that these negative attitudes toward the federal government can and will be felt by wildlife managers, making predator management only more difficult. One wolf biologist, commenting on wolf reintroduction, wrote that "certainly it has been observed over and over again that wolves which 'arrive' on their own are more acceptable by folks who are not generally keen on wolves than wolves that are shoved down their throats by Big Brother" (Fairchild 1993). Another wolf biologist expressed the same sentiment: "the local residents in the wolf area do not feel that naturally recolonizing wolves have been shoved down their throats. When wolves are physically moved into an area by agency actions, I believe they are less likely to be accepted than if they walk there on their own" (Boyd 1993). These are examples of how negative attitudes toward government can affect wildlife management. One of these biologists went on to say, "I sincerely fear that by having the government reintroduce wolves that they will forever be tainted" (Fairchild 1993). Resource managers should realize that an anti-government attitude does exist and will interfere with effective wildlife management. Unfortunately, we can offer no suggestions or solutions to this problem.

In summary, our brief review suggests that Wyoming people have undergone transitions in their attitudes toward wolves. The early mountain men considered the species a mere annoyance, western emigrants feared and hated the wolf, and pioneering livestock producers viewed them as an economic threat. Eventually, once it occurred only in low numbers, the wolf gained some measure of respect. We suggest that generally negative attitudes toward government form the basis for much of the current opposition to wolf reintroduction and recovery, rather than any fear and hatred of the species itself.

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PART III
CONFERENCE ABSTRACTS

Home Range, Habitat Use, and Socio-spatial Characteristics of Wolverines in Central Idaho

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We determined wolverine (*Gulo gulo*) presence, ecology, spatial characteristics, movement, demographics, social structure, and habitat use in central Idaho from 1992-1995. Our study area encompassed approximately 8,000 km^2 of primarily roadless and wilderness habitats. The study area was characterized by montane coniferous forests at lower elevations and subalpine habitats associated with talus rock scree and open mountain tops at higher elevations. Nineteen wolverines were captured and instrumented with intraperitoneal implant transmitters. We monitored wolverines weekly by ground and aerial telemetry, collecting more than 1,200 relocations. Annual home ranges of resident adults averaged more than 400 km^2 for females and more than 1,600 km^2 for males. Adult home ranges were segregated by sex, with female home ranges overlapping less than 10% and male home ranges overlapping less than 15%.

Offspring of both sexes remained associated with the natal area for up to 2 years, which corresponded with sexual maturation. Juveniles and subadults associated with resident kin, including their mother, the resident male, and siblings. Evidence of resident adults associating with subadults has not previously been described for wolverines. Periods of association lasted as long as 7 days with individuals traveling together or localizing at foraging sites. The extended association of subadults and adults may be related to the highly dispersed nature of food resources and may account for the large home range sizes of resident females. Adult male home ranges encompassed up to 3 female home ranges. Snow-tracking sessions were conducted to document scent-marking and foraging behavior. Food resources were widely dispersed but consistent in timing and presence, which may cause formation of traditional foraging routes. These sites were revisited both within a season of use and between years and were shared within kinship groups. Urination was the primary method of scent-marking observed during this study. Distinct seasonal shifts in elevation use ($P < 0.05$) by several individuals were recorded, with higher elevation habitats used during summer months. Movement to lower elevations during winter months may be correlated with increased presence of carrion attributable to the fall big-game hunting seasons.

The reproductive rate for 4 adult females was less than 1 kit per female per year. Females used secluded high elevation cirque basins for natal den sites. Human disturbance at maternal dens resulted in den abandonment but not kit abandonment. Kits remained with the adult female for approximately 3 months after weaning at 9 to 10 weeks of age. Females commonly left dependent kits at rendezvous sites consisting of large boulder talus or riparian areas associated with mature overstory and dense timber deadfall. Boulder talus associated with subalpine habitats was also used for resting and foraging sites.

Ungulate species, including mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), moose (*Alces alces*), domestic cow (*Bos bos*), and domestic horse (*Equus* spp.), were present in similar proportions in both summer and winter scat and foraging site collections. Other prey items included 5 species of carnivores, 12 rodent species (including 5 sciurids) and 1 lagomorph species. Avian species constituted 4.9% of species occurrences while insects, primarily ants, constituted 5.9%. Four male wolverines dispersed at sexual maturity, with 2 emigrating distances greater than 185 km. Two of these individuals appeared to establish at the new location while the other 2 returned to the study area. Six wolverines died during the study, with predation accounting for 50% of the mortality.

Evaluation of Methods to Inventory and Monitor Mammalian Carnivores in Yellowstone

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With the notable exception of long-term research on grizzly bears (*Ursus arctos*), and more recent studies on mountain lions (*Puma concolor*), pine martens (*Martes americana*), and coyotes (*Canis latrans*), we know very little about Yellowstone's mammalian carnivores. They are typically secretive, nocturnal, and exist at low population densities. In many cases, we do not even have reliable methods to determine presence let alone estimates of abundance and other important demographic parameters. During the winters of 1992-93, 1993-94, and 1994-95 we evaluated 3 field techniques for their suitability to inventory and monitor species of the order Carnivora. Forty-two hair snare stations, 33 remote camera stations, and 80 snow-track transects were operated for 2803 and 2013 effort-days and 425 km, respectively. These methods were then evaluated based on their site variability, efficiency, precision, bias, and maintenance costs, as well as their utility to estimate presence, distribution, and abundance.

Response to baited hair snares and camera stations varied with location and between years. In comparison, snow-track transects yielded consistent results. Sixty percent, 76%, and 100% of sites produced sign of carnivores with hair snares, camera stations, and snow-track transects, respectively. Hare snares received 0.012 visits per night while camera stations yielded 0.113. Snow-track transects produced 33.0. Hare snares detected 70% of known carnivore species. Camera stations and snow-track transects detected 50% and 100%, respectively.

All 3 methods evaluated exhibited significant advantages and disadvantages. For example, while hare snares can provide DNA evidence allowing identification of individuals, they require regular maintenance. In addition, hare snares and especially camera stations were actively avoided by several species. Unlike snow-track transects, however, camera stations and hair snares performed well in cold temperatures and under most other climatic conditions. Still, camera stations were costly in terms of expense and maintenance. Transect sampling, in comparison, enabled identification of 3 additional species and proved to be a simple, inexpensive survey method that required little maintenance. Whereas camera stations and hair snares are baited with food and scent lures and thus bias habitat use data, transect surveys cover large areas and can provide valuable information on precise habitat use and food habits if scats are found. For example, we successfully extracted DNA from fox (*Vulpes vulpes*) scats. Snow-track transects require skilled, full-time labor (2 individuals) able to track approximately 30, 2- to 5-km transects per winter season. Furthermore, species identification using snow-track transects can be difficult under certain climatic conditions, particularly given the similarity of many species' track characteristics. The aforementioned problems associated with each method result in questionable species identification. Upon evaluation, we consider reliability to be poor to fair for tracks and snared hair, and good only for camera stations.

Although specific research objectives and logistical considerations will influence selection and use of these methods, we suggest employing a combination of all 3 to determine presence and distribution of mammalian carnivores. We strongly recommend initial, large-scale surveys using snow-track transects conducted under the constraints of stratified random sampling. This should allow coverage of large areas (required for carnivores with large home ranges) in multiple habitat types. Because poor climatic conditions can render most winter days (e.g., ~60% in this study) unacceptable for snow-track transects, we further recommend augmenting these transects with hair snares and camera stations when important species are suspected to occur and/or probable sign requires positive identification.

Not finding evidence of a particular species when it is present and incorrectly concluding it is absent is a common problem in presence/absence surveys of carnivores. It is statistically analogous to a Type I error. Without assigning a probability value to a given level of effort, biologists are violating fundamental, reliable methods of scientific inquiry. We need to further develop and test new methods. A variety of traditional and novel abundance estimators (and associated techniques) for monitoring change are discussed.

A Preliminary Study of Habitat Use and Distribution of the Red Fox in the Northern Yellowstone Ecosystem

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Preliminary analysis of data was presented on the first year of a 2-year study beginning winter of 1994-95. We examined habitat use, phenotypic and genotypic variation, and parasitic fauna of red foxes (*Vulpes vulpes*) in the northern Yellowstone ecosystem. The study area was divided into 3 regions based on differences in habitat and elevation. We identified these regions as lower, middle, and upper. Using Global Positioning System devices, foxes were snow-tracked to obtain information on habitat use, prey base, and movement. Seventy track sets were examined across 26 transects in the middle and upper regions. This resulted in approximately 40 kilometers of fox tracks ranging in length from 100 meters to 1,500 meters. Several foxes were captured this winter in addition to 4 trapped previously and 6 collected from road kills.

The Geographic Information Systems database, created from data collected during the winter of 1994-95, includes 330 habitat points along track sets. At each point, we measured habitat type, cover type, distance to nearest ecotone, slope, aspect, snow depth, snow hardness, sink depth, and squirrel, weasel, grouse, and hare crossings. We also located 33 forage points on the track sets and examined the same set of parameters. In addition, 8 bed sites were located and described. The 330 habitat points were located approximately 100 meters apart, yielding an estimated total of 40 kilometers of fox tracks during the 1994-95 winter.

Red fox habitat use will be analyzed by comparing movement data and data collected at habitat and forage points to habitat availability in the northern Yellowstone ecosystem. Distribution of foxes will also be examined, especially in relation to known coyote (*Canis latrans*) pack territories. Additional comparisons will be made of parasitic fauna and disease titers between foxes and coyotes.

Influence of Social and Environmental Factors on Behavioral Budgeting by Yellowstone Coyotes

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The influence of social and environmental factors on the foraging ecology of coyotes (*Canis latrans*) is relatively unknown. We examined the influence of social and environmental factors in relation to behavioral budgeting (time-activity) of coyotes in Yellowstone National Park by observing 54 coyotes (49 residents from 5 packs, plus 5 transients) for 2,507 hours from January 1991 to June 1993. We found that 4 environmental variables significantly influenced the amount of time coyotes devoted to resting, traveling, hunting small mammals, and feeding on carcasses; namely snow depth, ungulate carcass biomass, habitat type, and prey density. Age and social status of the coyotes were the social factors that significantly influenced behavioral budgets. We observed that, during times of deep snow and high carcass biomass, pups fed less on carcasses and spent more time hunting small mammals than did alpha and beta coyotes.

Pups were restricted from feeding on carcasses by older pack members. Hence, they adopted a different foraging strategy and spent more time hunting for small mammals. Our observations suggest that resource partitioning (mediated through defense of ungulate carcasses) occurred among resident coyote pack members in Yellowstone. Parental care of the pups was terminated by winter and, thereafter, pups fended for themselves. Resource partitioning appeared to be a mechanism for regulation of pack size. Dispersers were low-ranking individuals, spent little time with other pack members, were subordinate in interactions with other coyotes, and had little or no access to carcasses. Philopatric coyotes were higher-ranking, more dominant, spent more time with other pack members, and had greater access to carcasses.

Coyote Population Demographics on Yellowstone's Northern Range

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This study examines the population demographics of 5 coyote (*Canis latrans*) packs in Lamar Valley (LV) and 7 packs in Blacktail Deer Plateau (BDP) in Yellowstone National Park from 1989 to 1994, prior to wolf reintroduction. Focal observations were used to determine pack size, litter size, social status, and pack affiliation of coyotes. Focal observations of scent-marking and territory defense were used to determine pack territory boundaries in LV. To ascertain BDP territory boundaries, 127 radio-collared or radio-implanted coyotes were tracked from fixed radio-telemetry stations using programs INDATA and HOME RANGE (50% harmonic mean contour). Territory landscape attributes were determined using U.S. National Park Service data layers with Geographic Information Systems. Estimated small mammal biomass was obtained from a concurrent Northern Range study.

Mean January pack sizes of 5.90 in LV and 5.42 for BDP were not significantly different ($t = 0.59$, $P = 0.60$). Mean litter sizes of 3.64 and 5.45 pups for the same respective areas were not significantly different ($t = -1.58$, $P = 0.89$). Mean territory litter size was negatively correlated with estimated mean small mammal biomass (adj. $R^2 = 0.58$, $P = 0.004$, $n = 12$). Pups typically dispersed in the fall or late winter at a rate of 13.4% before the end of their first year. The annual rates of mortality for pups and adults were 40.2% and 8.0%, respectively. Average territory size was 1,005 hectares in LV and 768 hectares on BDP. Estimated small mammal biomass per territory was significantly different between LV (2.48 kg/ha) and BDP (1.75 kg/ha) ($t = 3.33$, $P = 0.008$). Winter ungulate carrion biomass also appears to be greater in LV. Reintroduced wolves will probably change coyote population demographics in Lamar Valley and Blacktail Deer Plateau.

A Pre-wolf Disease Survey in Yellowstone National Park

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Whenever an animal is translocated, its resident micro- and macro-organisms are also transported. Therefore, disease concerns must be addressed for any wildlife reintroduction or translocation. To prepare for potential gray wolf (*Canis lupus*) reintroduction, a base-line study of canine diseases was conducted in Yellowstone National Park from 1991 to 1994.

Because wolves could potentially be infected with harmful diseases in the new environment, 1 objective of this survey was to identify diseases in the Yellowstone ecosystem that could negatively influence gray wolf reintroduction. Specifically, the diseases of concern were canine parvovirus, canine distemper, and infectious canine hepatitis. Reintroduced wolves could also potentially bring diseases with them that could be harmful to Yellowstone fauna, especially if wildlife did not have previous exposure. Therefore, the second objective was to determine which canine diseases were present in Yellowstone wildlife, particularly canids and mustelids.

The last objective was to determine if zoonotic canine diseases (that is, diseases transmitted from wildlife to humans) were already present in the Yellowstone ecosystem and to understand their disease ecology to assess the significance of adding wolves to this ecosystem. Specifically, the zoonotic

diseases of concern were a tapeworm, *Echinococcus*, and rabies.

The pre-wolf disease survey was a multi-faceted study, which involved: 1) disease sampling associated with the Yellowstone Coyote Ecology Project, 2) data obtained from the Yellowstone Disease Monitoring Program, 3) a hantavirus study conducted in Yellowstone National Park, and 4) literature review.

The pre-wolf disease study was closely tied to the Yellowstone Coyote Ecology Project conducted from 1991 to 1994 that provided a unique opportunity to thoroughly investigate diseases of Yellowstone coyote (*Canis latrans*) populations. We utilized the coyote as the primary model because closely related species, such as coyotes and wolves, are generally susceptible to similar diseases. In addition, coyotes and reintroduced wolves will share territories, carcasses, and other mechanisms supporting disease transmission. The coyote disease study involved sampling from live animals, post-mortem necropsies, and demographic study.

Disease information from live coyotes was gathered using: 1) physical examinations to evaluate general health status and detect clinical signs of infectious disease, 2) external parasites collected during the physical exam along with ear swabs, 3) blood serum for serologic testing, and 4) fecals for detection of internal parasites.

Post-mortem examinations were conducted on 54 adult coyotes and 41 pups. Each carcass was necropsied to determine the cause of death, identify specific or general pathological conditions, and to collect tissues for further examination.

Demographic data, such as reproduction, pup survival, and mortality factors were gathered with the help of radiotelemetry and field observations. Adult coyotes were trapped in the fall with padded, offset-jaw leghold traps with tranquilizer tabs. The adult coyotes were anesthetized with ketamine and xylazine, ear-tagged, radio-collared, and sampled as previously described.

To gather data on pup survival, 8-to-12-week-old pups were surgically implanted with an intraperitoneal transmitter possessing a mortality signal. In addition to providing social and behavioral data, intraperitoneal telemetry allowed biologists to recover many pups within 24 hours after death, which significantly increased our ability to determine the cause of death. Pups were captured by hand, anesthetized with both ketamine and xylazine or Telazol, then implanted and eartagged prior to sample collection for the disease survey. These procedures are described by Slade et al. (*this volume*).

In addition to the coyote disease investigation, results from the Yellowstone Wildlife Disease Monitoring Program were reviewed. The monitoring program provides a valuable avenue to opportunistically gather disease information from carcasses that are recovered throughout the year.

A hantavirus study conducted in Yellowstone National Park in spring of 1994 was also utilized for the pre-wolf investigation. The life cycle of *Echinococcus multilocularis*, which uses coyotes and foxes as definitive hosts, includes a larval stage that infects an intermediate host, such as mice and voles. Therefore, small mammals collected for the hantavirus study were also inspected for *Echinococcus* larvae. Examined carcasses suspected of having larvae were sent to the Wyoming State Diagnostic Laboratory for further examination.

A broad array of internal and external parasites was identified from Yellowstone coyotes. These parasites were collected during both live sampling and necropsies. However, none of the parasites collected have been reported to be harmful in free-ranging gray wolves.

Implants were surgically placed in 59 coyote pups. Slade et al. (*this volume*) describe the fate of these pups. The most significant finding relative to the pre-wolf survey was the detection of a parvovirus outbreak in coyote pups in 1991 and again in 1992. At least 11 of 31 pups died at about 3 months of age due to parvovirus. The Yellowstone Disease Monitoring Program documented a pine marten (*Martes americana*) from the Old Faithful area that died of canine distemper in April of 1993.

The hantavirus study conducted in Yellowstone during the spring of 1994 collected 616 small mammals, and every carcass was opened and visually inspected for *Echinococcus*. No *Echinococcus* larvae were detected. However, published literature reports the presence of *E. multilocularis* in or near the Yellowstone ecosystem. Seesee and Worley (1976) reported *E. multilocularis* in 2 foxes from the Gallatin Valley, and Seesee et al. (1993) reported this tapeworm in coyotes and foxes in Gallatin and Madison counties. Feigley (1981) reported *Echinococcus* cysts in 2 muskrats (*Ondatra zibethicus*) from the East Gallatin River. Although *Echinococcus* was not detected during this pre-wolf survey, literature review

supports the likely presence of *E. multilocularis* in the Yellowstone ecosystem, which involves the coyote / fox - rodent cycle.

A thorough literature review by Johnson (1995) was conducted to evaluate the potential role of rabies in Yellowstone wolf populations. Rabies has not been reported in Yellowstone National Park. The review, which correlated the disease ecology of rabies with its geographic distribution and distribution among species, concluded that the addition of the wolf to the Greater Yellowstone Ecosystem is unlikely to contribute additional risks associated with rabies to humans, domestic animals, or wildlife. Nonetheless, steps were taken to prevent even the remote chance of wolves becoming infected with rabies. To address rabies concerns, wolves for translocation were captured from areas known to be free of terrestrial rabies. Also, wolves were serologically tested for rabies and all test results were negative. In addition, all wolves were vaccinated with a killed rabies vaccine to protect them from even the most remote chance of exposure.

Coyote serology demonstrated that the common canine diseases tested for are present in Yellowstone as they are in most parts of North America. Therefore, Yellowstone populations of susceptible fauna are, as a whole, immunologically protected. There is essentially no risk if these diseases were brought along with the wolves. Even so, the potential transport of these diseases was minimized by examining each and every translocated wolf for signs of infection.

Johnson et al. (1994) attributed the death of wolf pups in Glacier National Park to canine parvovirus and / or canine distemper. Because these diseases are endemic to the Yellowstone ecosystem, they could potentially have a negative impact on developing wolf populations in Yellowstone. Therefore, disease monitoring is included as an objective of the Yellowstone Wolf Recovery Project. Other potential hosts, such as canids and mustelids, can be monitored for these diseases on an opportunistic basis. Diseases infecting wolves can also be monitored as part of present or future ecological studies (see Fuhrmann, *this volume*).

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Predator-Prey Relationships between Large Carnivores and Cervids in and around Glacier National Park, Montana

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Breeding wolves (*Canis lupus*) have been present in and around Glacier National Park for almost 10 years. Information from this area can be used to predict the effects of predators on cervid populations and behavior in the Greater Yellowstone Ecosystem and throughout the northern Rocky Mountains. This information will identify possible management alternatives to ensure healthy populations of both predator and prey. Since the initiation of our study in 1992, wolves, cougars (*Felis concolor*), bears (*Ursus* spp.), coyotes (*Canis latrans*), and humans have all killed radio-tagged, female, white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*) to varying degrees. Cougar predation was the greatest mortality factor for both deer and elk. Grizzly bears (*Ursus arctos*) and wolves were the primary predators on moose. Currently, deer and elk populations appear to be declining and the moose population is increasing. Wolves and cougars selected white-tailed deer as their primary prey item. Cougars killed a greater proportion of male deer than did wolves, but there was no difference in the age class of deer killed by wolves or cougars. Spatial and habitat variables affected prey encounter, detection, and capture by predators. Wolves traveled and killed deer in areas of high deer density in 1992-93 but not in 1993-94. Wolves killed deer in areas of greater hiding cover in 1992-93 but not in 1993-94. There was no relationship between snow depth or canopy and kill sites; however, depth of prey tracks did appear to be related to kill sites in 1993-94. The density of deer at wolf and cougar kill sites differed in both winters. Hiding cover was similar at cougar kill sites and wolf kill sites in 1992-93, but differed in 1993-94. There was no difference in canopy at wolf kill sites versus cougar kill sites in either winter. The more severe winter of 1992-93 and the resultant change in prey distribution probably accounts for most of the between-winter differences.

Wolf Abundance in Relation to Landscape and Prey

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Analysis of data from 28 North American studies suggests that the numerical response of wolves (*Canis lupus*) to ungulate biomass may be saturating rather than linear. A saturating response may be the result of an intrinsic spatial limitation of wolf densities. In this study, we explored the possibility that a saturating response may result from changes in the spatial distribution of prey. Implicitly, a linear numerical response assumes a spatially uniform distribution of prey, yet elk (*Cervus elaphus*), the primary prey species on the Northern Range (NR) of Yellowstone National Park, exhibit a highly clustered distribution.

We explored the implications of spatial clustering for predator-prey encounter rates using a point-process model to characterize the observed distribution of elk across the Northern Range. The model constituted a Poisson distribution of elk herds with the spatial distribution of individuals within each herd being uniformly circular and the number of animals in the herd drawn from a geometric distribution of herd sizes. The model was fitted to the observed locations and sizes of elk herds on the NR between 1986-1991 using a maximum-likelihood fitting procedure. We then used the model to explore how changes in elk density, caused by (1) increases in the number of herds and (2) increases in herd size, affected the probability of a wolf encountering an elk within a given search radius. Our analysis showed that higher elk densities caused by increases in the number of elk herds elevated the encounter rate, but higher elk densities caused by increases in herd size had a negligible effect on predator-prey encounter rates. Our finding that the encounter rate depends primarily on the number of herds rather than the number of animals within a herd is an intuitive and robust result that arises as a natural consequence of the observed clustering of elk on the NR. Interestingly, increases in elk density on the NR between 1986 and 1991 (there was a 3-fold variation in total density between the lowest and highest years) resulted entirely from increases in herd size. This suggests that from the viewpoint of a searching predator, increases in the biomass of elk on the NR may not translate into increased prey availability. This finding is also consistent with empirical observations that have shown that prey selection by wolves in Jasper National Park is based on the number of elk herds (Weaver 1994).

In addition to prey density, the number of wolves occupying the NR will be determined by habitat availability. Evidence from heterogeneous landscapes similar to the NR has shown that wolf habitat use is strongly governed by sinking depth in snow during winter, which directly limits wolf movements and also influences the spatial location of prey (J.

Weaver, P. Paquet pers. commun.). Sinking depth is a complex variable that varies in relation to snow depth and the snow density profile, which, in turn, vary temporally throughout the winter (Farnes and Romme 1993). However, work in Jasper National Park has shown that wolves generally restrict their movements to areas with snow depths less than 20-28 inches (about 51-71 cm) (J. Weaver, P. Paquet pers. commun.). Moreover, in Yellowstone the vast majority of elk are found in areas with a snow depth of less than 20 inches (Farnes 1993).

We calibrated a spatially explicit model to predict snow depths across the northern section of Yellowstone National Park. The model included estimated, empirical relationships between snow depth and the following landscape attributes: (1) slope, (2) aspect, (3) vegetation type, (4) distance along the rain shadow, and (5) cumulative snowfall measured at the park weather stations. The model was used to construct a Geographic Information Systems (GIS) layer of snow depth for the northern third of the park. Assuming a criterion of less than 24 inches snow depth as an indicator of habitat suitability for wolf occupancy, we performed a GIS analysis of the region. The analysis suggests that, in any given year, the total area suitable for wolf occupancy varies depending on snowfall. In a typical year, approximately 60% of the northern section of the park is suitable for the establishment of wolf territories. We are conducting further field research to improve the model. In particular, we are investigating the relationship between sinking depth, snow depth, and snow density.

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The Case of Yellowstone's Predator Pelicans: Ecology and the National Park Service Wildlife Division, 1920-35

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Beginning in 1924, Yellowstone National Park briefly carried out experiments to control the numbers of pelicans on Yellowstone Lake. This issue became public knowledge in September 1992 when Rosalie Edge published the Emergency Conservation Committee's inflammatory "Slaughter of the Yellowstone Park Pelicans." Although control had stopped years before, this unfavorable publicity was nevertheless unpleasant for the National Park Service.

The story of Yellowstone's pelicans takes on new significance if viewed as an example of the coevolutionary changes in ecological ideas and management agendas that took place during the dynamic period from 1920 to 1935. The pelicans feeding at Grouse Creek occupied the center of a complicated web of human relationships between the National Park Service's Washington office, Yellowstone Park personnel, fish culturalists of the Bureau of Fisheries, fishermen visiting Yellowstone, mainstream actors in the 1920s conservation movement, more "radical" conservationists like Rosalie Edge, scientists studying birds and parasites, and finally, Joseph Dixon and Ben Thompson of the National Park Service's Wildlife Division.

Perplexing management dilemmas are not new in Yellowstone. Although the players have changed, Yellowstone managers have never made decisions in a "vacuum." People, such as Assistant Chief Ranger George W. Miller, made wildlife management decisions within the greater context of national conservation interests, as well as changing ideas and attitudes among scientists. Letters of protest and support to Horace Albright from scientists all over the country in 1932 illustrate the nature of the relationships that surrounded Yellowstone at that time, and bring to light the contribution of our evolving scientific knowledge and understanding of natural resources to management direction. The growth of ecological ideas and conservation efforts surrounding the pelicans from 1920 to 1935 were significant precursors to the renewed emphasis on scientific management of natural resources beginning in the 1960s.

American Martens, Fishers, Lynx, and Wolverines: A Technical Conservation Assessment

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Scientists from Forest Service Research, the National Forest System, and independent institutions worked together to produce an assessment of the scientific basis for conserving forest carnivores in the western United States, a group that includes American martens (*Martes americana*), fishers (*Martes pennanti*), lynx (*Lynx canadensis*), and wolverines (*Gulo gulo*) (Ruggiero et al. 1994). This conservation assessment reviews what is known about the biology and ecology of these species, the management implications, and what information is needed for the development of scientifically reliable conservation strategies. Narratives for each individual species elucidate the state of knowledge within a conservation biology framework with emphasis on factors that affect population persistence. Additional narratives synthesize findings as the basis for discussing overall management implications that arise from the state of knowledge. Specific information needs are identified and a research approach is presented toward the development of conservation strategies for the 4 species.

Both the quality and quantity of knowledge are explicitly addressed in this assessment. Much of what is known about these forest carnivores is derived from just a few designed studies, combined with anecdotal information. Some of this knowledge merely documents the presence of animals in an area or habitat type, without addressing key issues of population ecology necessary for analysis of habitat requirements and persistence probabilities. Such knowledge can be misleading for conservation purposes, and this potential problem is addressed in the assessment. Overall, huge gaps in knowledge were identified for all of the species considered. Thus, the production of reliable conservation strategies is not possible and an evaluation of conservation status is problematic.

All species addressed in this assessment have distributions in the western United States that are limited to boreal forest ecosystems. Boreal forests are characterized by extensive landscapes with a major component of structurally complex, mesic coniferous stands that are characteristic of the late stages of forest development. The center of the distribution of this forest type, and of these forest carnivores, is the vast boreal forest of Canada and Alaska. In the western contiguous states, the distribution of boreal forest is less continuous and more isolated than to the north, so forest carnivore populations and their habitats are more fragmented at the southern limits of their ranges. Also, forest carnivores tend to be wilderness species that are largely intolerant of human activities, and they tend to have low reproductive rates and large spatial requirements by mammalian standards. All of these factors

contribute to the sensitive nature of these animals relative to human influence and the changing Western landscape.

The smallest bodied of the forest carnivores, the American marten, is also the most widespread, abundant, and best known. Still, its conservation status varies by area, with some populations showing no human impact and others possibly endangered. Distributional losses have been particularly extensive in the Pacific Northwest (i.e., Washington, Oregon, and northern California). Martens avoid non-forested areas almost completely, at least in winter, when they seek out complex structure near the ground (see Bissonette *this volume*).

The fisher is larger bodied than the marten, occurs at lower densities, and is known mostly from studies conducted in the eastern U.S. and Canada. Fishers have undergone extensive distributional losses, especially in the Pacific Northwest, and are given state and federal designations that reflect this status. Our knowledge of fishers in the western U.S. is based on only 4 field studies. These studies indicate a close association with mesic late-successional forests, an avoidance of non-forested habitats, and an affinity for physical structure near the ground like that of the marten.

The only cat among the forest carnivores, the lynx occurs in eastern Washington, where 2 studies have been conducted, and in the mountains of Idaho, Montana, Wyoming, and Colorado. The range of the lynx appears to be steadily retreating northward, as reflected by state and federal designations. It associates with late-successional forest for resting and denning, but uses early successional stands for hunting snowshoe hares, its primary prey. Lynx populations in the lower 48 states do not exhibit the dramatic cycles of those farther north. Our lack of knowledge about alternate prey, dispersal abilities, and responses to landscape attributes precludes better understanding of how lynx may be affected by human alterations of forests.

Wolverines are the largest, widest-ranging, least known, and most protected of the forest carnivores. Populations in the lower 48 states are limited to forested habitats, perhaps because of the wilderness character of these lands. Wolverine populations may receive important ingress from Canada. Only 4 field studies on wolverines have been completed in all of North America (see Copeland et al. *this volume*), and information from the western contiguous states is mostly anecdotal. Mature and old growth forests may provide important denning and/or rendezvous sites for wolverines. Only 1 study has been conducted where logging had been done. Very large areas will likely be needed to conserve wolverine populations.

An ecosystem approach to management will be central to the success of all conservation strategies given the complexity of ecological processes that likely affect persistence probabilities for these species. Complex physical structure associated with mesic late-successional stands will be important for conserving these forest carnivores, and immediate management attention will be needed to conserve populations that are already isolated and threatened. Until further research is completed, additional forest fragmentation via activities such as clear-cutting should be avoided in areas where forest carnivore conservation is of concern.

This conservation assessment leads to the conclusion that concern about the status of forest carnivores is justified and conservation strategies will be needed to assure the persistence of populations of these species. Additional information at multiple spatial scales is required to develop scientifically reliable conservation strategies, along with a substantial, sustained commitment to research.

Acknowledgments

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Vocal and Spatial Responses of Coyotes to Reintroduced Wolves in Yellowstone National Park

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How do coyotes (*Canis latrans*) solve the multiple problems of resource defense, relocation of separated pack members, territorial maintenance, and interspecific competition with gray wolves (*Canis lupus*)? Part of the answer lies in the suite of long-range vocalizations that coyotes use to address these complex sets of inter- and intra-pack problems. In this study we analyzed coyote vocalization behaviors from January to July of 1995 and, in addition, assessed coyote litter production and coyote spatial responses to reintroduced gray wolves. We monitored known coyote packs in 2 study areas in the Northern Range of Yellowstone National Park: Lamar Valley served as the treatment area, where gray wolves were present in 3 enclosures from January to March, and then free-ranging from April to June; and Blacktail Plateau served as the control, where gray wolves were absent throughout the study. Data collected were divided into 2 periods: pre-wolf release (winter), and post-wolf release (spring/summer). In addition, Lamar Valley was subdivided into "wolf" and "wolf-adjacent" areas across all seasons. We spent more than 700 hours in Lamar Valley and the Blacktail Plateau during 1995 and used more than 400 of these hours in the analysis. Data collected included the type of call, pack of origin, and vocal responses. For all areas, we corrected for the number of packs audible from a given vantage point based on known territorial boundaries derived from the previous 6 years of observations.

We found a highly significant set of wolf effects on coyote vocalization bouts. A vocalization bout is defined as a clump of non-independent calls separated by a >5-minute interval. Bout rates served as an overall index of all types of vocal activity and were calculated on a per pack, per 24-hour basis. In winter, while gray wolves were kept in 3 holding pens in Lamar Valley, the number of bouts per pack in Lamar Valley coyote territories containing wolf pens and Lamar Valley coyote territories adjacent to wolf pens did not differ significantly from each other, but were nearly triple the rate of the control ($P < 0.05$). In summer, we divided the coyote territories into wolf-use areas, where wolves superimposed their home range, and wolf-adjacent areas, where coyote territories were adjacent to wolf-use coyote territories. In both Lamar Valley wolf-use and wolf-adjacent coyote territories, the overall bout rates were significantly elevated above the control. Unexpectedly, the Lamar Valley wolf-use coyote packs had a lower bout rate ($P < 0.05$) than the coyote territories where wolves didn't travel.

The most frequent component of all coyote vocalization bouts is the group-yip howl, or the long-range territorial announcement call. This call, given by 2 or more animals, is frequency modulated

(meaning it rises and falls in pitch repeatedly) and is interspersed with repeated yipping. As was also the case for coyote bout rates, there were closely matched values for wolf-pen and adjacent wolf-pen rates, both of which were triple the rate of the control area ($P < 0.05$). In summer, the coyote packs in wolf-adjacent territories had a rate 3 times higher than in coyote packs in wolf-use areas, and 8 times higher than the control ($P < 0.05$ for both).

Lone howls are relocation calls given by separated pack members and do not seem to be directly associated with territorial defense. Lone howl rates in the summer and winter were significantly elevated above the control area in both wolf-use and wolf-adjacent coyote territories. Barks and yips, which function as alarm and threat calls, showed extreme variability. The rates were not significantly different between the study areas and exhibited the expected seasonal patterns characteristic of all coyote long-range vocalizations: bout rates, group-yip howls, lone howls, barks, and yips all declined from winter through spring in both treatment and control areas.

Bout intensity rates (defined as the number of discrete calls per bout) were consistent across all seasons and study areas. Coyote bout intensity rates appear to be stable, while both within-bout profiles (or the different types of calls contained within a single bout) and overall bout rates (or the frequency of calling episodes) seem to be responsive to changes in external stimuli such as the presence of gray wolves.

National Park Service patrol rangers kept records of coyote and wolf vocalizations and sightings while on patrol around the wolf pens during the winter portion of this study. The rates observed at the 3 wolf pens were similar, yielding an overall base rate of 10-20 bouts per 24-hour period, per coyote pack. This was consistent with other observed rates.

Coyotes showed a general pattern of spatial and behavioral avoidance of wolves, with the marked exception of coyotes' agonistic behaviors associated with wolf-coyote interactions both at carcasses and at coyote denning areas. In Lamar, the Crystal Creek wolf pack, which numbered 6 animals, spent 50% of its time from late March through early July in 4 known coyote territories. The litter sizes of these 4 coyote packs were lower than that of neighboring packs. In 3 out of the 4 wolf-use coyote territories, wolves were observed excavating traditional coyote den sites. We documented 1 of these excavation episodes at the Norris pack. Two of the 4 wolf-use coyote packs used den sites in non-traditional areas at the periphery of their territories. Mapped locations of den sites for the 2 study areas indicate that placement had been stable for the 5 years prior to wolf reintroduction. Thus, these location changes may be 1 of the earliest reliable indicators of spatial displacement of coyotes by wolves.

Yellowstone Coyote Pups: Capture, Marking, and Follow-up Study

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Each June from 1990 to 1993, we located coyote dens, captured pups, implanted them with radio transmitters, recorded their physical condition and general health status, and monitored adult and pup behavior in 15 packs found in the Lamar Valley and Blacktail Plateau of the Northern Range of Yellowstone National Park.

To find dens, we used aerial flyovers, tracked radio-collared adults, observed unmarked adults from vantage points, and explored traditional den sites. Two methods were used to catch pups: the "strand" method, where we surprised pups outside the den and sealed off entrances; and the "ferret" method, where we inserted a wire with a wooden head into the den and startled the pups into rushing out. About 2/3 of the pups were caught by the "strand" method.

Pups were 8 to 12 weeks old when captured in mid-June and weighed 4-8 pounds. They were eartagged, measured, examined for external parasites and ear mites, and had blood drawn for seriological analysis. Pups were then implanted with intraperitoneal radio transmitters.

During the 4-year period, 88 pups were observed at the various den sites (though additional pups undoubtedly were not observed). Of the 88 observed pups, 70 were captured and, of these, 59 were implanted. There were no deaths associated with capture and implanting. Of the 59 implanted pups, 28 survived at least through the first winter, 28 died prior to or during the first winter, and the fate of 3 pups remains unknown. Twenty-nine carcasses were recovered, including some unimplanted pups. The sex ratio was about equal: of the 59 implanted pups, 31 were males and 28 were females. Deaths were equally distributed among males and females, with 14 of each sex dying, while 16 males and 12 females survived.

Most of the pups died during the neonatal period, from birth (in April or May) to 5 months of age. During 1991 and 1992, an epidemic of parvovirus occurred and was the principal cause of death, with at least 11 of the 19 neonatal deaths being attributed to this disease (see Johnson et al. *this volume*). The surgical implantations of intraperitoneal transmitters were highly successful, which is consistent with the findings from numerous other studies.

Predation of Elk in Northwest Wyoming

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We investigated predation rates of 164 elk (*Cervus elaphus*) captured and radio-collared as neonates in northwest Wyoming during 1990-1992 and monitored through 1994. Neonatal mortality (birth to 15 July) averaged 15% annually and was higher ($P = 0.04$) for male than for female calves. Predation by black bears (*Ursus americanus*) and coyotes (*Canis latrans*) accounted for 68% of all neonatal mortality. Mountain lions (*Puma concolor*) killed 2 additional calves that were 4.5 months old and another that was 12.5 months old. Calves killed by predators were born earlier ($P < 0.002$) than calves that died from other causes, though predation of individual calves was unrelated to weight at birth. Thirty percent of all first-year mortality was due to predation. Elk older than 12.5 months died only as a result of hunting. Predation rates of calves that were born and summered outside Grand Teton National Park did not differ from survival rates of calves that summered inside Grand Teton National Park, where elk densities were twice as high. The similarity in mortality suggests that predation was not density-dependent.

Movements and Food Habits of Gray Wolves Released in Yellowstone National Park

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In late March 1995, after 10 weeks of acclimation in holding pens, 14 gray wolves (*Canis lupus*) making up 3 groups were released in the Lamar Valley of Yellowstone National Park. Initially, each group of wolves restricted movements to areas around the acclimation pens. Total area used was small and measured about 125 km^2 for the Crystal Bench group, 90 km^2 for the Soda Butte group, and 25 km^2 for the Rose Creek group. Distance traveled per day was also low, averaging 6.1, 3.1, and 1.7 km per day for the Crystal Bench, Soda Butte, and Rose Creek groups, respectively.

After about 3 weeks, an abrupt increase in movements signaled the beginning of an exploratory period. Area used increased to about 550 km^2 for the Crystal Bench and Soda Butte groups, and 1,000 km^2 for the Rose Creek group. Average travel distance per day was 22 km for the Crystal Bench and Soda Butte wolves, compared to 30 km for the Rose Creek group.

After this exploratory period, the Crystal Bench wolves returned to the park and settled into a 390 km^2 area between the Lamar and Pelican Valleys traveling an average of 5.4 km per day. The alpha female in this group excavated and explored 5 holes and behaved as if she were going to whelp, though she did not. Her pseudo-pregnancy was likely the result of rising prolactin concentrations.

The Soda Butte wolves settled while exploring because female 014 whelped one pup. Movements became localized in an area north of the park in the Absaroka-Beartooth wilderness. In mid-July, when the pup was capable of traveling with the pack, they moved south to Yellowstone where they remained through mid-September.

On 26 April, the Rose Creek alpha male was shot and killed. His mate, who was alone at the time, whelped 8 pups. She was later captured with her pups and transported to the Rose Creek acclimation pen where she remained until early October.

Two wolves traveled alone the first month post-release. A male pup from Crystal exited the pen after the other wolves and did not rejoin the pack until early May. The female pup from Rose Creek exited the pen with the 2 adults and traveled with them for 6 days before she separated and became a loner. Her movements did not exhibit an exploratory phase. Rather, she had an ever-increasing area of use before she settled in the northwestern portion of the park.

The Crystal wolves were located infrequently as a group from late March through late July. The adult pair (004M and 005F) were always located together (n = 51 locations), but various combinations of yearlings (singles and duos) were tracked traveling separately. In early August, this pattern changed and the pack began traveling together. The Soda Butte wolves were always located together through April, but were rarely together after whelping (i.e., May to August). In September, this pattern changed once more and they resumed traveling together (n = 51 locations).

The primary prey taken by all groups of wolves was elk (*Cervus elaphus*). Of 17 collected wolf kills,

15 were elk. Seven of these elk were calves (short-yearlings) and 6 were old elk. The Soda Butte group also killed one old cow moose (*Alces alces*) and a mountain goat (*Oreamnos americanus*). While traveling alone in April, the lone male pup from Crystal Bench killed an elk calf, and in September the lone female killed an old cow elk. There is no evidence that the wolves killed deer (*Odocoileus hemionus*) or bison (*Bison bison*). Kills observed opportunistically during tracking flights from 31 March through 14 May revealed a kill rate of 6.3 and 3.4 days/kill for the Crystal Bench and Soda Butte groups respectively. Observers in the Lamar Valley, who watched for wolves daily, recorded the Crystal wolves feeding every 5.2 days (observation period 11 May—6 July). Kill utilization was moderate (i.e., carcasses articulated with hide and hair present on leg bones). Most of the kills had been visited by coyotes (*Canis latrans*) and 4 of them were visited by grizzly bears (*Ursus arctos*).

Are High Elevation Populations of the Red Fox Isolated in the Greater Yellowstone Ecosystem?

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Red foxes (*Vulpes vulpes*) have been present in Yellowstone National Park since its inception, although they have been the focus of little research. Park records indicate that they have been found in all 3 traditional coat-color phenotypes: red, cross, and black. However, many Yellowstone red foxes have also been described as having "light yellow" and "gray" coats, colors that have not been reported for this species anywhere else in the world.

Extensive work was done on the genetic control of coat color in foxes during the early 1900s due to the value of their fur. Production of the traditional coat colors (red, cross, and black) is controlled by 2 loci, each with 2 alleles. Additional loci control coat color development for mutations that have occurred on fur farms, and at least 17 viable mutants have been discovered, none of which correspond to the novel color phases found in Yellowstone. A mutation at a homologous locus in mice, sheep, and foxes is responsible for converting coat color from black to either yellow or gray. This suggests that the novel color morphs in red foxes could be the result of a single mutation event.

A similar situation exists in the Cascade mountain fox (*V. v. cascadensis*), where 2 populations of red foxes are isolated by elevation. High elevation populations are only found in the subalpine region, while low elevation populations are found below a belt of coniferous trees in the surrounding scrub and farmland. In addition, montane foxes are smaller than lowland foxes and Canadian red foxes (*V. v. abietorum*). It is thought that the difference may be the result of a founder effect that occurred during the Wisconsin glaciation. We are currently examining the degree of isolation that occurs between the high and low elevation populations of the red fox in the Greater Yellowstone Ecosystem (GYE) to determine if a similar situation exists.

Park records for the last 100 years indicate that the 2 novel color phases of the red fox, namely light yellow and gray, have been present in the park since the late 1800s. Analysis of the records suggests that the novel color phases occur most frequently at higher elevations. Sightings of the novel color phases increase dramatically at elevations greater than 2,000 meters, the approximate boundary of subalpine habitat. Analysis shows that a significantly greater proportion of novel color phases is found at high elevations (Fisher's Exact test, $P < 0.0001$).

Six foxes have been trapped, with additional data

collected from 5 road kills and 1 predator-killed fox. Elevations range from 1,926 m to 2,987m for the trapped foxes, and from 1,630 m to 2,438 m for the road-killed foxes. Several morphological variables were significantly related to elevation: head girth ($r^2 = 0.857$, $P < 0.01$), neck girth ($r^2 = 0.820$, $P < 0.01$), and chest girth ($r^2 = 0.618$, $P < 0.01$). Genetic analysis (conducted in R. Wayne's laboratory at UCLA) was performed on a 300 bp sequence of mtDNA. To date, scorable sequences have only been obtained from 6 of the foxes, those occurring at elevations of 1,630 m, 2,072 m, 2,110 m, 2,145 m, 2,850 m, and 2,987 m. These sequences are identical, in scorable regions, except for a 1 base-pair substitution found in the road-killed fox from 1630 m.

These preliminary results are consistent with the possibility that some degree of isolation exists between the high and low elevation foxes in the GYE. A founder event during the Wisconsin glaciation or selective differences could explain the variability seen in the red fox populations. Further genetic analysis and increased sample sizes are needed to determine whether populations are indeed isolated. We are currently increasing our sample size and investigating these questions with microsatellites to try to provide a clearer picture with respect to the amount of gene flow between the high and low elevation populations of red foxes.

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