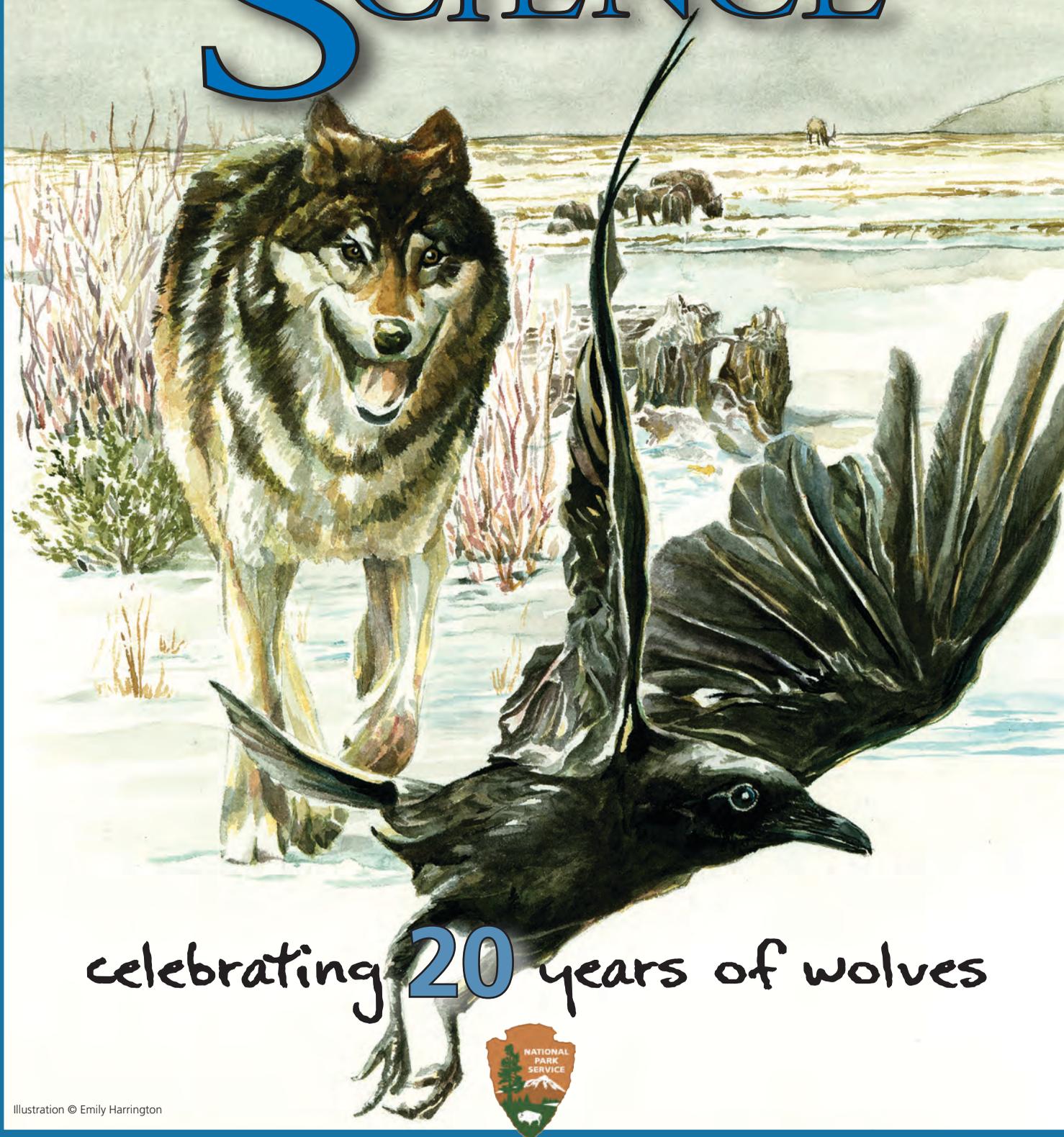


YELLOWSTONE SCIENCE



celebrating **20** years of wolves





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The Complications of Wildness

After a 70-year absence, 41 wolves from Canada and northwest Montana were reintroduced to Yellowstone National Park between 1995 and 1997. Numbers grew, meeting management targets; and wolves were delisted in 2009 (except in Wyoming), but were then relisted in 2010, delisted again in 2011, delisted in Wyoming in 2012, then listed again in Wyoming in 2014. It's complicated. Everything with wolves is that way. Most people rate wolves among the most controversial wildlife to live with; a colleague from India rates them as more controversial than tigers—a species that occasionally kills people.

The back and forth of listing and delisting does not affect the status of wolves in the park—they're protected either way. It's untrue that they are immune to influences from outside the park, but some refer to wolves in Yellowstone as “country club” wolves or wolves that live in a world of fewer conflicts. That may be partially true, as the park is managed as natural, unlike the human-dominated landscapes found elsewhere where wolves run into trouble...and people, too. This idea of natural is important and has been a long-term park goal. It's hard to imagine how this was accomplished without wolves.

Does natural mean wild? Many consider wolves to be a symbol of the wilderness (grizzly bears, too); wolf-less landscapes seem to be missing something. Part of this dedicated issue on wolves is about what it means to have this wildness back. Another part of having wolves back is people. Visitor enjoyment has been a big part of their return—a sensation almost—a craving to see them, even know them. It's something real in this contrived and digital age. Life and death. Real nature with no bars in between. Most don't get this in our daily lives, so it can be a thirst slaked by only the real thing. There are not many places other than Yellowstone to go for this. Of course, there are other perspectives, such as the life and death of a wolf is better left up to humans.

And this, in a nutshell, is the problem wolves have: wildness in a modern age. Wildness is hard to manage for, and people have divergent views on the subject. Ecologist Paul Errington called it “the pricelessness of untampered nature.” But we like to tamper. Thoughts like these stem from fundamentally different world views, which come from people's values. Somehow wolves have been, and continue to be, caught in the middle. It seems impossible that anything like this could be resolved.

But we try. We have the park, which is all of ours. And we have policy that says we need to keep it natural...whatever that is. But you can be sure that includes wolves and their kind, which is why this beloved place is different. It's wild, now especially. This edition of *Yellowstone Science* is dedicated to the last 20 years of wolf recovery in Yellowstone. We hope you enjoy this view into the complicated, rewarding world of bringing wildness back.

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PHOTO © R. DONOVAN

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Lessons Learned from the Yellowstone Wolf Restoration Project

Bruce Babbitt

In the twenty-one years since I signed the final decision documents, Yellowstone wolf restoration has continued to yield important new insights and many surprises, in the process attracting world recognition as a model of ecological restoration. Back in the 1970s, after passage of the Endangered Species Act, proposals to bring back the wolves generated little but continuing controversy. Again and again the effort seemed ready to collapse in acrimony and congressional resistance. Even the most optimistic proponents were unsure that the wolf would return within our lifetimes.

How this restoration effort could succeed against such long odds and in such a short time is a question that deserves exploration. Exactly how did the wolf cast off the image of reviled outlaw to inspire the most successful restoration effort of our time? How did public opinion swing so dramatically from negative to positive? Can the gray wolf story instruct us in ongoing efforts to save and restore endangered species, protect threatened ecosystems, and confront global warming?

The first lesson that I take from the Yellowstone experience is the imperative to continually explain, in language accessible to the public, the ecological case for restoring endangered species and their habitats. Aldo Leopold set an unforgettable example with his account of shooting one of the last wolves in the Escudilla Wilderness, only to watch a “fierce green fire dying in her eyes,”¹ an epiphany that has ever since inspired so many of us to action.

A second lesson from the Yellowstone experience is that change typically comes up from the grass roots, growing slowly from the sustained efforts of determined citizens. Defenders of Wildlife and the redoubtable Renée Askins (founder of the Wolf Fund in 1986 for the sole purpose of reintroducing wolves into Yellowstone) were among the many who led the way. Others must now carry on to complete the task of defining a

place for wolves on landscapes outside park boundaries and to restore other endangered species across the land.

An especially important part of the grass roots process was the manner in which advocates, park leaders, and scientists came together to design and use the Environmental Impact Statement decision process as an outreach opportunity to organize innumerable public meetings that awakened public opinion in favor of restoration.

And not least, the personnel of the National Park Service and the U.S. Fish and Wildlife Service were the unsung heroes of this process, persevering in the face of intense opposition from elected officials and local interest groups. They deserve our respect and thanks and continuing support.



Bruce Babbitt (pictured below wolf watching with Doug Smith) served as the Secretary of the Interior during the Clinton administration (1993-2001) when the initial wolf reintroductions occurred. He was Governor of Arizona from 1978 to 1987.



NPS PHOTO

¹ Leopold, A. 1966. *A Sand County Almanac*. Oxford University Press, New York, USA.

Wolf Restoration in Yellowstone: Reintroduction to Recovery

*Douglas W. Smith, Daniel R. Stahler, Matthew C. Metz, Kira A. Cassidy,
Erin E. Stahler, Emily S. Almberg, & Rick McIntyre*

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Anthony R.E. Sinclair, long-time researcher in the Serengeti of Africa, suggests that to understand an ecosystem, one also must know its human history. For the Serengeti, he refers to the 1889 outbreak of rinderpest that killed 95% of Africa's cattle and many wild ungulates, and the 19th century ivory trade, both of which drastically altered the plant-animal associations of the 20th century. When first studied in the 1960s, no one was aware of this history, which impeded an in-depth understanding of the ecosystem (Sinclair 2012). Yellowstone, too, has had human interventions

that have affected its short and, sometimes, long-term ecological relationships; but compared to the Serengeti, our human history is better documented. Historic interventions into Yellowstone include the fur trade, market hunting, predator control, fire suppression, elk and bison reductions, rewilding of black and grizzly bears, and now wolf reintroduction. It is this last one which is the focus of this issue. Although wolf reintroduction lasted only three years and recovery has been a relatively recent historical event, this human intervention is likely to have impacts lasting well into the future.

Since the first *Yellowstone Science* special issue on wolves in 2005 (10th anniversary of reintroduction), a lot has happened and our understanding has improved. Wolves are no longer in the “colonization” phase of recovery, which dominated the story in the 2005 issue. Glimpses of a new Yellowstone are taking shape. Gone for most of the 20th century, wolves and other carnivores have made a comeback; but wolves are arguably the most notable as they are considered the dominant North American carnivore (based on distribution and abundance; Mech 1970). Bears were never eliminated, but were reduced; and cougars have now recolonized as well. With these increased carnivore densities, and including other factors, elk have declined and bison have increased, ushering in what now has to be considered a new era in Yellowstone (White et al. 2013). This new time may be the most “natural” in all of Yellowstone’s long history.

“Natural” is what early park managers and outside scientists struggled to define (Pritchard 1999). This is ironic because at the time, most large carnivores were gone. Surely part of the definition of “natural” would include them, but public attitudes were strongly anti-carnivore; and this had a significant influence on policy (Pritchard 1999). Given this cultural backdrop, the human intervention of wolf reintroduction in the 1990s may be the most deliberate and high profile among these recent management actions. What follows is an update since the 2005 special issue on wolves, 20 years in. Likely the story will change each decade, but at least we can hope all of these carnivores will be around for some time, helping to keep Yellowstone as natural as it can be.

Human Attitudes and Wolf Recovery

In the first special wolf issue of *Yellowstone Science*, a change in human attitudes was highlighted as the most important factor in making wolf recovery possible. Humans are still the most important factor in wolf management, both inside and especially outside of the park. It is worth a brief review of the intertwined policy and people who pulled off this effort.

An early voice arguing for change before it was popular, Aldo Leopold mentioned Yellowstone as a place to restore wolves, “Yellowstone and its adjacent national forests. . . some of considerable size in which. . . [wolves] may be allowed to continue their existence without molestation” (Leopold 1944). He also added, “Are we really better off without wolves in the wilder parts of our forests and ranges?” (Leopold 1991). Ultimately, Leopold’s

vision for Yellowstone was realized and recognized when the first wolf pack to naturally form in Yellowstone in over 70 years was named the Leopold pack.

Another significant step was in 1975-1977, when John Weaver conducted a formal survey to look for wolves—he found none—and once again restoration was recommended through a reintroduction (Weaver 1978). Then Douglas Houston, in his landmark book *The Northern Yellowstone Elk*, did the same, calling Yellowstone “ideal” for wolves and that their absence was “the single greatest departure from the objective of maintaining natural ecosystems” (Houston 1982), harking back to the early park managers who tried to define the meaning of “natural,” yet without wolves (or other carnivores). By the time Houston was recommending restoration, the U.S. Fish and Wildlife Service had already produced a Recovery Plan which was revised in 1987 (USFWS 1980, 1987). Both documents helped clear the way for more planning that culminated in approval—bipartisan approval—from Congress to restore wolves to Idaho, Montana, and Wyoming.

In short, the strategy was to nurture a new population that had immigrated from Canada into northwest Montana and to reintroduce wolves to central Idaho and Yellowstone. The goal was 30 breeding pairs across the region and approved management plans from the three states. In 1995 and 1996, and only in Yellowstone in 1997, 76 wolves from Alberta, British Columbia, and northwest Montana were released into central Idaho and Yellowstone: 41 in Yellowstone (14 from Alberta, 17 from British Columbia, 10 from northwest Montana), and 35 in central Idaho (Bangs and Fritts 1996). The West’s new wolf era was underway. Some said this was the most significant wildlife conservation event of the 20th century for the United States. Changing human attitudes were revising the mystique of the old west—it would not go quietly or completely, nor should it. And, it still can be the “wild west,” perhaps even wilder with the carnivores.

Looking back, the process to restore wolves to Yellowstone went surprisingly smoothly. Early U.S. Fish and Wildlife Service work, combined with the vision of National Park Service (NPS) Director William Penn Mott, the quiet leadership of Yellowstone Superintendent Robert Barbee, the detailed planning of the Recovery Team, support from the Clinton administration and Secretary of the Interior Bruce Babbitt, and final implementation by Edward Bangs and Steven Fritts of the U.S. Fish and Wildlife Service, with big assists from

Yellowstone planners John Varley and Wayne Brewster, were the reasons for the success. Michael Finley was park superintendent when reintroduction occurred. Public support was significant, truly a ground swell of grassroots efforts from a variety of sources (The Wolf Fund and Defenders of Wildlife both at the forefront, plus many others). It is hard to imagine how such a controversial program achieved the success it did. Behind the scenes, there were many others, most notably Norman Bishop, an NPS employee who worked on his own time to educate the public about restoration and why to support it. Later the Yellowstone team led by Michael Phillips, and then Douglas Smith, carried the program to successful completion. Of course, most credit is due to the wolves; they only needed a little help.

Colonization to Saturation

Now, 20 years forth, some perspective on what happened can be achieved. Just by eyeballing the graph of annual park wolf counts (figure 1), we can characterize two phases over the last 20 years: Phase 1 is up to about 2008, where population growth was mostly positive; Phase 2 is where growth was mostly flat or even negative. This first period we refer to as the “colonization” phase (wolf numbers reached 174 in as many as 16 packs parkwide), and the second period the “saturation” phase (wolf numbers during this time hovered around 100 in 10 packs).

Since 1997, after releases were completed, average population growth was about 10% per year, but year-to-year variation was greater, ranging from +62% to -43%. This characterization helps us understand much of what is happening ecologically and behaviorally. Will there be a Phase 3? Interestingly the northern Yellowstone elk herd, after precipitously declining, also appears to be stable since about 2010 (figure 2). Has some kind of equilibrium been achieved between wolves and other carnivores, elk, and bison?

With fewer elk, we suspect there are fewer vulnerable elk. Wolves make their living from vulnerable prey, and not just available prey, because prey are also dangerous to wolves. We conclude this because elk probably now exist below carrying capacity, unlike when there were more than 20,000 elk (“The Challenge of Understanding Northern Yellowstone Elk Dynamics after Wolf Reintroduction,” this issue, for more details on the wolf-elk relationship). Elk below carrying capacity generally means there are plenty of resources for all; whereas, at carrying capacity, comparatively more elk will not have enough resources, be in poorer condition, and therefore be more vulnerable to wolf attacks. Anecdotally, our capture crews support the characterization of elk being in good nutritional condition in recent years. The

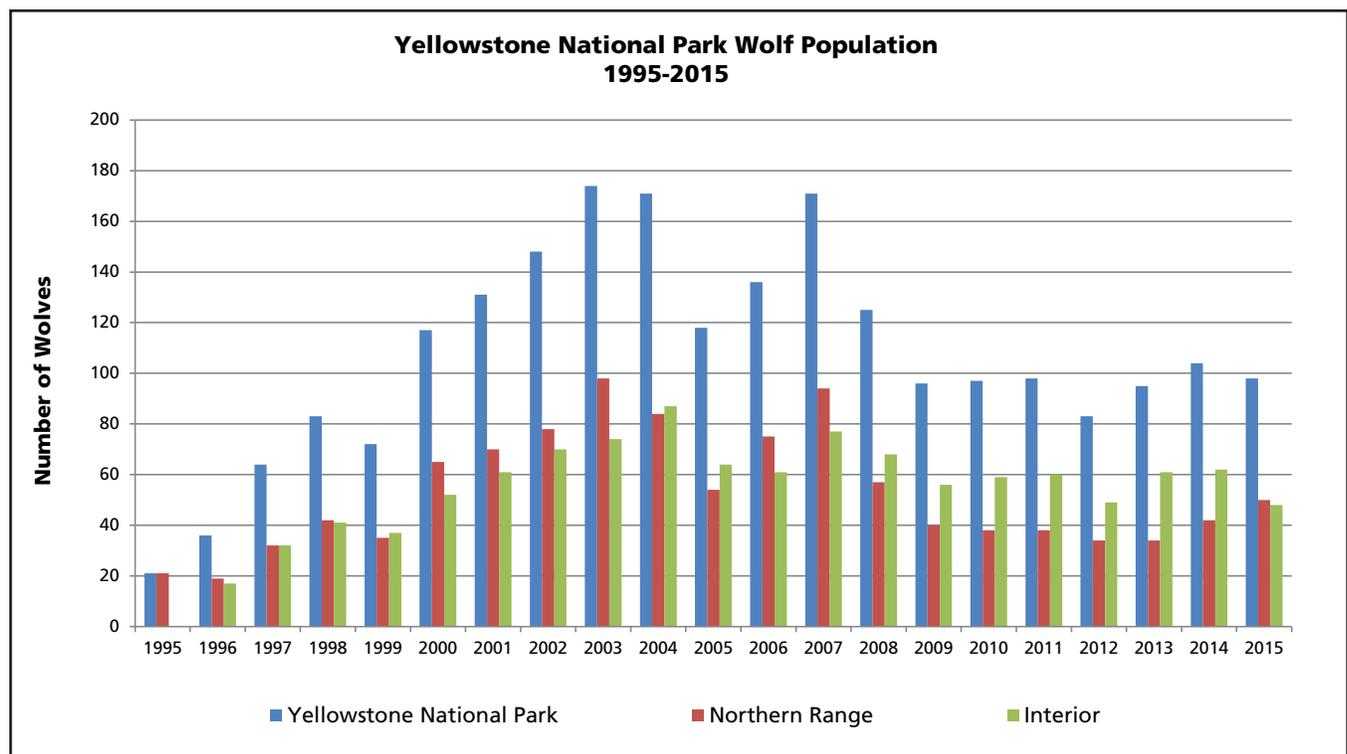


Figure 1. Yellowstone National Park wolf numbers in early winter, 1995-2015.

contract capture crew, who catch and collar elk, tell us that Yellowstone elk are the leanest, meanest elk in all of western North America. Why? Probably because they are predator-tested and below carrying capacity. How would you like to be a wolf faced with killing one of these elk, an animal five to seven times your size and you have nothing to use but your teeth and pack mates?

Another factor impacting wolf numbers is disease. In fact, disease could be considered the defining feature of Phase 1, or the outcome of growth and high wolf density. During Phase 1 when population growth was mostly positive, there were three outbreaks (1999, 2005, and 2008) of canine distemper virus (CDV) that caused the population to decline (figure 1; “Infectious Diseases of Wolves in Yellowstone,” this issue). After the first two declines, the wolves immediately increased the next year; we call this compensatory reproduction, and it likely occurred because there was abundant food in the form of vulnerable elk. After the third CDV outbreak in 2008, the wolves did not increase the next year; 2009 happened to be the year an epidemic of sarcoptic mange peaked within the park. We also learned the spread of

both CDV and sarcoptic mange were somewhat dependent on wolf density; packs in areas of lower density had lower exposure rates to both CDV and mange (Almberg et al. 2012, 2015). Mange is a chronic infection and may be here to stay, but now with lower wolf densities will there be another CDV outbreak? We know that CDV does not impact only wolves, but probably all carnivores in Yellowstone. So how will this dynamic affect wolves and other wildlife in the future? These disease outbreaks may be even more complicated. Interestingly, during CDV outbreaks, black wolves appear to survive better than gray, or at least wolves that carry the black coat gene (“Yellowstone Wolves at the Frontiers of Genetic Research,” this issue). This interaction between coat color and disease resistance is far from worked out but is an area of intense research.

Another interesting aspect of the saturation phase is it appears wolves have occupied most of the suitable wolf habitat in Yellowstone (figure 3). Habitat requirements for wolves include protection from humans, year-round availability of ungulate prey (Mech and Boitani 2003), and enough space so pups are protected from other packs

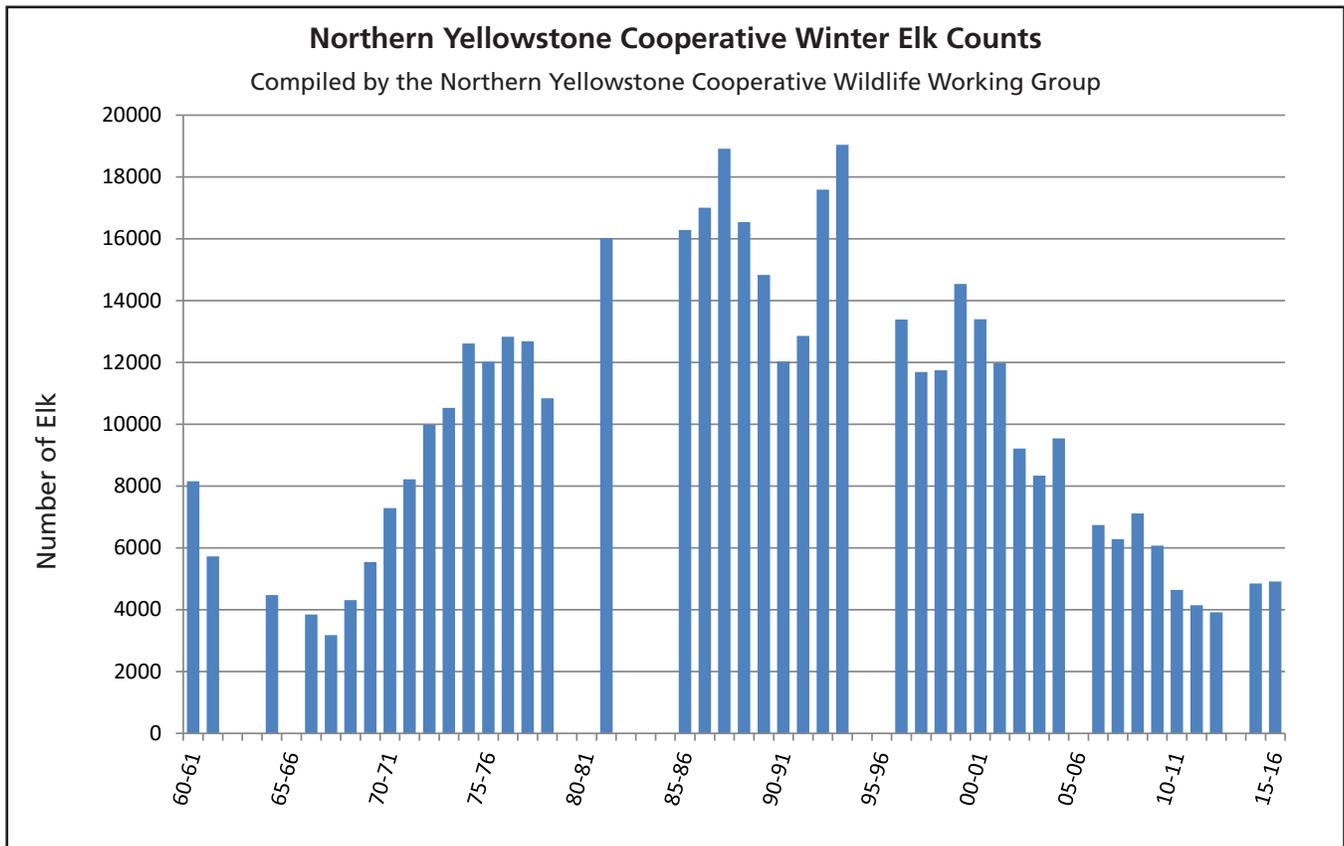


Figure 2. Winter counts of the northern range elk herd in Yellowstone National Park and adjacent areas of Montana, 1960–2016. Counts were not adjusted for elk sightability, and gaps represent years when no official count was conducted or when sightability was so poor due to weather conditions that a count was not released.

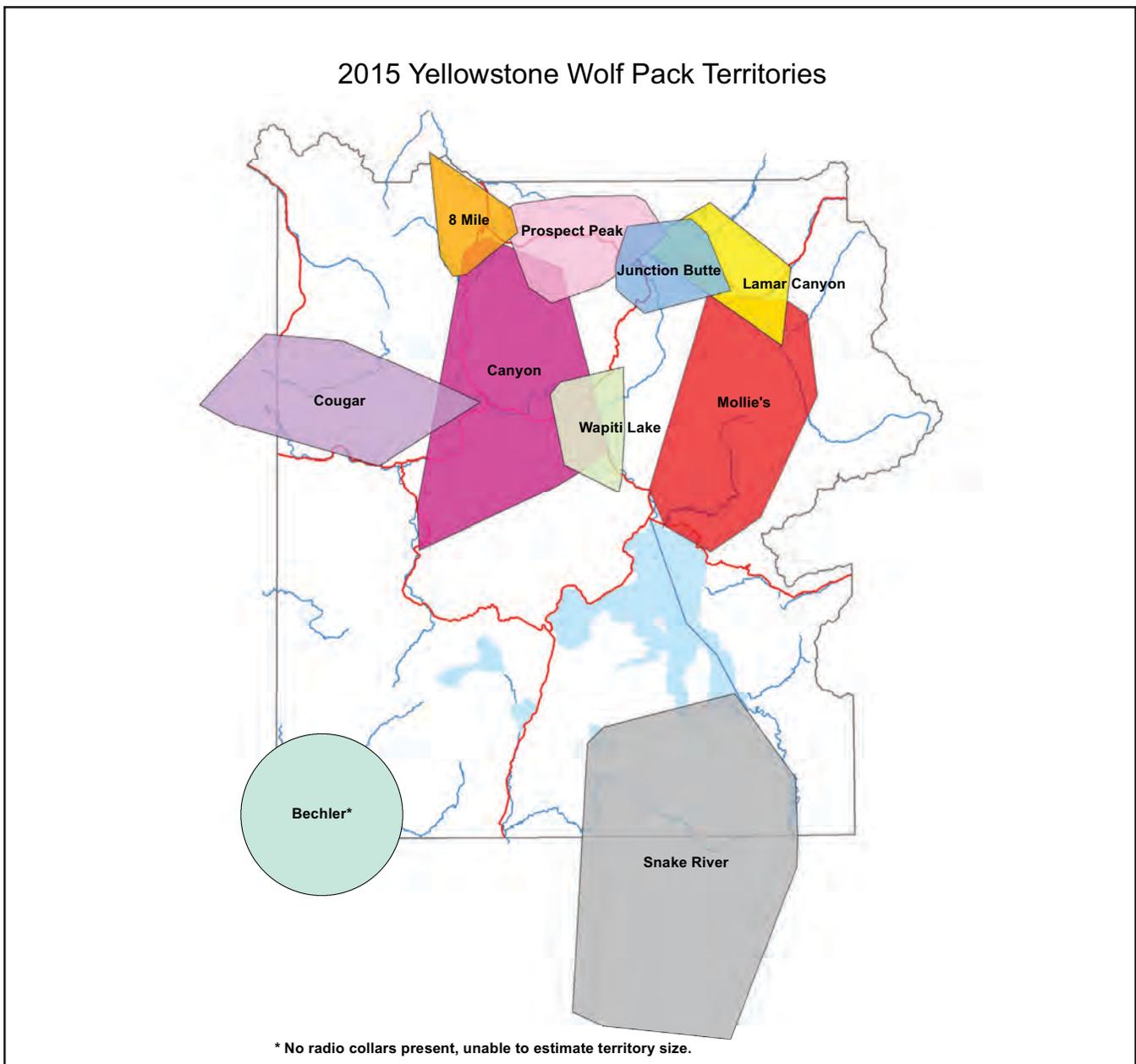


Figure 3. Wolf pack territorial boundaries for packs living primarily in Yellowstone National Park in 2015.

(Smith et al. 2015). For Yellowstone the first requirement is universally met. But with the park being such a harsh winter environment, many ungulates migrate out, making large portions of the park unsuitable for year-round wolf occupation. For example, due to the large population size and only partially migratory nature of northern Yellowstone elk, the northern range of Yellowstone is fully occupied (figure 3). No other area within the park has as many wolves or is contiguously occupied. Other areas of occupation are Pelican Valley, but to exist here wolves have to range widely or switch to eating bison in the winter because all the elk migrate out. Thorofare, Bechler, and Snake River regions are also occupied; but

wolves living in these areas must range widely and often have to leave the park. The Madison-Firehole River area and Hayden Valley contain wolves that often migrate to the northern range in winter. These factors have caused wolf territory size to vary accordingly: northern range wolf pack territories are smaller, averaging 274 km²/106 mi² (range = 58-1151 km²/22-444 mi²); whereas, interior territories are comparatively larger and average 620 km²/239 mi² (range = 105-1675 km²/41-647 mi²).

What Protection Brings

Besides organizing across the landscape, wolves also organize themselves into social units called packs. In



NPS PHOTO - D. STAHLER

fact, this behavior is what makes wolves so unique from other wildlife. Referred to as cooperative breeding, few mammals live this way; and the resulting sociality drives much of wolf life history. Most wolf packs outside Yellowstone suffer high levels of human-caused mortality. In a study of wolf mortality in Idaho, Montana, and Wyoming, it was found that about 80% of wolves were killed by humans (Smith et al. 2010). This influences pack structure. Conversely, low human-caused mortality in Yellowstone allows for richer age structures and more complex social organization within wolf packs, including very different roles for old individuals within the group (“Territoriality and Inter-Pack Aggression in Gray Wolves,” this issue). This protection from human hunting has also led to larger packs. Average pack size was about ten wolves through 2008; when the population declined, so did wolf pack size but not by much, to around nine wolves. The range of pack sizes was from 2 (considered the minimum size for a pack) to 37, which may be the largest pack ever recorded. This pack, the Druid Peak pack of 2001, was so large it was socially cumbersome and only rarely observed together. Ultimately, this pack split into four different packs (Druid Peak, Geode Creek, Agate Creek, and Buffalo Fork) over the course of fall and early winter.

These complex social groups may be a hallmark of wolf packs in Yellowstone and have been intriguing to study. Some of these packs stick around for a long time, with an average of about 12 years, but some are longer. Mollie’s pack (originally Crystal Creek pack and renamed after the late Director of the U.S. Fish and Wildlife Service) and Yellowstone Delta pack (originally Soda Butte pack) are two examples, and notably both packs are from first year (1995) reintroductions. We’re not sure why these two packs have persisted so long; but some possibilities are that they staked out a good territory before other wolves could (the benefit of being first), they don’t live in a competitive environment like the northern reaches of the park, and there have been some long-term individuals in these packs that may have been the “social glue” (“Wolf Turf: A Glimpse at 20 Years of Wolf Spatial Ecology in Yellowstone,” this issue, examines some of these ideas).

Socially complex packs usually have pups, but importantly, not as often as presumed. Some say 90% of wolf packs in any given year produce pups; but in the protected confines of Yellowstone, we find that the number of breeding packs each year is lower than that—about 70–80% reproducing packs each year. Why this is so could be due to many factors: death of a breeder, limited food,

disease, or competition between packs, collectively referred to as density dependence.

Beginning with low density and high food abundance early on, wolf reproduction was super-charged, particularly on the northern range. Ample food availability, coupled with increasing wolf density, led to more deviations from a monogamous, single-pair breeding structure within packs; about 25% of wolf packs in Yellowstone had more than one litter. Only recently has this started to drop. But average litter size is about 4.7 pups with about 3.1 pups surviving until December of that year (“Motherhood of the Wolf,” this issue). Typically pup survival is about 70%; but some years, particularly the ones of CDV outbreaks, pup survival can be less than 20%.

The Value of Yellowstone

As a whole, Yellowstone wolves have added to our understanding and appreciation of wolves everywhere. Crowds of visitors continue to come to view them. This was made possible by early park managers who had a vision and fought a decades-long struggle that led to Yellowstone being more “natural,” or at least more pristine than when it was established. This protection, or “natural baseline” as some early scientists called it, has led to greater insights into how nature works. Protection of the park has allowed for extensive research and insights into wolf ecology, from coat color disease immunity to discovering matrilineal pack organization, as well as the other topics covered in this issue. What a rarity in this modern-day sea of humanity. So despite all the historic human interventions and disturbances, each one and each time adding to our knowledge, Yellowstone has remained and thrived—largely because of the love so many have for it. Wolves are just one more thing making it slightly more natural and wild; and as Durward Allen said, “wildness needs wolves” (Allen 1979).

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NPS PHOTO - N. HERBERT

Motherhood of the Wolf

Daniel R. Stahler, Douglas W. Smith, & Daniel R. MacNulty

“She is the creature of life, the giver of life, and the giver of abundant love, care, and protection. Such are the great qualities of a mother.” – Ama H. Vanniarachchy, archeologist and scholar

For many of Yellowstone’s species, spring’s arrival not only brings relief from winter’s challenges, but also resets the biological calendar that governs individuals’ lives. As April’s temperatures rise and its expanding daylight weakens the veneer of snow and ice, many animals enter a new phase of their life history through the process of birth. The female raven at her cliff ledge nest, a cow bison on the big sage flats, and a mother wolf down inside a boulder den—all share in the culmination of their reproductive efforts from the previous months. There are many challenges for animals of any sex and age to simply survive from one life stage to the next. For a mother charged with the great expense of gestation, birthing, lactation, and successful raising of offspring, the costs are extraordinary. Because of certain individual traits, or social and environmental conditions, some mothers are more successful than others. While awe and admiration is deserved for all who become mothers, a biologist studying animal reproduction is particularly interested in asking: What are the qualities of a great mother? What factors play most significantly in shaping success at this key life-history stage?

Individuals’ life histories are the patterns of growth, reproduction, and survival over their lifetimes. Variation in growth rates, age of maturity, reproductive performance, and lifespan are the result of both species’ evolutionary histories and the environments to which populations of individuals are exposed. For highly social species, social conditions can play a particularly influential role in individuals’ life histories, even beyond that of prevailing ecological conditions. Wolves are a great example of the role sociality plays in this regard, as our scientific investigations on Yellowstone wolves effectively show. Through group hunting (MacNulty et al. 2012, 2014) and carcass use (Wilmers et al. 2003), pack defense of territory (Cassidy et al. 2015), advantages to the infirmed (Almberg et al. 2015), or the assistance of nonbreeding helpers in raising young (Stahler et al.

2013), individual wolf survival, and the ability of pups to survive, is often influenced by the qualities of the pack.

Reproduction is of great interest to biologists given its importance to population dynamics through recruitment, and to evolutionary processes through changes in heritable traits passed from parents to offspring over successive generations. Scientists studying a variety of species have demonstrated that reproduction in social organisms is shaped by numerous morphological, behavioral, and life-history traits, as well as environmental conditions faced by breeders (Clutton-Brock 1988). However, little is known about the relative influence of different traits, particularly in the context of environmental conditions that determine their value in adapting to changing environmental conditions. Interestingly, although wolves are among the most-studied mammals in the world (Mech and Boitani 2003), surprisingly little has previously been researched on which traits drive their reproduction. Here, we describe how our detailed monitoring of female breeders in Yellowstone has allowed us to better understand wolf reproduction. Using an impressive 14-year dataset (1996-2009) on individually known females’ annual pup production, we were able to simultaneously evaluate and rank the effects of individual traits, pack size and composition, and ecological factors influencing female reproductive performance (Stahler 2011, Stahler et al. 2013).

For Yellowstone’s wolf packs and the community of biologists and wolf enthusiasts who follow their lives, great excitement surrounds the arrival of pups each spring. Through this great maternal feat and the actions of the females’ mates and pack members, much of our ecological and cultural perception of the wolf pack revolves around having and raising pups. But before describing our findings, a brief overview of wolf natural history will help place the importance of reproduction in context.

Wolves live in territorial family groups that cooperate to capture prey, raise young, and defend resources from

competitors (Mech 1970). Wolves have a brief life history relative to other large carnivores, including early first reproduction, high fecundity, rapid development, and relatively short lifespans. The basic social unit of wolf populations is the mated pair and their offspring (Mech 1970). Due to delayed dispersal, wolf packs typically consist of multiple age and sex class compositions. Wolves are true cooperative breeders, with the care of offspring performed by both parents, as well as by other pack members. Wolves are sexually dimorphic (males and females have different size ranges), with males about 16-24% larger than females (MacNulty et al. 2009a), and have a multi-year growth pattern (MacNulty et al. 2009a, Stahler et al. 2013). Differences in body size between males and females are presumably shaped by selection pressures related to their respective reproductive strategies and roles in hunting and territoriality.

In Yellowstone, as in most wolf systems, breeding occurs between January and March. Following a 61-63 day gestation period, offspring are born underground in dens by late April. With typically just the dominant male and female mating within a pack, wolves have long been classified as having a monogamous mating system (Mech 1970). However, sexual dimorphism, unbalanced reproductive success of both sexes, and occurrences of multiple litters produced by different females in a pack suggest the evolution of a more flexible mating system. In fact, we've documented about 25% of our packs each year exhibiting exceptions to monogamy, with both dominant and subordinate females and males participating in breeding activity. This phenomenon is believed to be influenced largely by Yellowstone's prey abundance, wolf density, and more complex pack struc-

tures containing multiple, unrelated, opposite-sex pack members (Stahler 2011).

Our research simultaneously assessed and ranked the strength of factors driving female reproductive success. Specifically, we evaluated how a mother's age, body size, coat color, genetic variability, and pack size and composition influenced litter size and pup survival. The role of environmental stressors such as competition and disease were also evaluated. By capturing, radio-collaring, weighing, and monitoring individuals through time, as well as applying molecular techniques, we were able to measure individual traits and reproductive performance for breeding females. We measured two components of reproductive performance for each female breeder: litter size (pups emerging from dens) and litter survival (pups surviving until their first winter). Early litter sizes averaged 4.7 pups, with one litter as large as 11. The number of pups surviving until independence averaged 3.1 per litter and ranged up to 9. Pups are generally weaned at 5-9 weeks of age, then fed by various pack members via meat regurgitation until the pups can accompany adults to carcasses by autumn. To evaluate the role of body mass, we used age-specific weights taken from a female growth model. Results showed females grow rapidly in their first year of life, then more moderately until reaching maximum body size just before three-years-old. This age corresponds to when females typically begin reproducing.

We first looked at what individual traits are characteristic of a successful mother. Reproductive performance improved with increasing body mass, with larger females having larger litters and better pup survival (figure 1a). This pattern is consistent with many other

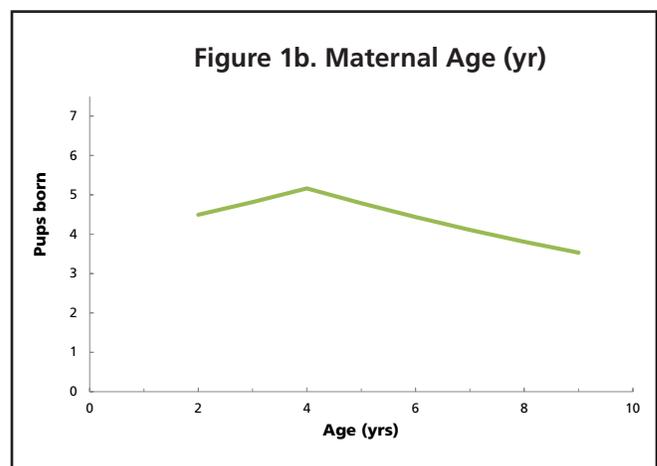
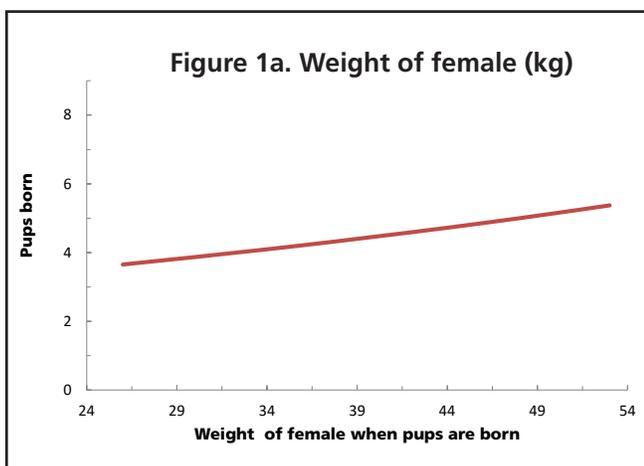


Figure 1. Effects of (a) body mass and (b) age on the number of pups first emerging from dens (pups born) in Yellowstone National Park, 1996-2009.

mammals, where larger body size indicates healthier individuals better able to invest resources towards reproduction. For wolves, the reproductive benefits of large size, combined with rapid growth and early age of first reproduction, indicate the first couple years of life are important to a female's lifetime reproductive success. As with other species, we found age-specific reproductive performance in wolves, a previously undetected pattern (figure 1b). Females showed no improved success following their first reproduction, but exhibited senescence (i.e., age-related deterioration in performance) around age five, which was the median lifespan for wolves during our study.

Although measures of individual genetic variation were not correlated with success, we found a surprising effect of coat color. Other work on Yellowstone wolves established that gray or black coat color is determined by the *K*-locus, a gene that is associated with immunity in other vertebrates (Anderson et al. 2009). Interestingly, gray females had a 25% greater litter survival than black females. While the mechanism for this effect is currently unclear, it is possibly due to how a female's color genotype influences physiological trade-offs important to reproduction and survival.

As in other cooperative breeding species, group size is an important predictor of a mother's success. Early litter sizes peaked when eight wolves were present, after which they decreased with additional pack members. This latter pattern may reflect costs on maternal condition incurred from intrapack competition for food or social stress during the breeding season. In contrast, pup survival was enhanced with increasing pack size (figure 2a). In addition to having more helpers to

provision young, larger packs have numerical advantages during intergroup and intraguild competition for resources like food (Wilmers et al. 2003) and territory (Cassidy et al. 2015) which contribute to offspring survival. Importantly, the positive influence of helpers was strongest for small packs, indicating there is a threshold below which packmates are critical to breeder success.

However, it is not just a numbers game. Just as individuals vary in quality, we've learned so do packs. With variation in sex and age composition, group size alone fails to identify the true costs and benefits of pack members on a mother's success (Stahler 2011). For example, mothers benefited more from additional male helpers than female helpers. This makes sense in light of the demonstrated importance of males as more proficient hunters (MacNulty et al. 2009a) and aggressive defenders of territory (Cassidy et al. 2015). On the other hand, mothers experienced reduced litter survival in packs containing multiple breeding females. Cooperation presumably has its limits when mothers compete for resources needed to raise their own pups in a multi-littered pack. Regarding helpers' ages, mothers benefited the most in packs with more prime age wolves (2-5 years) than yearlings and older helpers, likely due to these individuals being higher quality foragers (MacNulty et al. 2009b).

Finally, besides a mother's and her family's qualities, her environmental surroundings can be important. We found higher wolf density (figure 2b) and disease outbreaks had significant negative effects on pup survival. Our finding of negative density-dependent effects is likely due to increased competition and strife with other packs under high wolf densities. Outbreaks of canine distemper virus were associated with pronounced pup

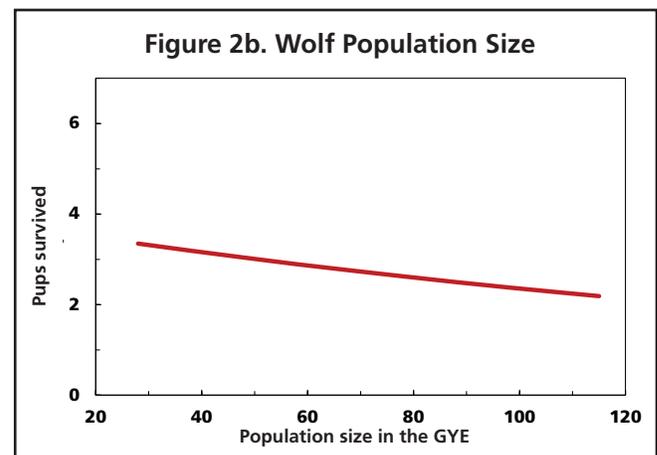
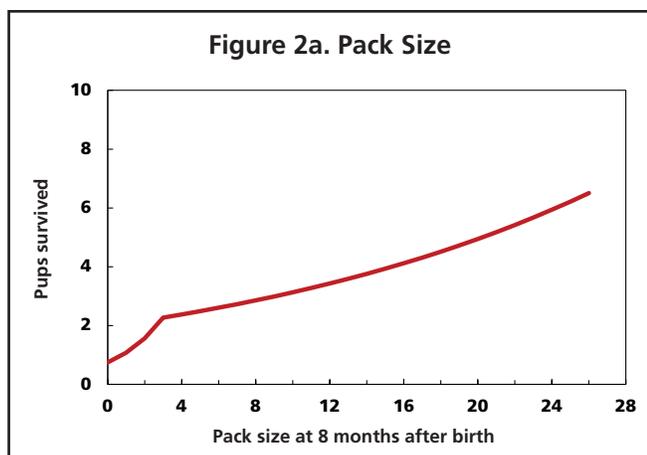


Figure 2. Effects of (a) pack size and (b) wolf population size (number of wolves/1000km² in the northern GYE) on the number of pups in a female's litter surviving until independence (pups survived) in Yellowstone National Park, December 1996-2009.

mortality. Although unpredictable, disease prevalence is a critical factor for female reproduction and may be a strong selective force in wolf systems, especially if linked to individual traits that offset its negative effects (e.g., coat color).

Having shown what the qualities of a successful mother wolf are, we then asked: What is the relative importance of different traits under varying environmental conditions? A sensitivity analysis, which allowed comparison of effects across a common scale, indicated body mass is most influential, followed by pack size. Reproductive gains due to larger body size and cooperative breeding appear to mitigate losses associated with population density and disease effects. These findings highlight the adaptive value of large body size and sociality for wolves, in promoting a mother's success in competitive environments.

Our work on Yellowstone wolves helps to clarify how life history, sociality, and ecological conditions interact in this cooperatively breeding carnivore, and ranks the adaptive value of different traits. Future work aims to explore how similar traits influence male reproduction, breeding strategies, and the link between food, territory, and reproduction. Knowledge about which traits promote fitness in the context of environmental challenges may help predict how wild populations will respond to global climate change, disease, habitat alteration, and human exploitation. Ultimately, we hope this knowledge serves the conservation of this controversial but charismatic and ecologically important carnivore. If decades of research and management around the world have taught us one thing, it is that wolves are resilient in the face of great challenges. Studies such as these from Yellowstone help explain why.

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Yellowstone Wolves at the Frontiers of Genetic Research

*Daniel R. Stahler, Bridgett M. vonHoldt, Rena M. Schweizer,
& Robert K. Wayne*

Nearly four decades following the eradication of the gray wolf in Yellowstone National Park, a new microbial species was discovered in the Lower Geyser Basin which revolutionized the world of molecular biology and wolf genetics (Guyer and Koshland 1989, Varley 1993). This microbial species was a heat-loving bacterium, *Thermus aquaticus*. It produces a heat-stable enzyme known as *Taq* polymerase that, for the first time, enabled scientists to replicate DNA on a massive scale using a series of simple steps involving the heating and cooling of DNA. Only bacteria adapted to the hot springs' environment produced this heat stable *Taq* polymerase that could survive these temperature fluctuations. *Taq* polymerase was featured as the molecule of the year (1989) on the cover of *Science* magazine (Guyer and Koshland 1989); and sales of *Taq* polymerase, related products, and equipment generated billions of dollars in revenue. The inventor of the DNA amplification process (the polymerase chain reaction or PCR) using *Taq* polymerase, Kary Mullis, was awarded the Noble Prize in 1993. Since the 1980s, PCR has revolutionized the fields of forensics, human medicine, infectious diseases, and molecular and population genetics. In a fascinating chain of events, the discovery of an obscure species adapted to Yellowstone's harsh geothermal waters opened the portals of scientific investigations for many organisms on the tree of life, and highlighted the importance of biological diversity for human society.

Beyond the obvious benefits to our own species, we need look no further than the Canidae family (wolves, dogs, coyotes, jackals, and foxes) to see where such molecular techniques have significantly advanced our understanding of ecology, evolution, and conservation. From unraveling the complex evolutionary histories of wolf-like canids and origins of dog domestication, to revealing the structure and function of genes, to addressing questions significant to canid conservation, few non-human species have been at the frontiers of

genetic research as have wolves and their relatives. For Yellowstone wolves, the application of molecular DNA techniques puts this population in a particularly bright spotlight. Here, we provide an overview of the role genetics has played in the recovery of Yellowstone wolves and the variety of questions addressed by an ever-advancing field of molecular research.

The importance of genetics was first applied during the reintroduction years as founding individuals were selected from different packs in different parts of Canada and released into both Yellowstone National Park (YNP) and the central Idaho wilderness. As a result, a genetically diverse population comprised of many unrelated individuals became the foundation for what resulted in a rapidly expanding breeding population throughout Idaho and the Greater Yellowstone Ecosystem (GYE). This met an important conservation goal of any successful species recovery program by establishing a genetically diverse network of subpopulations (vonHoldt et al. 2010). When maintained at adequate sizes and connected through genetically effective dispersal, populations are found to be more resilient to the fitness costs associated with inbreeding, small population size, and isolation, and better equipped to adapt to changing environmental conditions.

With all founders genetically sampled, the next critical component to the YNP's genetic research was establishing a sampling protocol for their progeny. From the beginning, efforts have been made to collect genetic samples from all wolves handled during capture and radio-collaring events (figure 1), as well as from any deceased wolves discovered. Additionally, scats and hair left behind on the landscape have been collected and used, depending on sample quality or degree of degradation. From these sampling methods, DNA is extracted and amplified from whole blood, tissue, or scat, and banked for a variety of molecular applications. In addition to the genetic sampling, the Wolf Project team and collaborators have remained committed to collecting a



Figure 1. Genetic samples are collected from every live-captured wolf and investigated mortality. Blood draws (top photo) yield quality DNA for a variety of genotyping techniques. Ear biopsy punches (bottom photo) provide samples used to culture cell lines to test the effects of specific cell level challenges on genes.

variety of demographic, life history, morphological, behavioral, disease, and ecological datasets through time. The integration of such rich data over a significant period of years has rarely been achieved for any species in the wild, let alone for a reintroduced population of known founders and their descendants.

Molecular Techniques & Markers Applied to Yellowstone Wolves

Advances in the molecular tools and techniques, and their application to ecological, evolutionary, and behavioral studies, have risen dramatically over the last two

decades. Since wolves returned to Yellowstone, we have assessed the genetic composition, or genotypes, of individuals using a variety of molecular markers and approaches. Using PCR to amplify and sequence nuclear DNA, which individuals inherit from both parents, the nuclear genome has been surveyed for short repetitive DNA fragments known as microsatellite loci, single nucleotide polymorphisms (SNPs), or genome sequences. Microsatellites are often highly variable and are useful for resolving recent population dynamics, such as dispersal, paternity, and relationships. This information is used to estimate reproductive success through parent-

age assignments, although it requires a relatively large proportion of the breeding population be genetically represented. One drawback to using such repetitive DNA is that it is limited with regard to the proportion of the genome that can be surveyed. Often, a study consists of 8-40 loci, a small fraction of the genome, which limits the ability to make inferences about evolutionary patterns, complex population structure, or even resolve parentage in closely kin-structured animals like wolves. The next level at which YNP genetic data has been surveyed is with respect to variation in SNP loci. SNPs are single nucleotide polymorphisms, or variable sites, that segregate alleles (a variant form of a gene) in a population and can be genotyped across the entire genome. This data type is part of the next generation of genotyping techniques and can provide valuable information regarding regions of the genome that contain recent changes putatively linked to adaptations or are preserved stably over long evolutionary periods. The last level at which Yellowstone wolves have contributed towards conservation genetics is in genome sequencing. Here, we can scan the entire collection of >2 billion nucleotides and address similar questions but with much deeper resolution, as well as sequence genes that are expressed, or transcribed, in response to specific biotic or environmental conditions. Collectively, these genetic markers have allowed us to explore questions ranging from population structure and gene flow, to reconstructing pedigree relationships, understanding the dynamics of coat color, life-history strategies, and natural selection on the genome.

Major Projects & Findings

Pedigree construction and application

Scientists and the public alike have been eager to explore the genetic lineages of Yellowstone wolves. Using genotypes from 26 microsatellite loci, we assessed the relationships and genetic similarity of 200 Yellowstone wolves to infer patterns of parentage, breeding pair characteristics, and general pack formation assembly rules (vonHoldt et al. 2008). From the microsatellite data, we reconstructed the population genealogy, allowing us to detail pack formation, dissolution, and assess kinship ties among packs (figure 2). We also found Yellowstone wolves avoid inbreeding with close relatives. Knowing genealogical structure and how it influences behavior and demography allowed us to better evaluate the success of this wolf recovery—a valuable contribution to the field of conservation genetics (vonHoldt et al.

2008, 2010). We have also integrated the wolf pedigree with life-history data and demographics to demonstrate powerful new methods for exploring co-evolutionary dynamics (Coulson et al. 2011). Using Yellowstone's genealogy, we can calculate the level of heritability (the degree to which a trait measured in an individual is correlated with the same trait measured in its parents) for various life-history traits (e.g., reproductive success, fecundity, lifespan, behavior, coat color). As more wolves are sampled and newer genotyping methods applied, we will continue to build and improve the accuracy of the Yellowstone wolf pedigree for a variety of applications.

Population genetics

In order to evaluate the success of wolf recovery on a broader regional scale, we assessed genetic diversity and connectivity across the three recovery areas (Greater Yellowstone Ecosystem, Montana, and Idaho; vonHoldt et al. 2010). We analyzed DNA samples from 555 Northern Rocky Mountain wolves, including all 66 reintroduced founders in Idaho and YNP, for variation in 26 microsatellite loci over the initial 10-year recovery period (1995–2004). The population maintained high levels of variation with low levels of inbreeding and throughout this period expanded rapidly. We found significant genetic differences between the three recovery areas, and we verified effective dispersal (dispersal with subsequent reproduction) events between each of the recovery areas. Genetic connectivity was one of the primary stipulations for wolf delisting in the Rocky Mountains. This provided great insight into the landscape ecology of wolves through the scope of molecular genetics, and gives us a baseline and methodology by which to evaluate genetic structure and connectivity in the future.

Coat color (K-locus)

The discovery of genetic variants that affect phenotypes (i.e., the observable traits influenced by an organism's genes and its environment) is a rarity when studying natural populations. Research that has done so used model species that can be bred in a laboratory allowing for the genetic basis of traits to be uncovered through phenotypic assessments of offspring. Although not model species, gray wolves are unique in that their relative, the domestic dog, has been the focus of extensive genetic research and was the fifth species to have their genome sequenced. Thus, we have a great library of genetic information on traits such as coat color, and what genes are contained in the genome that can be

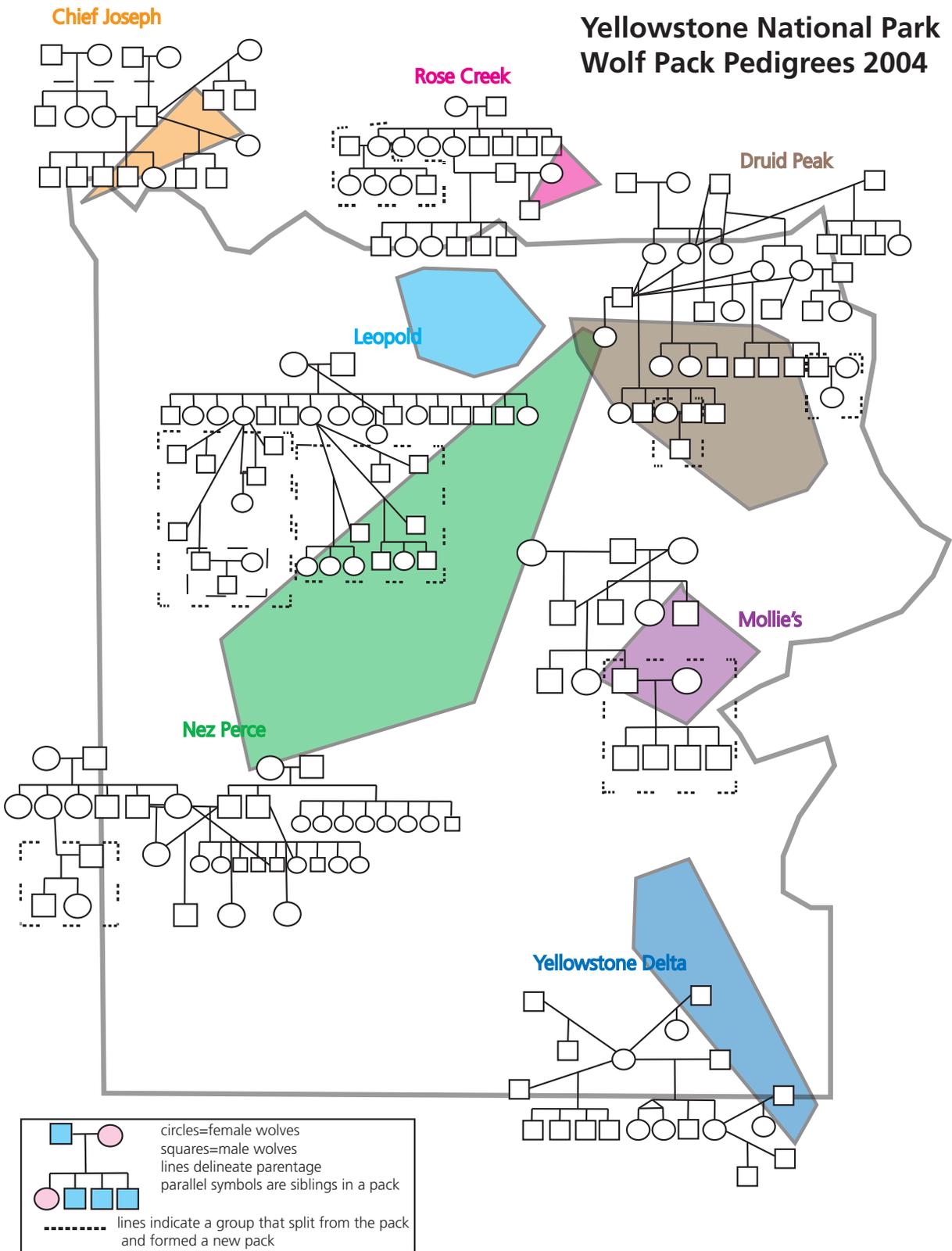


Figure 2. This map depicts some of Yellowstone National Park's wolf packs that existed in 2004 from which detailed pedigrees have been constructed from genetic data collected since reintroduction. Each pedigree reflects known breeding pairs and their offspring produced throughout the years. For some packs (Rose, Druid Peak, Leopold, Mollie's, and Nez Perce), hatched lines around groups of individuals represent new pack formations that resulted from offspring of pack founders. Such pedigrees demonstrate not only the close family structure of wolf packs, but some of the complex social organization and breeding behavior of Yellowstone wolves.

utilized for an understanding of phenotypic variation in wild wolves. Specifically, black coat color has been investigated in Yellowstone wolves and found to be due to a single gene (a β -defensin gene termed CBD103 or the *K*-locus), with all black coated individuals carrying a 3-nucleotide deletion linked to this coat color phenotype, a mutation believed to have originated in domestic dogs of the Old World (Candille et al. 2007, Anderson et al. 2009). We demonstrated through use of our pedigree data this single mutation was responsible for all black wolves in YNP and that the black allele was dominant over the gray (figure 3). This result set the stage for studies that explored the link between genetics, viability, fitness, and selection (e.g., Coulson et al., 2011, Stahler et al. 2013, Hedrick et al. 2014, Schweizer et al. unpublished data). Remarkably, it was found that the *K*-locus gene is involved in immune function, suggesting an additional role in pathogen defense. In fact, ongoing research is showing black wolves have greater survivorship during distemper outbreaks (Cubaynes, unpublished data).

Another study (Schweizer, unpublished data) used a “capture” array (a method that allows one to subsample and sequence regions of the genome) to sequence the *K*-locus in over 200 Yellowstone wolves, as well as wolves from other populations. This allowed for levels of genetic variation to be measured among different populations, as well as the ability to estimate how strong positive selection has been in each one. We found Yellowstone wolves have undergone selection for the mutation that causes black coat color to a greater extent than other populations of North American wolves, and selection strength may have increased since the founding of the Yellowstone population. This may be related to patterns of canine diseases, immunity, and fitness advantages of the black heterozygotes (Coulson et al. 2011). Furthermore, the origin of the *K*-locus in wolves may have come from hybridization events between dogs and wolves in northwest North America (Schweizer, unpublished data).

NPS PHOTO - D. STAHLER



Figure 3. Yellowstone wolves come in two general coat color types – gray and black. Research on our population has found black coat color is due to a single gene mutation and is linked to variation in wolf fitness.

Finally, we are applying emerging techniques in cell culture science to study the adaptive value of coat color variation. This involves techniques that allow cell lines of wolf fibroblasts (skin) and keratinocytes (keratin-producing cells) to be initiated from wolf ear biopsy punches taken during capture. Transformation of these cell lines provides an infinite source of DNA and RNA, and allows a non-invasive method to test the effects of specific cell level challenges on genes. For example, we are testing skin cultures with various viral and bacterial antigens to determine how black and gray wolves respond differently to these stressors. We can then test the response to specific antigens and our hypothesis that the black coat color gene is involved in immune response. This basic design can be used to probe the function of any genetic variant and will be a critical tool for understanding adaptation in future studies. The Yellowstone Wolf project is one of the only studies using stem cell lines in wild animal research.

Behavior & health

Behavioral studies of aggression in Yellowstone wolves are ongoing, with aggression linked to specific phenotypes and with possible links to genetic and regulatory variants (e.g., Janowitz et al., unpublished data). We have used genealogy to estimate the heritability of the level of aggression an individual will display during interpack interactions. Our preliminary heritability analysis identified that a simple additive genic model of inheritance was not sufficient to explain this complex behavioral trait. Rather, we found this behavior is influenced by both an intricate foundation of genetic and regulatory features, as well as an environmental influence. We can also apply these research strategies to explore the molecular influences on disease susceptibility, such as mange infections. To investigate the impact of genetic and epigenetic variation on mange infection, we are currently assessing how molecular variation segregates with infection severity classification, time to recovery, and frequency of reinfection.

Gene expression

It is commonly thought genetic variation is the key to adaptation and surviving environmental and biotic challenges, such as global warming and a change in predator or prey diversity. This is likely true for change occurring across generations, but the mechanisms for adaptation across an individual's lifetime concerns gene expression. Whenever we eat, sleep, exercise, or relax, a

select set of genes is turned on and off, like a molecular switch, which is critical for daily survival as a response to life challenges, such as strife, starvation, or disease. However, we are largely ignorant of the scale of gene expression response and its limits in natural systems. For the first time ever in a wild vertebrate population, we have characterized gene expression using next generation sequencing techniques (RNA-seq.). This effort involved a whole new collection scheme, as previous blood preservation techniques only preserved DNA. Our new focus is to also collect RNA, the set of molecules that reflect which genes are expressed. Charruau (Charruau et al. 2016) explains the factors that govern gene expression in model species and humans, such as sex and dominance rank, do not strongly influence gene expression in blood from wolves. This may reflect the highly cooperative and integrative nature of wolf society. Overwhelmingly, gene expression patterns in wolves are instead related to age and disease. Wolves age rapidly, as most individuals die by age five or six, and exhibit evidence of extreme injury and disease throughout this period. This rate of aging is matched by an equally rapid rate of gene expression senescence; a six-year-old wolf has experienced as much change in gene expression, over a similar subset of genes, as an elderly human. Our results also highlight how disease, such as mange, may cause secondary effects on gene expression, in addition to a primary pathogen response. We discovered wolves have a component of gene expression response related to mange that likely reflects tissue damage and healing due to scratching associated with the infection. These results establish a critical baseline for future studies of wolves across changing environments and in human dominated landscapes with distinct stressors. Further, we provide a new precedence and protocol for similar studies of other wild vertebrates.

Wolves & the age of genomics

We have entered the age of genomics, and wolves are at forefront being among >10 genomes having been described (Freedman et al. 2014, Zhang et al. 2014). However, these are genomes from Old World wolves used to study dog domestication and high altitude adaptation. North American wolves have a unique and divergent ancestry that needs a separate assessment. We finished the genome sequencing of 302M, a famous Yellowstone wolf that fathered many offspring. For this wolf, we have the highest sequencing resolution (an average of 50-fold coverage of each nucleotide) compared to any other

wolf to-date. We also sequenced his mate (569F) and an offspring (570M), and are in the process of sequencing four more offspring. These sequences will provide a definitive estimate of mutation rate in wild wolves, a value that is an essential parameter in determining the evolutionary rate of genes and how selection alters the genome. It will enable us to build population models of how favorable and deleterious variation accumulates in populations (Marsden et al. 2015) and understand selection at the *K*-locus (black coat color gene). The complete genome also defines diagnostic North American wolf markers that can be used to probe admixture with dogs and coyotes (e.g., vonHoldt and Wayne 2012). The sequencing of 302M, a legacy wolf of the YNP population, will place genetic research in YNP in the limelight and exemplify its cutting edge nature to the public.

Genetic Research: Present & Future

The impact of humans has radically altered natural spaces worldwide and will be more severe in the future. This impact will disproportionately affect large predators, so we need to establish a genetic baseline and develop predictive tools in order to calibrate and predict genetic responses in the future. The genetic research done in YNP is in large part aimed at this need. We have established a genetic baseline using a wide variety of genetic markers. We have shown the population is genetically healthy and unlikely to suffer genetically in the future, if genetic exchange between populations continues. We have established a complete population pedigree of more than 350 wolves, which is the basis for understanding the genetic underpinning of wolf behavior and physiological traits. We have advanced the understanding of the genetic basis of coat color in YNP wolves and probed its role in survivorship and disease resistance. For the first time, we have a detailed map of the North American wolf genome and can measure mutation rates on individual genes that influence phenotype and adaptation. We now understand the basic factors influencing gene expression and regulation that can limit response to future environmental stressors. We plan to expand this research and integrate data on disease and behavior to explain genetic and epigenetic patterns. These efforts will continue to keep Yellowstone wolves on the frontier of genomic research.

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Dan Stahler (see page 16).

The Challenge of Understanding Northern Yellowstone Elk Dynamics after Wolf Reintroduction

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The status and trend of the northern Yellowstone elk herd has been an enduring conservation issue throughout the history of Yellowstone National Park. It is the largest of about seven migratory elk herds that graze the park's high-elevation meadows during summer. But unlike the other herds, the northern Yellowstone herd has a history of spending winter primarily within the park, ranging across the low-elevation grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries along the park's northern border and adjacent areas of Montana. As the size of the northern herd has fluctuated over time, concerns have alternated between worries of too few and too many elk. Consensus about the appropriate size of the northern Yellowstone elk herd has been elusive.

This cycle of discontent originated in the late 19th century when concern focused on dwindling elk numbers due to market hunting and poaching (Houston 1982). Early 20th century protectionist policies, including the elimination of wolves and cougars, boosted elk numbers and stoked concern that the herd was too large. In response, park managers and hunters shot, trapped, and relocated tens of thousands of elk between 1920 and 1968, pushing the pendulum of public concern back toward concerns about too few elk. Then in 1969, the park implemented a policy of ecological process management known as natural regulation (Leopold et al. 1963), where elk numbers were allowed to fluctuate according to prevailing environmental conditions. Outside the park, the State of Montana used hunting to manage elk numbers. Except for the drought, fire, and severe winter

of 1988–1989, conditions during 1968–1994 were generally favorable for elk survival and recruitment, and their numbers soared (figure 1). In turn, so did criticism that overabundant elk were destroying winter range vegetation.

A key outcome of this latter 20th century period, one that remains integral to understanding current elk dynamics, was a substantial increase in the distribution and abundance of elk wintering in the Yellowstone River valley outside the park. High elk densities inside the park, protection and restoration of winter range outside the park, and changes in the structure and timing of hunts in Montana more than doubled the winter distribution of elk north of the park (Lemke et al. 1998). It is unclear whether this shift represented a new condition or the return to a former one because historic records about the extent to which the northern herd wintered north of the park are ambiguous and debated (Houston 1982, Wagner 2006). Regardless, the expanded distribution of the northern herd into Montana raised concerns about overgrazing and agricultural damage on non-park lands. In 1976, the State of Montana lifted an 8-year ban on hunting migrant elk outside the park in December through February. In later years, the limited-permit late season hunt targeted mainly adult female elk with a goal of limiting numbers of elk wintering outside the park. During 1976–1995, the late season hunt removed an average of 965 total elk per year (range = 0–2,409 elk); whereas, the annual fall hunt removed 520 (range = 194–2,728 elk; Lemke et al. 1998).

Consistent with expectations that hunting alone would not limit the size of the northern elk herd (Houston

1982, Mack and Singer 1993), a record high number of 19,045 elk were counted in January 1994 (figure 1). But it did not last. In December 1994, three months before the first set of reintroduced wolves exited their acclimation pens near the lower Lamar River, managers counted 2,254 fewer elk than during the previous winter for reasons not fully explained by harvest, since only 772 elk were removed during the preceding fall and late hunts (Lemke et al. 1998). And so began the latest major drop in northern Yellowstone elk numbers. By 2013, managers counted 3,915 elk, only 743 more than the herd’s lowest count in 1968. Similar to previous declines, this one was met with widespread public consternation. Except this time wolves, not humans, received most of the blame.

When the policy of natural regulation was adopted to guide elk management in the park, predation was not considered essential to controlling elk numbers. Rather, food limitation alone was thought sufficient to limit the elk herd (Cole 1971, Houston 1976). Nevertheless, the policy’s subsequent emphasis on maintenance and restoration of ecosystem processes paved the way for wolf reintroduction in 1995–1997. As a result, understanding the extent to which wolves are responsible for the latest decline in the northern elk herd is vital to gauging the consequences of a core prescription of natural regulation. It is also necessary to testing broadly important ideas about the ecological role of top predators. In particular, the hypothesis that wolves are ecosystem engineers that have suppressed elk herbivory and triggered large-scale recoveries of aspen and willow in northern Yellowstone (e.g., Ripple and Beschta 2012, Painter et al. 2015) assumes that wolves are a principle cause of the

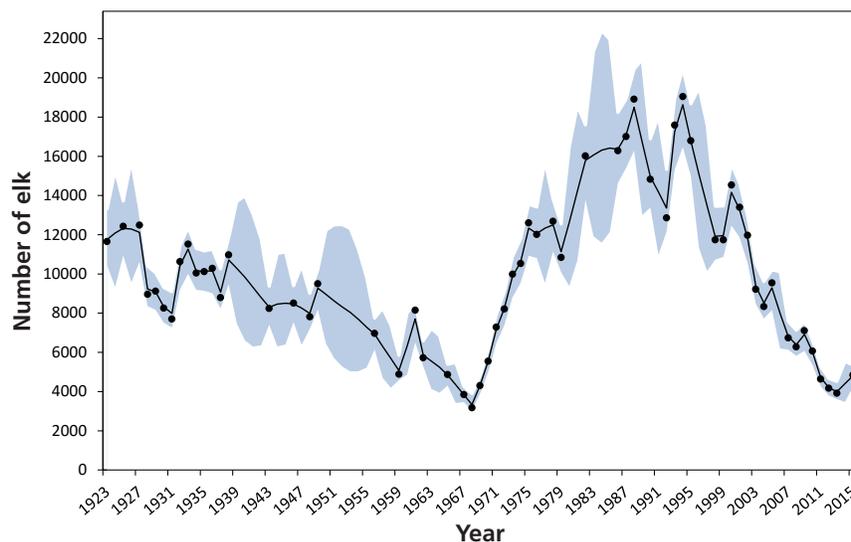


Figure 1. Counts (circles) and fitted trend line for abundance of the northern Yellowstone elk herd, 1923–2015. Shaded area indicates uncertainty about the trend. Data are from the Northern Yellowstone Cooperative Wildlife Working Group.

elk decline. However, scientific consensus about the role of wolves in driving the dynamics of the northern herd has yet to emerge, despite 20 years of research by numerous federal, state, and academic investigators.

An overarching reason for the impasse is that wolf reintroduction was neither a controlled nor replicated experiment. Political and financial constraints aside, such an experiment was impossible because there were no comparable elk herds living under similar environmental and management conditions. The northern Yellowstone herd was, and remains, a unique population. Also, numerous factors besides wolves affect elk population growth (e.g., summer precipitation, winter severity, and other predators including humans) and none were held constant. On the contrary, these factors varied enormously in the years after wolf reintroduction. Under these uncontrolled and unreplicated conditions, highly confident conclusions about cause and effect are difficult (perhaps impossible) to obtain. The challenge of inferring causation helps explain why the debate about the influence of wolves on northern Yellowstone elk dynamics is unsettled and why it will remain so for the foreseeable future.

In lieu of an experiment, the only tool scientists have to disentangle the cause(s) of the recent elk decline is long-term observation. This approach attempts to infer causation from strong correlation between annual measures of key system attributes (assuming these are known and measurable) across the observed range of variation. Spurious correlations can be avoided, or weakened, by collecting and integrating time series data on multiple expressions of the relationship of interest. For example, analysis of the correlation between elk population growth rate and wolf population size is strengthened by complimentary data on the relationship between elk calf recruitment and wolf predation rate.

A virtue of the northern Yellowstone ecosystem is it has been monitored longer and more intensively than most other ecosystems. As a result, many different time series data exist that are pertinent to understanding the forces that shape the dynamics of the northern elk herd. But there are obstacles with these data. First, the data are discontinuous. Financial and logistical constraints hinder faithful collection of annual data as well as limit some monitoring to short time periods. This leads to data gaps which obscure the link between cause and effect.

Second, the data are not necessarily accurate. Take for example the annual northern Yellowstone winter

elk count, which has evolved over the last century from ground surveys taken over multiple days to aerial surveys conducted in a single day (Lemke et al. 1998). Modern aerial counts are known to be underestimates of true abundance (Houston 1982, Coughenour and Singer 1996, Singer et al. 1997, Eberhardt et al. 2007); but scientists, managers, and the public have mainly ignored this bias and interpreted the counts as estimates of true population size. Highlighting the danger of this approach, Singer and Garton (1994) estimated aerial surveys during 1986-1991 overlooked 9-51% of the northern elk herd, and the fraction of missed elk ranged from 9-30% in years with "good" sighting conditions to 35-51% in years with "poor" sighting conditions. This means ignoring annual changes in sightability can distort understanding of population trend. For example, counts during 1987 (17,007 elk) and 1988 (18,913 elk) suggested an increasing population, yet sightability-corrected counts for these years indicated a slight decrease (1987 = 23,350 elk; 1988 = 22,779 elk; Coughenour and Singer 1996). Fortunately, an outcome of the current elk decline is that researchers and managers have teamed up to build a statistical tool that will allow them to correct future elk counts for imperfect sightability, which will in turn strengthen inferences about the effects of wolves and other factors on elk population trend.

Despite uncertainty about the northern Yellowstone elk data, there is little doubt that wolves have contributed to the recent decline of the northern elk herd. What is in doubt is the size of that contribution. How much of the decline is due to wolves? The basic biology of wolves suggests that they have a modest influence on elk dynamics. The wolf has the bite force, body size, and cooperative behavior to kill a wide array of ungulates ranging from diminutive deer to one-ton bison (Mech et al. 2015). But it lacks the massive size, retractable claws, supinating muscular forelimbs, and specialized skull configuration (Peterson and Ciucci 2003) that would allow it to be a consistently high-success hunter of any one particular prey species.

Instead, the wolf is a consistently low-success hunter of a wide range of prey. Its strategy is to find the easy mark: a prey animal that is easily killed because of its small size, old age, poor health, or treacherous surroundings. The problem is that easy marks are generally rare and often inconspicuous. Wolves find their mark by relentlessly sifting through the available prey pool, testing prospective victims. Wolves cast a wide net and test many more prey than they actually kill. This is why the

success of wolves hunting elk in northern Yellowstone has rarely exceeded 20% (Smith et al. 2000, Mech et al. 2001) and drops to less than 10% when only adult elk are considered (MacNulty et al. 2012).

Selective hunting behavior of wolves determines the age distribution of prey they kill. Roughly half of elk killed by wolves in northern Yellowstone are calves, a pattern that has changed little since wolf reintroduc-

tion (Smith et al. 2004, Wright et al. 2006, Metz et al. 2012). Also unchanged has been the age distribution of the adult (more than 2 years-old) female elk they kill: 89% of 640 wolf-killed adult female elk in northern Yellowstone during 1995–2011 were more than 10-years-old (figure 2a), and the annual mean age of these elk varied between 13- and 16-years-old (figure 2b). Nearly half (48%) of 606 wolf-killed elk documented in the

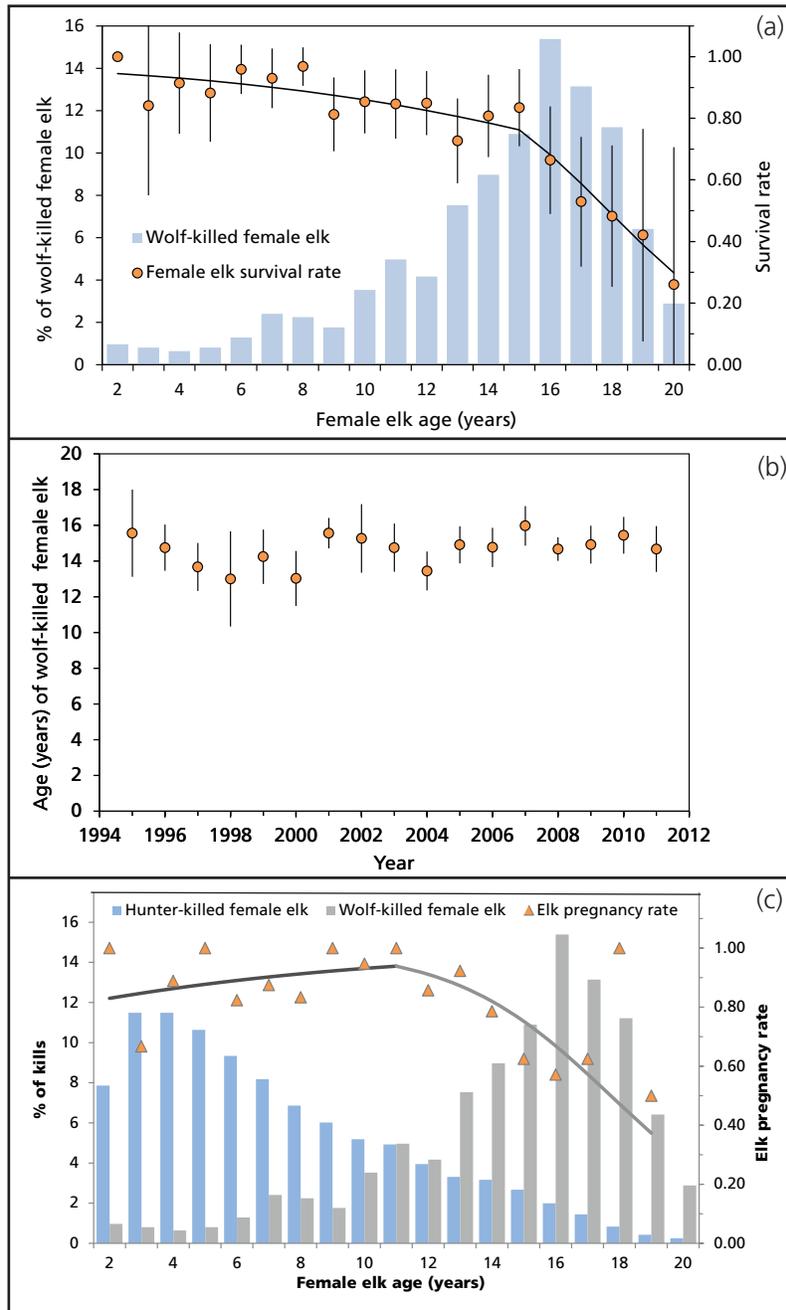


Figure 2. Demography of northern Yellowstone adult female elk in relation to predation patterns of wolves and humans. (a) Age distribution of wolf-killed female elk ($n = 624$ kills) during 1995-2011 (left ordinate) and annual survival rate of female elk ($n = 173$ females) during 2000-2012 (right ordinate). (b) Mean age of wolf-killed female elk ($n = 640$ kills) during 1995-2011. (c) Age distribution of female elk killed by wolves during 1995-2011 ($n = 624$ kills) and humans ($n = 6,862$ kills) during the late hunt, 1996-2009 (left ordinate) in relation to elk pregnancy rates ($n = 230$ females) during 2000-2014 (right ordinate). Harvest data are from Wright et al. (2006) and Montana Fish, Wildlife and Parks.

Madison headwaters area of Yellowstone National Park during 1996–2007 were also calves (Becker et al. 2009). Older elk (10–13 years-old) also represented the largest overall share of adult females killed by wolves. However, the mean age of wolf-killed adult female elk was nearly 6 years younger in the Madison headwaters (9.1 years, 95% CI = 8.6, 9.7, n = 220) than in northern Yellowstone (14.7 years, 95% CI = 14.3, 15.0, n = 640). Extreme winter conditions and other factors contribute to a shorter lifespan and make elk more vulnerable to wolf predation in the Madison headwaters area (“Wolf Effects on Elk Inhabiting a High Risk Landscape: The Madison Headwaters Study,” this issue).

Selective wolf predation is important to the fate of the northern Yellowstone elk herd because it results in higher survival for the subset of elk that are rarely killed by wolves. This is evidenced by the relatively high mean annual survival (84–97%) of 2- to 8-year-old female elk in northern Yellowstone during 2000–2012 (figure 2a). Because this subset includes the most fertile females in the population (figure 2c), selective predation may reduce the impact of wolves on elk abundance (Wright et al. 2006, Eberhardt et al. 2007). On the other hand, selective predation also means wolves are major predators of elk calves, and calf survival may be the most important driver of elk population growth (Raithel et al. 2007). Thus, the effect of wolves on calf survival is arguably the single largest determinant of their role in the decline of the northern elk herd (Proffitt et al. 2014). But it is also one of the least understood aspects of wolf-elk interactions.

Existing information about the effect of wolves on calf survival in northern Yellowstone is not clear-cut. Long-term data on the composition of wolf-killed prey show that elk calves represent a large proportion of wolf-killed elk, particularly in summer (62%) and early winter (49%; Metz et al. 2012). Although suggestive, wolf-kill data do not measure calf survival per se. Barber-Meyer et al. (2008) provided a proper analysis of calf survival in northern Yellowstone by using radio-telemetry to track the fates of 151 newly born calves during 2003–2005 when wolf numbers peaked in northern Yellowstone (Cubaynes et al. 2014). They found that wolves accounted for only 14–17% of calf deaths and that overwinter calf survival was high (mean = 90%). It is likely the sample of calves entering each winter was too small (n = 12–16) to provide an unbiased estimate of overwinter survival. However, a comparable radio-telemetry

study of northern Yellowstone calf survival conducted before wolf reintroduction (1987–1990) followed a larger sample of calves entering winter (n = 16–25) and found a similarly high rate of overwinter survival (mean = 86–94%) except in the severe post-fire winter of 1988–1989 (mean = 16%; Singer et al. 1997).

By contrast, summer survival rates of calves in 1987–1990 (mean = 65%; Singer et al. 1997) were more than twice that of those in 2003–2005 (mean = 29%; Barber-Meyer et al. 2008). Although at least some of the decrease was due to how the recent study defined the summer survival interval (capture date to October 31) to be two months longer than in the earlier study (capture date to August 31), it is notable that the proportion of calves killed by grizzly bears and black bears jumped from 23% (1987–1990; Singer et al. 1997) to as much as 60% (2003–2005; Barber-Meyer et al. 2008). This change aligns with an increase in the number of grizzly bears in the Greater Yellowstone Ecosystem during 1982–2007 (Kamath et al. 2015). These patterns would minimize the influence of wolves on calf survival, if not for the sheer number of elk calves among wolf-killed elk (Metz et al. 2012).

A similar discrepancy applies to cougars, which also commonly kill elk in northern Yellowstone. Like wolves, the composition of elk killed by cougars is dominated by calves (Ruth et al., *in press*). Moreover, the average total number of cougars inhabiting northern Yellowstone increased 76% from 1987–1993 to 1998–2004 (Ruth et al., *in press*). Yet, the proportion of cougar-killed radio-collared calves changed very little between 1987–1990 (1.5%; Singer et al. 1997) and 2003–2005 (2.6%; Barber-Meyer et al. 2008). Spatial mismatch between winter distributions of wolves, cougars, and radio-collared calves most likely explains why these predators killed so few radio-collared calves during 2003–2005 despite the prevalence of calves in their diets (Barber-Meyer et al. 2008).

As a result, questions persist about whether wolf, bear, and cougar predation adds to or replaces other sources of calf mortality, such as winter severity and other predators (Singer et al. 1997). On average, are wolves killing calves in northern Yellowstone that would otherwise survive their first year of life? A strong negative relationship between a proxy for calf survival (number of calves per 100 adult females counted in late winter; calf:cow ratios) and wolf population size (figure 3) is consistent with the hypothesis that wolves are an additive source of calf mortality. But inferring causation from this correlation is not foolproof. Calf:cow ratios are a composite of

fecundity and calf survival, and may be confounded by changes in female age structure (Bonenfant et al. 2005). In addition, parallel changes in wolf abundance and other factors that affect calf survival, (e.g., bear/cougar abundance) confound assessment of a wolf effect.

Between the potential bias of analyzing calf:cow ratios and the high cost of radio-collaring and tracking calves, there are few, if any, good options for annually monitoring overwinter calf survival and the factors that affect it. In an effort to develop an alternative, researchers have started visually tracking the fates of calves observed at heel among about 70 radio-collared adult female elk that winter in northern Yellowstone. Although these observational data are also error-prone, they provide a valuable auxiliary dataset for assessing the validity of calf:cow ratios, as well as permit analyses of adult female reproductive success that account for the effects of individual-level factors such as age. Continued emphasis on assessing the effects of wolves on calf survival is an essential step toward greater understanding of the impact of wolves on the abundance of the northern Yellowstone elk herd.

Whereas debate about the magnitude of the effect of wolves on elk abundance is unresolved, there is a growing understanding that factors besides wolves contributed to the decline of the northern elk herd. Foremost among these are other predators, especially humans. In contrast to the age-selective predation patterns of wolves, cougars, and bears, human hunters participating in the northern Yellowstone late season hunt primarily

ly killed the most fertile adult females (figure 2c). This likely represented a random sample of the female elk age distribution because the late hunt emphasized antlerless elk. By itself, regulated hunter harvest of young adult females is unlikely to reduce elk numbers. This is evidenced by substantial growth of the northern herd from 1976 to 1988 (figure 1) when hunters harvested large numbers of antlerless elk in the absence of much carnivore predation. And because hunters killed relatively few calves, high calf survival likely offset the removal of young adult females.

Elk calves enjoyed a large, perhaps unprecedented degree of protection from predation during the first 10–20 years of the natural regulation era. This began to change by the late 1980s when it became clear that a recovering grizzly bear population was increasingly preying on elk calves (French and French 1990). Growing cougar numbers and eventual wolf reintroduction increased predation pressure still further. By the early 2000s, the once predator-sparse environment of northern Yellowstone National Park was filled with record numbers of wolves, cougars, and grizzly bears preying on elk calves. Meanwhile, hunters continued to harvest substantial numbers of mainly young adult female elk during the late hunt. From 1995–2002, the late hunt annually removed between 940 and 2,465 total elk (figure 4). In 1997, severe winter conditions pushed many elk north of the park where they were exposed to hunter harvest. This resulted in the greatest number of elk harvested during the late season hunt (2,465 elk) since it was reinstated in 1976. And together with elk harvested during the preceding fall hunt, the total number of hunter-harvested elk during winter 1996–1997 represented the second largest removal of elk (3,320 animals) in the natural regulation era (figure 4). Record numbers of winter-killed elk suggest many harvested animals would have died of starvation had they avoided hunters. With continued declines in elk numbers observed during annual counts, the State of Montana reduced the number of late-hunt permits to less than 200 beginning in 2005 and suspended the hunt indefinitely following the 2009 season. While the fall season hunt continues, antlerless elk harvest has averaged less than 50 animals per year or less than 2% of the observed elk population since 2010 (Loveless 2015). The decline in hunting opportunity has fueled debate on the effects of predators on the northern herd, with the hunting public questioning the maintenance of high predator densities at the expense of hunting opportunity.

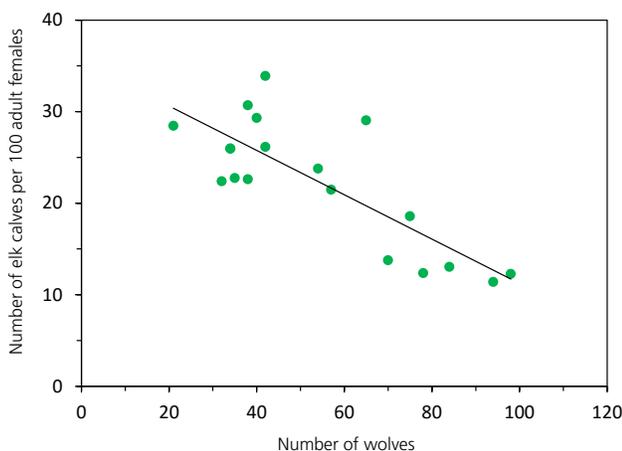


Figure 3. Elk recruitment rate (number of calves per 100 adult females) in relation to wolf population size in northern Yellowstone, 1996–2015. Wolf numbers correspond to animals living mainly inside Yellowstone National Park. Data are from the Northern Yellowstone Cooperative Wildlife Working Group and the Yellowstone Wolf Project.

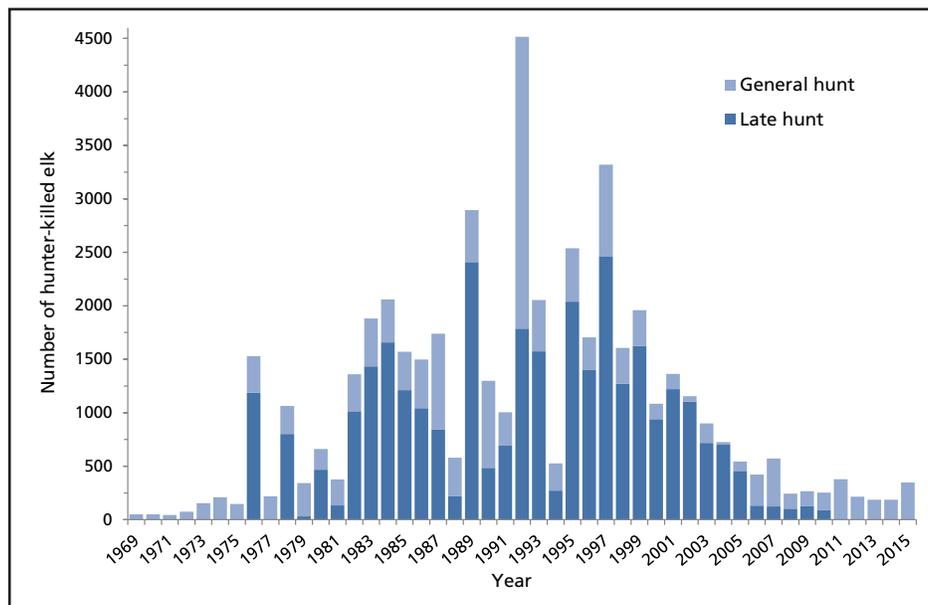


Figure 4. Annual number of northern Yellowstone male and female elk harvested by hunters in Montana Hunting District 313 (north of the park boundary) during the natural regulation era, 1969–2015. The final late season hunt occurred during the winter 2009–2010. Data are from Lemke et al. (1998), Vucetich et al. (2005), and Loveless (2015).

The decade following wolf reintroduction involved a level and pattern of predation on the northern herd it probably had not experienced since the market killing era (1872–1882) when wolves, cougars, and bears were probably still fairly abundant. The level of predation between 1923 and 1968 was also quite high, but this was mainly from humans (Houston 1982). As a result, the age of hunter-killed elk was not biased toward calves (e.g., Greer and Howe 1964) as it is with carnivore-killed elk. By contrast, the period between 1995 and 2005 involved a combination of carnivores killing calves and hunters killing young, fertile females. Wolf predation on old females may have also had a role, if diminished calf recruitment shifted the female age distribution toward older, more vulnerable age classes. Under conditions of intense predation across all ages of elk, it is difficult to imagine how the northern herd could have avoided a steep drop in abundance. Indeed, the mix of carnivore- and human-caused mortality that defined this period may partly explain why the rate of decline after wolf reintroduction was greater than it was during 1923–1968 (figure 1) when humans were the only major predator.

Declining ungulate abundance with increasing predator diversity has also been observed in moose and caribou systems (Gasaway et al. 1992, Peterson 2001). These studies suggest each additional predator species (i.e., wolves, grizzly bears, black bears, humans) results in a stepwise reduction in ungulate abundance. However, the dynamics and mechanics of this relationship are

poorly understood. For example, little is known about how changes in the relative abundance of different predator species offsets (or exacerbates) the impact of predator diversity on ungulate abundance. In addition, it is unclear whether the combined effects of multiple predators on shared prey is the sum of their separate effects, or whether predators interact synergistically (or antagonistically) such that their combined impact is greater (or less) than the sum of their individual impacts.

The ability of grizzly bears to usurp wolf-killed elk (Ballard et al. 2003) suggests the potential for a synergistic effect; whereas, diminished cougar predation on elk calves in the presence of wolves and grizzly bears (Griffin et al. 2011) suggests a possible antagonistic effect. There is also the possibility that good forage conditions buffer elk against predation in systems with as many predators as Yellowstone (Griffin et al. 2011). Clearly, progress toward understanding the fate of the northern herd requires continued attention to northern Yellowstone as a multi-predator system.

A continued focus on the role of humans is also necessary. Cessation of the late hunt and reduced antlerless harvest during the general hunt in recent years provides a unique opportunity to assess whether adjusting human harvest can offset the impact of multiple carnivores on the abundance of the northern herd. Increased ungulate abundance in response to fewer predator species, including humans (Peterson 2001) together with evidence that human harvest has an overriding influence

on adult female elk survival (Brodie et al. 2013) and elk population growth (Vucetich et al. 2005) suggests the northern herd may at least stabilize in the years ahead. If so, it will highlight how the fate of the northern herd is ultimately in the hands of humans, much as it has been since at least 1872.

The final actor in the northern Yellowstone saga that cannot go unmentioned is bison. A common refrain among those of us who were on the ground in northern Yellowstone during the late 1990s is that where we once saw herds of elk, we now see herds of bison. This has fueled speculation that bison are competing with elk and increasing bison numbers have contributed to the decrease in the northern elk herd following wolf reintroduction. This is an interesting reversal of perspective from the 1970s and 1980s, when the concern was about too many elk outcompeting bison and other ungulates. Studies during that period concluded that competition between elk and bison was minimal (Houston 1982, Singer and Norland 1994, Barmore 2003). Whether or not this still holds true is the subject of ongoing research.

No matter how much science tells us about what drives northern Yellowstone elk population dynamics, science alone is unlikely to resolve stakeholder concerns about too few or too many elk. This is because these concerns are less about science and more about competing visions of what northern Yellowstone should look like. What is indisputable is that the current version of the northern Yellowstone system (i.e., fewer elk wintering mainly outside the park, more bison wintering mainly inside the park, lower human harvests, high carnivore predation from multiple predators) is unlike any that has existed since managers conducted what was perhaps the first systematic count of the northern herd a century ago (Bailey 1916). How long this version lasts and what the next one may look like are fascinating questions. The answers will only be revealed if northern Yellowstone's many stakeholders continue to support long-term coordinated monitoring and assessment.

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Understanding the Limits to Wolf Hunting Ability

Daniel R. MacNulty, Daniel R. Stahler, & Douglas W. Smith

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One of the best known facts about wolves is that they kill hoofed animals (ungulates) for a living. In North America, these include everything from deer and mountain goats, to bison and muskoxen. Less understood is how wolves kill these animals. This may seem trivial, but misconceptions about wolf hunting behavior are a key source of the misunderstanding and mythology about wolves. Beneath many debates about wolves is a fundamental confusion about the ability of wolves to kill ungulates.

The root of this confusion is the presumption that wolves are outstanding hunters. This is an understandable view. Few other mammalian predators can kill prey so much larger than themselves. Wolves also hunt in packs, and there are few spectacles in nature as impressive as a swarm of wolves chasing and taking down a large ungulate. People may have a special appreciation for this because not long ago most humans also made

their living by cooperatively hunting big game. The key difference, of course, is that humans hunted with tools. The spectacular ability of wolves to cooperatively kill ungulates several times their size with only their teeth as weapons often elevates them to a place in the human imagination reserved for powerful natural and supernatural forces, such as tornadoes and Moby Dick.

Human imagination has played a big role in popular (mis)understanding of wolf hunting behavior because direct sightings of wolves chasing and killing prey have been rare. Most wolves inhabit areas too densely forested or too remote to allow regular observation of their hunting behavior. As a result, general knowledge about wolf hunting behavior has been heavily influenced by hearsay, nonobjective accounts, and interpretations of tracks in snow. Although Murie (1944) compiled the first scientific observations of wolf hunting behavior, this remained a murky area of science until the stud-

ies of Isle Royale wolves by Mech (1966) and Peterson (1977). These researchers pioneered the technique of using small fixed-wing aircraft to observe wolves from the air. This allowed the researchers to witness and record an unprecedented number of wolf-prey interactions, all of them involving moose, the only ungulate on the island. Their surprising finding was that most moose escaped unscathed, even when cornered by more than a dozen wolves. Subsequent observations of wolves hunting Dall sheep (Haber 1977, Mech et al. 1998), muskoxen (Gray 1983), bison (Carbyn et al. 1993), white-tailed deer (Nelson and Mech, 1993), and caribou (Mech et al. 1998) confirmed that most wolf predation attempts usually fail.

Why are wolves so often unsuccessful in catching their prey? Although the outcome of any species interaction is contingent on the traits of each species, traditional explanations about the low success rate of wolves have mainly focused on the role of prey traits. The central hypothesis has been that wolf-killed prey “must be disadvantaged in some way, for they would have escaped if they were not” (Mech 1970). Because aerial observations often provide only coarse details about wolf-prey interactions, researchers have used the remains of kills to infer how prey traits affect wolf hunting success. By comparing the traits of wolf kills to those of animals killed for other reasons (e.g., hunters, vehicle collisions), researchers have shown that wolves primarily kill young, old, and debilitated animals, which comprise a small fraction of the total prey population (reviewed by Mech and Peterson 2003). The conclusion from this research is that wolves are often unsuccessful because most prey populations are dominated by individuals they cannot catch.

But why can't wolves catch these individuals? To answer this question, one must appreciate how the traits of wolves constrain their ability to kill. The most obvious trait is skeletal. In general, wolves lack a specialized skeleton for killing. Its front-most teeth, the incisors and canines, are their only tools for grabbing and subduing prey; and these wear out with age (Gipson et al. 2000). Also its skull is not mechanically configured to deliver a killing bite like some other mammalian carnivores, such as felids and hyaenids. Specifically, a relatively long snout reduces the force of jaw-closing muscles that is exerted at the canine tips during the bite (Wang and Tedford 2008). In addition, the joint where the jaw connects to the skull does not allow the jaw to be locked or

heavily stabilized when biting prey (Peterson and Ciucci 2003). Wolves also lack retractile claws and supinating, muscular forelimbs, which precludes them from grappling prey as do other large carnivores (e.g., cougars, grizzly bears).

Less obvious traits, including age, body size, and social behavior, can further limit wolf hunting ability. This information derives from observations of wolves hunting elk in northern Yellowstone National Park. This research differed from past efforts because it was based on the behavior of individually-identifiable wolves with known life histories. These animals were either members or descendants of the population reintroduced to Yellowstone in 1995-1997 (Bangs and Fritts 1996). Observers could measure the hunting behavior of individual wolves because (1) many were radio-collared and/or had distinct features (e.g., pelage markings, color, body size and shape), and (2) it was possible to watch wolves for extended periods from fixed positions on the ground, often from overlooks that afforded a bird's-eye view without the tight-circling and fuel restrictions of a fixed-wing aircraft. Ground observations provided extra time to carefully dissect the identities and roles of different pack members, as well as to record the entire sequence of a wolf-prey interaction from start to finish (MacNulty et al. 2007). Ground observations were made possible by northern Yellowstone's sparse vegetation and year-round road access.

Yellowstone research showed that the hunting ability of wolves, like the escape ability of their ungulate prey, decreases with age due to physiological senescence (MacNulty et al. 2009a). Top-performing hunters were 2-3-years-old. This highlights how age-specific change in hunting ability transcends differences between pups and adults to include differences between adults and old adults. Moreover, decline of hunting success with age suggests that temporal fluctuations in the age composition of the wolf population might contribute to the impact of wolf predation on elk numbers. And among wolves of the same age, smaller ones were generally worse hunters than larger ones because absent specialized killing morphology, sheer mass was necessary to topple an adult elk that is 2-6 times larger (MacNulty et al. 2009b). Indeed, male wolves were better than females at dragging down elk precisely because they were heavier. On the other hand, a lighter build may have given females an advantage when sprinting after fleet-footed elk.

Analyses of the effect of pack size on the success of wolves hunting elk revealed that group hunting behavior did little to offset age- and size-specific constraints on individual hunting ability (MacNulty et al. 2012). Packs with four wolves were more successful than packs with fewer wolves; but in packs with more than four wolves, pack size had no measurable effect on the outcome of wolf-elk interactions. Results suggest this was due to wolves holding back (i.e., free riding) to avoid injuries which arise from being kicked, trampled, or stabbed with antlers. This pattern held regardless of whether a wolf was a pup or an adult and suggests wolves in large packs may join a hunt simply to be at hand when a kill is made.

By contrast, the success of wolves hunting bison increased across pack sizes over which elk capture success was constant (4-11 wolves) and leveled off at a group size over 3 times larger than that of wolves hunting elk (13 wolves; MacNulty et al. 2014). Wolves were probably more cooperative hunting bison than elk because a single wolf has practically no chance of killing an adult bison by itself; whereas, a single wolf has about a 2% chance of killing an adult elk by itself. Low solo capture success is expected to foster cooperation because it leaves ample scope for an additional hunter to improve the outcome enough to outweigh its costs of active participation (Packer and Rutan 1988).

The bottom-line is that the wolf's own biology enforces strict limits on its capacity to kill ungulates. It is precisely these limits that prevent the wolf from behaving as a runaway killing machine (Mech et al. 2015). Nevertheless, proponents for and against wolves rarely begin their arguments with a recognition of what wolves cannot do. Instead, both sides typically exaggerate the predatory power of wolves to advance their respective views about the ecological virtues and vices of wolves. Bridging the gap between these two views requires a shared understanding of the limits of wolf hunting ability.

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Dan MacNulty see page 33.

Territoriality and Inter-Pack Aggression in Gray Wolves: Shaping a Social Carnivore's Life History

Rudyard Kipling's Law of the Jungle Meets Yellowstone's Law of the Mountains

Kira A. Cassidy, Douglas W. Smith, L. David Mech, Daniel R. MacNulty, Daniel R. Stahler, & Matthew C. Metz

When Rudyard Kipling wrote *The Jungle Book* in 1894 and included the famous line “For the strength of the Wolf is the Pack, and the strength of the Pack is the Wolf,” he would have had no idea that over a century later, scientific research would back up his poetic phrase. Recent studies in Yellowstone have found that both the individual wolf and the collective pack rely on each other and play important roles in territoriality. At a time when most fairy tales and fables

were portraying wolves as demonic killers or, at best, slapstick gluttons, Kipling seemed to have a respect or even reverence for the wolf. Wolves in *The Jungle Book* raise and mentor the main character Mowgli, with the pack's leader eventually dying to save the “man-cub” from a pack of wolves. Kipling may have extended intra-pack benevolence to a human boy for literary sake, but he was clearly enthralled with how pack members treat each other. As wolf packs are almost always family units, most commonly comprised of a breeding pair and their offspring from several years, amiable behavior within the pack is unsurprising. By contrast, wolf packs are fiercely intolerant of their neighbors, their rivals. And this competition is proving to be an important facet in the life of a wolf and its pack.

Although many animals live in groups, only some are considered territorial (willing to fight other groups or invading individuals to protect their territory). African lions, meerkats, chimpanzees, and mongooses regularly attack and even kill non-group members (Heinsohn and Packer 1995, Doolan and MacDonald 1996, Wilson et al. 2001, Cant et al. 2002). Even nomadic hunter-gatherer human groups fought; the often lethal conflicts ranged from primitive to complex warfare (Wrangham and Glowacki 2012). For this behavior to evolve, it must afford group members a survival advantage. Wolves likely evolved to be territorial because it benefits them in several ways: repelling intruders makes it easier to protect vulnerable pups at the pack's den, and securing territory with abundant prey ensures an uncontested

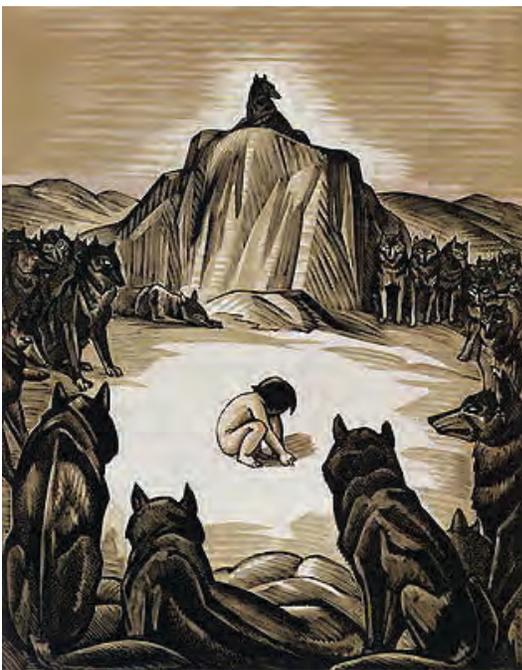


Illustration by Charles Maurice Detmold from *The Jungle Book* by Rudyard Kipling, Macmillan & Co., London, UK, 1894.



The Agate Creek pack, led by several adult females, chases the Oxbow Creek pack (out of frame). Within a few minutes, the Agate Creek pack caught and killed a female from the Oxbow pack, effectively reducing that pack to only two wolves.

food source (Kittle et al. 2015). Success in both these aspects of life—reproducing and eating—perpetuates the genes of high-performing individuals. And in the case of the wolf, the ones best at reproducing and eating are aggressive with their rivals. In fact, of all the dead

wolves recovered in Yellowstone, intraspecific (wolf vs. wolf) strife accounts for two-thirds of natural mortality (figure 1).

Although inter-pack conflict is not rare, wolves display a variety of nonaggressive territorial behaviors that di-

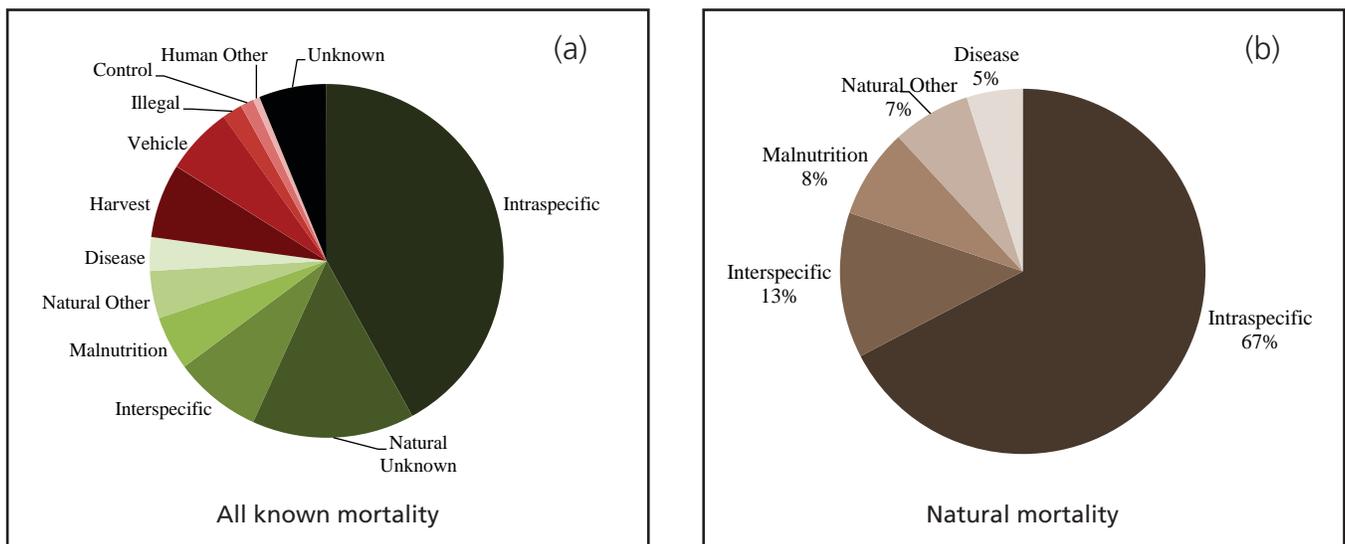


Figure 1. Causes of mortality for Yellowstone National Park collared wolves (1995-2015). (a) All causes of mortality; (b) Natural, known causes of mortality.

minish the risk of confrontation. They scent-mark within territories and along boundaries, and these scents can be detected by other wolves for 2-3 weeks (Peters and Mech 1975). They also howl, to signal their location and strength to neighboring packs (Harrington and Mech 1983). When these behaviors fail to separate neighboring packs or one pack decides to engage another, the ensuing confrontations are almost always aggressive. In these cases, each pack tries to displace the other and, if possible, catch and kill an adversary.

But what makes one pack better or more successful at aggressive encounters with another group? Is it simply a numbers game? Does the larger pack always win? If so, that would fit well with the first line of Kipling's writings: "The strength of the Wolf is the Pack." Using data gathered during direct observations of 121 aggressive encounters between packs from 1995-2011, we were able to test these questions. As expected, pack size was important to successful conflicts. The larger group was more likely to win (Cassidy et al. 2015), as seen in groups of African lions, chimpanzees, and hyenas (Mosser and Packer 2009, Wilson et al. 2002, Benson-Amram et al. 2011). And just one wolf can make quite a difference; a pack with one more wolf than its opponent has 140% higher odds of winning (or 2.4 to 1). If a pack of 10 fought a pack of nine 100 times, the pack of 10 would win about 71 of the encounters.

If the strength of the wolf is the pack, it makes sense that wolves have evolved to live in large groups. Between 1995 and 2015, Yellowstone packs averaged 9.8 wolves and frequently grew to 20, with the largest pack recorded at 37 members. But living in such a large family isn't always beneficial to other aspects of wolf life. The most efficient pack size for successful elk hunting is only four wolves (MacNulty et al. 2012) and eight for reproduction (Stahler et al. 2013). Living in a large group often means each individual wolf gets less to eat (Schmidt and Mech 1997). The largest packs tend to exhibit more fission-fusion behavior (Metz et al. 2011), much like chimpanzees and hyenas (Lehmann and Boesch 2004, Smith et al. 2008). They may be able to get away with being less cohesive because when they break into smaller groups, each wolf gets more food; and as long as each group is larger than its neighbor's full size, it is still likely to win in a territorial contest.

Wolves do several things to indicate that on some level, they might realize pack numbers give them an advantage. They will often disperse in same-sex cohorts. These pack mates, typically siblings, look to join an op-

posite sex individual or, even better, a cohort of opposite sex wolves. Most packs in Yellowstone have formed this way. Becoming an immediately-sizeable pack is critical to establishment and persistence on the wolf-dense northern range (wolf density in Yellowstone's northern range has ranged from 20.1 to 98.5 wolves/1000km² and averages 52.9, almost double the average wolf density in northeastern Minnesota and 10 times higher than Denali National Park [Fuller et al. 2003]). While each year new wolf pairs form, since 1995 only two simple packs—packs made up of one male and one female—have successfully raised pups and established a territory in the hyper-competitive northern range (Leopold, which formed early on in 1996; and Swan Lake, which formed at the western edge of high-wolf density territories).

Although infanticide, the killing of pups, has been recorded in gray wolves (Latham and Boutin 2012, Smith et al. 2015), it is less common than in bears and wild felids, and occurs when one pack attacks the wolves at the den site of another pack. Spring is the most effective time for one pack to impact another; den-attacks are more likely to result in adult and pup mortality, sometimes even wiping out an entire litter (Smith et al. 2015). Unlike wolves, female bears and felids become sexually receptive after they stop lactating, thus motivating males to kill nursing juveniles and mate with the female, replacing a rival's offspring with their own (Hausfater and Hrdy 2008). By contrast, female wolves come into estrus only once per year for about a week (Asa et al. 1986). So although mating competition is intense for a short time, there is no immediate advantage for outside males to kill dependent young. In fact, the evidence suggests that newly established breeding males attend the pups as if they were their own. There are several cases of a new dominant male joining a pack, either when the dominant female is pregnant with the previous male's pups (e.g., the Lamar Canyon pack in 2015) or after the pups were born. This suggests the new male realizes the value in raising unrelated pups; it ensures his pack size increases and remains competitive against neighboring packs. He can then breed with the female the next mating season—an incredibly long-vision for individuals that, in Yellowstone, only live an average of 4.6 years (MacNulty et al. 2009a).

During 121 aggressive interactions recorded in Yellowstone, 71 escalated to a physical attack and 12 resulted in mortality. We also recorded seven cases of apparently altruistic behavior, where one wolf was being attacked by a rival pack and its pack mate disrupted the attack

by running close by or even jumping into the middle of the group of wolves. In four cases the victim escaped. Kipling penned a similar scenario wherein Mowgli was saved from a rival pack of wolves by his lead male wolf, who was injured and eventually died—effectively giving his life for his pseudo-offspring. The risky behavior exhibited by the altruist is difficult to explain; but if successful, it enjoys the benefits of maintaining a packmate, who usually shares its genes (kin selection [Hamilton 1964]) and may reciprocate or aid them in the future (reciprocal altruism [Trivers 1971]). Whether it is through rescuing a pack mate, raising unrelated offspring, or traveling in a large pack to defeat rivals, “The strength of the Wolf is the Pack” rings true.

But there is the second part: “The strength of the Pack is the Wolf.” Could Kipling be right? Could there be some pack composition influence: that one individual has a disproportionate effect, maybe helping its pack beat an opponent in an aggressive encounter, even when outnumbered? While statistically holding pack size fixed, we tested for effects from all age and sex categories. We also tested to see if residents were more likely to defeat intruders. This home-field-advantage hypothesis was not supported; even intruders were likely to win if they were larger. But Kipling would be happy to know

that some types of wolves have a significant and positive effect on their pack’s success: adult males and old adults (6 years or older; Cassidy et al. 2015). Adult males are the most aggressive wolves in the pack, and having one more than a rival meant 65% higher odds of winning (1.65 to 1). Males are 20% larger and more muscular than females (Morris and Brandt 2014), though this actually hinders males during some stages of prey hunting, as their bulk makes them slower (MacNulty et al. 2009b). This sexual dimorphism probably evolved as an adaptive response to intense inter-pack competition and protection of the family unit through fighting. A male wolf’s aggressiveness actually increases throughout his entire lifespan, even as hunting ability and body size diminish into old age (MacNulty et al. 2009a, b).

Perhaps related to the value of adult males to territoriality, we have recorded several cases of an unrelated male joining an already established pack as a subordinate member. Even though the new male could be viewed as competition for breeding rights with the females, he is accepted, perhaps for the positive influence he has on pack success when encountering a neighbor. Conversely, in 20 years we have never recorded an unrelated female joining an already-established group. Females did not have an effect on conflict success. Their

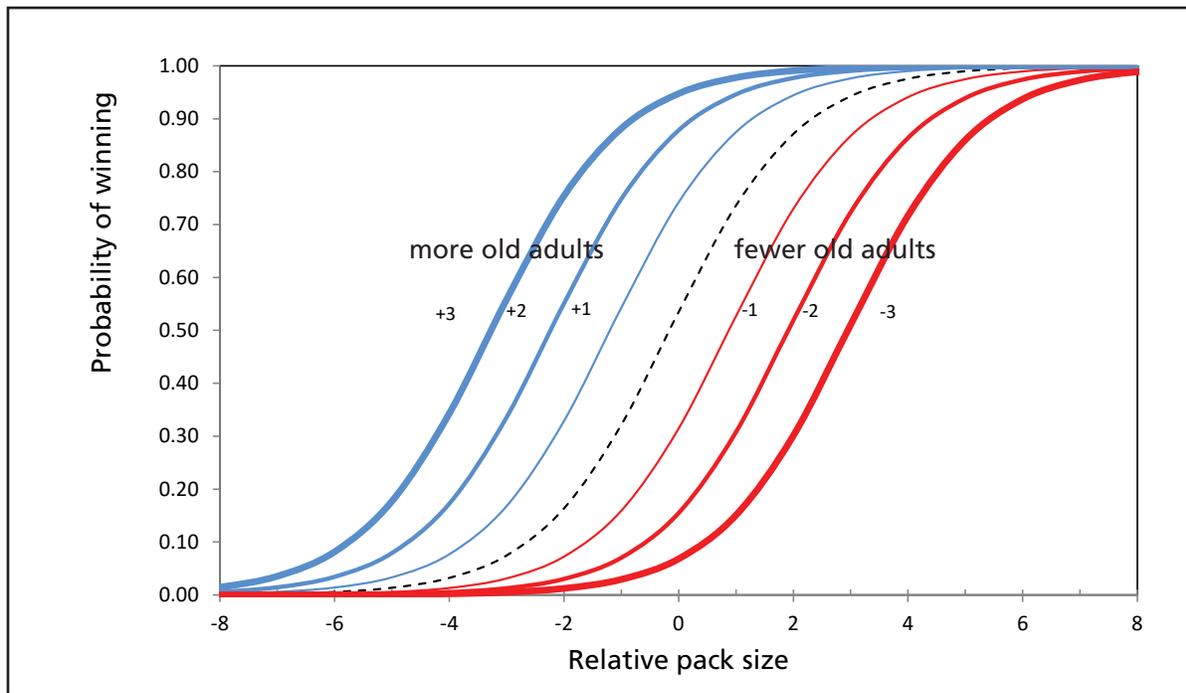


Figure 2. Predicted values for the probability of a wolf pack winning an aggressive inter-pack interaction based on relative pack size (RPS) and old adults. Red lines indicate probability of winning while having relatively fewer (-1, -2, -3) old adults than an opponent. Blue lines indicate probability of winning while having relatively more old adults than an opponent. Data collected from 1995-2011 in Yellowstone National Park.

aggression stays approximately constant throughout their entire lifespan and may drop slightly during their most reproductively-active years, likely a product of self-preservation.

But the most influential factor in whether or not a pack defeated an opponent was the presence of an old wolf. A pack with one old wolf more than the opposition has 150% greater odds of winning, making age more important than having a numerical advantage (figure 2). But why? Old wolves are past their physical prime, participating less and less in hunts as they age, instead relying on the younger, faster, stronger wolves to risk bison and elk hooves and antlers to provide food for the entire pack (MacNulty et al. 2009b). Even the lead wolf in *The Jungle Book* eventually became so old that he rarely left his lair yet was still the leader, as Kipling wrote in one of the last lines of wolf code or “The Law of the Jungle”:

***“Because of his age and his cunning,
because of his grip and his paw,
in all that the law leaveth open,
the word of the head wolf is law.”***

What old wolves possess is experience. They’ve encountered competitors many times, seen pack mates killed, participated in killing rivals. They may avoid a conflict they figure they can’t win, upping their chance of survival. Having an experienced wolf allows a pack to draw from past knowledge, increasing the odds that even a small pack can defeat a larger pack.

As death by rival pack is by far the most common cause of natural mortality, the packs that can reduce this risk by being larger than their neighbors, having more adult males, or having old adult pack members are the ones most likely to acquire and maintain productive territory. Those territories include safe places to raise pups, lots of prey, and separation from humans and roads. One pack in Yellowstone, the Mollie’s pack (originally called the Crystal Creek pack) has persisted for over 21 years, likely because it has traditionally been one of the largest packs with many adult males and long-term, old members. This pack has had only six dominant males and five dominant females in their entire history—reigns that help explain the pack’s success and longevity.

The loss of an old adult or an adult male, through natural- or human-causes, reduces the competitive strength of the pack, likely affecting the remaining pack members’ long-term survival, reproduction, ability

to hold productive territory, and ultimately the entire pack’s persistence. Over 100 years ago, when Kipling wrote “For the strength of the Wolf is the Pack, and the strength of the Pack is the Wolf,” he couldn’t know his creative writings would someday be interwoven with wolf research. But maybe that is why *The Jungle Book* is still such a classic; although Kipling’s premise of wolves raising a human boy is obviously fictitious, the way he describes the heart of the wolf pack and the ways the pack treats its family versus rivals is based in truth and, now, supported with science.

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Kira Cassidy is a research associate with the Yellowstone Wolf Project. After graduating from Southern Illinois University in 2007, Kira started as a biological technician with the Wolf Project in 2008. For two years Kira worked on the Druid Road Management crew and participated in six winter studies, all but one following the famous Druid Peak pack. In 2013 she completed a MS degree at the University of Minnesota, advised by wolf biologist Dr. L. David Mech. Her projects focused on territoriality and aggression between wolf packs. In 2014 Kira accompanied a film crew to Ellesmere Island, Canada, to document arctic wolves. Living next to a wolf den for six weeks fostered Kira's desire to help communicate science through media, art, and writings for the public. Kira's current projects focus on wolf pack behavior and sociality. Results from some of these projects highlight the importance of old adults in a wolf pack and led Kira to consider connections to other social species, including humans. This was the topic of Kira's TEDx talk in Bozeman, Montana, in April 2016.



LEADING THE WAY: Women in Science



Lisa Koitzsch, Kira Cassidy, Erin Stahler, & Brenna Cassidy

Early on, almost all people who studied wolves were men (with the notable exception of Lois Crisler who wrote *Arctic Wild* in the 1950s). Whether or not this influenced the science being done is debatable, and perhaps unknowable; but men and women often approach the same situation or problem differently. This may be especially evident in research concerning who was the “leader of the pack.” Arguably, the very first wolf biologist, Adolph Murie, who studied wolves in Mount McKinley National Park (now Denali National Park and Preserve) in the 1930s and 40s set the stage for years to come in this area of behavioral study. Murie closely observed wolf behavior in the park and at one point in his book *The Wolves of Mount McKinley* wrote, “He [the alpha male] seemed more solemn than the others, but perhaps that was partly imagined by me, knowing as I did that many of the family cares rested on his shoulders.” More recent research in Yellowstone and Ellesmere Island indicates it may be the alpha (now called the dominant breeder) female who runs the show.

- Doug Smith

Lisa Koitzsch currently works as a technician for the Yellowstone Wolf Project. She graduated from Johns Hopkins University with a BA in Humanities and French Literature and worked for several years in publishing and administration. During the two intensive months of winter study, her main focus is downloading location data from GPS-collared wolves, creating maps of clustered wolf locations, and coordinating searches of these clusters, which typically represent feeding and resting locations, in order to estimate wolf-pack predation rates. Lisa has worked with the wolf project every winter since 2008, when she and her husband, Ky, were hired as a two-person crew to conduct necropsies on wolf-killed prey. In addition to her current work with the Yellowstone Wolf Project, Lisa and Ky are working on a three-year noninvasive study estimating winter population size and vital statistics of moose in Yellowstone National Park’s Northern Range.

Kira Cassidy (see page 42)

Erin Stahler (see page 54)

Brenna Cassidy is a Biological Technician with the Yellowstone Wolf Project. She graduated from University of Wisconsin-Stevens Point as a Wildlife Ecology major in 2012 and moved to Yellowstone National Park shortly after to participate in her first winter study. Since then, she has done six winter studies and has spent most of that time with the Junction Butte pack. Brenna has worked on a number of projects in Yellowstone including the Raptor Initiative, the Core Bird Program, and the Yellowstone Cougar Project. Studying multiple species has allowed Brenna to travel throughout the park by plane, foot, canoe, and skis. Seeing the park through the eyes of multiple species has shown her that each has a important role in the interconnected ecosystem of Yellowstone.

A Peak Life Experience: Watching Wolves in Yellowstone National Park

Rick McIntyre



NPS PHOTO - B. CASSIDY

After 18 summers of working as a seasonal naturalist in Denali National Park and Glacier National Park, I transferred to Yellowstone in the spring of 1994 and worked as a seasonal naturalist with the title of Wolf Interpreter. All of my programs were on the subject of the upcoming wolf reintroduction.

In May 1995, as I was returning to Yellowstone for my second summer, my goal for the season was to see at least one of the newly reintroduced wolves. I thought, with my experience in spotting wolves in Denali and Glacier, I might have a chance of seeing one over the course of the summer. None of the people working on

the planning of Yellowstone's wolf reintroduction program expected wolves to be easily seen by park visitors after being released. This was partly due to the intense hunting and trapping pressure the wolves had experienced in their home provinces in Canada. From that previous experience, the wolves would very likely avoid crowded sections of the park where visitors might see them from the road corridor.

In the early morning of my first full day in the park, I saw the entire six-member Crystal Creek pack in Lamar Valley and helped visitors to see them as well.



Rick McIntyre and Lizzie Cato. Lizzie was born and raised in Raleigh, NC, and grew up enjoying the outdoors. A graduate from Colorado State University, Lizzie holds a bachelors degree in wildlife biology. Lizzie works full time on the road observation crew doing daily ground tracking and helping educate visitors on the Yellowstone wolves. Photo © K. Lynch.

Unexpectedly, the wolves turned out to be very visible, and large crowds showed up in Lamar Valley every day to see them. The excitement level of spotting wolves that first summer would have been similar to seeing the Beatles standing on a street corner at the height of their popularity. Being in the middle of so many crowds during that period, it was clear that when Yellowstone visitors got a glimpse of the reintroduced wolves, it was truly one of the peak experiences of their lives. I frequently saw people crying with joy, and at times had citizens run over and hug me because I was the nearest uniformed representative of the National Park Service.

I continued to work for the Interpretation Division as the Wolf Interpreter through the fall of 1997 and also volunteered with the Wolf Project during my time off. I switched to a biological technician position with the Wolf Project in the spring of 1998 and am still in that position.

As word spread of the visibility of wolves in Yellowstone, we began to have problems with overenthusiastic visitors who would either walk toward nearby wolves for a closer photo or drive toward where wolves were trying to cross the road. One particular incident motivated us to come up with better ways to manage visitor-wildlife interactions.

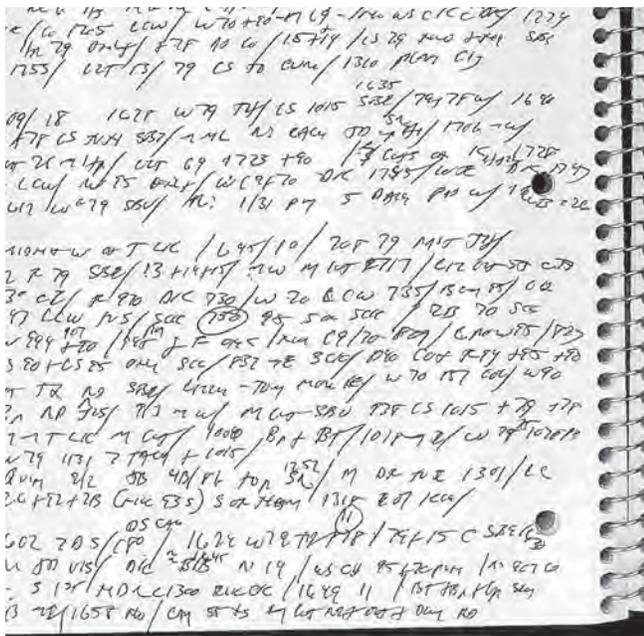
During a busy Memorial Day weekend, Druid alpha male 21M was trying to return to the pack's den with food from a carcass. As he approached the road near

the den, visitors drove to the likely crossing point and stopped to photograph him. Due to the cars blocking his route, the wolf backed off, went west, and tried to cross at another point. Once again people drove to that site and intercepted him. Wolf 21M went further and further west and was repeatedly blocked each time he tried to cross. He had to go five miles west of the den before he could cross the road, then had to walk another five miles east to finally reach his pups at the den.

After that pivotal incident, Wolf Project, Interpretative, and Law Enforcement staff worked together when wolves were approaching the road and developed techniques of temporarily stopping traffic in both directions when crossings were imminent. We also developed park regulations requiring people to stay a minimum of 100 yards from wolves and prohibited any actions that changed the natural behavior of wolves. In addition, we gradually developed a protocol of using aversive conditioning techniques on wolves that had become too habituated to people, cars, and roads. Due to the unique situations we were experiencing, much of what we did during those early years was trial and error. A key early decision was for all of our staff to be oriented toward being interactive, cooperative, inclusive, and collaborative with park visitors and local residents about wolf sightings. That policy has paid off in many unforeseen ways over the years.

Looking back over that early period, it is now clear a number of positive trends developed organically among park staff and visitors. Very quickly an informal cadre of "wolf watchers" naturally formed in areas where wolves were most likely to be seen, such as Lamar Valley. Comprised of long-term repeat park visitors and local residents, the wolf watchers, without any planning or instructions, became role models of proper behavior regarding watching and photographing wildlife.

In many cases, it was the regular wolf watchers, arriving before sunup in wolf viewing areas, who would be the first to spot wolves. Without any oversight, the more experienced watchers would quietly view the animals from the road corridor or short distances from the road, and usually act in ways that would not interfere with the behavior of the animals. Later, as more visitors arrived on the scene, the wolf watchers would graciously offer to show them the wolves through high quality spotting scopes, identify the wolves in sight, explain the behaviors of the animals, and convey the story of the park's wolf reintroduction program. Without being aware of it, those newer arrivals would settle into the same quiet



After a long day at work, Rick spends the evening hours creating a hand-written account (like the one above) of the day's events and then creates a computerized version. Rick's twenty-one years of meticulous observations are estimated to contain 11,000 pages of material.

and respectful behavior exhibited by the wolf watchers and would model that same behavior as they took the initiative to speak to additional visitors that came on the scene. Beyond that, people who went through that experience continued to behave in that manner when they saw wildlife in other sections of the park.

The Wolf Project developed methods of informal roving interpretation in those situations where we would speak to individuals, families, and crowds about the wolf story in Yellowstone, emphasizing how wolves fit into the overall mission of the National Park Service. In other situations, we conducted more formal talks on the side of the road to school groups, college field trips, wildlife tour groups, and other groups about wolves. During recent years, the number of those roadside talks has averaged well over 200 annually. In these interactions we emphasize proper respectful behavior around park animals, especially wolves. We speak about how overenthusiastic people might inadvertently block wolves trying to cross the road. In addition, we talk about the issue of animal habituation in a national park and how wolves used to being around crowds of people, roads, and cars might leave the park during legal wolf hunting seasons and naively walk toward a party of hunters or be hit by fast-moving cars.

The ground-swell of interest in the park wolves led to support for the Yellowstone Wolf Project in many forms. People who had seen wolves in the park talked to their friends about their experiences. Websites and emails spread the word about Yellowstone wolf packs and famous individual wolves. All this created greater interest and notoriety regarding the Yellowstone wolves. When budget cuts came to the park, donations to the Wolf Project through the Yellowstone Park Foundation became an important source of support for wolves and the program. Those donations, large and small, all came about through this intimate observation experience visitors had with wolves, Wolf Project staff, and wolf watchers.

Another organic development was the impact of crowd sourcing on wolf research. Wolf watchers often spotted wolves before Wolf Project personnel came on the scene. Many wolf watchers became experts in identifying individual wolves and in noting their behavior. All this added up to more wolf observations than would have been possible with limited staffing. A large number of critically important behavioral sequences that have been published in Wolf Project peer-reviewed scientific papers originated with the watchers. They truly are citizen scientists!

Having worked for the National Park Service for over 40 years, it is professionally invigorating to be in the middle of a crowd of park visitors who are experiencing the thrill of seeing wild wolves living out their lives in Yellowstone. It is clear from watching the faces of these people and hearing their excited comments that each person is having a peak life experience they will fondly remember the rest of their lives. For any ranger, from any era of our 100-year history, what better sums up the mission and purpose of our agency?

Just after writing that last paragraph, I had a conversation with a woman who perfectly illustrated that last point. I was showing some wolf pups to several people when the woman came up to me and thanked me for helping her and her friends see the pups. She went on to say several years earlier she had come to the park with a troop of girl scouts. Her entire group saw wolves on one particular day, and they all listened to a talk I did on wolves. She then said, "Let me tell you something—it was a life changing experience for all of us."



Infectious Diseases of Wolves in Yellowstone

Emily S. Almberg, Paul C. Cross, Peter J. Hudson, Andrew P. Dobson, Douglas W. Smith, & Daniel R. Stahler

The summer of 2005 began with such promise for wolves in Yellowstone. The population had been at an all-time high the last few years, and the wolves appeared to be in good condition. Several packs had been particularly busy during the breeding season, and early summer pup counts suggested another healthy crop of new wolves rising through the ranks.

And then something changed.

While monitoring dens to count pups, we noticed huge declines in pup numbers. The Slough Creek pack started out with 18 pups among three litters; by August, these numbers had declined to three lethargic pups. Similar things were happening across the northern portion of the park. We were soon looking at the worst pup survival rates since wolf reintroduction; by the end 2005, total wolf population numbers in the park had dropped by over 30%. That was the summer we came to understand the importance of infectious diseases for wolves in Yellowstone.

Parasites and pathogens are often overlooked in studies of wild populations. This is due, in part, to the logistical issues of studying disease impacts; often there are few outward signs of illness, bodies are seldom recovered soon enough for disease tests, and the proximate cause of death (e.g., injuries from other wolves) are often more obvious than a predisposing illness. As a result, viruses, bacteria, worms, and mites were historically perceived as factors that only impacted weak individuals or randomly caused outbreaks in overly-dense populations. This perception may have been reinforced by the history of over-hunting that reduced wildlife populations to low densities with reduced rates of disease transmission, leading us to forget or underestimate the ability of disease to cause significant amounts of mortality.

Following the summer of 2005, the Yellowstone Wolf Project expanded its monitoring efforts to include parasites and pathogens to better understand the cause

of poor pup survival in 2006 and the overall health of wolves. That winter, the Wolf Project collected blood serum, as they always do, during their annual capture and radio-collaring efforts. Blood serum contains a record of many of the pathogens the animal has been exposed to over the course of its life. When we analyzed the serum, the results were clear: wolves in Yellowstone had just experienced a massive outbreak of canine distemper virus (CDV; Almberg et al. 2009). CDV is a close relative of measles, and is one of the most significant diseases of domestic dogs and wild carnivores worldwide.

We now know wolves in Yellowstone have experienced three major outbreaks of CDV in 1999, 2005, and 2008 (figure 1); and during these outbreaks many other carnivores, including coyotes, foxes, cougars, black and grizzly bears, and likely badgers, were also infected (“canine” distemper is a misnomer—the virus actually infects a wide range of carnivore species; Almberg et al. 2010). Outbreaks of CDV are particularly lethal for young animals. Wolf pup survival in the northern region of the park during outbreak years was only 23%, as compared to 77% in non-outbreak years. Adults appeared less affected; but among those exposed to CDV for the first time, survival is roughly half of what it is normally. Once an individual survives a CDV infection,

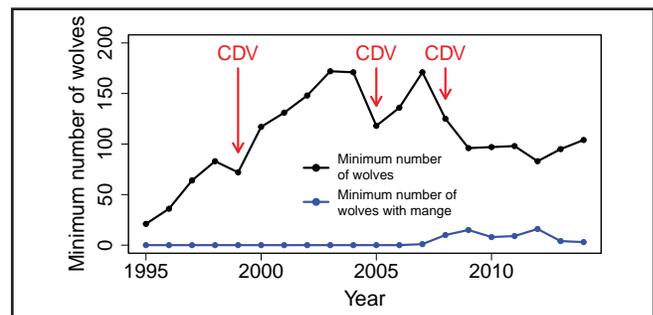


Figure 1. Minimum number of wolves (black) and those infected with sarcoptic mange (blue) in Yellowstone National Park, 1995-2014. Years of canine distemper virus (CDV) outbreaks are marked in red.

it is thought to be immune for life. As a result, it may take several years before an area has enough susceptible individuals to support another outbreak.

We don't know where CDV is circulating during non-outbreak years, but we are fairly certain it is absent from large carnivores in Yellowstone during that time. Previous research suggests it is unlikely that domestic dogs are playing any significant role in the ecology of the virus in the Greater Yellowstone Ecosystem and that it is circulating at a fairly large spatial scale among a variety of other carnivore species (e.g., raccoons, skunks, and coyotes) throughout the region (Almberg et al. 2010). It remains to be seen whether some of the more recent lower densities of wolves will help reduce the frequency and extent of any future outbreaks within the park.

In addition to CDV, there is another parasite that has had measurable impacts on wolves in Yellowstone: the microscopic mite, *Sarcoptes scabiei*. Introduced as part of predator-eradication efforts in the early 1900s, sarcoptic mange presumably persisted among other fur-bearing species until reappearing within Yellowstone packs in 2007. The mite burrows into its host's skin, where it causes the infected individual to scratch itself to the point of hair loss (figure 2). These hairless lesions can result in an estimated doubling of energy expenditure to keep warm during winter months (figure 3), decreased body condition, and an increased risk of mortality.

In the first few years after mange was detected among wolves in Yellowstone, the mite successfully spread to nearly all packs in the northern region of the park, and caused fairly prevalent and severe infections (Almberg et al. 2012). Monthly monitoring, in part supported through citizen science efforts (www.yellowstonewolf.org), has shown individuals can recover from infections;



Figure 2. A wolf pup infected with sarcoptic mange in Yellowstone. The hairless lesions are characteristic of this infection. NPS photo.

but they have no long-term immunity. Individual infections can last anywhere from months to years, and infection waxes and wanes within the population over time and seasons. Furthermore, we now know the impacts of the mite on an individual wolf depend on the context. An infected wolf living in a large, healthy pack survives just as well as an uninfected wolf; however, as pack size decreases or the proportion of infected pack mates increases, infected individuals are much more likely to die (Almberg et al. 2015). We suspect that larger packs with many healthy pack mates are able to offset the effects of the mite by providing food and helping to defend the territory of those that are sick.

Wolves, like all the large mammals in Yellowstone, are infected with a diverse array of pathogens. We know that nearly all wolves in Yellowstone become infected with canine parvovirus, canine adenovirus-1, and canine herpesvirus at some point in their lives. We have also detected canine coronavirus-1, canine adenovirus-2, and *Bordetella bronchiseptica*; but currently we have no estimate of how common these infections are or their impacts (although they can cause severe illness in domestic dogs). Some of the wolves carry *Neospora caninum* and *Echinococcus granulosus*, a protozoan parasite and a tapeworm, respectively, that use both wolves (and other canids, including domestic dogs and coyotes) and ungulates to carry out their life cycles.

E. granulosus has been the subject of much controversy and misinformation. There are two “biotypes” of *E. granulosus* circulating within North America. The northern biotype (strains G8/G10) that circulates among wolves, coyotes, domestic dogs, and wild ungulates is capable of causing an extremely rare and relatively benign, treatable infection in humans through the ingestion of infected canid fecal material (Foreyt et al.

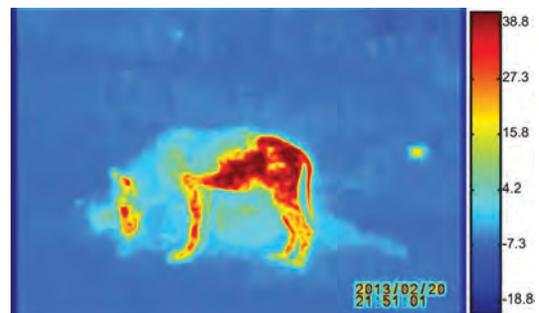


Figure 3. Thermal cameras have been used to estimate the heat loss associated with mange infections in wolves. This is a thermal image of a wolf in Yellowstone suffering from severe mange, with areas of hair loss illustrated in red. An uninfected wolf would look almost entirely blue. The color bar on the right shows the temperature in degrees Celsius. Photo credit: USGS.

2009). The domestic biotype, which circulates among dogs and domestic ungulates, particularly sheep, occurs throughout the sheep-herding regions of the world and is capable of causing more severe infections in humans (Thompson 2008). All reintroduced wolves were treated to remove parasites including *E. granulosus* prior to release; and although we lack definitive evidence, *E. granulosus* was likely present within the Greater Yellowstone Ecosystem prior to wolf reintroduction. The odds of people contracting *E. granulosus* are extremely low. In fact, to-date, not one wolf biologist ever tested has contracted *E. granulosus*, despite decades of potential exposures (Mech 2010).

All disease monitoring efforts to-date point to one obvious conclusion: parasites are everywhere! We have only looked for a small fraction of the parasites that are likely circulating, and yet we have ample evidence that wolves in Yellowstone routinely experience many different infections and have steadily acquired a characteristic community of pathogens since their reintroduction. While we have begun to understand the effects of sarcoptic mange, the impacts of other parasites remain unknown. For example, we now know we are more likely to detect viral parasites on dead wolves, regardless of the cause of death, than we are on live wolves sampled during capture. Of course, this information does not tell us whether parasites are just helping to finish off an individual that was already likely to die for other reasons (“compensatory mortality”) or whether these parasites are causing extra mortality that we currently fail to measure at the population level. It does point to the distinct possibility that we have consistently underestimated the role of parasites within the ecosystem.

We now recognize infectious diseases, along with prey abundance and social competition, as one of the key factors affecting wolf population dynamics. In addition to continuing to study the impacts of parasites on wolf numbers, we have begun to think about how parasitism of a top predator may have cascading effects through the food chain. For example, in the years of CDV outbreaks, we see higher rates of elk calf recruitment, presumably mediated through lower rates of predation. We have also begun to think about how wolves may be shaping the parasite populations of their prey. Theoretical and empirical work have demonstrated how predators may target infected prey, if the infection makes prey easier to catch. This may have the larger effect of helping to keep prey populations healthy—something to keep in mind

as other diseases, such as brucellosis and chronic wasting disease, continue to expand their range within the region.

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Emily Almberg recently completed her PhD at Penn State University studying the dynamics of sarcoptic mange in the wolves of Yellowstone. Currently, Emily is a disease ecologist with Montana Fish, Wildlife and Parks and is working on a range of wildlife health projects statewide.

Wolf Turf: A Glimpse at 20 Years of Wolf Spatial Ecology in Yellowstone

Erin E. Stahler, Douglas W. Smith, & Daniel R. Stahler

Territoriality is one of several well-known characteristics of wolf natural history that has presumably evolved in response to selection for behaviors advantageous to individual reproduction and survival. Worldwide, territory characteristics vary depending on ecological conditions (e.g., prey and competitor density), geographical features, seasonal changes, and human presence (Mech and Boitani 2003). However, what nearly all wolf populations share is an aggregation of territories where packs actively defend and compete for areas that provide access to critical resources, such as vulnerable prey and offspring rearing space. Numerous studies have converged on the idea that wolf spatial ecology is shaped primarily by prey, social interactions, and geography. And the last two decades of work in Yellowstone contributes to this understanding.

Looking at any single year of wolf pack territories in Yellowstone gives general pack location information and provides insight about the social and ecological conditions for that year (see map, page 9). But by comparing 20 years of territory maps, patterns emerge which tell a story about what parts of Yellowstone National Park are important to wolves (figure 1). Contrary to what is portrayed in a map, territory boundaries are not static or well defined. Instead, they are constantly changing, expanding and contracting, as packs compete with their neighbors. This can make defining and mapping wolf territories somewhat challenging. Various statistical methods exist for mapping territories, and choosing one method over another depends on the questions being asked or how a territory is defined. With all of these caveats in consideration, the annual mapping of territories still gives insight into some of the basic underlying factors driving wolf spatial dynamics.

Colonization after Reintroduction

In the first few years following reintroduction, wolves explored the landscape and established territories quickly. Some packs, like the Leopold pack, began

concentrating their movements in a specific area right away (i.e., Blacktail Plateau). While other packs, like the Soda Butte pack, roamed more widely and shifted considerably from year-to-year before finally choosing an area to settle down. During this initial colonization period, packs competed over specific areas of the park even though plenty of unoccupied habitat was available. For example, the Druid Peak pack in 1996 displaced the Crystal Creek pack to take over Lamar Valley. However, overall competition was relatively low due to lower wolf densities. Less competition early on translated to more flexibility in movement because what often limits a pack, other than available prey, is constraint caused by neighbors. From 1998 and on, a mosaic pattern of wolf territories began to emerge, which is typical for established wolf populations. Territories in the northern portion of the park (known as the northern range) started compressing in size as wolf density and number of new packs increased. With these changes came increased strife and competition.

Northern Range vs. Interior

When examining a map depicting all recorded locations of radio collared wolves over the last 20 years, a striking pattern emerges (figure 2). The story this map tells is one different from a map of the park's geothermal features or prime visitor attractions. It's a story of what geographical and ecological features of Yellowstone's 2.2 million acres are most attractive to wolves. One obvious pattern is the high concentration of wolf use on the northern range, with greater dispersion in the interior. These two major areas of the park are characterized by differences in elevation, vegetative communities, and weather patterns—all of which influence seasonal ungulate densities and, therefore, predator use. Packs living in the interior (e.g., Mollie's, Cougar, Yellowstone Delta, Bechler) cannot rely on elk, their favored prey, year-round. At the onset of winter, most elk migrate to the northern range or outside the park, leaving little behind but the more formidable and difficult to kill bi-

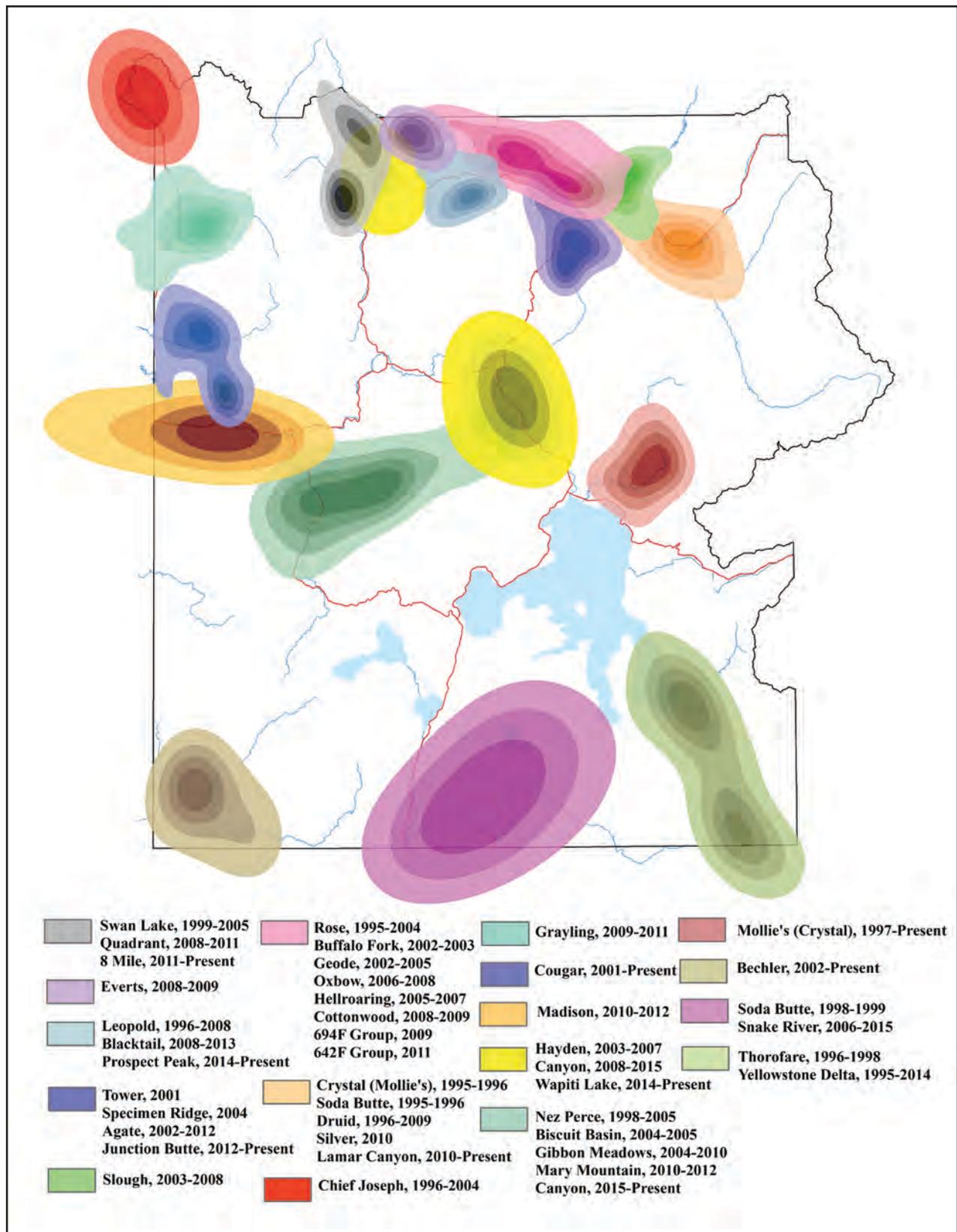


Figure 1. Spatial distribution of wolf pack territory use in Yellowstone National Park over 20 years (1995-2015). Aerial locations of collared wolves were used to generate Kernel density estimations for geographic areas used by different packs over time. Gradients of color from light to dark depict increasing concentrations of use, identifying areas most important to Yellowstone wolves.

son. Because the northern range is important wintering range for most ungulates, especially elk, wolf density is higher. One result of higher density is greater turf wars which can lower individual wolf survival (Cubaynes et al. 2014). A more beneficial outcome is that there may be greater opportunities to find potential mates, which can lead to new pack formation.

From a spatial perspective, we see wolf territories on the northern range overlapping more. Packs may avoid using these areas of overlap simultaneously to reduce conflict—howling may help mitigate this. However, despite wolves’ attempts to avoid each other, there seems to be a link between overlap, conflict, and pack turnover. In particular, the Hellroaring and Tower Junction areas consistently have the most territorial overlap between packs throughout all years and also have the highest rate of pack turnover, often due to loss of individuals resulting from conflict (figure 3). In addition, higher pack turnover may also be associated with proximity to the park boundary in which human influences (i.e., wolf harvests or illegal poaching) may play a role. Losing individuals to either natural or human-caused mortality may be a tipping point that disrupts the social dynamics of a pack and their ability to maintain a territory (Cassidy et al. 2015). So, why do packs try and establish themselves in this area time and time again? Likely because it is prime winter habitat for elk and has landscape features conducive for successful hunting. Several river drainages converge in this area, and the valley bottoms may provide prime areas for wolf-elk encounters (Hebblewhite et al. 2005, Kauffman et al. 2007).

Contrary to territories on the northern range, wolf packs in the interior have more interstitial space between territories and experience less inter-pack competition. If we think of packs as distinct family lineages, those in the interior tend to experience longer persistence, or lower pack turnover rates, due in part to fewer territorial contests. For instance, the Crystal Creek pack, which was renamed Mollie’s in 2000, is the only pack in Yellowstone to persist for the last 20 years. In addition, Almborg et al. (2012) found packs in the interior have a lower risk of disease transmission likely due to lower territory overlap and wolf density. Disease was a major contributor toward the demise of three packs on the northern range, but we have not seen this in the interior. However, living in the interior is not easy; a limiting factor for packs may be finding vulnerable prey during the winter. It has not been uncommon for interior packs (e.g., Mollie’s, Hayden, Canyon, Cougar, Nez Perce, Mary Moun-

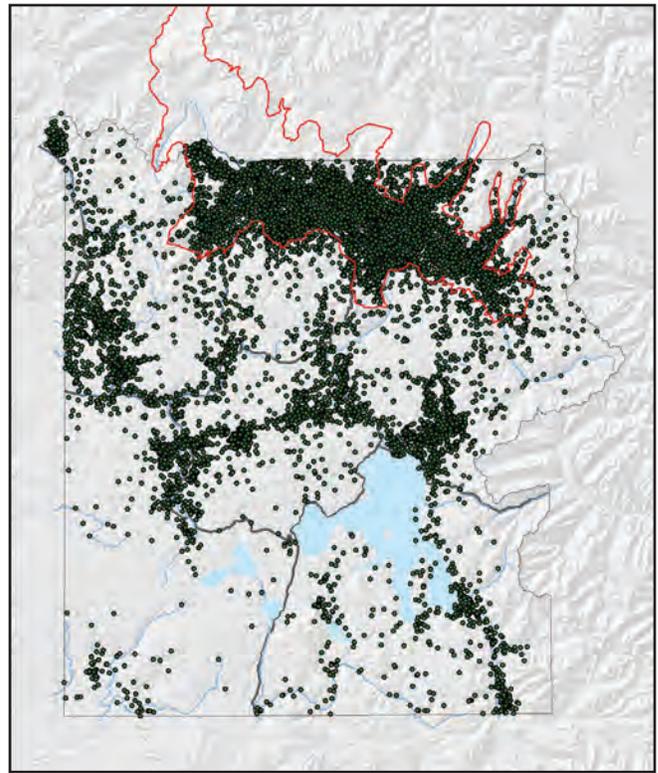


Figure 2. All aerial locations of collared wolves within Yellowstone National Park from 1995-2015. The distribution of points shows the greatest concentration of use in Yellowstone’s portion of the northern range (outlined in red). This region of the park holds the best year-round prey availability. Note: locations of collared wolves outside the park are excluded.

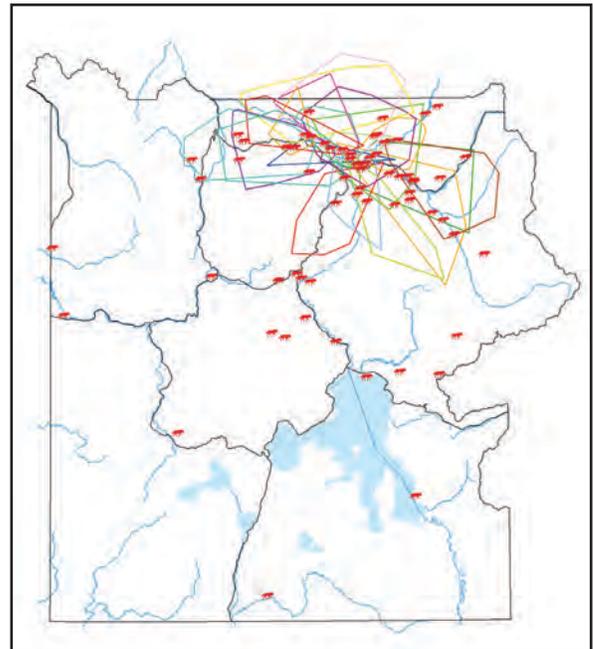


Figure 3. Location of radio-collared wolves killed by other wolves in YNP from 1995-2015. Polygons represent wolf territories, and areas of overlap generally correlate with wolf kills.

tain) to travel into the northern range for short periods during winter—a time when vulnerable prey is less likely available in their own territory. For example, during the winter of 2011-2012, the 19-member Mollie's pack spent more time on the northern range making kills than in their home range of Pelican Valley. What caused this behavior is likely a combination of factors. First, there was a large number of wolves with little access to vulnerable prey in their core territory of Pelican Valley. Second, the absence of a dominant male—killed the previous fall—may have caused pack females to seek potential mates during the breeding season on the northern range where there was a greater probability of encountering a mate due to density. Seasonal territory shifts to find prey is not uncommon and is characteristic in other wolf populations worldwide (Mech and Boitani 2003). Since most of these movements happen during the winter, this suggests both hunting opportunities and hormones influence wolf extra-territorial forays in Yellowstone.

Geography & Individual Knowledge

In addition to how seasonal prey abundance and wolf density shape the spatial ecology of Yellowstone wolves, geography plays an important role. As we look at wolf territories throughout the years, packs utilize a core area, often in the middle of their territory. Interestingly,

these regions remain relatively constant through time, both for the same pack from year-to-year and among packs from different time periods (figure 4a and 4b). These core areas are usually surrounded by distinct topographical features, such as significant mountainous terrain and major river drainages, and serve as natural boundaries (much like a moat surrounding a castle). Such boundaries appear to influence territorial movement patterns and inter-pack encounters, and likely help mitigate the costs of territorial defense. Whether for offspring rearing space or hunting opportunities, some regions are just prime areas for wolves. Kauffman et al. (2007) suggested wolf territories are influenced by physical landscape features that favor hunting success.

Other areas provide great homesites; we see the same den and rendezvous sites used year after year, even by unrelated individuals from different packs. These landscape features clearly influence wolf spatial patterns in consistent ways; however, we also see how the role of kinship and individual knowledge transfers are important. For example, we see cases where females inherit their mother's breeding position and continue the spatial legacy of their relatives (e.g., 478F of Cougar Creek). In other cases, dispersed individuals return to their natal lands with their own newly formed pack (e.g., 302M of Blacktail). Together, these patterns reflect the collec-

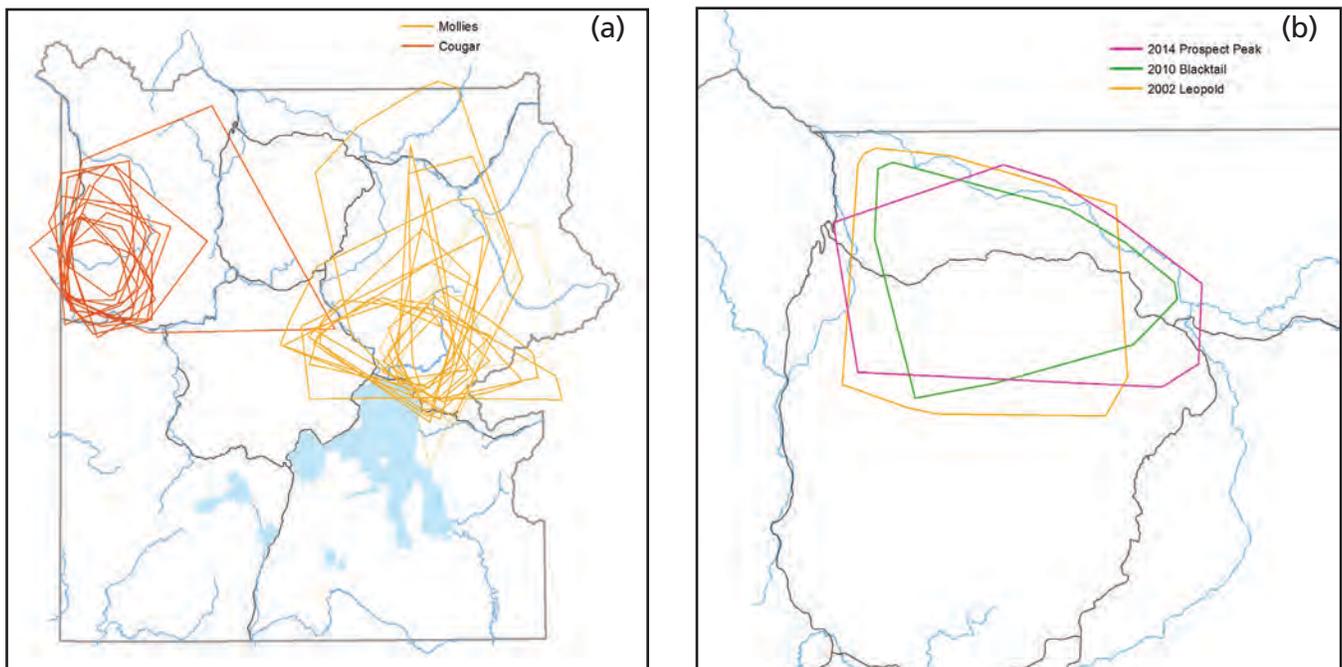


Figure 4a. Annual territory polygons overlaid for two long-term packs (Mollie's and Cougar Creek) show consistent use of a core area. This pattern suggests certain geographic areas within the park contain reliable resources that are valuable for wolves. 4b. An example of a core area occupied by three different packs over a twelve year period.

tive influences of individuals and their surrounding environments on wolf territory use.

There is more to be learned about the spatial ecology of Yellowstone's wolves. Future work aims to evaluate how kinship ties between packs may influence spatial and temporal organization on the landscape, and how territorial quality can be measured and correlated with wolf survival and reproductive success. For now, each location recorded from a collared wolf contributes a valuable piece towards understanding the territorial mosaic for Yellowstone wolves. When combined with the other long-term datasets, a richer picture and better understanding of this creature is revealed.

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Temporal Variation in Wolf Predation Dynamics in Yellowstone: Lessons Learned from Two Decades of Research

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Beginning with the pioneering work of Adolph Murie (1944) in Mount McKinley (now Denali National Park) in 1939-1941, ecologists have long been interested in evaluating the factors influencing wolf predation dynamics. Murie, who had just recently studied coyote ecology in Yellowstone National Park (YNP), was hired to assess wolves' relationship with Dall sheep. Through detecting and evaluating >800 Dall sheep skulls, Murie suggested wolves tended to kill vulnerable prey, an observation that has since been found to be a driving force in wolf predation dynamics (Mech and Peterson 2003). Because wolves are coursing predators who typically hunt large prey, selecting vulnerable individuals minimizes their risk of being injured while hunting. Murie's study provided the first glimpse into wolf-prey relationships, and many ecologists have spent significant time since trying to advance our understanding of wolf predation dynamics.

Among studies of predation, wolf-prey relationships are among the most well studied and best understood. In fact, the study of wolves and moose on Isle Royale National Park, which began in 1958 and continues today, is the longest running predator-prey study in the world. Since 1971, researchers have evaluated predation dynamics for wolves preying on moose, which are the sole ungulate (hoofed mammal) on Isle Royale. Central to the evaluation of how wolf predation influences moose population dynamics, has been collecting information about kill rate (kills per wolf per day) and predation rate (annual percent of moose population killed by wolves). This work has shown that the influence of wolf predation on moose population dynamics varies considerably over time (Peterson et al. 2014), highlighting that the influence of predation is not static but rather temporally dynamic.

Long-term studies like the one on Isle Royale are relatively unique. Wolf restoration in Yellowstone, however, provided a significant opportunity to conduct a similar long-term study in a much different ecological system. That is, while Isle Royale is characterized by its simplicity, YNP is best described by its complexity, as it is home to high densities of multiple large predators (e.g., wolves, cougars, grizzly bears) and eight different species of ungulates, including elk, bison, and mule deer. Moreover, Yellowstone is also affected by differing management strategies inside and outside of the park (e.g., human hunting). Currently, our research investigating wolf predation dynamics in YNP has been ongoing for two decades. Here, we will only discuss our work for a subset of packs that are intensively monitored and primarily live on the northern range of the park.

For many studies investigating wolf predation, kill rate estimates from winter provide the foundation. A common observation among these studies is that wolves kill more frequently as winter progresses, which has been primarily attributed to prey being easier to capture as snow depth increases (e.g., Huggard 1993, Post et al. 1999). Our work in YNP supports this previous research, as we observe kill rates are greater in late winter (March) than in early winter (mid-November to mid-December; Smith et al. 2004, Metz et al. 2012). Additionally, late winter kill rates are highest in years when winter is more severe (Mech et al. 2001; Yellowstone Wolf Project, unpublished data). However, in multi-prey systems, understanding how wolf predation influences prey population dynamics also requires knowing what prey species wolves are selecting. Historically, elk are the dominant species killed by northern range wolves (average 92% of wolf kills during a particular winter). Of note is that while the average was 95% in the first ten years, the average has declined to 88% in the last ten years.

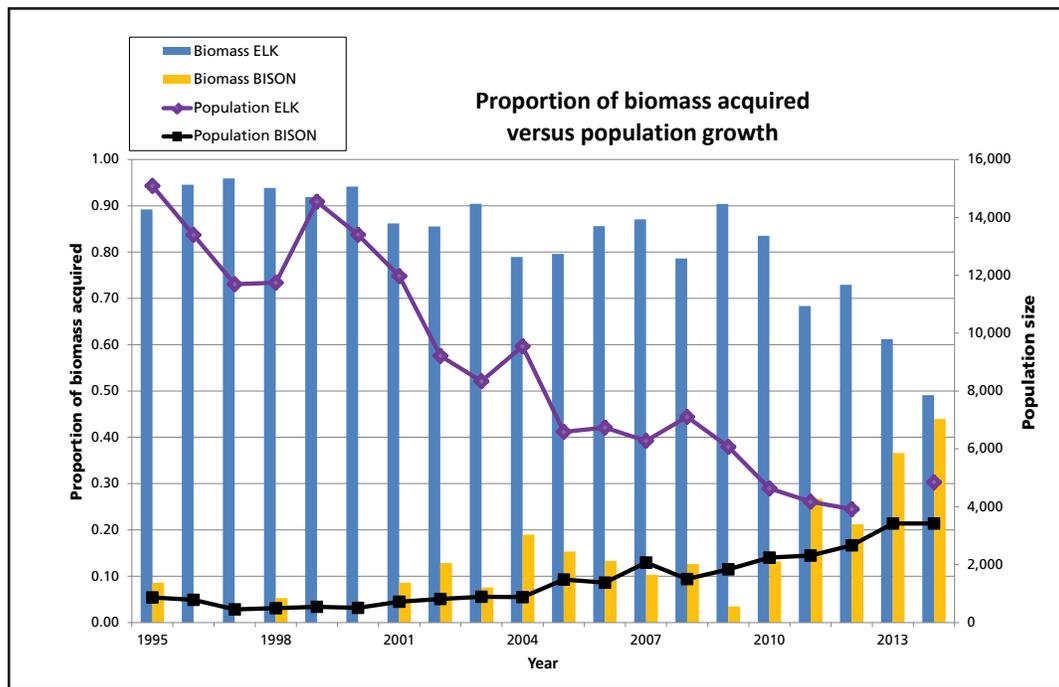


Figure 1. Proportion of biomass acquired by northern range wolves during winter from elk and bison in comparison to ungulate population abundance (1995-2014).

Ending here, though, would provide an incomplete picture of how dramatically the northern range wolf-prey system has changed over the last two decades. Twenty years ago in the winter of 1995-1996, there were at least 15,000 elk and ~900 bison on the northern range; today, there are at least 5,000 elk and ~3,500 bison (figure 1). And although wolves rarely kill bison during winter (1.6% of wolf kills), they also welcome a free meal as bison make up 5.3% of all acquired carcasses (i.e., killed or scavenged). Moreover, bison comprised an average of 6% of the biomass acquired by wolves during winter over the first decade (1995-2004), but 20% over the last decade (2005-2014; figure 1). This shift in the importance of bison in the diet of northern range wolves emphasizes the finding on Isle Royale (among others) that temporal variation in predator-prey dynamics is a critical, and likely universal, characteristic of large carnivore-prey systems.

This increased use of bison is also likely driven by there being fewer vulnerable elk within the current, less dense elk population. And although elk could be the perfect-sized prey for wolves, wolves still incur risks while hunting them and are therefore selective about the type of elk they take. Specifically, during early winter when adult elk are less vulnerable, wolves typically select for calves. But as snow depth increases and nutritional conditions decline, wolves select for adult males during late winter (Smith et al. 2004, Metz et al. 2012). Additionally, when wolves prey on adult elk, they select for older adults (Wright et

al. 2006). This selective nature of wolf predation should be even more prominent during other seasons of the year. Unfortunately, our understanding of large carnivore-prey dynamics had been primarily limited to winter because prey remains were difficult to consistently detect during snow-free periods.

About a decade ago, a new window of opportunity was opening that would allow for a detailed look into how large carnivore predation dynamics differed throughout the year. Led by the pioneering work of Anderson and Lindzey (2003) studying cougar predation in southeast Wyoming, large carnivore-killed prey could be routinely located through searching carnivore GPS location “clusters” (i.e., spatially and temporally-related GPS-collared carnivore locations; figure 2). With this new technique, precisely evaluating seasonal predation dynamics became possible. Our work in YNP has been at the forefront of this research, and we have examined wolf predation dynamics from May-July (encompassing elk calving season) through searching GPS clusters since 2004. Combining the data collected in spring (May) and summer (June and July) with data from winter, we have been able to evaluate precisely how wolf predation dynamics differ among the seasons of the year.

Ecologists had long expected seasonal differences in predation dynamics because of seasonal differences in prey availability and vulnerability. For the northern range wolf-prey system, ungulate migration affects prey

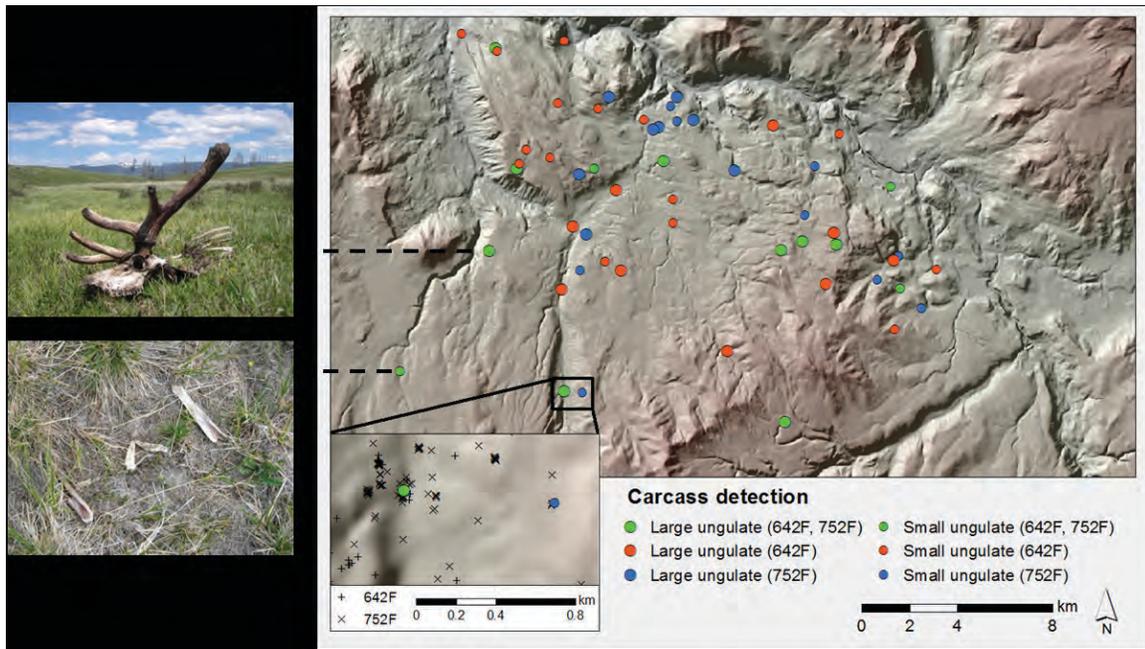


Figure 2. Example of carcasses found via GPS clusters. Here, 54 ungulate carcasses found via the GPS clusters of wolves 642F and 752F of the Blacktail pack in the spring-summer of 2010 are displayed. The inset map in the bottom left corner displays the GPS locations of each wolf. Notice both wolves have locations at a large ungulate carcass, but only 752F has locations at the small ungulate carcass. Not all carcasses a pack acquires are visited by all pack members. We use multiple GPS-collared wolves in a pack to estimate the pack's "missing" carcasses (Metz et al. 2011).

availability, with most ungulates being more abundant within YNP during spring-fall. Through our work, we found the nutritional condition of ungulates killed by wolves is generally poorest during late winter and spring (figure 3). These seasonal differences in animal movement patterns and nutritional condition, along with the appearance of highly vulnerable neonate (newly born) ungulates during spring, drive seasonal variation in predation dynamics in YNP.

In comparison to winter, deer and bison are more prominent among wolf-killed prey in spring-summer. However, deer still make up a relatively small percent (9%) of all wolf kills found during this period. Bison (5%) also represent a small portion of wolf kills during spring-summer, although wolf-killed bison neonates are being increasingly detected in recent years (Yellowstone Wolf Project, unpublished data). Similar to winter, scavenging adult bison can also be an important food item for wolves in spring-summer. In particular, wolves sometimes scavenge adult female bison in the spring that likely die from birthing complications. Despite the use of these other species, elk (85%) is the dominant species killed by wolves during spring-summer. Among elk kills, wolves especially select for highly vulnerable neonate calves (64%) during summer. Wolves are one of many predators of elk calves in the predator-rich system

of YNP; and although predation has been the leading cause of elk calf mortality since wolf restoration, bears are the dominant predator (~60% of deaths compared to ~15% for wolves; Barber-Meyer et al. 2008). Ultimately, the combined effects of predators (e.g., bears, wolves, cougars, coyotes) and climatic conditions play a critical role in elk calf survival rates (Griffin et al. 2011) and elk population growth rates (Raithel et al. 2007).

The most pronounced seasonal change in wolf predation dynamics is that kill rate differs throughout the year. Specifically, the number of prey that wolves kill per day peaks during summer, although kill rates of non-neonate elk (i.e., ≥ 6 months old) reach an annual minimum (figure 4a). Consequently, most wolf-killed prey during summer are neonates (62%) that provide little biomass. Most kills are neonates because adults are in better nutritional condition (figure 3) and are increasingly dangerous to hunt. Evidence for this increased risk is provided through the observation that wolves are most likely to be killed by an injury sustained from an ungulate during summer (figure 5). Our impression of seasonal variation in kill rate is also markedly different if we instead think about how much biomass wolves acquire. When doing so, the amount of food acquired by wolves is highest during late winter and spring when ungulate nutritional condition is poor (figure 3), and reaches its annual minimum during

summer (figure 4b) when ungulate nutritional condition improves.

This seasonal pattern of biomass acquisition is driven by wolves being coursing predators whose own mortality risk varies throughout the year (figure 5). In comparison, cougars (ambush predators) display little seasonal variation in rates of biomass acquisition (Knopff et al. 2010). The differing rates that each of these carnivores acquires food throughout the year provides insight into their life history. That is, the seasonal curve for wolves (figure 4b) suggests wolves evolved to absorb the costs

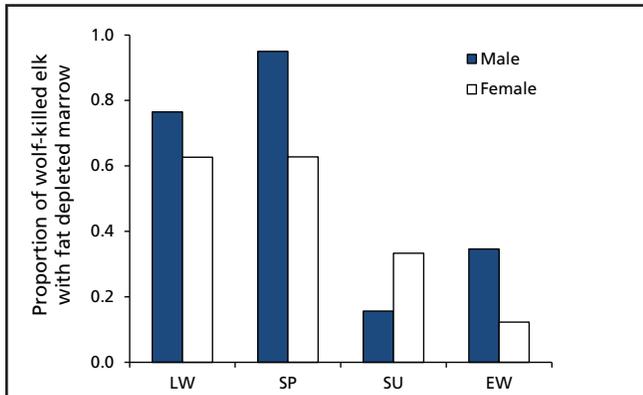


Figure 3. Proportion of wolf-killed adult elk from 1997-2014 with fat-depleted bone marrow ($\leq 70\%$). (Late Winter [LW], Spring [SP], Summer [SU], Early Winter [EW]).

of reproduction (i.e., gestation and lactation from approximately mid-February to mid-June in YNP) during periods of the year when they acquire food in great excess of their energetic demands. Conversely, cougars can breed at any time of the year, although they tend to have young while neonate ungulates are being born (e.g., Elbroch et al. 2015). Ultimately, our work identifies summer as the limiting period of the year for wolves, and suggests that measuring kill rate during summer is required to understand how food acquisition affects wolf population dynamics.

The identification of summer as the limiting period for wolves is novel; yet the primary reason we began investigating predation dynamics 20 years ago was the same as Murie 75 years ago—to characterize the influence of wolves on prey population dynamics. This is a complicated topic with many factors that influence the strength of wolf predation on prey populations. Yet, for the simple system on Isle Royale, the percent of the moose population killed by wolves (i.e., predation rate) is a strong predictor of moose population growth rate, with the moose population being likely to decline when the predation rate exceeds 10% (Peterson et al. 2014). For Yellowstone, wolves' predation rate (% of elk population killed by wolves) is a poor predictor of elk population

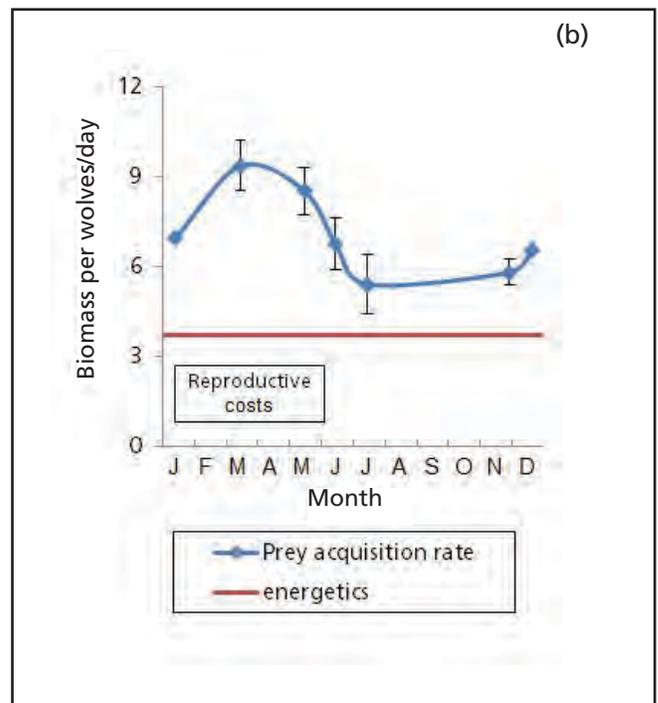
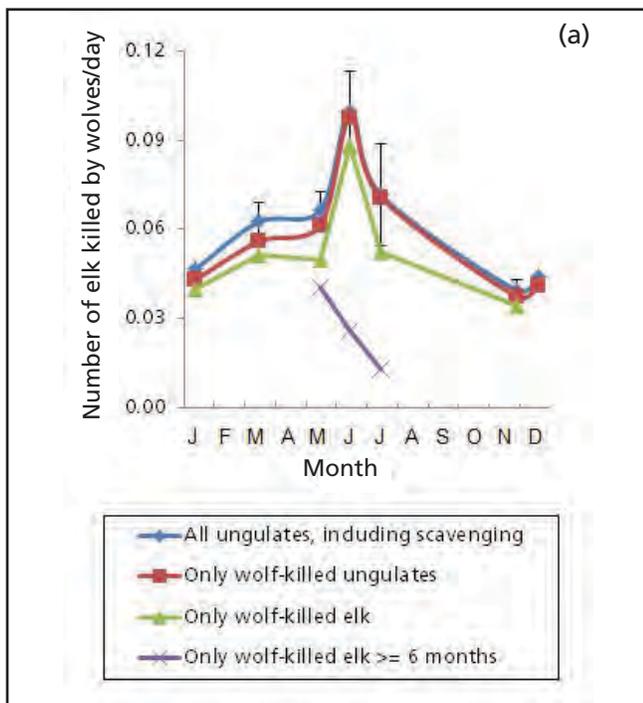


Figure 4. Seasonal variation in feeding ecology rates of northern range wolves (1995-2015). The lines connecting adjacent data points highlight the average trend that exists between sampling periods (a). In (b), the red line represents the estimated minimum daily energetic requirement for northern range wolves (~3.7 kg per wolf per day) and “reproductive costs” identifies the period where breeding female wolves experience the energetic costs of gestation and lactation.

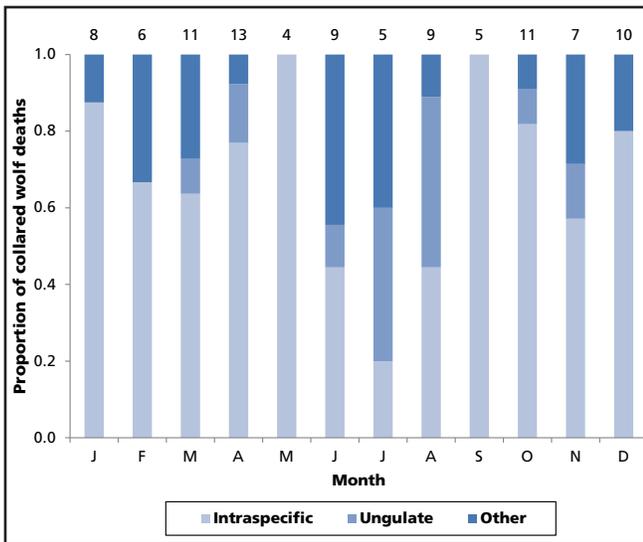


Figure 5. Monthly variation in cause of death for 98 radio-collared wolves in Yellowstone National Park (1995-2015). All wolves with human-caused (i.e., management-related, vehicle strike) and unknown causes of death were excluded. The number above each bar represents the number of radio-collared wolf mortalities found during that month.

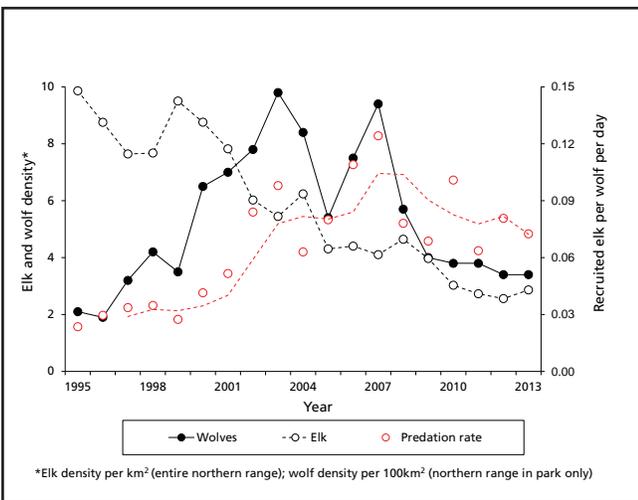


Figure 6. Temporal variation in northern range wolf-elk dynamics (1995-2014). Dashed lines for predation rate and kill rate represent 3-year moving averages.

growth rate (Vucetich et al. 2011), likely because wolves are one of many factors (e.g., other predators, human harvest, climatic conditions) influencing elk survival. Nonetheless, wolf predation rate has increased in recent years (figure 6). This increase in the proportion of the elk population killed by wolves is due to the smaller elk population, rather than an increase in kill rate (i.e., how frequently wolves kill elk). If Isle Royale provides guidance to the consequences of temporal variation in predation rate, then the influence of wolf predation on the northern range elk population has likely increased in the most recent decade.

Our ability to estimate predation rate in YNP has been strengthened over the last decade because we have been able to precisely estimate seasonal wolf predation patterns. In doing so, we have gained a detailed understanding of many aspects of wolf predation. What we have learned so far indicates YNP's predator-prey system is temporally dynamic and much more complicated than just a wolf-elk system. Whether the first decade or the second is most representative of future wolf-prey relationships in YNP is unknown. Our findings, so far, provide significant insight into the annual cycle of wolf predation dynamics, and will allow for us to better understand why future conditions are similar or different to those witnessed during the last two decades.

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Shirl Ireland, who paints at the Heritage and Research Center once a week, uses the biological collections, including these wolf skulls, for both subject matter and reference material. Illustration © S. Ireland

Why Wolves Howl

John & Mary Theberge

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It was a deep-freeze January morning, with mist peeling back in strands off the open riffles of the Lamar River like a series of gossamer curtains hiding a stage, eventually revealing the willow flats of the far shore. Out there, initially invisible, was the big Druid Peak pack. Their howls filtered to us through the mist.

When they became visible, most of the pack were bedded while others were drifting around. But the black beta male, by that time famous, or infamous, known simply as “302” seemed anxious to move on. He trotted briskly downriver, disappearing briefly behind a mist curtain, and then reappearing on a knoll.

After looking back at his pack, he threw up his head and howled. Short, deep howls, breaking both up and down in pitch. The pack ignored him. He trotted on and then howled again. This time a few wolves got up and started his way. Then others. Soon the whole pack was down in the willows and into a draw that led them out of sight.

Why did he howl? The off-the-cuff explanation, overheard from a woman standing nearby, was that he was telling his fellow pack mates to get off their butts and follow.

She may have been right. This situation was one where a clear expression of intent seems to have been involved, at least subjectively. We have seen it infrequently both before and since. Sometimes the pack moves, but not always. Most often a move is initiated in silence. Over the span of a few minutes, one wolf after another gets up and heads out the same way. Or, one wolf howls, the whole pack joins in, and then they move off more or less together. Regardless, as a prelude to a move, howling is used inconsistently.

That inconsistency is shared in most of the 22 social or environmental situations we identified in Yellowstone. And that inconsistency is based on considerable underlying motivational complexity, not only in wolf howls, but in all animal vocal communication.

Triggers

Competing triggers that may cause wolves to howl include some basic, but surprisingly slippery concepts. Intent itself, if based on memory and learning, can trigger vocalization, as anyone knows whose dog barks to be let in. Was 302’s intent based on remembering a similar, successful experience either learned directly or

observed? Or, did he think it out, on-the-spot reasoning, which is much more problematical?

Intent can be classified by levels of complexity (Dennett 1983) and involve recursion or sequential reasoning such as we humans use all the time (Chomsky 1988, Corballis 2011). These higher levels of intent require a well-developed prefrontal cortex that wolves simply do not have. A preponderance of biologists would assert that non-human animals cannot engage in complex reasoning, especially reasoning that involves conceptualizing a number of steps (Hauser et al. 2002, Chomsky 1953).

Instead, the primary basis of vertebrate vocal communication is believed to be emotion (Suddendorf 2013), a conclusion reached by Charles Darwin in *The Expression of Emotion in Man and Animals* (which is still widely quoted). Even in chimps, “the production of sound in the absence of the appropriate emotional state seems to be almost an impossible task” (Goodall 1986). We share many midbrain structures for emotions with other vertebrate species. Included in the term “emotion” are the concepts of “internal drives” (Grandin 2005) or “internal motivational states” (Lord et al. 2009). Were 302’s howls that day really motivated wholly or in part by hunger, exploratory behaviour, or care soliciting? Possibly those innate feelings caused adaptive neurohormonal adjustments in him; excitation of the sympathetic nervous system resulted in more cortisol or other biochemicals in the blood, and the result was that he howled. The biochemistry of emotions is a complex and active research area. If the outcome of such howls often enough was that the pack joined in on what turned out to be successful hunts, then natural selection would favour howling in that particular context without having any reasoned-out intent. After all, even bacteria communicate and coordinate with no brain at all: “Some bacteria move in voracious swarms called wolf packs, as do lions, wild dogs, and killer whales...” (Moffett 2011).

Language

Did 302’s howls actually express anything? That is, did his howls contain any specific information? From research we conducted years ago largely with captive wolves, we learned wolves have an amazing ability to distinguish differences in harmonic overtones in each other’s howls, which makes individual recognition possible from a distance (Theberge and Falls 1967). Similarly, Palacios et. al (2007) identified structural differ-

ences in the fundamental frequencies of the howls of different wolves. We also learned that a higher level of excitement is reflected in higher pitched vocalizations (Theberge and Falls 1967), a trait in common with most mammals (Morton 1977). So 302’s howls conveyed that it was he who was howling and he was to some degree excited or disturbed. Perhaps that was enough. His pack mates could recognize the situation and read into it that he wanted them to follow. But was other information coded in his howls?

The vast majority of biologists define language as requiring sophisticated syntax, that is, grammar and sentence structure to convey meaning; and they attribute that ability solely to humans (Corballis 2011, Pinter 1994, Chomsky 1953, Kruglinski 2009). Neurobiology backs this up. Only primates have a Broca’s area, situated in the left prefrontal cortex, and a Wernicke’s area, in the left parietal cortex; both are fundamental to expressing and understanding language.

What about signalling or simple sounds that convey specific information referring to specific objects (called “referential communication” by Seyfarth and Cheney [2003] or “protolanguage” by Bickerton [1995])? Such signalling is well-known for species of primates (Cheney and Seyfarth 1990) and rodents (Slobodchikoff 2012), where different calls refer to different predators and elicit different avoidance responses. These vocalizations represent situations under intense selection pressure. We do not know yet if wolves exhibit referential howling. To find out, we have made hundreds of digital recordings for computer-based sonographic analysis.

Whether language or protolanguage, or emotion or reason-driven, it is clear that wolf howling touches on deep concepts. For centuries these concepts have occupied the thoughts and writings of psychologists, physiologists, neurobiologists, ethologists, and ecologists—included are intelligence, reason, cooperation, language, cognition, and consciousness. We ultimately hope our research may help shed light on these difficult topics. But the place to start is with descriptions of when wolves howl. The why, the really tough part, comes later.

Yellowstone

Yellowstone is an ideal place to study wolf howling with known and radio-collared animals, and open habitats where animal behavior may be observed. So in 2001 we turned to Yellowstone. Our starting place, besides our own studies, were statements reported about howling

playing a role in territoriality during the breeding season, but not nailed down with quantification (Peters and Mech 1975, Harrington and Mech 1979, Harrington and Asa 2003).

Disconcertingly, we soon learned it takes a considerable effort to amass large enough sample sizes to draw statistically valid conclusions. The main reason is the inconsistency mentioned earlier. Some field trips yielded few howls where context could be identified. Howling is probably secondary to scent (Harrington and Asa 2003), despite the richness of both motivational triggers for wolf howling and the richness of social and environmental situations that wolves get into.

NPS PHOTO - J. PEACO



The inconsistency springs from another source and has yielded some interesting conclusions. The other source is a dramatic seasonal variability. Howling is four times more common in February than in May, the extremes of a smooth curve of change, except for a sudden drop at the end of February. We abstracted this pattern from more than 11,000 howls noted over a 10-year period by Yellowstone Wolf Project's Rick McIntyre. This pattern mirrors the annual pattern of serum levels of testosterone and estradiol in wolf blood. This finding indicates the reproductive state underlies wolf howling, not only during the breeding season but all year. The same pattern is found in other social carnivores that are monestrous (have only one confined and regular breeding season per year), such as coyotes and dingoes. No such seasonal pattern of vocalizations exists in polyestrous species (e.g., African lion and spotted hyena.)

Even more noteworthy are the 1,509 howling responses by pack mates and foreign wolves. They, too, were seasonal. Foreigners answered increasingly more often than pack mates from October (the time when wolf packs travel more extensively in their territories) to the end of February (the end of the breeding season). We interpret this period is one dominated by between-pack territoriality and mate-finding concerns. Then, abruptly, the situation changes—almost all answers throughout the denning and summer seasons are by pack mates. Defended territoriality, so prominent in fall and winter, almost ceases to exist. Replacing it is a near-complete shift to within-pack concerns, likely accompanied by a different set of dominant emotions. Wolves are into pup rearing and except for hunting forays, show little concern over neighboring packs.

Paralleling the seasonal frequency of between-pack howling are aggressive encounters between packs quantified by Yellowstone Wolf Project's Kira Cassidy (2015), who drew almost exactly the same curve as ours. The drop in aggressive encounters is sudden at the beginning of the denning season, even though actual inter-pack killing is highest in April, likely because the presence of pups restricts the defensive behavior of the pack being attacked (Smith et al. 2015). Summer is a time of relative between-pack harmony on the range, and fall and winter is a time of territorial and mate-finding tensions.

Other conclusions about the howls of Yellowstone wolves are on the horizon. One features two qualitatively different types of group or pack howls, which may lead to quite solid evidence of emotion versus reason in their utterance. We are anxious to flesh that one out.

The End of 302

It was late September 2009, and 302 was several years older. By then he had left the Druid Peak pack and emerged as the alpha male of the large Blacktail Plateau pack that lived to the west. Snow had fallen on and off for several days. 302 and his pack were on the Swan Lake flats, and they howled frequently when split up between opposite sides of the busy park road. It was classical disturbance howling, one of the key and most consistent situations triggering howling, whether caused by humans, bears, vehicles, or by foreign wolves. To our amazement, disturbance howling appeared to trump discretion. He and his pack were well out of their normal defended territory, trespassing on lands claimed by the Quadrant pack. They had interfaced with that pack before. Wolf packs know their boundaries well. After several days the resident pack came, attacked, and killed 302.

We have seen howling lead to several other wolf deaths. It is quite clearly a two-edged sword. It can be both adaptive and maladaptive, further complicating interpretation.

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The Plight of Aspen: Emerging as a Beneficiary of Wolf Restoration on Yellowstone's Northern Range

John Klaptosky

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed tree in North America and is native to Yellowstone National Park's (YNP) northern range, a 250,000 acre area including the valleys of Yellowstone, Lamar, and Gardner rivers. Aspen make up a small component of vegetation on Yellowstone's landscape, and most stands on the northern range are less than five acres in size. However, aspen remain a persistent species because of its root-suckering ability, allowing aspen stands to proliferate as successive generations of shoots arise from a continually expanding root system. As a result of this characteristic, aspen usually occur in clones of genetically-identical individuals (Barnes 1966). Aspen seedling establishment is not common because of short-lived seed viability and demanding seedbed requirements. Major disturbance events, such as the 1988 Yellowstone fires, may play an important role in the preparation for aspen seedling establishment. Following the 1988 fires, there was widespread germination of aspen seedlings in burned areas (Kay 1993, Romme et al. 1997); however, most of

those seedlings have since been browsed by ungulates (Romme et al. 2005, Forester et al. 2007), yet some have persisted in scattered high-elevation sites (Hansen et al. 2016). Although pure, self-sustaining stands exist, aspen is generally regarded as a species that requires major disturbance, such as fire or clearcutting, to reduce competition from other tree species and to stimulate growth of aspen suckers (Bartos and Mueggler 1979, Mueggler 1989).

Schier (1975) reported when major disturbances such as fire are excluded from the environment, aspen may be replaced by conifers, provided there is a seed source nearby. Many aspen stands in Yellowstone coexist along the edges of conifer forests or as a component of mixed conifer environment. Schier (1975) also stated aspen established on drier sites often revert to shrub-steppe community types, and heavy browsing by elk (*Cervus elaphus*) can hasten this transition. Additionally, as a result of multiple years of browsing, aspen develop a shrub-like form, which can be seen extensively on Yellowstone's northern range (figure 1). Aspen in



Figure 1. The sprouting of new shoots each year, coupled with the continual hedging by elk, give aspen their shrub-like appearance.

this shrub-like form are a common appearance in aspen stands throughout the northern range, demonstrating aspen's resiliency to persist on the landscape in spite of heavy browsing.

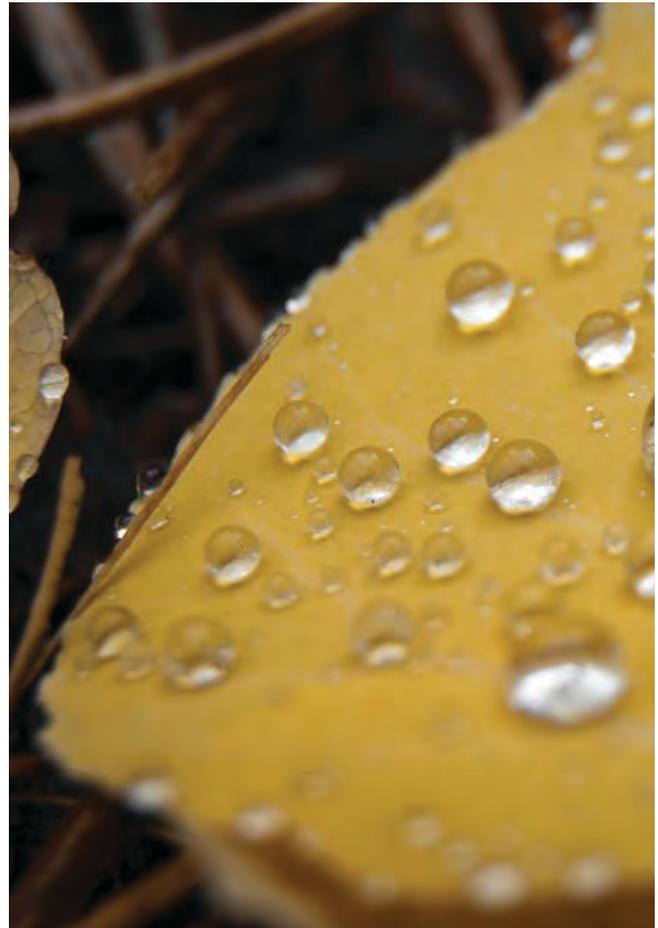
Warren (1926) provided one of the earliest data sets regarding aspen of Yellowstone in his classic study of beaver and aspen. Warren reported that aspen and beaver were abundant along most streams in the Tower Falls area. In the 1950s, reexamination of the status of beaver in the Tower Falls area (Jonas 1955) revealed no sign of beaver, where an estimated 200 had lived in the early 1920s. Aspen along streams and ponds had all but disappeared. It appears beavers eliminated the older aspen trees and elk browsed the young clone trees (Barmore 1967). It is during the same time period when Warren was conducting his study that park records reported on the extirpation of wolves (*Canis lupus*) from Yellowstone. Throughout the 20th century, other researchers on the northern range documented the failure of existing clones to regenerate replacement of overstory stems (Rush 1932, Grimm 1939, Kay 1990, Romme et al. 1995, Larsen and Ripple 2005). It is estimated aspen historically covered 4-6% of the northern range (Houston 1982) but have declined to cover 1-2% of the landscape (Renkin and Despain 1996).

The decline of aspen is of concern because it is a unique and important species in the park. Aspen is one of the few upland deciduous tree species present in the ecosystem, and is noted for very high rates of net primary productivity (Hansen et al. 2000). Aspen forests are important for biodiversity; they support a greater variety of plant associations than the typical conifer forests of the area, as well as increase bird species richness and total abundance (Turchi et al. 1995, Dieni and Anderson 1997, Hollenbeck and Ripple 2008).

The character of aspen stands has also changed from variable age classes to a recent state of mature, declining stands of older stems (Meagher and Houston 1998). According to Mueggler (1989), western aspen matures between 60 and 80 years, deteriorates rapidly after about 120 years, and in rare cases reaches ages over 200 years. According to age sampling done between 2003 and 2005, where 30 samples were randomly collected across the northern range and aged, the existing aspen overstory in the park established sometime between 1864 and 1919, with an average tree age of 119 years (YNP, unpublished data). This establishment period is consistent with other age structure analyses done on northern

range aspen (Warren 1926, Romme et al. 1995, Larsen and Ripple 2003).

Aging aspen stands on the northern range are rapidly declining. As a result of stand deterioration, the reduction in crown area facilitates aspen suckering because apical dominance is weakened, and more solar radiation reaches and warms the surface floor (Schier 1975). In aspen, auxin (a plant hormone that causes elongation of cells in shoots) produced in undisturbed growing stems/trees is translocated downward into roots where it inhibits sucker formation, a phenomenon known as apical dominance (Farmer 1962, Eliasson 1971a,b, Schier 1973, Steneker 1974). Interference with or disturbance of the auxin supply (such as fire disturbance or mechanical damage like stem browsing) changes the hormonal balance in the roots, which enables growth promoters (such as cytokinins) to initiate the regenerative process. During aspen regeneration, variation in stand development may be affected by clones with inherently poor suckering capacity (Schier 1975), clonal genetic differences in susceptibility to pathogens (Mielke 1957, Wall 1971, Copony and Barnes 1974), as well as a host of insects.



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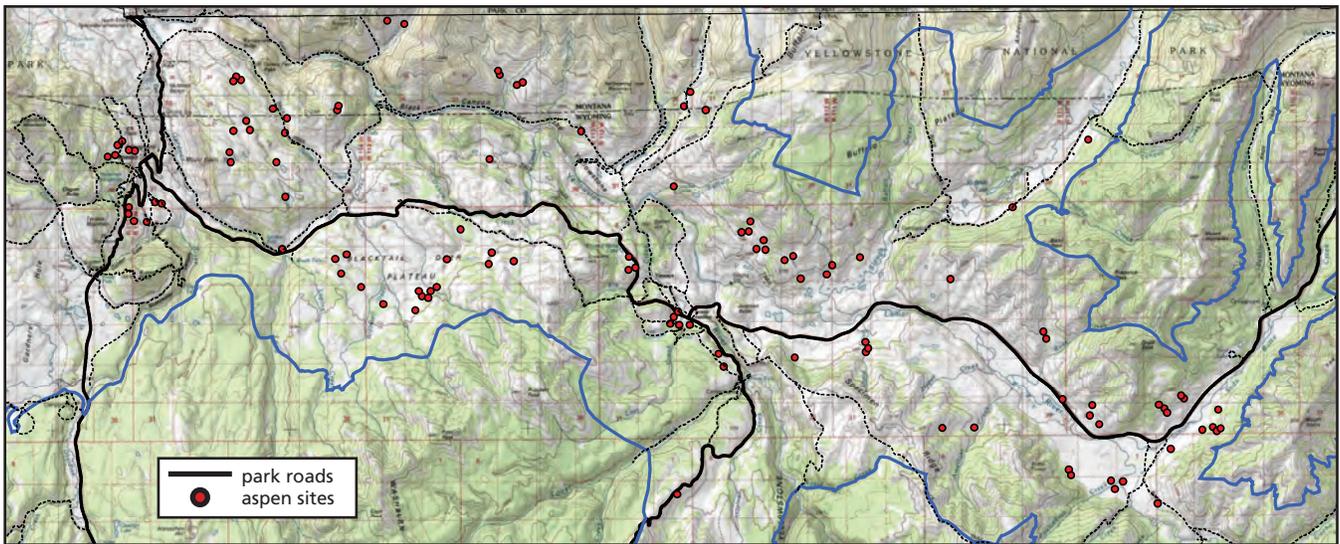


Figure 2. Map of northern range aspen sites.

Wolves and Aspen

After almost 70 years of absence, wolves were reintroduced into Yellowstone in 1995. By the end of 1998, 112 wolves formed 11 packs in the Greater Yellowstone Ecosystem (GYE; Smith et al. 1999). Four packs established themselves on the northern range. In 1999, 113 permanent plots were established in aspen stands (defined as a group of aspen trees within 30 meters of one of its cohorts) across the northern range to assess the role of reintroduced wolves on elk use and aspen response (Ripple and Larsen 2000; figure 2). An inventory of YNP northern range aspen stands was created from a set of 1:24,000 color infrared aerial photographs taken in October 1998, at the conclusion of the fire season. A scanning stereoscope was used to identify grid cells containing large-stem aspen. A comprehensive list of cells containing aspen was compiled from the photographs to produce the inventory. Beginning with a live mature aspen tree running into the stand towards the centroid of the clone, a 1 x 20 meter transect was established. A metal tag was attached to the aspen start tree, and the transect was marked with nine-inch spikes for reference. From 1999-2013 (with the exception of year 2000), there has been an effort to visit and collect data for all 113 aspen sites annually near the end of the growing season in August/September. For 10 of those years, between 106 and 113 sites were visited. For the other four years, 60-90 sites were visited. Collected data included aspen stem height, current annual growth of the leader stem (the tallest stem when in shrub form), evidence of browsing from the prior year, and a count of new suckers.

Wolves' primary prey species is elk. According to the Northern Yellowstone Cooperative winter elk count data, there has been a reduction of elk from 19,000 in 1993-1994 (the last census data prior to wolf reintroduction) to 5,000 in 2015-2016 (YNP, unpublished data, see page 8). As the number of elk has declined on the northern range, there has been a significant reduction of elk use in the number of browsed aspen stems (YNP, unpublished data; figure 3). It also appears the physiological response of apical dominance is beginning to express itself in aspen, as evident by the production of fewer suckers and increased stem height (figure 4). Given the decline in elk, the influence of apical dominance, and the significant average increase in stem height, the

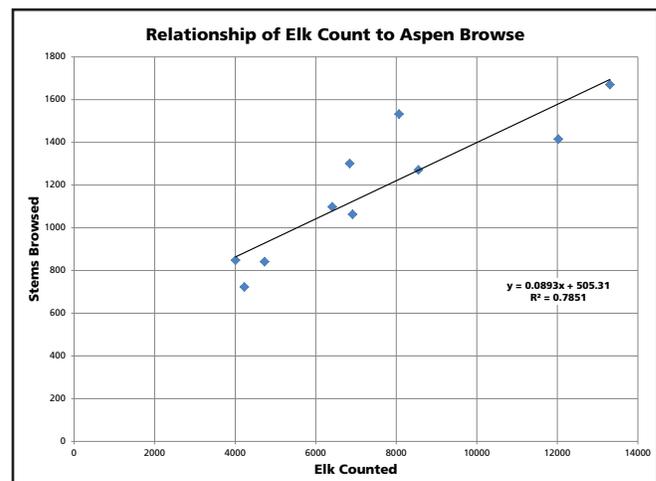


Figure 3. Elk show a strong preference for aspen. Where a minimum of 100 sites was sampled and elk data was available for the year, the correlation between the number of elk and the amount of browsed stems is nearly 80%.

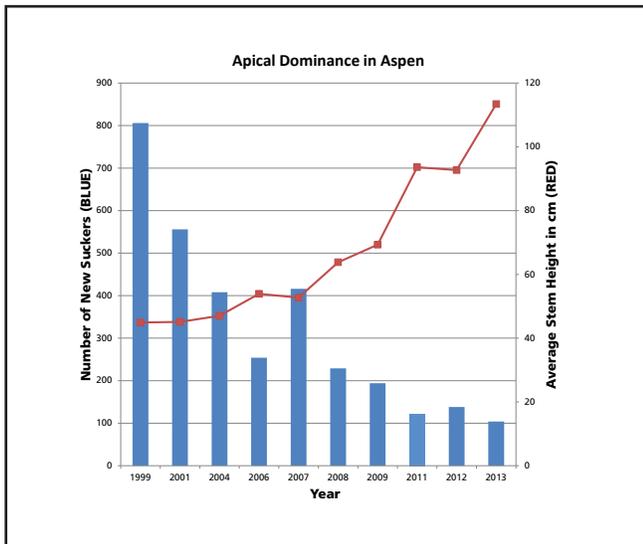


Figure 4. In 1999, the first year the aspen plot transects were read, 91% of aspen stems were browsed and 34% of 2,369 stems measured were suckers of the year. In this scenario, intense browsing is taking place, apical dominance is minimized, and energy is being devoted to sucker production rather than to stem elongation. However, by 2013 browsing was at 58% and new sucker production fell to 7%. In this scenario, with reduced browsing pressure and apical dominance asserting control, suckering was minimized and energy reserves were allocated to stem elongation. (Data reflects at least 100 sites sampled per year).

early stages of stem elongation should be evident on the northern range landscape. Comparing the average stem heights for sites from 1999 (the first year aspen plots were read) to 2012 it appears aspen stand recovery is beginning to take place on the northern range (figure 5).

Are Aspen Benefitting from Wolves?

Together with other factors that influence the number of elk such as predation from bears, cougars, and hunting, aspen appears to be benefitting from the reintroduction of wolves. Barring any unforeseen circumstances, these large predators are here to stay in Yellowstone; and their continued presence on the northern range should help maintain the elk herds at lower densities, providing a long-term benefit to aspen, unlike the decades that followed the discontinuation of culling activities and the ensuing increase of elk on the landscape. Since the successful restoration of wolves along with other large predators in Yellowstone, the gradual decline in elk has significantly reduced browsing pressure, allowing for apical dominance to increasingly express itself in aspen. This physiological process is translating into the emergence of widespread aspen stand recovery, in spite of

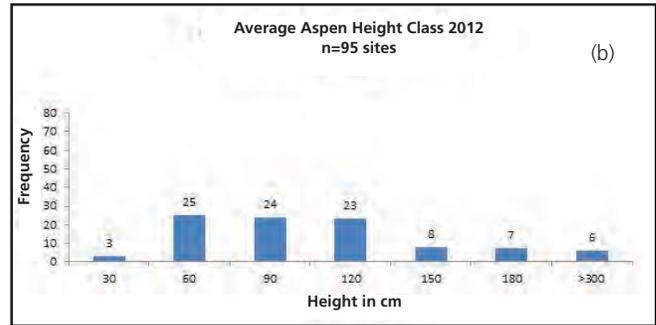
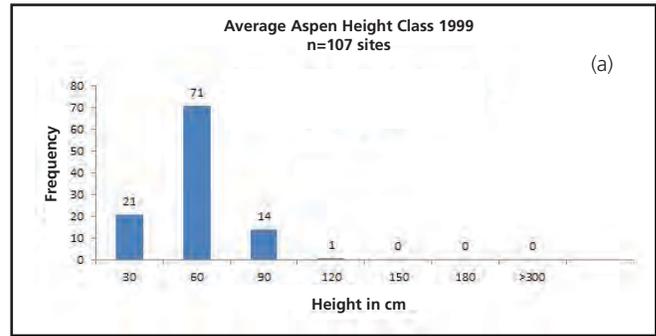


Figure 5. In 1999, (a) approximately 86% of plots sampled had an average aspen stem height of 60 cm or less, and no stems measured were greater than 100 cm. However, by 2012, (b) only 27% of plots sampled contained average aspen stem heights less than 60 cm and more than one-third were greater than 100 cm in size.

continued levels of browsing across the northern range. In light of this recent development, it is premature to say aspen have recovered or will return to anything like historic levels both in range and size. Many existing stands of mature aspen trees on the northern range established and flourished at the tail-end of the Little Ice Age, a period where conditions were predominantly wetter and cooler. These environmental conditions do not exist on the northern range today, so aspen is expected to behave and adapt differently. Recent data are highly encouraging and suggest a positive trend forward for aspen. How this plays out on the future landscape remains to be seen.

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John Klapotsky acquired a master's degree in Park and Resource Management (with an emphasis in Sustainable Systems) from the University of Slippery Rock, Slippery Rock, PA. He began his career with Yellowstone National Park in 2003, and has since served as a biological science technician in the vegetation department at the Yellowstone Center for Resources. John began his work with aspen in 2003, as the lead field technician for a research project involving the history of aspen browsing on Yellowstone's northern range.



The Big Scientific Debate: Trophic Cascades

Douglas W. Smith, Rolf O. Peterson, Daniel R. MacNulty, & Michel Kohl



PHOTO © J. OLSON

Wolves generate controversy. Usually it's of a cultural kind, like how they should be managed or should we have them at all. Scientific debates tend to take the back seat. Probably the most intense of these is the impact of wolves on their prey because the answer may influence wildlife management. In Yellowstone, a somewhat unique controversy, largely centered within scientific circles, has cropped up and questions how wolves impact ecosystems—if at all (Peterson et al. 2014). This is interesting because wolves and other carnivores (not bears) have been functionally absent for most of the 20th century; and now with their return, a comparison can be made. Sounds straightforward, but it's not. Nature is complex.

The debate has centered on the phenomena called “trophic cascades” or how species interact within a food web (i.e., how nature is organized, if one can characterize the near impossible complexity!). Specifically, a trophic cascade refers to a predator's impact “trickling down one more feeding level to affect the density and/or behavior of the prey's prey” (Silliman and Angelini 2012). The question then, simply put, is: Have wolves impacted

plants? Here we are referring to just woody plants—primarily willow and aspen. For most of the 20th century these woody plants have been suppressed, or not grown tall, due to elk browsing (which led to National Park Service reductions in elk); then coinciding with wolf recovery, some plants showed signs of “release” from the suppression of browsing (Painter et al. 2015). Most studies agree with this scenario (with some exceptions), and the debate is about why the sudden growth.

Theoretically the argument is framed as “top-down” vs. “bottom-up.” Top-down is predators eating prey, reducing their number (or changing behavior), and causing fewer plants to be eaten. Bottom-up is sunlight causing growth in plants, and plants providing food to a certain number of prey which then determines the number of predators. So which is more important? Because Yellowstone had few predators for decades, and now that they're back, we can compare the system before and after predator recovery. Because this was not a properly run experiment, there are many uncontrolled variables, which has led to disagreement. The first problem to be solved is to determine how this works. Early on the idea

of a “landscape of fear” was presented: without wolves, elk were unconstrained to roam the landscape (Brown et al. 1999). With wolves this changed and some places made elk vulnerable to attack, so elk avoided these “risky” places. In short, this change in elk behavior explained why willows exhibited signs of release before elk populations became really low (Beyer et al. 2007). This is a behaviorally mediated trophic cascade. Others disagreed (Marshall et al. 2013). It was just fewer elk or a numeric effect (Kauffman et al. 2010). Which is it? Or is it both?

Yet another argument was site and water availability; fewer elk was not enough (Marshall et al. 2013). Alternatively, it was attributed to weather or climate change (Despain 2005). When conditions were right or the climate was favorable, woody plants grew despite elk. Also beavers had been lost about the same time elk increased in the early 20th century, and the loss of beavers changed streams in a way that reduced willow and aspen (Wolf et al. 2007, Bilyeu et al. 2008). Beavers were a linchpin. Determining the cause of changes in willow growth was complicated—too many factors varied simultaneously.

In short, we have competing and very complex arguments. Is there any way to resolve this debate? Some say we need to design the right experiment, despite the vast size and cost of such an undertaking. Importantly, and other than the climate hypothesis, no one is arguing that top-down effects are not important, or that natural predation has no impact on the lower trophic layers. What is being debated is the extent that changes in woody plants are due to the effects of wolves (and other carnivores) on elk and how these top-down influences ripple through the food web. Part of the disagreement comes from crediting wolves as the only agent, ignoring cougar recovery and increases in bear numbers, and of course elk management outside of the park (which also reduced elk and kept them in the park). Another criticism is that too much impact has been attributed to elk, that other factors like water availability need inclusion in any explanation. In dry areas with reduced elk herbivory, no willow response was observed.

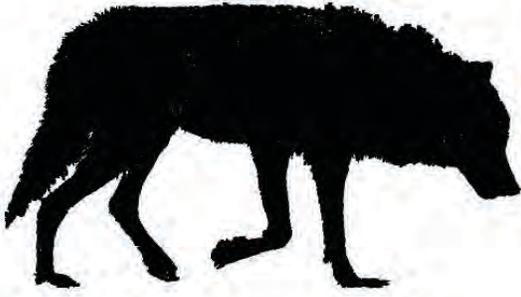
Another question is the distribution of willows. There has been no increase in the area of willow and aspen, only a height increase in existing stands, which may be dependent on beaver occupation. Maybe the changes to Yellowstone mid-20th century were so significant that a couple decades of fewer elk is not enough to erase the long-term damage on woody plants (Wolf et al. 2007).

Lastly, and most recently discovered, is an important elucidation of how wolves and elk really interact across the varied landscape of Yellowstone. Possibly the most intense debate centers on what wolves do to elk. This is the behavioral vs. numeric argument typically framed as one or the other. But what happens if that’s not how wolves and elk really interact? After years of painstakingly collaring wolves and elk, an answer may be emerging. Elk do respond behaviorally to the risk of wolf predation, but not all the time; they avoid risky areas only when wolves are active. This is a fascinating discovery and suggests the increase in woody vegetation is potentially attributable to a combination of fewer elk responding to wolf activity. Elk are not avoiding risky areas but are aware of wolves. These factors together may have allowed some woody plants to show signs of release on appropriate sites (enough water) after decades of suppression. So many factors are involved, including the possible impact of a changing climate. But it would also be difficult to say it’s only weather. Surely, we’ve made progress, but we’re not there yet.

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YELLOWSTONE



KINGDOM: Animalia

PHYLUM: Chordata

CLASS: Mammalia

ORDER: Carnivora

FAMILY: Canidae (dog family)

GENUS: *Canis*
(Latin word meaning “dog”)

SPECIES: *lupus*
(Greek word meaning “wolf”)

COMMON NAMES: gray wolf,
timber wolf

NAMES IN OTHER LANGUAGES:
Spanish: Lobo, French: Loup,
Italian: Lupo, Swedish: Varg,
Norwegian: Ulv

GROUP OF WOLVES: pack/
family (one of few eusocial
species)

AVERAGE LIFE SPAN (YNP):
4-5 years

**AVERAGE LIFE SPAN (OUTSIDE
YNP):** estimated 2-3 years

**OLDEST WOLF KNOWN IN
YNP:** 12.5 years - 478F of the Cou-
gar Creek pack

**OLDEST WOLF KNOWN IN
THE ROCKIES:** B2 released in
Idaho at estimated 4 years of age;
died at age 13.8 of unknown causes

**CAUSES OF MORTALITY IN
ADULTS (YNP):** natural causes
77% (intraspecific 42%, natural
unknown 15%, interspecific
8%, malnutrition 5%, other
4%, disease 3%); human causes
17% (harvest 7%, vehicle 6%,
illegal 2%, control 1%, other 1%);
unknown causes 6%

**CAUSES OF MORTALITY IN
ADULTS (GYE):** human causes
77%; natural causes 23%

**PROPORTION OF POPULATION
>5 YEARS OLD:** 18%

SEX RATIO: 50:50

PELAGE: gray or black (ratio
50:50), rarely white

BLACK COAT COLOR: caused
by *K*-locus gene thought to
have originated from historic
hybridization with domestic dogs
500-14,000 years ago

LOCOMOTION: tetrapedal,
digitigrade

AVERAGE RATE OF SPEED:
5mph

TOP SPEED: 35mph

AVERAGE BODY MASS: males-
110 lbs (50 kg); females-90 lbs (41
kg)

**HEAVIEST KNOWN WOLF
IN YNP:** 148 lbs (wolf 760M of
Yellowstone Delta pack with no
food in stomach)

HEIGHT AT SHOULDER: males-
81 cm average, females-77 cm
average

LENGTH: 181 cm average

BODY TEMPERATURE:
100-102.5 F (37.3-39.1 C)

RESPIRATION: 10-30 breathes
per minute

HEART RATE: 70-120 beats per
minute

EYES: blue at birth, light yellow to
gold to brown as an adult

NUMBER OF BONES:
319 males, 318 females

NUMBER OF TEETH: 42

SMELL: excellent, although un-
measured. Estimated to be thou-
sands of times better than humans

VISION: excellent night vision; no
red or green cones, but have blue
and yellow cones

HEARING: little is known, but
probably similar to dogs (relatively
normal hearing abilities compared
to other mammals)

DENTAL FORMULAE: incisors 3
top/3 bottom, canines 1/1, premo-
lars 4/4, molars 3/2 (on each side)

FEEDING HABITS: generalist car-
nivore (Mech and Boitani 2003);
scavenges when possible and has
been known to eat small amounts
of vegetation

PRIMARILY FEED ON (YNP):
Winter: elk (>96%), bison (3-4%
and increasing in recent years;
deer (1.5%); Spring: elk (89%),
bison (7%), deer (7.1%); Summer:
elk (85%), bison (14.1%), deer
(<1%)

**ELK KILLED PER MONTH PER
WOLF:** 1.83 elk/wolf/month
during winter

WOLF FACTS

ELK KILLED PER YEAR PER

WOLF: 18-22 elk/wolf/year (all age classes, including neonate calves)

KILOGRAM PER WOLF PER DAY NEEDED FOR SURVIVAL:

3.25 kg/wolf/day; can eat 15-20% of body weight in one sitting

CURRENT YNP POPULATION:

99 in 10 packs

CURRENT GREATER YELLOWSTONE POPULATION:

510

CURRENT NORTHERN ROCKIES POPULATION:

1,782

CURRENT NORTH AMERICAN POPULATION:

67,100-74,100 (53,600-57,600 of these in Canada)

AVERAGE HOME RANGE SIZE IN YNP (NORTHERN RANGE):

274 km² (range=58-1,151 km²)

AVERAGE HOME RANGE SIZE IN YNP (INTERIOR):

620 km² (range=105-1675 km²)

AVERAGE HOME RANGE SIZE IN YNP (PARKWIDE):

428 km²

AVERAGE PACK SIZE (YNP):

9.8

PERCENT OF POPULATION THAT ARE LONE WOLVES (YNP):

2-5%

PERCENT OF POPULATION THAT ARE LONE WOLVES (NORTH AMERICA):

10-15%

HIBERNATORS?:

No, active all year

MATING SYSTEM: usually monogamous, but about 25% of packs have multiple breeding pairs under polygamous matings

PERIOD OF COURTSHIP:

mid-February

GESTATION:

63 days

BIRTH PERIOD:

mid-April

BIRTH LOCATION:

den

TYPICAL DEN TYPES:

excavated under large roots, boulders, hill-sides, caves with a tunnel leading to an enlarged chamber; several entrances and chambers may be present

DEN EMERGENCE:

10-14 days

AVERAGE LITTER SIZE (YNP):

4.4 at den emergence, 3.2 survive until late December

MAXIMUM LITTER SIZE RECORDED (YNP):

11

SPLIT LITTERS?: multiple fathers per litter have not been detected in wild gray wolves

WEANING: 5-9 weeks from milk, then brought food (regurgitation) for another 3 months

MILK CONTENT: 6.6% fat; 144 kCal per 100 grams

RENDEZVOUS SITES: used as wolf pups get older as a central homesite; time spent there and number of homesites varies widely between packs

AVERAGE FEMALE AGE AT FIRST LITTER (YNP): 2.7 (Stahler et al. 2013)

ONSET OF FEMALE REPRODUCTIVE SENESCENCE:

4-5 years

INTERBIRTH INTERVAL: can be every year

EYES OPEN: 12-14 days

WOLVES SEEN IN YNP: 3,573 consecutive days (February 2001-November 2010)

BITE PRESSURE: 1,200 psi

DISPERSAL: both sexes, YNP average age 2 years, 1 month; range 1-4 years

HOWLING FUNCTION: many uses, including intrapack communication, advertising territory, coordinating social activities

DISTANCE HOWLING CAN BE HEARD: forest=11km (6.6 mi), open areas=16 km (9.6 mi)

LONGEST TERM PACK: Crystal Creek/Mollie's, 1995-present

LONGEST TIME AS ALPHA MALE: 8 years; 712M, currently alpha male of the Canyon pack

LONGEST TIME AS ALPHA FEMALE: 8 years; uncollared white alpha female of the Canyon Pack

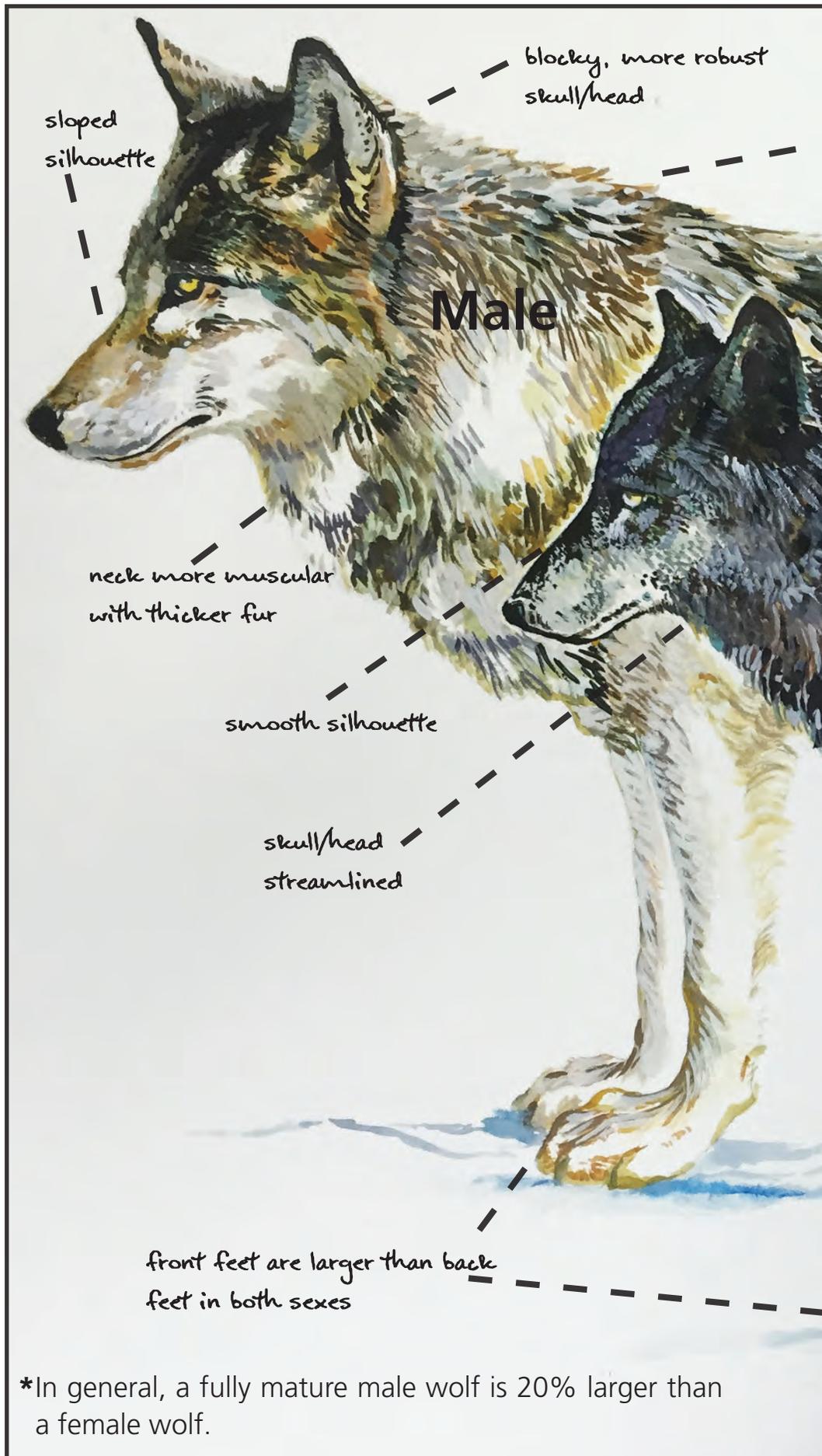
LARGEST PACK RECORDED IN YNP: Druid Peak, 37 wolves (2001); may be the largest ever recorded (42 wolves seen together in Wood Buffalo National Park (1974) but unknown if they were a single pack)

MOST PUPS BORN TO A SINGLE PACK IN YNP: Leopold pack, 25 pups, at least 4 litters (2008)



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Male vs. Female Wolves*

larger, massive shoulders,
stand out from body

shoulders do not stand out
and are proportional to the rest
of the body

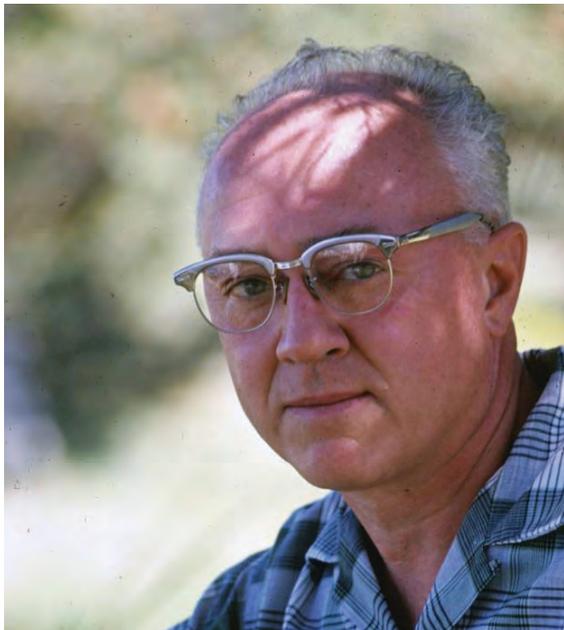
Female



FIVE QUESTIONS

Three scientists at the forefront of wolf ecology answer the same questions about wolf biology and management

L. David Mech, Rolf O. Peterson, & Douglas W. Smith, as interviewed by Charissa Reid



Durward Allen 1910-1997

In 1958, while a professor at Purdue University, Durward Allen began what continues to be the longest running predator-prey study ever conducted in the world at Isle Royale National Park. His first graduate student was David Mech, who was pursuing a PhD. In 1970, Allen's final graduate student, Rolf Peterson, also acquired his PhD as part of the Isle Royale Study. Dr. Allen turned the study over to Peterson in 1974, and Peterson continues to share leadership of the Isle Royale study 46 years later. Both Mech and Peterson went on to distinguished careers and are known as two of the foremost authorities of wolves in the world. Durward Allen died in 1997.

Doug Smith studied under Peterson and Mech, working on the Isle Royale Study from 1979 to 1994 and in Minnesota in 1983. Smith came to Yellowstone to work on wolf reintroduction as a project biologist in 1994 and eventually became the Wolf Project Lead, a position he has held for 20 years.

1. Do you have any memories of Durward Allen you'd like to share?

MECH: I was Durward Allen's first graduate student, and he assigned me the privilege of launching the Isle Royale wolf and moose study. He became a great mentor and friend. Besides our joint interest in the study, we both were keen on writing. "You really don't know how to write until you put a million words through the typewriter," he once told me. He had done so long before, having written several books and many articles. What I remember most about Durward was his wry wit and wonderful way with words. One particular winter evening at camp on Isle Royale, Durward was pecking away on an old Smith Corona typewriter, trying to finish one more article. After an especially bad bout trying to get the old machine to work, he looked up and dryly announced, "Ya know; this old typewriter would make someone a damn good boat anchor!" That typified

Durward's wry utterances and forever made me think of him when I saw an old typewriter.

PETERSON: Durward Allen took up backpacking when he was nearing retirement age, primarily to get a glimpse of the interior of Isle Royale from the ground while writing a book on the island in the early 1970s. He was used to the canvas-and-leather era of camping in the Northwoods, and on his first solo backpacking trip he took along a bag of potatoes. But soon he adapted to the go-light routine of backpacking. In autumn 1972 he hiked 27 miles on a loop trail; and on the last night, still 10 miles out, he felt some tightness in his abdomen which he figured was from the waist-belt of the backpack, just a nylon strap. He hiked to Washington Creek campground the next day, his departure point for the

trip back to the mainland in a few days. But he hardly slept that night because of continuing gut discomfort, and he was unable to arise in the morning. He crawled on all-fours a couple hundred yards to the ranger station, and a call was made to the air taxi to come right away to fly Durward to a hospital in Hancock, Michigan. He spent almost a week there as doctors puzzled over what his problem was – all the symptoms of appendicitis except one, as his white-blood-cell count was normal. Finally, a colleague from Purdue University drove to Hancock and took Durward home to Indiana, where doctors operated and found that his appendix had ruptured but only very slowly, and in fact there was nothing to remove. Durward concluded he was one of the lucky few people who might have survived appendicitis without the intervention of modern medicine – he often mused on how he might have gotten along if he'd been a mountain man 150 years earlier. But next time he backpacked, he had a padded waistbelt.

SMITH: I had heard a lot about Durward Allen before meeting him. First from Erich Klinghammer, who was a colleague of his at Purdue University, then later from Rolf Peterson, who was his student. I volunteered for

Erich at Wolf Park in Battle Ground, Indiana, in the spring of 1979. Being from Germany (and a former student of Konrad Lorenz), he was impressed by anyone who had worked at something for a long time; some called it the “German alpha male effect.” And that was Durward – an expert, a book author, and one of the pioneers in the nascent field of wildlife management, or I should say wildlife biology. In fact, I credit Dr. Allen for my educational interest in wildlife. In 1979, so many students were majoring in Wildlife Biology that one professor at Utah State where I interviewed called Wildlifers, as they were referred to at the time, “a dime a dozen.” Then I met Dr. Allen at Wolf Park in Indiana. Nervous and almost clumsy, I spent part of an afternoon with him talking while watching a captive pack of wolves at Wolf Park. At one point I got around to the conversation at Utah State when I asked: *Should I even major in wildlife given there were so many students doing so?*, then I repeated the comment I heard by the Utah State professor. Quickly, almost interrupting, he said, “wildlife managers are a dime a dozen, wildlife scientists are not.” I enrolled that fall in Wildlife Biology at the University of Idaho.

2. Are wolves in Yellowstone National Park different from other North American wolves, or do we just know more about them?

MECH: It depends on what you mean by different. Every population is different from other populations, but there is uniqueness to the origin of the Yellowstone wolves in that they were translocated from two fairly separated areas in Canada, meaning that their original gene pools were different. That differs from most colonizing populations of wolves in that ordinarily, the colonizers would all be from, basically, the same gene pool, whereas in Yellowstone they are from two separate gene pools. What practical difference this makes or what scientific difference this makes is certainly unknown and could be argued about, but I think that there's at least some reason to believe that because these two gene pools were merged in Yellowstone, that makes that population unique.

It's pretty clear that because of the great surplus of prey that was available to the population when it was first reintroduced, the kinds of things that we saw, like a pack of 37 wolves, were a result of there being that much food, which reduced the competition within the packs and between the packs during the first several years

of reestablishment. The population that exists now is much more similar to other populations in that they have pretty much equilibrated with their prey. Actually, if you look at the, say, maximum pack size of the wolves in Yellowstone over all the years, the largest pack was in 2001, which was just six years after reintroduction. And, since that time, the maximum pack size has consistently decreased, such that the maximum pack size by 2015, was only about half of the maximum pack size in 2001.

The Yellowstone population from the beginning has been the most scrutinized wolf population in history anywhere in the world. The percentage of the number of wolves collared with even VHF radios and the amount of time that they've been observed from the ground has all produced tremendous amounts of data, which the biologists have turned into very informative publications. That means that things that we might not have been able to find in other wolf populations the biologists were able to find in Yellowstone. The question comes down to this: are some of the new findings a result of the increased scrutiny or are they a result of other

factors like the fact that the population originated from two separate gene pools? That question hasn't been answered and may not even be answerable, so it does remain a question.

PETERSON: I don't think Yellowstone wolves are fundamentally different from other wolves in North America. The wolves introduced in 1995 were certainly placed in a unique situation, with extremely abundant prey in a large protected environment. Although one could never predict exactly what wolves would do in those circumstances, the general pattern of rapid population increase and then a leveling out is what one would expect (and hope for) in that situation. The unique features of their individual lives are fascinating, but they are no more unique than almost any other animal would prove to be if we invested the effort to learn about them with the same intensity.

SMITH: Wolves in Yellowstone are not different than wolves anywhere else. And I think a lot of people sometimes mention that they are...because, for one, we've learned so much about them that there seems to be a lot of different, new things about those wolves. Secondly, and perhaps most importantly, what really characterizes wolves in Yellowstone, and this is primarily the northern part of the park, the northern range, is that they occur at very high density. And that's unique across North America.

Wolves are an animal that lives in ecosystems at fairly low densities. Because of the very large elk herd that was present in Yellowstone at the time of reintroduction, wolf numbers built up to arguably the densest wolf population North America's ever seen. What's interesting is the northern range inside Yellowstone National Park is almost exactly 1,000 kilometers squared. The number of wolves we have in northern Yellowstone on the northern range is the unit of measure for wolves worldwide. Very typical wolf densities for, say, Canada is 10 to 15 wolves per 1,000 kilometers squared. In Alaska, it's not uncommon to have single-digits wolves per 1,000 kilometers squared. Where there's a lot of white-tail deer, say in Wisconsin or Minnesota, you might have 30 to 40 wolves per 1,000 kilometers squared. Here in Yellowstone, our peak density for several years was in the 80 to 100 wolves per 1,000 kilometers squared.

So what pervades a wolves' social behavior and ecology on the northern range of Yellowstone is this unique high

density. Our wolf pack territories are 200 to 400 square miles. Arctic wolf pack territories being up to 1,500 square miles. What wolves do here in this very competitive environment is very different than what wolves do someplace else, but that doesn't make them different.

Secondly, and this is as important, we have had better looks at wolves. Our monitoring is more intense. We're probably one of the more intensive monitoring programs worldwide. And why is that? Because we have a road bisecting all the good wolf habitat in the park. Wolves up to this point in time have always been a remote wilderness species. They live in faraway places. And almost all the monitoring of them has been through radio collars and airplanes. Yellowstone is the best example of continuous year-round not only aerial monitoring, but ground monitoring as well. Rick McIntyre went out every day for fourteen years and saw a wolf 97 percent of the days he went out. There's nothing that can match that worldwide. Even though each day is just a little bit of information, you add all that up, we get great looks at wolves. This is also aided by the fact that we've been very successful radio collaring wolves.



Rolf Peterson, Douglas Smith, and David Mech examine a wolf kill near Crystal Creek along the Lamar River in 1999. NPS Photo.

3. What has been Yellowstone's most significant finding or contribution to wolf research or management?

MECH: I don't know any other place in the world one could get such information that the MacNulty papers have produced on the effect of pack size and the wolf – individual wolf ages and sizes, how they affect wolf hunting behavior. I don't think that kind of information could ever have been obtained anywhere else in the world. And it is unique and I think very significant to the whole field of wolf/prey interactions. We didn't know anything like this before, and so I think that those findings were some of the most important.

The recent findings related to pack size and composition affecting the winning of pack interactions, aggressive interactions, comes a close second, I would say. We've known from many populations that wolves kill each other, but we certainly had no idea about the level – or we certainly had no level of detail similar to what Kira Cassidy has found in Yellowstone with the wolf packs attacking each other. That's pretty unique information.

What's most surprising to me has been many of the observations of the multiple breeding in some individual groups of wolves that we don't even – they're not even family packs; that is, there's groups of wolves that get together, like several males getting together; or there's one female that I think was observed breeding with five males and that type of thing. That's really surprising to me. I wouldn't have envisioned any of that; and it's one of the things, incidentally, I wonder about as to whether it's a result of some of the differences in genetics or whether it's a result of the more intense scrutiny that these packs have had. I wouldn't be able to answer that question myself.

PETERSON: I think the ecosystem role of the wolf that has been demonstrated in Yellowstone will prove to be the most important lasting contribution. Although the top-down significance of wolves is not a unique scientific result from Yellowstone alone, the huge audience that is paying attention makes the findings from Yellowstone all the more important. Prior to the introduction of wolves to Yellowstone, the long-running controversy over elk management had been referred to as the biggest controversy in wildlife management of the 20th century. Perhaps that is arguable; but in any case wolf predation played an important role, along with recovery of griz-

zly bears and cougars, in reducing a hyperabundant elk population.

SMITH: We've had a great window into ecosystem functioning. "How do ecosystems function?" has been the hottest scientific debate going. A lot of the trophic cascades arguments are a window into how ecosystems work. And that's been a really vibrant debate. We're coming out with new information on that.

The second thing that we've learned is how wolves work in the absence of human exploitation. And really, this is why we establish national parks. There are two things we've discovered, and it probably does not occur in wolf populations outside of protected areas like Yellowstone. And that is, one, wolves have organized themselves into matrilineal groups. The other thing that we're finding, and this is even more evolving science, is there appears to be an interaction between a coat color, whether you're a black wolf or a gray wolf, and disease immunity and aggression. Those two things are currently being studied.

Early wolf biologists, all males, thought the supreme leader of the pack was the alpha male. It appears that it's the female. Female offspring tend to stay in the pack. It's called philopatry. Male offspring tend to leave. They disperse. And they do this because wolves don't want to inbreed. When you have a tendency for males to leave and females to stay, the daughters are within the pack waiting for their opportunity for mom to die.

Second finding: There appears to be a relationship between coat color and disease immunity. And what that means is black coat color is dominant to gray coat color in wolves. If you get a black and a gray allele, the black allele is dominant and you're gonna be a black wolf. But you're heterozygous black. So you maintain the possibility to have gray offspring because you're carrying that allele. It's just masked by the dominant gene. So that's one way to get a black wolf is you get a black copy of the gene and you get a gray copy. And it always comes out black. You could also get two recessive gray alleles. That's the only way to get gray. So you get two gray alleles, you get a gray wolf. And then you could also be black because you get two copies of the black allele and that wolf is black. What we're finding out is if you get

both copies of black, you have a higher probability of dying from a disease.

Homozygous black wolves die at a higher rate when they're born, right after they're born, than hetero-

4. What is the most pressing issue or conservation challenge facing wolves in Yellowstone?

MECH: Yellowstone wolves are pretty well protected. I don't see any major problems affecting their conservation. I would be very, very surprised if that population didn't persist for as long as the park persisted. I don't see any big threats to their conservation. In the long term, I see that the relationship between the number of wolves and the number of prey being something that should be followed for a very long period. Each predator/prey – or let's say each wolf/prey population is unique, and Yellowstone's wolf/prey population, or wolf/prey system, comprises or is comprised of elk and bison and sheep and deer and moose and pronghorn and all; and it will be very interesting over the years to see any changes in the proportion of all these different prey animals that make up the wolf kill. I mean that's going to shift as numbers of the different prey animals change. So, for example, the elk population has dropped considerably and now we're starting to see wolves taking more bison.



David Mech and Durward Allen examine a wolf kill circa 1960. Photo © D. L. Allen

zygous black or gray wolves; but heterozygous black wolves have a survival advantage, probably because of an immune system gene. We're trying to figure out what they're dying from.

Sooner or later, they're going to be taking more pronghorn, I believe, and probably preying a little harder on the sheep and deer. A really good, close look at the changes in that dynamic over the years would be pretty valuable.

PETERSON: From the human standpoint, the key conservation challenge is to preserve and protect the Yellowstone ecosystem, with the national park at its core. The presence of wolves gives an important boost to this challenge; but the fundamental challenge has been there for many decades, as Yellowstone is an island in a sea of human-dominated ecosystems that press on Yellowstone from all sides. For the wolves themselves, I think their special challenge is to become specialized predators of bison – everyone hopes that will happen.

SMITH: Social science. I sometimes say – wolves are one of the most studied mammals in the world and that's because they're controversial. The real frontier for wolves is human attitudes. But people are the tough part. For us in the park it's tough because people come here from all over the world to see them and love them. Then wolves cross the line, and two of the three states want to reduce the wolf population. They have a different group of constituents that have different demands on wildlife than our people do. The boundary issues are going to be very pressing.

To be honest, it's been difficult, but it's ended up going well. You've got wolves far from Yellowstone that Yellowstone has no business commenting on. And then you've got wolves in the park, which is all our business. And then you've got wolves in between. And those are the wolves that we have to reach some kind of compromise about. And I think, in general, we have.

Montana has responded to our request to reduce harvest right next to the park. Wyoming has small hunt units with limited quotas. We talked to them. So it's going well. Maintaining that balance into the future is going to be a challenge.

5. Why did you choose to dedicate your professional career to the study of wolves?

MECH: As a teenager I was always interested in fur trapping, and the most challenging animals to trap are carnivores, and so I became interested in carnivores. And before graduate school, I had the opportunity to help with some research on black bears, and in that process I also ended up catching some coyotes and bobcats, and so the larger carnivores interested me a great deal and I worked with some professors on them. And when the Isle Royale Wolf Moose Project became available, it was actually offered to me as a graduate project. I jumped at it and was hooked on wolves ever since because of the challenges involved both in studying the wolves and the challenges that the wolves face in their lifestyle.

PETERSON: It wasn't just wolves as a focal species that interested me, it was wolves in the complete context of an ecosystem, where wolves influence the abundance of their prey, which in turn impacts a myriad of plants and other animal species, including impacts that we probably aren't clever enough to measure or even guess about.

SMITH: I've been interested in wolves since I was about twelve, thirteen years old. I have two older half-brothers; they're 20 and 25 years older. For Christmas one bought me Dave Mech's book *The Wolf*. I still have it. That book came out in 1970. And my brother who saw this interest that I had I think just randomly saw this book on a bookshelf. In those days there was no Amazon.

At fifteen, and I know this well – at fifteen I started writing wolf biologists. And this is back in the day of pen and paper or typewriter. And oddly, again, that was unique to the age. I was fifteen in 1975. They all wrote back typed letters, not form letters. At fifteen, everybody said, “No thanks.”

So at eighteen I wrote them back again. I wrote all the same wolf biologists back. Dave Mech, Rolf Peterson, Lloyd Keith, Lu Carbyn, Erich Klinghammer, the big five, and said, “I don't want a paid job; I don't want a volunteer job. I just want to hang out with you. I just want to observe what you're doing. And it's for an educational project. I'm a senior student. I want to go for a school project for six weeks.” And so to this day, I have a soft spot in my heart because I get two or three either

high school or college kids every year wanting to do the same thing. And I can't bring myself to say no because one of those five wrote me back and it was a captive study.

Erich Klinghammer. He was doing behavioral research on captive wolves associated with Purdue University. I drove over there in the middle of the winter with my mother. My father had died. He just wanted to look at me in person and see is this some kind of wacko high school kid. At the end of the interview he said, “You can come.” And so in the spring of 1979 I went to Wolf Park to hand rear wolf pups.

It's been a love of my life to study them. I am tirelessly still loving it.



Current staff and volunteers who are part of the Durward Allen legacy through their studies and work with Peterson and Mech. Back row: Ky Koitzsch, Daniel Stahler, Roberta Ryan, Douglas Smith; Front row: Kira Cassidy, Lisa Koitzsch, and Erin Stahler. (Matthew Metz, not pictured)

SHORTS

Wolf Effects on Elk Inhabiting a High Risk Landscape: The Madison Headwaters Study

Robert A. Garrott, P.J. White, Claire Gower, Matthew S. Becker, Shana Dunkley, Ken L. Hamlin, & Fred G.R. Watson

The effects of wolves on elk in the Greater Yellowstone Ecosystem have been contested among laypersons, politicians, and scientists—with some claiming devastation, others suggesting healing restoration, and most seeing something in between. In 1991, Montana State University initiated a study of about 400 to 600 elk inhabiting the Madison headwaters area in the west-central portion of Yellowstone National Park. The elk herd was nonmigratory and remained within the park year-round; therefore, the animals were not subject to harvest by human hunters. This high-elevation area has complex terrain, accumulates deep snow, and supports a mosaic of habitats including large tracts of burned and unburned forests interspersed with geothermal areas, meadows, rivers, and small lakes. The area is also an important winter range for bison that seasonally migrate west from their summer range in Hayden Valley. Prior to wolf restoration, coyotes were the only abundant mammalian predator, with some grizzly bears during spring and a few mountain lions. The study was initiated seven years before reintroduced wolves recolonized this portion of the park and continued thereafter, providing a rare opportunity to compare the responses of individual elk and the population as a whole to the restoration of a top predator that had been absent for approximately 70 years.

The protocol for the study was based on maintaining a representative sample of radio-collared female elk with biologists conducting extensive field work from November to May each year to monitor their behavior, nutrition, movements, pregnancy, survival, and population trends in response to forage, snow, predators, and other conditions. From 1991 to 2009, scientists amassed more than 12,000 person-days of field work and evaluated 15,000 observation periods of elk groups; 6,500 snow urine samples for assessing elk nutrition; 2,000 serum and fecal

samples for assessing elk pregnancy; 1,000 plant samples for assessing biomass and nutrition; 17,000 measurements of vegetation; 4,175 kilometers (2,594 miles) of snow tracking along wolf trails; and 750 carcasses of ungulates killed by wolves. Also, 4,300 snow cores and more than 24,000 hours of wind data were collected to model spatial and temporal dynamics of the snow pack.

Prior to wolf restoration, the probability of an elk dying was related to its age, body condition, and snow pack. The primary cause of death was starvation, with younger and older elk more likely to die than elk in the prime of their life (3-9 years old) that have uniformly high survival rates. Elk rely on their teeth to obtain and break up plant materials, which are further broken down by microbes in their four-chambered stomachs to obtain energy and protein. Teeth wear with age, so older elk become less efficient at obtaining nutrients and accumulating the fat and protein reserves needed to survive winter when the availability of nutritious foods is low. This is especially true in the Madison headwaters region where high concentrations of silica in the soils and fluoride in the waters accelerate tooth wear—thereby leading to a shortened life span compared to elk in other areas. In addition, calves are smaller in body size, and as a result have smaller stores of fat and protein to metabolize during winter when forage was scarce. Deep, prolonged, or hard snow conditions also increased the risk of starvation of young and old elk by limiting access to forage under the snow and requiring more energy for them to forage and move about the landscape. As a result, the proportion of elk in the population dying from starvation each winter varied among years depending on winter severity. However, elk that frequently used geothermal areas (where heat from the interior of the earth reduced or eliminated snow pack) were less vulnerable to starvation.



ILLUSTRATION © E. HARRINGTON

Wolves recolonizing the Madison headwaters area strongly preferred elk as prey and killed comparatively fewer bison, even though bison were more abundant than elk from midwinter through spring. Bison kills were more frequent during late winter when animals were in poorer condition. The wolves' preference for elk probably reflects the formidable challenge of killing bison, which form groups to aggressively and cooperatively defend themselves and their young. In contrast, elk do not use group defenses and generally flee when attacked. Wolves strongly selected calves and older elk, which are the age classes most vulnerable to starvation mortality during winters of average to severe snow pack. However, the survival of elk calves was lower and less variable among years after wolf numbers increased, suggesting predation limited the recruitment of animals into the breeding population. The survival of adult female elk was 5-15% lower following wolf recolonization, primarily in the middle to older age classes. The diets and nutrition of elk remained similar to those prior to the arrival of wolves. Elk pregnancy rates remained high, but elk abundance decreased rapidly as breeding females were killed and wolf predation on calves consistently reduced recruitment to low levels. As elk numbers decreased due to wolf predation,

wolf kill rates remained high and wolf numbers continued to grow. As a result, predation removed a higher portion of the elk population each year until elk became scarce. Thereafter, wolf kill rates decreased, strife among packs increased, wolf numbers declined, and packs began to hunt elsewhere for most of the year.

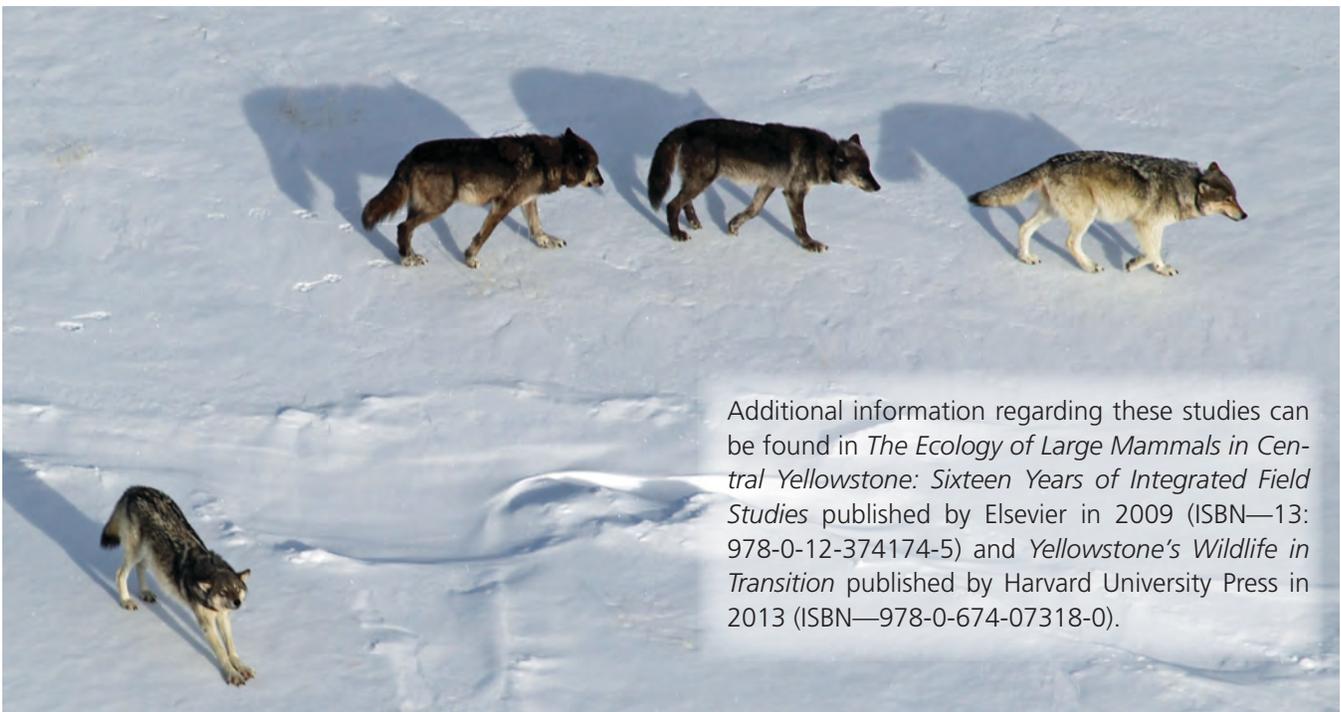
After wolves established in the Madison headwaters, the probability of an elk dying was strongly influenced by factors other than its physical condition, including characteristics of the landscape and weather that increased its susceptibility to predation by wolves. Elk at higher elevations with deeper snows were more likely to be killed by wolves, as were elk in thermal areas or meadows where they could be chased into habitat boundaries of deeper snow or burned timber with down-fall that impeded their escape. Conversely, elk on steep slopes with shallow snow and good visibility, or in areas where they could quickly escape to deep, swift, and wide rivers after encountering wolves, were less vulnerable to predation. As a result, in less than two decades, elk went from being numerous (~400-600 individuals) and broadly distributed throughout the Gibbon, Firehole, and Madison drainages during winter to scarce (less than 25 individuals) and constrained to relatively small refuges in the Madison drainage where

they were more likely to observe approaching wolves and escape if detected and attacked. Wolves killed nearly all of the elk in the Firehole and Gibbon drainages where susceptibility to predation was high. Many of these elk were strong and in good condition, but were caught in “terrain traps” where they were unable to flee effectively. Wolves also substantially lowered adult survival and limited recruitment in the Madison drainage; but less than two dozen elk persisted in areas with shallower snow bordered by the swift, deep, and wide Madison River. Encounters with wolves remained high in these areas, but adult elk were sometimes able to flee to nearby refuge habitat.

Ultimately, this study demonstrated how behavioral, physical, and environmental factors interact to influence the vulnerability of elk to predation by wolves and, in the end, revealed wolves can have a dramatic effect on the abundance and distribution of elk across the landscape. While the Madison headwaters study may represent what could be considered a “worst-case” scenario with respect to the impacts of wolf restoration on elk, the processes documented in this study are similar to those documented in other wolf-elk systems throughout the Greater Yellowstone Ecosystem by other research teams. Integrating the results from this impressive body of scientific work, we conclude the impacts of wolf restoration can be substantial for elk herds spending winter in forested, mountainous environments where elk are quite vulnerable to predation due to a heterogeneous landscape with deeper

snow pack. Predators tend to be more diverse and numerous in these areas due to lower susceptibility to human harvest and less conflict with livestock production. Conversely, the impacts of wolf restoration can be modest for elk herds spending winter in open, low-elevation valleys where elk are less vulnerable to predation due to a more homogeneous landscape with shallower snow. Also, predators tend to be less numerous in these areas due to high susceptibility to harvest and culls after livestock depredations. Over time, higher survival and recruitment in lower elevation valleys should lead to an increased proportion of elk spending winter in these areas. Indeed, a review of migratory elk populations throughout the Greater Yellowstone Ecosystem indicates broad-scale distribution shifts are occurring, with a higher portion of elk spending winter on lower-elevation ranges.

Certainly, many factors other than wolves, including human harvests, drought, and predation by bears and mountain lions, have had substantial effects on elk populations living in the Greater Yellowstone Ecosystem. However, the restoration of an additional top predator was a transformational event that eventually facilitated and maintained a substantive decrease in elk numbers and many other indirect effects to decomposers, other herbivores, predators, producers, and scavengers throughout the ecosystem. As a result, this bold restoration effort also led to a substantially improved understanding of the role of apex predators in terrestrial communities.



Additional information regarding these studies can be found in *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies* published by Elsevier in 2009 (ISBN—13: 978-0-12-374174-5) and *Yellowstone’s Wildlife in Transition* published by Harvard University Press in 2013 (ISBN—978-0-674-07318-0).

NPS PHOTO - D. STAHLER

Pelican Valley & Mollie's Pack

Douglas W. Smith, Travis Wyman, Daniel R. Stahler, & Daniel R. MacNulty

NPS PHOTO



Unlike the northern range, wolf work in the interior can be tough. So tough, it was originally envisioned as aerial monitoring only, which is how most wolf studies accomplish the task of remote study. Bob Garrott and his team had successfully mastered ground data collection in the Madison-Firehole river drainages, but work elsewhere seemed infeasible. Most of these other locations were far from roads.

Then in 1998, the idea of working in Pelican Valley came up—a long famous place and what some would call the “heart” of Yellowstone. Situated in the middle of the park and vital to much wildlife, it certainly fits. A pack of wolves lived there, named Mollie’s pack (after the late Director of the U.S. Fish and Wildlife Service who held her ground on wolf reintroduction despite criticism), and they seemed unique. Initially there were many hurdles to overcome; one was the uncertainty of success and, perhaps more importantly, some significant safety issues. The plan would entail camping out for two weeks in winter without a shelter and observing from a high point above the valley or an observation point (OP). Before that though, the first task was to see if the wolves were even in the valley enough to make observation worthwhile. A quick plotting of radio locations revealed wolves were in the valley a significant portion of the time, especially in late winter. We decided we might just have a project!

Clearing this new research with rangers and administrators took time. The administration’s desire was for us to use Pelican Springs cabin, but if we did we would not be able to see the valley. A daily ski across the valley would

disturb any wildlife we wished to observe. The decision was made to camp at the OP above the valley and stay put—no wildlife disturbance. In 1999, with scant winter equipment, we did just that. It proved to be a wise decision.

Once the hardship and struggle of hauling two weeks of gear across Pelican Valley was accomplished, with subpar equipment (especially sleds) and up a large hill, major scientific insights followed. At first we just watched and gathered behavioral data. Quickly, we realized there were few elk, and later no elk due to the harsh environment, so Mollie’s pack wolves had adapted to eating only bison in the winter.

Quickly the story became about wolves and bison. Formidable prey compared to elk, killing bison presented a different challenge to the wolves. Several bison kills were witnessed, and a few were filmed, wetting the appetite to learn more and how their strategy differed from killing elk. Bison commonly stand their ground, whereas elk commonly flee—a major difference we noticed right away. Wolves facing a 1,000-2,000 pound animal presented a unique set of problems; taking the bison head on was out of the question. Wolves would have to work the environment to their advantage. Watching and waiting for the right moment to attack was critical. Wolves seem to have all the time in the world, so they were never in a hurry and waited. When they decided to attack, they chipped away: attack, wound, and wait; attack, wound, and wait...Using this strategy, some kills took up to nine hours. The wolves also had to use terrain to their advantage. Wind-blown



hills had no snow and the bison favored such terrain for better footing; between the hills were troughs that collected snow, so the wolves favored these areas for attack as the snow hampered bison defense.

Confrontation between bison and wolves was stunning to watch; rarely observed nature in action. Pressuring bison for hours, wolves gradually drove them into deep snow and then jumped on them, many wolves at times, hanging from muscle and hide by their teeth. Once on firm ground, the bison shook the wolves off like water droplets, finally swinging their horns at them. Seemingly undeterred, the wolves waited for their next chance, or inexplicably left the bison, sensing an unseen cue or sign that made them abandon the effort.

At times, persistence paid off and a kill was made. But then another problem cropped up: who gets the spoils? This time of year a large bison carcass is a food bonanza. Every critter far and wide came in to grab what they could: weasels, foxes, coyotes, ravens, eagles, magpies, and grizzly bears. Once bears arrived it was over for the wolves. The carcass now belonged to them. Virtually every documented carcass in Pelican Valley from March through October attracted grizzly bears. It was not a matter of if but when, and the wolves had to grab as much meat as they could before the bears moved in. Up to 24 bears have been observed on one wolf kill at the same time. In March during our study, these carcasses became small “eco-centers” and most of the action in the valley occurred here.

Through time, our science became more sophisticated with fixed locations to observe from at regular intervals throughout the day, in addition to opportunistic observation of behavioral interactions. These observations indicated bison organized themselves differently when wolves were present in the valley versus when they were gone. Bison stayed closer to areas of good footing when wolves were around, and straying into riskier areas to forage when wolves were absent. Eventually the bison cow/calf groups left, probably because of wolf pressure, leaving about 40-80 hardy bulls for the wolves to deal with. So the valley changed, but in a vigorous way, and in fact gained some with the addition of wolves as they provided the carcasses that life hinged on in late winter.

Of course, we changed too. We purchased better equipment, especially sleds and light teepees that made living there for two weeks tolerable. We also dug into the snow and made caves to sleep in, and other years cut snow blocks with a saw to make an igloo. Crawling in either shelter, you could escape the near-constant roar of the wind or at night be oblivious to a foot of overnight snow that collapsed tents. For 16 straight years we managed the storms and wind that made Pelican Valley famous; and like with all things, we told stories, building memories that grew into a fondness for the place. After these years of study, it was felt our objectives had been achieved, so we turned things back to the valley, to the animals and plants that endure this harshness in the heart of Yellowstone.

Wolf Management: Den Closures, Habituation, & Hunting

*Douglas W. Smith, Kira A. Cassidy, Daniel R. Stahler, Erin E. Stahler,
& Rick McIntyre*

Although wolf reintroduction to Yellowstone National Park (YNP) was a very deliberate management action, and initially almost all of our work was management related, most of the wolf program today is monitoring and research. One reason for this is that there is almost no human safety threat posed by wolves. Why this is so is not entirely clear, but wolves seem to be naturally wary of people, or perhaps centuries of persecution have made them this way. Wolves are also less interested in human foods than other carnivores because they do not eat daily and are accustomed to the feeling of hunger. Therefore, it does not drive their behavior. Wolves commonly go days and sometimes a couple weeks without eating, so they do not become desperate for a meal. Wolves will feed on garbage, but when doing so are usually still wary of people (until conditioned). Overall, wolves are probably the least dangerous large carnivore. This does not mean we are not alert to the occasional wolf that may have received human food and is gradually losing its fear of people. Rather our management is not dominated by human-wolf interactions. Mostly we are focused on the flip-side, managing wolves so they are adequately protected from people—the other side of the National Park Service mandate. With Yellowstone being probably the best place in the world to view free-ranging wolves, much of our wolf management is geared toward people.

Protection of Wolf Dens & Rendezvous Sites

First and foremost are dens. Research has shown that wolves can be sensitive to human disturbance in the first six weeks after pups are born (Frame et al. 2007). Studies that have experimentally disturbed wolves during this time period found that sometimes the den will be relocated (Frame et al. 2007). Any time young pups are moved there is a risk of mortality, so this is the time period we try to protect wolves the most. The original Federal Special Regulations recommended protecting

areas around dens until June 30. After this date, pups are mature enough to withstand disturbance and den relocation. In Yellowstone, we have only used this date as an approximate guideline because some circumstances are unique to a park. For example, we keep a den in Lamar Valley and a rendezvous site (the above ground site that wolves use after a den) in Hayden Valley, both popular viewing areas, closed for longer not only to protect wolves but also to allow for visitor enjoyment—a key national park policy objective. If we opened these areas, many people, with no ill intent at all, would approach the wolves hoping to see or photograph one, especially a pup, which would displace the wolves and make them less visible afterward. Despite our protection, many people mistakenly walk into the Hayden Valley rendezvous site. Packs that use this area have low pup production. The correlation between few pups and high disturbance is a concern. This possible relationship has caused us to keep the area closed after the recommended June 30 deadline, wanting to err on the side of resource protection. Finally, remote dens are left unmanaged mostly because it is unlikely they will be disturbed.

NPS PHOTO



Wolf den sites are commonly found under tree roots.

Human Safety

Although the risk of human injury from a wolf is almost zero, it is not actually zero, so another management activity is to keep wolves and humans apart. Our best tool for this is enforcing the park regulation that people must stay 100 yards from a wolf (or bear), and if the wolf moves closer, then the person must *maintain this distance*. This will keep wolves and people safe and prevent habituation.

When wolves and people do interact, Mark McNay, formerly of the Alaska Department of Fish and Game, summarized the outcomes for North America during the 20th century (McNay 2002). He found only 19 cases of aggression of non-rabid wolves toward people from 1900-2001; these encounters excluded 20 incidents involving dogs or defensive behavior (protection by wolves of other wolves). There were no fatalities. Since 1969, there were 18 aggressive encounters and 11 of them involved habituated wolves (McNay 2002). Clearly, habituation needs to be prevented. How is this done? Keeping wolves and humans apart is one way, but keeping human food from them (similar to bears) is another.

Since McNay's study there have been three fatalities in North America, but the circumstances were similar. Wolves lost their natural fear of humans through exposure. It appears for wolves to attack humans they must first become familiar with them, lose their natural fear, and then attack, although this is very rare. This is not the case with other carnivores which may attack a person on their first encounter. In YNP, we have removed two wolves proactively because they had probably obtained human food and were exhibiting inappropriate behaviors (e.g., closely approaching humans). One wolf chased a person on a bicycle and a motorcycle. Another wolf walked up to several people and closely inspected anything they had in their hands (i.e., thinking it was food). In another situation this wolf tore apart a back-pack looking for food. Unfortunately, aversive conditioning did not work, so we removed them.

Before removal, park staff try everything they can to discourage habituated wolves (YNP 2003). Typically this means aversive conditioning. Confused with hazing, which is opportunistic negative reinforcement, aversive conditioning targets individuals. We start gently and escalate if there is no response--yelling, horns, and sirens first, graduating into cracker shells and ending with non-lethal bean bags or rubber bullets fired from a shotgun (YNP 2003). Initially, this was recommended against. We subjected these methods to professional review before we formulated our policy, and some comments were "don't

bother with aversive conditioning, it doesn't work, just kill the wolf." This has been done in other places because wolves are so common and removing a tame one will have little impact on the population. This is true, but in a park setting we chose to respond differently. And to some people's surprise, we have found aversive conditioning to be effective.

Habituation

Since wolf reintroduction, 55 wolves in 127 incidents have exhibited habituated behavior (this is different from McNay's "aggressive" category). Thirty-eight of these wolves were aversively conditioned 76 times; 49% of these actions immediately changed the wolves' behavior. Another 42% were probably successful, but not clearly so; because in eight cases we did nothing and the wolf never approached a person again. Finally, in 13 incidents the wolf either died or disappeared within six months of the incident. This is strong evidence that aversive conditioning does change habituated wolf behavior.

Where was habituation most common? Of the 127 events, 102 (80%) were on park roads, 14 (11%) in developments, and 11 (9%) were in the backcountry. Clearly the roads are a hot spot, and this is where the park has focused outreach and staff to avoid human-wolf contact. Most roadside encounters were in the spring/summer (May, June, and July; figure 1). This time period is also when pups become yearlings and many habituated wolves are young. Young wolves (yearlings in particular) have a lot of free time since older adults typically hunt and care for pups. Although yearlings do care for pups occasionally, they have less investment in pups so they take care of them less. They also explore and range widely and have a strong curiosity—which can lead them to humans. Some

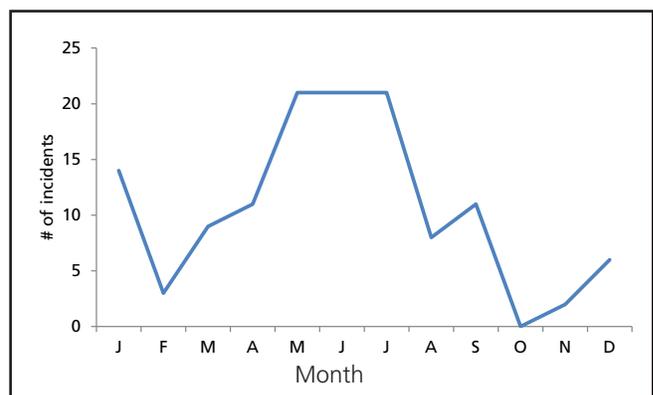


Figure 1. Wolf incidents with people by season in YNP 2002-2015. An incident is defined as closely approaching a person or lingering on the road near people.

have compared this to human teenager behavior. The lesson is to be alert to young wolves in spring.

Further, 54% of our habituated events have been confined to four packs, all of them road-adjacent packs: Canyon (23 incidents, 18%; pack lives in Hayden Valley area), Lamar Canyon (22 incidents, 17%), Druid Peak (13, 10%; Lamar Valley area combined with Lamar Canyon is 27% of incidents), and Hayden Valley (11 incidents, 9%; with Canyon, this is 27% of the incidents in the Hayden Valley area). Lamar and Hayden valleys are both open valleys with roads where visitors commonly encounter wolves. Arguably, these two valleys have more wolf-human proximity than any other location in North America. Certainly there are other places where wolf-human contact is more acute, but there might not be any other place where year-in and year-out wolves and humans coexist as much. Importantly, no one has been hurt, some aversive conditioning has occurred, and it has mostly been successful. Only one wolf (restricting the area to only these two valleys) has been removed.

Wolf Hunting Outside of Yellowstone

The last wolf management issue of concern is packs that primarily live in YNP, but wander outside of the park during the hunting season. Some of these wolves are legally harvested (figure 2). This is a difficult issue because the wolves are not aware of the boundary or the differing management objectives. These objectives are not mutually exclusive, but they are not the same. A gradual transition of regulations from inside the park to outside the park was necessary. Also, park wildlife that spend most of their

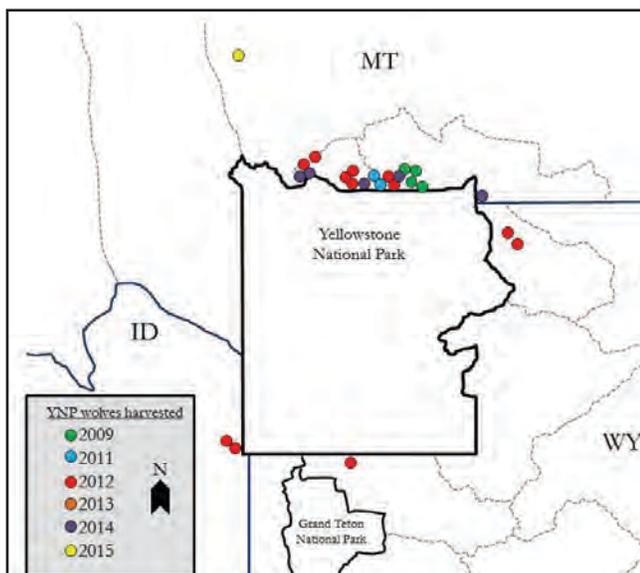


Figure 2. Harvest of wolves primarily living inside YNP outside of park boundaries by year.

time inside YNP are not conditioned to human hunting and are less wary and possibly more vulnerable to human take—wolves being one example. Many compare wolves to elk that are also cross-boundary, but migratory elk spend about half the year outside the park so they learn to be wary.

To accomplish this goal the states have created small hunting units with quotas next to the park. Montana has created two special hunting districts north of Yellowstone that limit the number of wolves that can be taken. Wyoming has also created relatively small hunting units next to YNP which allows for precise control of harvest. Both of these actions have limited the harvest of wolves that primarily live within YNP (figure 2). This regulated hunting will ensure that human-take outside of YNP will not impact the wolf numbers inside the park. These actions do not control what wolves will get harvested; but it does reduce the chances that a commonly observed wolf, cherished by the public, will be removed. It also preserves the social fabric within wolf packs by not removing too many wolves of high social rank, thereby preserving the natural functioning of the pack and population dynamics.

Overall, having wolves protected within YNP and harvested in a sustainable fashion outside the park is good for wolves in the long run. Such a mosaic of management practices protects wolves in some areas and limits them in areas of human conflict, which may reduce human dislike of wolves. Wolves are a polarizing issue for the public. Controlling problem wolves and hunting some of the others enhances acceptance of having them on human dominated landscapes. This is a foundational premise for all state agencies, and although questioned by some social scientists (Treves and Bruskotter 2014), has quelled some of the controversy over wolf restoration to the West. In the park, our mission is balancing wildlife protection with human enjoyment. It has taken some time; but we have achieved the proper balance for wolves to function as they should, and for people to observe and enjoy seeing wolves without harming them in a natural and wild setting.

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Winter Study

*Douglas W. Smith, Daniel R. Stahler, Matthew C. Metz, Kira A. Cassidy,
& Erin E. Stahler*

PHOTO © R. DONOVAN



Quinn Harrison digs out a mandible from the bone boiling pot. These collections are critical to predation research by the Wolf Project.

Winter study is the term used to describe our winter wolf research program. The study was mostly adapted after the winter wolf research project in Isle Royale National Park in Lake Superior, Michigan (Allen 1979) and partly after another project in the Brooks Range of Alaska (Dale et al. 1995). Historically, most wolf work has been done in the winter: packs roam together (unlike summer), leave easily observed tracks, and the white, snowy background make wolves easy to see from an airplane. Planes equipped with skis could land on lakes making huge swaths of otherwise

inaccessible country accessible. The Isle Royale research program established a winter study starting in 1959 which continues to this day, and named it simply “Winter Study” (Allen 1979). Researchers flew out to the island in early January (over Lake Superior and sometimes open water) and stayed for almost two months. They flew every day, weather permitting, looking for wolves, counting moose, and searching for moose killed by wolves. The results included annual estimates of wolf and moose numbers plus wolf predation rate—the proportion of the moose population killed by wolves annually (Mech 1966,

Peterson 1977, Vucetich et al. 2011). This work was the foundation for Yellowstone's winter wolf research.

Yellowstone is not Isle Royale. We are not an island, and we live on site year-round. There may be other times of year when data on wolves should be gathered. When designing our study we looked at another study in the Brooks Range of Alaska, where like Isle Royale they tried to string together many consecutive days flying, but varied the season and flew 30 consecutive days (weather permitting; Dale et al. 1995). The published results provided a good picture of how many and what kind of prey the wolves killed. We combined the two strategies: fly every day possible for two 30-day periods in early and late winter. We chose early and late winter because it was well known that wolf kill-rates change through winter, and book-ending winter would give us a good picture of the entire winter. So, since 1995 the Yellowstone Wolf Project has studied wolves for two, 30-day periods from mid-November through mid-De-

ember and again during the month of March. This has been our foundational research program and has generated some of our most important data. We have consistently done it every year, the same way; so data gathered are comparable, and changes can be tracked through time effectively.

This annual program has become a tradition for the Wolf Project, an annual ritual marking the passing of the seasons and years. Several hundred technicians have participated; the work is grueling, but some say it's the best experience of their lives. The work begins at first light to last light every day with one day off per week, and in March that can make for some very long days. One other difference for Yellowstone is we combine aerial surveys with ground surveys. Because Isle Royale and the Brooks Range are so remote, they have no road system, but we do. Using the road system, our design has three groups of volunteers, each assigned to a pack for 30 days. Their job is to be experts for that pack by keeping them in sight from the road. Simultaneously, when the weather permits, an airplane flies over all packs. This allows us to get a subset of data from three packs monitored both ways and monitoring by air only for the rest. In this way we can estimate what we are missing from air-only packs.

Importantly, winter study is fun. The park empties out, and it seems the wolves come alive. Winter is either moving in or out, and it's a wonderful time to be out every day. We have expanded into summertime studies now. As with time, all things change, and wolf research has too; but it would be hard to replace the tried and true winter-work, and we're happy for that.

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Piece by Piece: Wolf Project Sample Collections Go Beyond Ecology

Kira A. Cassidy, Deb Guernsey, Blaire Van Valkenburg, Quinn Harrison, Brenna Cassidy, & Erin E. Stabler



After being collected from the field and meticulously cleaned, the wolf skull collection is housed at the Heritage and Research Center in Gardiner, Montana.

Looking closely at a wolf skull can provide a glimpse into the life history of *Canis lupus*. The large teeth draw your eye first, especially the four canines—perfectly aligned, built for grasping prey and tearing muscle and tendon. A maze of nasal bones leads up to front-facing eye sockets—empty spaces once home to the hardwiring of a wolf’s strongest senses: olfaction and vision. And then the sagittal crest, that spike at the skull’s peak, that provides purchase to large masseter muscles for chewing through a femur to get the marrow, or holding on to a running, kicking elk or bison.

On top of those features evolution has bestowed upon the wolf, each individual also has a story to tell. Injuries, tooth wear, and infection (if manifested in the skull) can give details about the hardships a wolf encountered during its life. Following advice from Ron Nowak (a biologist specializing in wolf morphology who helped streamline the *Canis lupus* sub-species debate) the Yellowstone Wolf Project added wolf skulls to the list of biological samples collected. The collection has expanded our knowledge about gray wolves over the last two decades and continues to grow in size and depth.

These skulls are being used to assess rates of tooth wear and tooth fracture to compare with wolf populations from the past and other carnivores such as lions.

During times of food stress, carnivores tend to ingest more of a carcass by chewing and consuming bones. This practice leads to more rapid tooth wear and breakage; measuring it can help detect changes in carcass consumption in the last 20 years. When wolves were first introduced to Yellowstone, elk were very abundant. Consequently, wolves did not have to put extra effort into chewing bones to obtain nutrition. However, the number of elk has decreased and as a result the wolves may be finishing carcasses more completely and wearing their teeth more heavily. By tracking shifts in wolf tooth wear patterns through time, we can gain insights into how this large carnivore is affected by changes in prey availability. The effort to clean and process wolf skulls and teeth is incredibly time consuming and often underappreciated. Paleopathologist Sue Ware, for example, has cleaned, measured, and examined the skulls for evidence of cause of death, injuries, and abnormalities, spending countless hours in the lab processing and taking measurements.

In addition to skulls we also collect other samples—on both live and dead wolves—with the goal of answering specific biological questions. Genetic samples (either through whole blood collection or tissue samples) are sent to the University of California at Los Angeles, and have been used to construct a detailed pedigree of Yel-



Whole blood collected 14 and 20 years ago (from long-time alphas 21 and 42 of the Druid Peak pack) remain on file for future analysis. Samples to be sent for DNA analysis have to be stored in a freezer set at -80°C .

lowstone wolves. This information has been used to test the genetic health and viability of wolves in the northern Rocky Mountains (vonHoldt et al. 2008, 2010), to explore the process of domestication (Anderson et al. 2009, Janowitz Koch et al. 2016), and to investigate the effects of genes on heritable behaviors and traits (Hedrick et al. 2014, Schweizer et al. 2016).

Blood samples can reveal exposure to diseases by testing the serum for specific antibodies. These tests confirmed canine distemper virus (CDV) outbreaks coinciding with years of low pup survival and have provided insight into other, less fatal diseases, such as canine parvovirus, canine adenovirus, and canine herpesvirus (Almberg et al. 2009). In addition to serum evidence to the wolf's past, we collect whisker samples (1-2 per wolf during either capture or at death). These samples are analyzed to measure the isotopic signature of the wolf's diet from the previous six months. The species wolves prey on each have their own isotopic signatures based on the carbon:nitrogen ratio in their diets and pass this on to the wolves. This information has been an important addition to prey-selection work, especially with remote packs observed infrequently, as some packs seem to supplement their mainly elk-based diet with different species (e.g., deer, bison, and beaver).

Wolf scats have been collected to answer specific research questions related to prey-selection (Trejo 2012), disease exposure (Almberg et al. 2009), and genetic analysis (Ausband et al. 2010). These projects have helped hone data collection and analysis methods, including prey fur identification in a laboratory setting and viral stability in different climatic environments. During capture operations we take a variety of measurements of the wolf's body, including length, chest and neck circumference, and weight. These measurements have been used to model body mass changes between the sexes by age (MacNulty et al. 2009, Stahler et al. 2013).

With changes in the northern range elk herd size and composition, it has been essential to not only collect samples from wolves but also their main prey species. We visit many ungulate carcasses (killed by wolves and other causes of death) to collect a variety of samples. A tooth is used to determine the age of the prey and has helped confirm wolves often target the very oldest cow elk and youngest calves. Prey condition changes throughout the year with almost all elk in excellent shape in the late summer and fall as evidenced by high fat content in their femur marrow; however, by late winter many elk are in much poorer condition. By collecting



With over 1,300 elk mandibles collected, the Wolf Project assesses tooth wear patterns and jaw necrosis to determine age and condition of elk.

marrow samples all year, we can track the seasonal health of the herd to map the average and compare with those individuals killed by wolves. Collected samples from prey killed by wolves often have lower fat content than would be expected for that time of year.

Some samples can even be used to back-fill historic data on the health of the elk herd (Wright et al. 2003). We collect a metatarsus from each elk, as it is one of the last long bones to develop while the individual is still in utero. The development of this bone correlates well to the health of the elk's mother and can be affected by the mother's age but also the weather patterns and snow depth during her pregnancy and the previous summer's forage quality. To date, the Wolf Project has collected over 2,600 elk metatarses.

Many of the samples collected make their way from the field to holding freezers and then on to different labs throughout the country. However, the wolf skulls are housed in the park's Heritage and Research Center Museum. Given Yellowstone National Park's 144 years, and the ecosystem's thousands-of-years-long chronicle with wolves, it only seems fitting that the wolf skulls collected in Yellowstone represent this historic spirit. Over 160 wolf skulls are currently preserved in the museum

for everyone from students, researchers, and artists to enjoy. Each of the thousands of samples collected is unique and represents a concerted, sometimes exhausting, effort put into the collection process, with the end goal to advance the scientific knowledge and to reveal the intrinsic value of Yellowstone wolves, past and present.

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SNEAK PEEK

Coming Up in *Yellowstone Science*

Todd M. Koel

On the Rise: Native Fish Conservation in Yellowstone National Park

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Following the recession of glaciers some 8,000-10,000 years ago, native fish began dispersing to the Yellowstone region. By the late 1800s, the waters of Yellowstone supported 12 species (or subspecies) of native fish, including Arctic grayling, mountain whitefish, and cutthroat trout. These native fish species provided food for both wildlife and human inhabitants. After the establishment of Yellowstone Na-

tional Park in 1872, park inhabitants and visitors initially harvested fish for sustenance and survival in this wild, remote place. Early park superintendents noted the vast naturally fishless waters of the park, and asked the U.S. Fish Commission to stock them. The first nonnative fishes (fishes from outside the park) were planted in 1889-1890. So important were fisheries during this early period, this harvest-oriented, fish management program

accounted for over 310 million fish being planted in Yellowstone by 1955. In addition, between 1903 and 1953, some 818 million eggs were stripped from Yellowstone trout and shipped to locations throughout the country.

Popular publications describing the quality and abundance of fishing in Yellowstone became prominent. While most hunting was curtailed by early park management, the commercial harvest of fish was allowed to provide food for the hotels until 1917, the year after the National Park Service was created. During these early years, sport fishing became an accepted use of resources, and the phenomenal sport fishing experience that the park provided rose in notoriety. Yellowstone's recognition as an angling mecca was born. Largely due to the activities in Yellowstone and the popularity of its fisheries, recreational angling became a long-term, accepted use of national parks throughout the country.

Although Yellowstone has—and continues to be—an angling mecca with pristine waters supporting an abundance of fish, significant threats to the long-term persistence of native fish have emerged. Nonnative, predatory lake trout and exotic whirling disease were introduced to the vast, seemingly secure Yellowstone Lake ecosystem, home to the largest remaining concentration of cutthroat trout. In the early 2000s the impacts of an expanding lake trout population and whirling disease coincided with that of drought, resulting in a precipitous decline in cutthroat trout. Cascading effects through the ecosystem were documented. Grizzly bears are now seldom seen on cutthroat trout spawning tributaries, and few ospreys prey on cutthroat trout near the lake's surface or nest in adjacent trees. As measured by the frequency with which Yellowstone cutthroat trout are caught, angler success on Yellowstone Lake is less than one-half of what it once was prior to the existence of lake trout.

Coinciding with the cutthroat trout decline in Yellowstone Lake were changes in another previous stronghold for this species in the park, the Lamar River. Rainbow trout, which were intentionally introduced by park managers in the early 1900s and propagated at the Trout Lake hatchery near lower Soda Butte Creek, historically remained concentrated in the Yellowstone River below the falls at Canyon and the lower Lamar River. In the early 2000s, however, anglers began reporting catches of rainbow trout upstream more frequently. As rainbow trout hybridize with cutthroat trout, their spread has raised concerns about the security of the cutthroat trout in the upper Lamar River system. Additionally,

westslope cutthroat trout and fluvial Arctic grayling, native to the upper Madison and Gallatin drainages, were largely lost due to the historic stocking of nonnative fish in Yellowstone. Only a single, small aboriginal westslope cutthroat trout population remains, discovered in 2005 in aptly named Last Chance Creek, a tributary to Grayling Creek. No aboriginal fluvial Arctic grayling remain.

Yellowstone's native fish have underpinned natural food webs, had great local economic significance, provided unparalleled visitor experiences, and defined much of the park's 20th century historical context. To address recent and historical losses, and reverse declining trends in native fish populations and loss of ecosystem function, the National Park Service has sought to take actions that will ensure their recovery.

In the next issue of *Yellowstone Science*, significant accomplishments made in restoring native fish over the past decade will be described. In addition, research and development of methods to more efficiently control nonnative lake trout will be presented. The issue will include articles with a broader scope that describe the range-wide status of Yellowstone cutthroat trout and efforts to prevent the introduction of additional aquatic invasive species across the Greater Yellowstone Ecosystem. Of particular importance will be a description and recognition of the many partners who support and contribute to the Native Fish Conservation Program in Yellowstone, and research being undertaken to conserve Yellowstone's native fish through 2016, the National Park Service centennial year.

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NPS photographers included: Dan Stahler, Doug Smith, Erin Stahler, Kira Cassidy, Jim Peaco, Matthew Metz, and Neal Herbert.

If you are interested in donating photography for consideration in our publications, please contact us at yell_science@nps.gov.

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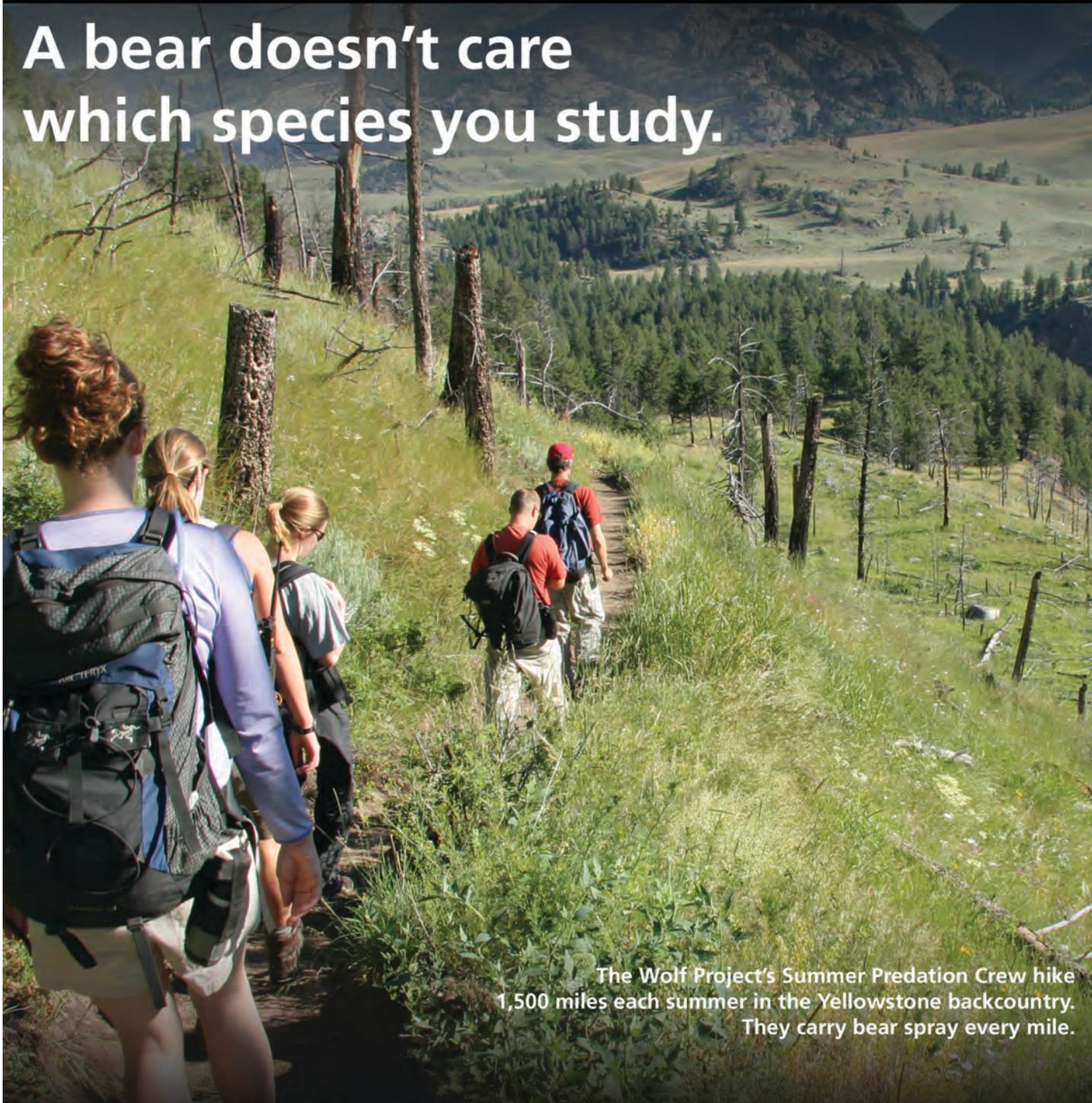
Back row (left to right): Ellie Schmidt, Quinn Harrison, Dan Stahler, Roberta Ryan, Lisa Koitzsch, Ky Koitzsch. Middle row (left to right): Jane Dentinger, Lizzie Cato, Erin Stahler, Brenna Cassidy, Kira Cassidy, Doug Smith, Lisa Lochner, Melissa DiNino. Front row (left to right): Grace Glynn, Anna Peterson, Becca Thomas-Kvzilik. Not pictured: Rick McIntyre, Matt Metz.



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