Biodiversity and the "Crystal" Salamanders of Yellowstone

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BIODIVERSITY IS A COMPLEX and nebulous concept. At its most fundamental level, biodiversity is defined as the number of species found in a region. Conservation efforts generally attempt to maximize and preserve the variety of native plants and animals. The number of organisms found in a healthy ecosystem is determined by several factors, including the heterogeneity of the habitat, with more diverse habitats generally able to support more species and more communities (Huston 1994). Yellowstone National Park currently contains dozens of mammal species, hundreds of bird species, and more than a thousand species of vascular plants. Counting animals and plants is comparatively easy next to characterizing the park's innumerable microscopic fauna, which include countless species of fungi, bacteria, and other microscopic organisms, many of which thrive in Yellowstone's famously extreme geothermal environments. Our estimate of species number increases every year with new discoveries.

Although the number of species in a region may be a rough proxy for the health of the ecosystem, it reflects neither the viability nor the full diversity of the species and populations. In general, a healthy ecosystem contains not only a diverse array of species, but also a large amount of variation within any given species. Physical and genetic diversity can be crucial to species persistence, and genetic diversity provides the variation necessary to meet novel ecological challenges, including disease outbreaks and environmental change.

The phenotype of an organism is the manifestation of its set of physical and behavioral characteristics, which are governed by a complex interplay between the genetic makeup of the organism and its environment. Phenotypic variation within a species is often closely tied to local habitat conditions, and specific environmental conditions can directly and sometimes dramatically modify phenotype. This flexibility is known as phenotype plasticity, and is considered part of the developmental toolkit necessary for survival in an unpredictable ecosystem. Certain phenotypes only occur under particular environmental conditions, and plastic phenotype variation can reflect the heterogeneity of the environment (Fig. 1). This phenotype diversity adds to the richness of a species, and may buffer against ecosystem change and species decline.

From Pond to Pond: Population Plasticity

Generation and maintenance of all levels of diversity motivate much of the research in the Hadly Lab at Stanford University. As a graduate student in Dr. Elizabeth Hadly's

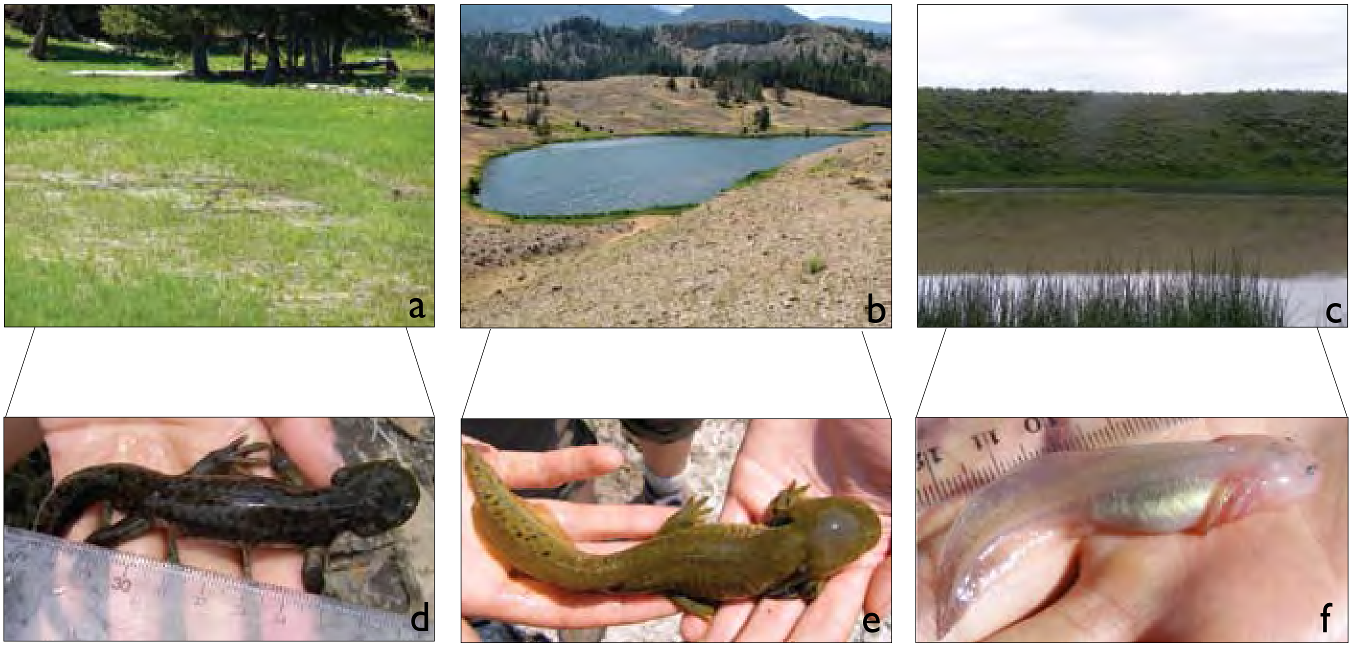

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Figure 1. Habitat–phenotype relationships in tiger salamanders. Ephemeral wetlands (a) support rapidly metamorphosing populations (d). Permanent ponds and fishless lakes (b) can support adults as well as reproductively mature paedamorphs (e); extremely murky ponds (c) support "crystal" juvenile populations (f).

group, I explore environmentally mediated phenotypes and developmental variation in amphibians. I investigate how changes in the environment affect the phenotype and genetics of populations. My dissertation research focuses on diversity of the amphibians of Yellowstone, specifically the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). I am particularly interested in the spectrum of developmental strategies employed by tiger salamanders in northern Yellowstone, where spatial and temporal environmental variability yields a wide variety of salamander phenotypes.

"This finding reminds us that novelty and biological mystery truly still exist."

Salamanders are extraordinary in their ability to respond to their environment, and their phenotype often dramatically reflects their developmental conditions (Gould 1977). Like most amphibians, tiger salamanders have a biphasic life cycle consisting of a larval aquatic stage followed by metamorphosis into a reproductively mature semi-terrestrial stage (Fig. 1d). In Yellowstone, ephemeral, rapidly drying ponds support only rapidly growing larval individuals that undergo metamorphosis at a small size. More permanent, resource-rich ponds often yield populations that metamorphose later in life and at larger body sizes. These leisurely individuals may even delay metamorphosis until their second year, overwintering at the bottoms of ponds as large juveniles (Koch and Peterson 1995). Individuals from more permanent environments are often more healthy and well-adapted than their rapidly growing counterparts (Semlitsch and Wilbur 1988).

Another Hadly Lab member, Judsen Bruzgul, demonstrated how Yellowstone salamander populations have modified developmental strategies over time (Bruzgul et al. 2005). Fossils of tiger salamanders from Yellowstone show that the amount of time individuals spent in the larval stage versus the terrestrial stage changed in response to climate fluctuations over the last several thousand years. When climate was warmer and ponds dried more quickly, salamanders spent less time in the larval stage and reached large sizes during the terrestrial stage. In contrast, when climate was cooler and wetter and ponds were more permanent, salamanders spent more time in pond environments and grew larger during their aquatic phase. These findings emphasize the ability of this species to adapt to environmental variability, and stress that changing conditions are quickly reflected in the physical characteristics of the population.

In extreme cases of life cycle plasticity, larval tiger salamanders may forgo metamorphosis altogether, developing instead as sexually mature larvae known as paedomorphs. One North American species of salamander, the Mexican axolotl (*A. mexicanum*), is exclusively paedomorphic in nature, metamorphosing only under the most stressful conditions. Tiger salamanders are facultatively paedomorphic, meaning that they will adopt paedomorphosis only under certain environmental conditions. Although this phenomenon has some genetic component (Voss and Smith 2005), it is driven predominantly by environmental factors, and paedomorphosis occurs in some individuals only when the environment is particularly permanent and habitable. Paedomorphic tiger salamanders are relatively uncommon, but have been found in several high elevation lakes in northern Yellowstone (Hill 1995, Spear 2004) and were collected from these environments in the last several years (Fig. 1e). Using genetic markers to model the genetic relationships within the population, we found little genetic difference between these paedomorphs and the rest of the Yellowstone salamander population. This underscores the fact that these paedomorphs are determined environmentally—rather than genetically—and that they require exceptionally stable and productive environments in order to be maintained in the population.

Salamanders may also show considerable variety in coloration. Color variation is extremely common in vertebrates, and often evolves rapidly. This variation is often co-opted and maintained as cryptic coloration, which allows individuals to blend into their environments. This type of camouflage provides an enormous selective advantage, as it renders organisms less visible to predators and prey. Specifically adaptive cryptic variation has been characterized in many vertebrates, from mammals (Hoekstra et al. 2006) to reptiles (Rosenblum et al. 2004) and amphibians (Storfer et al. 1999), and the adaptation can often be traced to small changes in single genes. Coloration frequently varies along environmental gradients, even within species, stressing that the selective advantage or disadvantage of a particular color is entirely context-dependent. Take a polar bear out of the arctic and put him in a jungle and he is very poorly disguised indeed. Likewise, flip a fish over in the water, and suddenly her light belly and dark back make her extremely conspicuous.

Yellowstone's "Crystal" Salamanders

In a multi-year study of amphibian phenotypic and genetic diversity, I discovered a particularly dramatic case of color variation. In two small adjacent ponds in northern Yellowstone, my assistants and I found numerous larval salamanders almost entirely devoid of pigmentation, giving them a distinctive crystalline appearance (Fig. 1f). Anomalous albinos appearing in otherwise normal populations have been recorded before, and at first I thought that these clear individuals would be unusual among a pond full of normal, dark green salamander larvae. But after hours of wading around with nets and fishing out dozens of individuals, each as clear as the last, I realized that these ponds contained something truly novel. Every individual was so thoroughly devoid of coloration that it was rendered largely transparent, with internal organs readily visible in sunlight. In some individuals, we were actually able to observe blood pumping through their tiny hearts. Their gills were pale pink and their skin was sparklingly translucent, giving them the appearance of being made of glass or crystal.

Excited about the discovery, I called my advisor, Liz Hadly. She noted that since the salamanders had dark, rather than red or pink eyes, as well as some coloration at the end of their tails, they must be physiologically and genetically capable of producing pigment. These individuals were therefore more accurately described as leucistic rather than albino. Closer inspection over the next several days revealed that most of them did in fact possess tiny melanophore pigment cells in their skin, but these cells were much smaller and at a far lower density than in normal individuals.

These two ponds have been examined numerous times by several different amphibian research groups in recent decades, and this is the first time anyone has observed and recorded this singular phenotype. According to Stephen Spear, who sampled salamanders across northern Yellowstone in 2002 and 2003, he found light colored adults in these particular ponds, but never any juveniles, suggesting that although metamorphs migrated to the ponds, active breeding and development of juveniles may not have been occurring. Has something recently changed in the environment that has caused the populations to exhibit this phenotype? Or have we simply missed this unique and extraordinary phenomenon? This finding reminds us that novelty and biological mystery truly still exist.

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The typically dark green cryptic coloration of a growing juvenile salamander found in Yellowstone. Skin pigmentation protects the salamander from the sun and allows it to blend with its pond environment.

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Crystal salamanders are almost entirely devoid of pigment. These were the only types of salamanders found at the survey location in northern Yellowstone.

Leucism, albinism, and various other forms of amelanism are rare, but their appearance is nearly ubiquitous throughout the animal kingdom. Albinos routinely appear in both vertebrate and invertebrate populations. Albinism and leucism have been documented in many North American species of salamanders (Hensley 1959). Amphibian researchers, including Robert Reese (1969), Ben Novak (Montana State University, pers. comm.), and Randal Voss (University of Kentucky, pers. comm.) have found light or transparent juvenile and adult tiger salamanders in the field, sometimes in large numbers. These and other color aberrations are generally caused by genetic mutations that disrupt pigment formation or inhibit the migration of pigmented neural crest cells. Because being extremely light in color is an enormous cryptic disadvantage in normal tiger salamander habitats, alleles for light phenotypes are unlikely to be maintained or fixed in the population. However, in extremely low-light environments such as the bottoms of turbid ponds, the necessity of camouflage and sun protection is removed, and genetic albinism may become very common.


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A light-colored adult found in a crystal salamander pond, possibly metamorphosed from a crystal juvenile. Compare to the more typical coloration of the adult in Figure 1d.

The ponds containing the crystal populations have high clay content, making them abnormally murky. It therefore seemed plausible that the low density of pigment cells was caused by genetic factors selectively advantageous in these environments. However, it was surprising both that this phenotype was exclusive to these locations, and that we did not find any normally pigmented salamanders in either of these two ponds. Given the large amount of genetic exchange with other local populations, we would expect some amount of phenotypic "spillover" if this phenomenon were exclusively genetic. Instead we found none.


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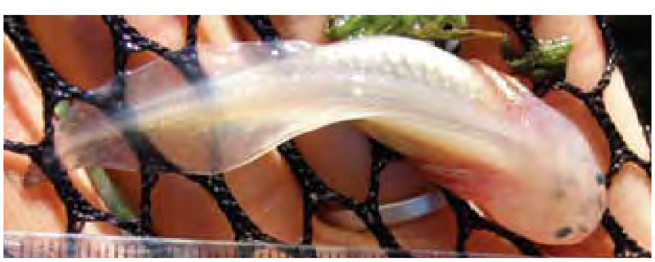

Above: A normally pigmented juvenile tiger salamander.
Below: A Yellowstone crystal salamander in a dip net.

Crystal Phenotype—Genetic or Environmental?

Back in the lab, we set out to determine the genetic relationships between ponds in this region, hoping to determine whether the phenotype was caused by genetic factors. My undergraduate assistants and I spent the remainder of the summer isolating and analyzing genetic material from tissue of these extraordinary individuals. Small tail clips were collected from all the salamanders trapped or netted from ponds in Yellowstone, and we used these tissue samples to examine the genetic makeup of the individuals and populations. The tail clips are quite harmless to the amphibians, which grow back the end of their tails after we return them to the wild. Using neutral genetic markers that can help determine recent relatedness (Spear et al. 2005), we have found that the crystal individuals fit neatly into the genetic context of the rest of the Yellowstone population. Individuals from within these ponds are not any more closely related to one another than we would expect any pond population to be, and they are not notably genetically distinct from neighboring populations. If this phenotype were caused by a single genetic mutation or even several interacting genetic factors, we would expect all of the individuals showing the phenotype to be closely related: direct offspring of a few progenitors carrying genes for the crystal phenotype. But our genetic analyses show that these ponds still exchange a large amount of genetic material with the surrounding populations—far too much for such a specific adaptation to persist at such a high frequency.

These genetic findings allow us to conclude that we are observing an ecologically determined phenotype. Now we need to determine what unique ecological factor produces these types of individuals. Perhaps these ponds are deficient in a chemical necessary for normal pigment synthesis, or perhaps the environment somehow blocks production, migration, or expansion of pigment cells. Larvae of several amphibian species, including *A. tigrinum*, express the optic pigment melanopsin in their epidermal tissue, which renders their skin slightly photosensitive (Provencio et al. 1998). Under low-light conditions, the melanophore pigment cells in the skin of tiger salamander larvae contract, causing individuals to pale within minutes or hours (Laurens 1917). It is possible that so little light penetrates the murky water of these ponds, the larvae are exhibiting a dynamic response to their environment. As the water level goes down over the course of a summer, and the individuals within are exposed to more sunlight, they appear to become less transparent (Stacey Gunther, Yellowstone National Park Research Permit Office, pers. comm.). This suggests that the melanophores expanded in response to increasing light exposure as the pond dried.

Certain transparent salamanders from outside of the park also appear to display photosensitivity, by darkening in response to brighter conditions (Ben Novak, pers. comm.). Although this type of photosensitivity is probably contributing to the crystal phenotype, these individuals certainly contain fewer melanophore cells than do normal salamanders, a phenomenon likely governed by longer-term environmental responses. Although the specific causes remain to be researched in depth, it is clear that this phenomenon is environmentally driven and that it is beneficial or at least neutral for individuals living in these abnormally murky pond environments.

The crystal salamanders enhance our concept of biodiversity, and are part of the rich biotic heritage of Yellowstone National Park. Here is a singular phenotype, matched superbly to the environment that causes it. In light of climate change in Yellowstone and elsewhere (McMenamin et al. 2008), these populations highlight the importance of the irreplaceable variance of the park's landscape, which fosters the deep diversity in its constituent vertebrate species.

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PHOTO COURTESY OF THE AUTHOR

Sarah McMenamin is a PhD candidate in the Department of Ecology and Evolution at Stanford University, and has been involved in Yellowstone research for four years. Sarah received her undergraduate degree magna cum laude from Mount Holyoke College in 2004.

Literature Cited

Bruzgul, J. E., W. Long, and E. A. Hadly. 2005. Temporal response of the tiger salamander (*Ambystoma tigrinum*) to 3,000 years of climatic variation. BMC *Ecology* 5:7.

Gould, S. J. 1977. Ontogeny and phylogeny. Cambridge: Belknap Press of Harvard University Press.

Hensley, M. 1959. Albinism in North American amphibians and reptiles. East Lansing: Museum of Michigan State University.

Hill, S. R. 1995. Migratory chronology of adult tiger salamanders (*Ambystoma tigrinum*) and survey of larvae of the tiger salamander in the northern range of Yellowstone National Park. MS Thesis. Montana State University, Bozeman.

Hoekstra, H. E., R. J. Hirschmann, R. A. Bundey, P. A. Insel, and J. P. Crossland. 2006. A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science* 313:101–104.

Huston, M. A. 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge: Cambridge University Press.

Koch, E. D., and C. R. Peterson. 1995. Amphibians & reptiles of Yellowstone and Grand Teton National Parks. Salt Lake City: University of Utah Press.

Laurens, H. 1917. The reactions of the melanophores of *Ambystoma tigrinum* larvae to light and darkness. *Journal of Experimental Zoology* 23:195–205.

McMenamin, S. K., E. A. Hadly, and C. Wright. 2008. Climatic change and wetland desiccation cause amphibian decline in world's oldest national park. *Proceedings of the National Academy of Sciences* 105 (44):16988–93.

Provencio, I., G. Jiang, W. J. De Grip, W. P. Hayes, and M. D. Rollag. 1998. Melanopsin: An opsin in melanophores, brain and eye. *Proceedings of the National Academy of Sciences* 95:340–345.

Reese, R. W. 1969. The taxonomy and ecology of the tiger salamander *Ambystoma tigrinum* of Colorado. PhD Thesis. University of Colorado, Boulder.

Rosenblum, E. B., H. E. Hoekstra, and M. W. Nachman. 2004. Adaptive reptile color variation and the evolution of the MCIR gene. *Evolution* 58:1794–1808.

Semlitsch, R. D., and H. M. Wilbur. 1988. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. *Copeia* 1988:978–983.

Spear, S. 2004. Landscape effects on genetic structure in tiger salamander (*Ambystoma tigrinum melanostictum*) populations across the northern range of Yellowstone National Park. MS Thesis. Idaho State University, Pocatello.

Spear, S. F., C. R. Peterson, M. D. Matocq, and A. Storfer. 2005. Landscape genetics of the blotched tiger salamander (*Ambystoma tigrinum melanostictum*). *Molecular Ecology* 14:2553–2564.

Storfer, A., J. Cross, V. Rush, and J. Caruso. 1999. Adaptive coloration and gene flow as a constraint to local adaptation in the streamside salamander, *Ambystoma barbouri*. *Evolution* 53:889–898.

Voss, S. R., and J. J. Smith. 2005. Evolution of salamander life cycles: A major effect QTL contributes to discrete and continuous variation for metamorphic timing. *Genetics*, 170:275-281.

NPS/KERRY GUNTHER

Presence and Distribution of White-tailed Jackrabbits in Yellowstone National Park

Kerry A. Gunther, Roy A. Renkin, James C. Halfpenny, Stacey M. Gunther, Troy Davis, Paul Schullery, and Lee Whittlesey

WHITE-TAILED JACKRABBITS (*Lepus townsendii*), the only hares which frequent Yellowstone National Park's grassland and sagebrush habitats, have persisted with very little fanfare in a limited range of the park since its creation in 1872. A January 2008 article published in the scientific journal *Oryx* and based on a study by Joel Berger, concluded that the park's jackrabbit population was extirpated (Berger 2008a), provoking debate and nationwide news coverage. Berger, a scientist at the Wildlife Conservation Society and professor at the University of Montana, inferred from historical publications that jackrabbits were once abundant across the northern portion of the park and claimed they were "virtually non-existent" by 1990–91, and that none had been seen there since (Berger 2008a). He also recommended the National Park Service (NPS) consider reintroducing white-tailed jackrabbits to restore ecological integrity.

After an Associated Press release about Berger's study (Brown 2008a), park staff received many phone calls and e-mails concerning jackrabbits. Some past visitors submitted anecdotal observations and others requested that the NPS immediately begin a jackrabbit reintroduction program. Berger later retracted his claim that jackrabbits were extirpated from the park (Berger 2008b), though he continued to imply that they were "markedly reduced in range" in Yellowstone National Park and jackrabbit abundance in both Yellowstone and Grand Teton national parks was caught in a "downward spiral" (Berger 2008c, Brown 2008b).

As a result of Berger's article and public interest, white-tailed jackrabbits became something of a mini-controversy and were given more thought and consideration in Yellowstone than ever before. Observations by the authors of this article and other anecdotal records did not support Berger's claims. Instead, they suggested that the jackrabbit abundance and distribution had not changed significantly in Yellowstone for at least the last 20 to 50 years and prompted a re-examination of the historical record.

Methods

Due to the interest and debate generated by Berger's research, we looked at historical information that might lend insight into the past abundance and distribution of jackrabbits in Yellowstone as well as contemporary park records and databases. We also queried biologists and naturalists who worked in the park on a long-term basis for information on current presence, abundance, and distribution. The methods we used in this study were a cost-effective means of obtaining basic, preliminary information on jackrabbits in a timely manner. We do not consider this study to be a substitute for a systematic survey of jackrabbit abundance and distribution in the park.

We reviewed materials located by the park's library and archive technicians, including books, journals, and naturalist reports, for information concerning the abundance and distribution of jackrabbits in the park. We also searched the park's road-killed wildlife and rare animal databases for records of jackrabbits. We reasoned the chances of observing wildlife would be greatest along roads and in developed areas because of the number of people and amount of time people spend in those areas. Both of these databases are therefore biased toward animals seen near park roads. Naturalist-tracker James Halfpenny also conducted three ground surveys to detect jackrabbit tracks and other sign in northern Yellowstone in 2008.

Our field experience in the park spans five decades. Therefore, we were able to use our personal observations of jackrabbits from living and working in Yellowstone to assess the species' presence or absence and current distribution. We also queried 12 other professional biologists each with 3 to 50 years of experience in the northern portion of the park, the only area where jackrabbits were reported to occur during historical (1872–1949) and contemporary (1950–2008) periods.

The apparently limited distribution of jackrabbits in Yellowstone suggests that much of the park is not suitable habitat. We plotted locations of jackrabbit observations, road-killed carcasses, and their sign (i.e., tracks and fecal pellets) and compared them to maps of vegetation habitat types, elevation, and average annual precipitation zones to evaluate if any of those factors influence jackrabbit distribution.

Results and Discussion

Historical Record

Evidence from Lamar Cave. Barnosky (1994) found bones of at least one white-tailed jackrabbit in one of the upper levels of her excavation in Lamar Cave on the northern range. Radiocarbon aging of a piece of wood excavated at the same level indicated that the bones were from 0 to 419 years before 1994.

Ludlow's Expedition. In 1875, Captain William Ludlow made a reconnaissance trip from Carroll, Montana (Territory), to the park and back, accompanied by naturalist George Bird Grinnell. Ludlow's report (Ludlow 1876), which contained Grinnell's descriptions of the wildlife they observed, never mentions seeing jackrabbits while in the park, nor were jackrabbits on the list of species they observed in the park. Berger (2008a) inferred from Captain Ludlow's 1876 trip report that jackrabbits were once abundant in the park. In the report's discussion of prairie hares (another name for the white-tailed jackrabbit), they stated:

> *This species is very abundant in some localities, while in others, quite as favorable for it, it is not found at all. In fact, the abundance or scarcity of the Prairie Hare in any district depends almost altogether on the number of wolves to be found in the same tract of country. Where all the coyotes and gray wolves have been killed or driven off, the hares exist in great numbers; but where the former are abundant, the latter are seldom seen. We saw none near the Missouri River, where the buffalos [sic] and consequently the wolves, were numerous; but at Camp Baker, where there are scarcely any wolves, the hares were very common.*

Camp Baker is approximately 200 km (125 mi) north of Mammoth Hot Springs and 460 m (1,500 ft) lower in elevation, so the habitat and winter snow accumulation were likely very different there. The report gives us no insight into the presence or absence, abundance, or distribution of jackrabbits in the park in the 1870s.

Milton Skinner's *The Yellowstone Nature Book.* Milton Skinner's *The Yellowstone Nature Book* (1926) is the earliest reference that we were able to locate which documents both the presence and distribution of jackrabbits in the park. A more exhaustive search of the archives may reveal others. Skinner reported that "These big gray jack rabbits with their large white tails are common between Gardiner and Mammoth Hot Springs, and may also be seen almost anywhere in the open northern sections of the Park."

The first half of Skinner's description refers to the same area where jackrabbits are regularly observed today—near Reese Creek, Stephens Creek, Rifle Range Flats, Rattlesnake

NPS/JANINE WALLER

White-tailed jackrabbit on Rifle Range Flats, April 2008.

Mad as a March Hare

The Facts about White-tailed Jackrabbits

Body length: 565–655 mm (22–25 in)
Tail: 66–112 mm (3–4 in)
Rear feet: 145–172 mm (6–7 in)
Ears: 93–113 mm (4 in)
(After Hall and Kelson 1959)

White-tailed jackrabbits (*Lepus townsendii*) are a familiar, if not entirely predictable, sight to anyone driving from Mammoth Hot Springs to Stephens Creek in the morning and evening. Scientific study of white-tailed jackrabbits is limited, and in many parts of the country, jackrabbits are considered agricultural pests.

White-tailed jackrabbits are found in prairie-grassland and grass-shrub steppe habitat types in western high plains and mountains. They are sometimes associated with croplands and pasture when uncultivated land is present along fence lines (Dubke 1973). However, white-tailed jackrabbits generally prefer grass-dominated habitats. They have also been found to flourish above treeline in the alpine zone and avoid forested areas (Bailey 1936).


NPS/STACEY GUNTHER

Description

Jackrabbits are members of Lagomorpha, a well-distributed order containing 81 species of rabbits, hares, and pikas. Hares and rabbits are grouped together in the Leporidae family. Despite their name, jackrabbits are actually hares in the genus *Lepus*. Jackrabbits are easily distinguished from true rabbits by their large ears, large feet, and generally large body size. Hares use their ears to listen for danger and to radiate body heat. The flow of blood through the thin tissue of the ears allows them to dissipate excess body heat and tolerate body temperatures up to 41°C (106°F) (Forsyth 1999).

The summer coat of the white-tailed jackrabbit is grayish brown, with a lighter underside. The ears are rimmed with black. In southern areas of its range, the winter coat is very similar to the summer coat, though often paler. Further north, where there is persistent and widespread snow cover, as in Yellowstone National Park, the winter coat undergoes a striking color change to nearly white. The white-tailed jackrabbit is the only species of jackrabbit in North America to consistently exhibit two annual coat molts.

Behavior

Hares differ from other lagomorphs in that they rest and breed in shallow depressions or scrapes, known as forms, which are often located under shrubs or bushes. White-tailed jackrabbits are rarely seen in groups; in fact, they may be the least social of the hares (Lim 1987).

White-tailed jackrabbits exhibit nocturnal activity patterns, presumably to avoid detection by predators. Generally, white-tails forage in the open at night, but are less active during the day and retreat to denser cover (Fautin 1946, Lechleitner 1958). A full moon can delay their nocturnal foraging by several hours (Flinders and Chapman 2003). Once under cover of darkness they feed on grasses, forbs, and shrubs, selecting the newest and most succulent plant material (Flinders and Hansen 1972).

In the presence of a perceived threat, jackrabbits use their hearing to avoid a confrontation if possible. If surprised at close range, they rely on cryptic coloration and behavior, such as remaining motionless. If necessary, jackrabbits attempt escape by running at speeds from 56 to 80 kph (35 to 50 mph) and cover 2–3 m (6–10 ft) with each bound. White-tailed jackrabbits will also swim to escape pursuit, paddling with their front legs (Orr 1940, Lechleitner 1958).

Breeding

Some hares exhibit energetic and unusual mating behavior in the spring. These potentially confusing displays have given us the expression "Mad as a March Hare" and the eccentric March Hare character in *Alice in Wonderland*. Jackrabbit mating begins with a vigorous pursuit of the female by the male. As the chase progresses, one jackrabbit will begin leaping while the other runs underneath.

Rabbits and hares are well-known for their prolific breeding abilities. White-tailed jackrabbits can breed in the spring following their birth and often have several litters annually thereafter. Jackrabbit reproduction is similar to that of other lagomorphs in that ovulation is induced, meaning that it requires an act of copulation. More than the black-tailed jackrabbit, white-tails show variation in their reproductive rate, ranging from a single litter per year to four litters annually. Litter size is similarly flexible, varying from 1 to 15. Gestation is 36–43 days, averaging 42 days (Kline 1963).

The young of jackrabbits, leverets, are much more precocious than other lagomorphs (young rabbits are referred to as kittens). Hare leverets, for example, are born fully furred and with their eyes open, while rabbit kittens are born hairless and blind. Jackrabbits can leave the form within 24 hours of birth, begin foraging at two weeks, and are usually weaned after a month, when rabbit kittens are still in a fur-lined nest underground.

In most areas, the breeding season of white-tailed jackrabbits averages 148 days and can extend from late February to mid-July. The timing of white-tail breeding in the northern Yellowstone ecosystem is not well documented.

Butte, Rescue Creek Trailhead, Gardner River High Bridge, and the Mammoth Terraces.

The second half of Skinner's description is more difficult to precisely interpret. Was he referring to areas where jackrabbits are regularly observed today as the "open northern sections of the Park"? Or was he referring to other northern sagebrush-grassland areas, such as Lamar Valley, Little America Flats, Junction Butte, Pleasant Valley, and Gardners Hole? We may never know. We were unable to locate any records of jackrabbits in Gardners Hole, only located documentation of one sighting in Lamar Valley, one set of jackrabbit bones from the Lamar Cave, and one vague reference to jackrabbits on the slopes of Mount Washburn. Therefore, it seems unlikely that Skinner was referring to those areas. The current range of jackrabbits in the park fits within the range described by Skinner in 1926, and we could find no evidence of range retraction or expansion since that time.

Park Ranger Newell Joyner's Article. In a short article entitled "The Prairie Hare" published in "Yellowstone Nature Notes," Joyner (1929) states: "In Yellowstone Park, particularly around the lower altitudes as at Mammoth, the hare attracts us not from an economic standpoint, but as an object of extreme interest."

Murie's Coyote Study. In some areas of the West, jackrabbits are an important prey species of coyotes. Adolph Murie conducted extensive research on coyotes in Yellowstone from 1937 through 1939. Murie (1940) stated that the jackrabbit "occurs only on the north side of the park and is not abundant, although tracks can always be found on its range" and that "the jackrabbit is often an important coyote food item in localities where it is abundant, but in Yellowstone it is of minor importance." Jackrabbit remains were found in 37 of 5,086 (<1%) coyote droppings he collected. If we subtract the approximately 3,500 coyote scats that were collected in interior areas of the park where jackrabbits were not present, jackrabbits still composed less than 1% (37 of 1,586) of the prey remains in coyote scats collected from jackrabbit range (Murie 1940). These results were similar to those of Olaus J. Murie's coyote study (1935), in which he identified only 10 occurrences (<1%) of jackrabbits from 2,145 individual food items collected from 64 stomachs and 714 feces of coyotes around Jackson Hole, Wyoming. As in the Yellowstone coyote study, not all of the Jackson Hole samples were collected within jackrabbit range. However, the finding of only 10 occurrences of jackrabbit remains suggests that they were either not a primary prey species of coyotes or were not abundant or widely distributed in that area. Since jackrabbits have a very limited distribution in Yellowstone and composed less than 1% of the diet of park coyotes in Murie's study, coyote predation on other species is unlikely to change significantly even if jackrabbits were extirpated.

Harold Brodrick's *Wild Animals of Yellowstone National Park.* Brodrick (1954) stated that jackrabbits were found in "open sections in the northern parts of the park. Has been seen on the highest slopes of Mount Washburn. Most frequently seen in the early morning and evening. Not numerous."

Contemporary Record

Streubel's Small Mammals of the Yellowstone Ecosystem. Donald Streubel (1989) reported that jackrabbits were found in northern Yellowstone, usually in open shrub-grass communities or in large openings in montane forests. Streubel never saw any jackrabbits in Lamar Valley, but suspected that it was likely good jackrabbit habitat due to the abundance of sagebrush-grassland habitat that dominates the valley (D. Streubel, pers. comm.).

Johnson and Crabtree's Small Mammal Survey. Kurt Johnson and Bob Crabtree (1999) reported that "White-tailed jackrabbits are uncommon on the Northern Range. Extensive surveys conducted in the Lamar Valley and Blacktail Plateau during 1990 and 1991 resulted in only one sighting. Whitetails are somewhat more common in the lower sagebrush habitats around the Gardiner and Mammoth areas."

Halfpenny and Marlow's Track Surveys. Halfpenny (2008) and Halfpenny and Marlow (2008) conducted three track surveys for jackrabbit along 6.8 km (4.25 mi) of the Old Yellowstone Trail road from the Heritage and Research Center in Gardiner to the park boundary at Reese Creek. Tracks were identified as those of jackrabbits by length of foot, length of stride, rotary gallop pattern, and absence of pads on the bottom of the foot. Only tracks that were within 2 m (6.5 ft) of the road or crossed the road were counted. On March 2, 53 separate sets of jackrabbit tracks were observed in snow that was 10–12 hours old. The tracks were relatively evenly spaced along the entire length of the survey route, with an average density of 12.5 sets of tracks per mile of road. In the March 14 survey, conducted nine hours after snowfall had ceased, 11 sets

JAMES HALFPENNY

Jackrabbit tracks are regularly found at low arid elevations.

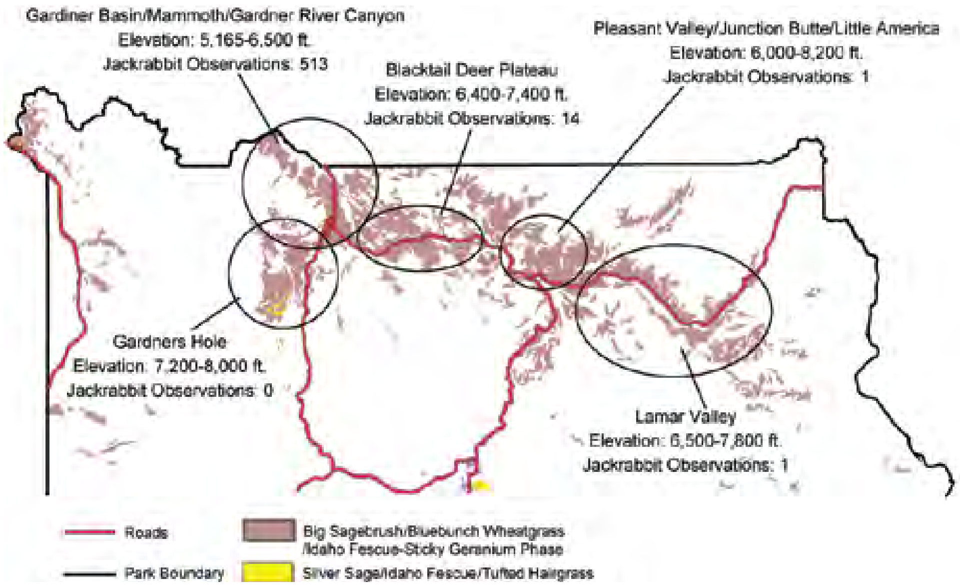

Figure 1. Concurrence of vegetation, elevation, and jackrabbit distribution in Yellowstone.

of jackrabbit tracks were counted with an average density of 2.6 sets per mile of road. In the March 15 survey, conducted 30 hours after snowfall had ceased, 47 sets of jackrabbit tracks were counted with an average density of 11.1 sets per mile of road. All jackrabbit tracks were field mapped and geo-referenced using a CyberTracker Global Positioning System.

Yellowstone Road-killed Wildlife Database. This database contains records of large mammals (>14 kg [30 lb]) killed by vehicles on park roads from 1989 through mid-September 2008. We found 13 incidental records of jackrabbits that were struck and killed by vehicles in the park. Small mammals (<14 kg [30 lb]) are generally not reported because they are frequently hit, generally do not damage the vehicles that hit them, and do not require removal from the road for safety purposes. Consequently, these records indicate a minimum number of vehicle-strike mortalities. However, these carcasses provide proof that jackrabbits have been present in the park since 1992. The observed distribution of road-killed jackrabbits is consistent with the distribution observed through our personal sightings of live jackrabbits, the sightings by the biologists we queried, and the sighting and sign records in the rare animal database. All of the road-killed jackrabbits were on the Old Yellowstone Trail road, the Gardiner to Mammoth road, the segment of road between the Mammoth Chapel and the Gardner River High Bridge, or the road across from the Mammoth Terraces.

Yellowstone Rare Animal Database. The rare animal database contains anecdotal sightings of wildlife recorded from 1887 through mid-September 2008. It is neither a systematic survey nor a complete record of wildlife presence, absence, or distribution. However, reports of jackrabbits in the database could lend insight into the species' historical and contemporary distribution. We assumed sightings reported as jackrabbits were correct because it is the sole hare species that occurs regularly in the park's grassland and sagebrush habitats (Berger 2008a).

Of the 559 records of jackrabbits and their sign in the database, 26 are from outside the park in the Gardiner Basin and Paradise Valley. Jackrabbit records from the park include observations of live animals (n=218), sign (tracks, n=128; fecal pellets, n=173), and carcasses (n=14). Because of the recent interest in jackrabbits, the sighting records from the park are biased toward observations made in 2008. Prior to 2008, people generally did not report jackrabbit sightings because they were considered common within the range they occupied in the park. The database contains 3 records from the 1940s, 1 from the 1980s, 15 from the 1990s, 13 from 2000 through 2007, and 501 from January to September 10, 2008.

The distribution of jackrabbits in the park appears to be influenced by the presence of preferred sagebrush and

Table 1. Observations of white-tailed jackrabbits in different habitat types.

Habitat Type	Number of Acres in YNP	Percent of Total Acres	Observations	Percent of Total Observations
Big Sagebrush/Idaho Fescue	31,037	1.4%	345	65%
Bluebunch Wheatgrass/Sandberg's Bluegrass-Needle-and-Thread Phase	2,087	<1%	85	16%
Mud Flow Mosaic[a]	1,153	<1%	60	11%
Big Sagebrush/Blue Bunch Wheatgrass	1,635	<1%	36	2%
Idaho Fescue/Bearded Wheatgrass-Sticky Geranium Phase	79,072	3.6%	4	0.8%
All Other Non-forested Habitat Types (n=17)	324,237	14.7%	0	0%
Total Non-forested Habitat Types (n=22)	439,221	20%	530	99%
Forested Types				
Douglas fir/Snowberry	55,084	2.5%	3	<1%
All Other Forested Habitat Types (n=42)	1,701,801	77.5%	0	0%
Total Forested Habitat Types (n=43)	1,756,885	80%	3	<1%

[a]Grassland mosaic covering large mudflows near the north entrance.

Sagebrush-grassland Area	Elevation (ft/m)	Number of Jackrabbit Sightings
Pelican Valley	7,800–8,100 / 2,377–2,469	0
Hayden Valley	7,700–8,100 / 2,347–2,469	0
Gardners Hole	7,200–8,000 / 2,194–2,438	0
Lamar Valley	6,500–7,800 / 1,981–2,377	1[a]
Pleasant Valley/Junction Butte/Little America Flats	6,000–8,200 / 1,829–2,499	0/1[b]
Blacktail Deer Plateau	6,400–7,400 / 1,950–2,256	14
Upper Mammoth Terraces	6,400–6,600 / 1,950–2,011	5
Gardiner Basin/Mammoth/Gardner River Canyon	5,200–6,500 / 1,585–1,981	513

[a]Jackrabbit observation was at 2,000 meters (6,560 ft)
[b]Bones of one white-tailed jackrabbit were found in Lamar Cave (Barnosky 1994)

Table 2. Jackrabbit observations in areas of sagebrush-grassland habitat, shown by elevation.

grassland habitat types (Table 1) and elevation (Table 2, Fig. 1). Based on the records in this database, jackrabbits do not use all habitat types in the park in proportion to availability. While approximately 80% of the park is covered by forested habitat types (Despain 1990), less than 1% (n=3) of the jackrabbit observations occurred there (Table 1). The other 99% (n=530) of the jackrabbit observations occurred in non-forested habitat, of which 65% (n=345) were recorded in big sagebrush (*Artemisia tridentata*)-Idaho fescue (*Festuca idahoensis*) habitat types.

The database contains no records of observations of jackrabbits, their carcasses, or their sign from the higher elevation sagebrush-grassland habitats (Table 2) of Pelican Valley, Hayden Valley, Gardners Hole, or the Pleasant Valley-Junction Butte-Little America Flats area, and only one record from Lamar Valley. The database contains just 14 records from the sagebrush-grassland habitat on the Blacktail Deer Plateau and 5 records from the Upper Mammoth Hot Spring Terraces. Most of the observations (96%, n=513) were in sagebrush-grassland habitat at elevations below 2,000 m (6,500 ft) in the Gardiner Basin, Mammoth Hot Springs, Gardner River Canyon areas.

It is unlikely elevation alone is the factor limiting jackrabbit range in the park. Jackrabbits are found as high as 4,200 m (14,000 ft) in Colorado (Lim 1987). Instead, elevation is likely a surrogate for precipitation in Yellowstone. Snow, the most common form of precipitation in the park, generally begins to accumulate earlier, attains greater depths, and lasts later into spring with increasing elevation (Despain 1990). Most of the jackrabbit observations in the park (96%, n=512) were in very arid areas where average precipitation ranges from just 25 to 40 cm (10–16 in) annually (Table 3). The remaining observations were from areas that receive between 40 and 46 cm (16–18 in) (3%, n=16) and between 46 and 76 cm (18–30 in) (1%, n=5). No observations of jackrabbits, their carcasses, or their sign were reported in areas that receive more than 30 inches (75 cm) of precipitation annually.

Records in the rare animal database—all from the 1940s—contain information of additional interest. In a 1941 record, "Four whitetail jackrabbits, or prairie hares were seen between Gardiner and the Stermitz ranch during the general antelope count on March 24. This is a greater number than is usually seen on a half day's ride over the lower game range." This sighting suggests that jackrabbits were present but not abundant in the Gardiner Basin in the 1940s. In another 1941 record, "A large prairie hare or white-tailed jackrabbit was found dead on the road near the new Gardner River bridge on February 27, cause of death–accident struck by car, pelage–white winter coat beginning to shed." In a 1947 record, "Four jackrabbits have also been winter residents of the Lamar Station area and have become very tame. One can almost pick them up before they move. They feed around the hay stack and from the hay fed to the horses in the corrals." This is the only reported sighting we found for Lamar Valley, although a more thorough search of the archives may reveal others.

Table 3. Observations of white-tailed jackrabbits in zones of differing annual precipitation.

Average Annual Precipitation (inches/cm)	Number of Acres in YNP	Percent of Total Acres in YNP	Observations of Jackrabbits	Percent of Total Observations
10–12 / 25.4–30.5	895	<1%	79	15%
12–14 / 30.5–35.6	5,228	<1%	91	17%
14–16 / 35.6–40.6	16,512	1%	342	64%
16–18 / 40.6–45.7	43,834	2%	16	3%
18–20 / 45.7–50.8	48,507	2%	1	<1%
20–30 / 50.8–76.2	512,298	23%	4	1%
30–40 / 76.2–101.6	628,006	29%	0	0%
40–50 / 101.6–127	483,517	22%	0	0%
50–60 / 127–152.4	266,867	12%	0	0%
60–70 / 152.4–177.8	149,075	7%	0	0%
70–80 / 177.8–203.2	40,709	2%	0	0%
Total	2,195,448	100%	533	100%

The Foothills of A High Mountain Ecosystem: Home of the White-tailed Jackrabbit

C. Hart Merriam was one of the first biologists to explore Yellowstone National Park. He described the plant and associated animal communities which occur at different elevation as "life zones." This concept describes the relationship of vegetation and wildlife communities to topography, climate, and elevation. The life zone concept is not as widely used today as in the past, (Smith 1974) but we are better able to interpret the limited information about the presence and distribution of the white-tailed jackrabbit within and around the park by applying the life zone idea to Yellowstone.

Yellowstone is part of a high mountain ecosystem within the central Rocky Mountains. The climate in mountain ecosystems varies dramatically with changes in elevation. Temperatures are warmer at lower elevations and cooler at higher elevations. The warmer temperatures at lower elevations increase evaporation, dry soils, and extend the growing season (Kershaw et al. 1998). Following Merriam's model, former Yellowstone biologist Terry McEneaney (1988) described four life zones that are represented in the park: *foothills, montane, subalpine* and *alpine*. In Yellowstone, white-tailed jackrabbits inhabit primarily the arid, low-elevation foothills zone and, to a lesser extent, the non-forested areas at the very lower elevations of the adjacent montane zone (Table 1).

The ***foothills zone*** occurs from the lowest elevations in the park (1,570 m; 5,165 ft) up to approximately 1,800 m (6,000 ft). It forms the transition between prairies and mountains. Vegetation is predominately open grasslands and sagebrush. Tree species include narrowleaf cottonwood and scattered Rocky Mountain juniper. Dry ridges in this zone may contain limber pine and wetter areas may support aspen. The upper reaches of the foothills zone in Yellowstone receives only 40–45 cm (16–18 in) of precipitation annually. The lower elevations of this zone which occur from the park boundary at Reese Creek east to Gardiner, Montana, and Rifle Range Flats, receive less than 38 cm (15 in) of precipitation annually, and contain "cold desert" vegetation. Big sagebrush, rabbitbrush, prickly-pear cactus, needle-and-thread, and junegrass are common.

The ***montane zone*** occurs immediately above the foothills at elevations from 1,800 to 2,300 m (6,000 to 7,600 ft). It contains a combination of open and forested habitats. Open valley bottoms dominated by sagebrush and grasslands are prevalent in the lower elevations of the montane zone. Forested areas occur at the upper elevations of this zone. Douglas fir is considered the defining tree species of these areas. Other trees in this zone include aspen, narrowleaf cottonwood, limber pine, lodgepole pine, Rocky Mountain juniper, subalpine fir, and Englemann spruce. Shrub species in this zone include big sagebrush and willow.

The ***subalpine zone*** extends from the upper edge of the montane forest at approximately 2,300 m (7,600 ft) up to the treeless alpine zone at approximately 3,000 m (10,000 ft). The subalpine zone is predominately forested, interspersed with non-forested areas.

The ***alpine zone*** is the treeless zone that occurs from timberline at approximately 3,000 m (10,000 ft) up to the top of the rocky slopes of Eagle Peak, the park's highest point at 3,462 m (11,358 ft). This zone is dominated by alpine tundra.

Latitude, geology, slope direction, and slope angle also influence the boundaries between life zones (Fisher et al. 2000). For example, north-facing slopes in Yellowstone are generally cooler and wetter than south-facing slopes. Due to these differences, the boundary between life zones can be as much as 200 m (700 ft) higher on south-facing slopes than on north-facing slopes (McEneaney 1988). Of 533 records of white-tailed jackrabbits in the Yellowstone rare animal database, 72% (n=384) occurred in the foothills zone, and 28% (n=149) occurred in the lower elevations of the montane zone. Most of the jackrabbit observations in the montane zone (87%, n=129), occurred below 1,900 m (6,500 ft). We were unable to locate any sightings of white-tailed jackrabbits in the alpine zone, and found only one reference to jackrabbits being observed in the subalpine zone (Brodrick 1954) in Yellowstone National Park.

Table 1. Rare animal database records of white-tailed jackrabbits in different life zones.

Life Zone	Elevation (ft/m)	Records of White-tailed Jackrabbits
Foothills	5,165–6,000 / 1,574–1,800	384
Montane	6,000–7,600 / 1,800–2,300	149
Subalpine	7,600–10,000 / 2,300–3,000	0
Alpine	10,000–11,358 / 3,000–3,462	0

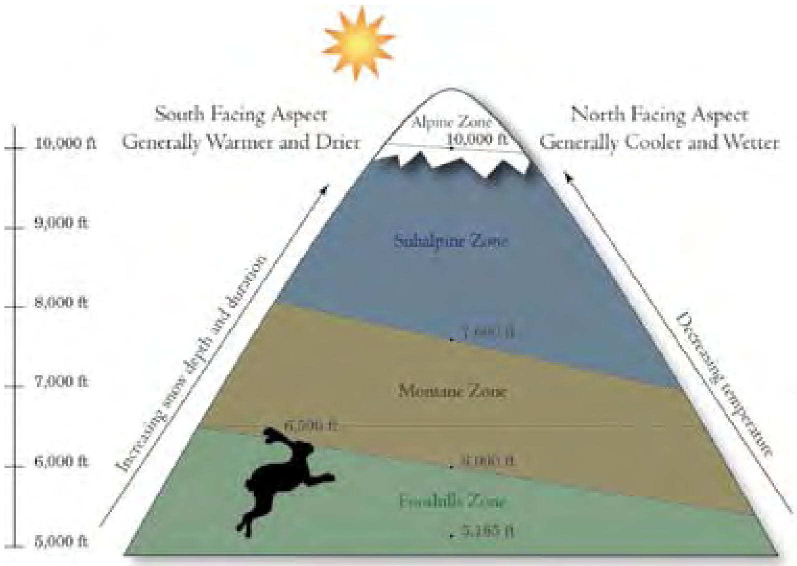

Figure 2. Jackrabbit distribution in the life zones of Yellowstone.

Observations by Park Biologists and Researchers. Our personal observations, as well as those of 12 biologists that we queried, indicate that jackrabbits are present but not abundant in northern Yellowstone. From the late 1950s through mid-September 2008, we regularly observed jackrabbits in the park's arid sagebrush-grassland communities below 1,980 m (6,500 ft), including the area from Beattie Gulch west of the park boundary at Reese Creek, east to Gardiner, Montana, south to the Mammoth Terraces, and southeast to the Gardner River High Bridge.

They are occasionally observed on Blacktail Deer Plateau (M. Haroldson, Interagency Grizzly Bear Study Team, pers. comm.; B. Crabtree, pers. comm.; J. Halfpenny, unpublished data), which we believe is at or near the upper elevational limits of the species' suitable habitat in the park. The Blacktail Deer Plateau receives 40–50 cm (16–20 in) of precipitation annually, which is 10–20 cm (4–8 in) more than the Gardiner Basin and 5–10 cm (2–4 in) more than the Mammoth Hot Springs-Gardner River Canyon area, the two places in the park where jackrabbits are regularly observed. Wind-aided snow removal may allow jackrabbits to inhabit the Blacktail Deer Plateau in winter (B. Crabtree, pers. comm.).

We found no records of observations of jackrabbits, their carcasses, or their sign in the large sagebrush-grassland habitats of Pelican Valley, Hayden Valley, or Gardners Hole, and only one anecdotal observation each from Lamar Valley and the slopes of Mount Washburn. However, these are high elevation sagebrush-grassland habitats with snow cover 30 cm or more deep that persists for three months or more (B. Crabtree, pers. comm., 2008), which may prevent jackrabbit access to shrub forage and shrub cover in winter. The winter diet of jackrabbits consists primarily of shrubs such as sagebrush and rabbitbrush (Bear and Hansen 1966, Lowery 2006), and suitable jackrabbit habitat generally consists of sagebrush-grasslands in arid areas with low winter precipitation (B. Crabtree, pers. comm.).

In addition, jackrabbits were observed beyond the park boundary in the Gardiner Basin and in Paradise Valley north of Yankee Jim Canyon to Livingston, Montana. Paradise Valley contains sagebrush-grassland habitat, is lower in elevation than the park, and has low winter precipitation and snow accumulation as well as wind-aided snow removal, making it suitable winter jackrabbit habitat. Since northern Yellowstone appears to be the terminus of jackrabbit range in this area, the connectivity provided by the Paradise Valley corridor likely facilitates immigration, emigration, and gene flow with populations outside the park.

Although we have not personally observed jackrabbits in the large sagebrush-grassland habitats of Pelican Valley, Hayden Valley, Gardners Hole, Lamar Valley, or the Pleasant Valley-Junction Butte-Little America Flats area, nor had any of the biologists we queried, we cannot conclusively determine whether or not jackrabbits inhabit those areas because they have not been systematically surveyed.

Conclusion

Historical references to the abundance and distribution of jackrabbits in Yellowstone are very limited. The few references we located all suggest that jackrabbits were never abundant and had a very limited distribution in the park. Because we did not conduct systematic surveys over the entire known range of jackrabbits in Yellowstone, we cannot determine their population numbers, trends, or precise distribution. However, a qualitative assessment of the data we collected suggests that the distribution and abundance of jackrabbits in the park has not changed significantly since the late 1950s. In addition, a review of the historical record does not indicate any significant change in distribution or abundance since the 1920s and 1930s. We found no evidence that jackrabbits were significantly more abundant or more widely distributed when the park was created in 1872 than they are today.

In 2008, jackrabbits are still regularly observed from the park boundary at Reese Creek east to Gardiner, Montana, and south to the Mammoth Terraces. Within eight months of their argued extirpation, we were able to collect more than 500 observations of jackrabbits, their sign, and their road-killed carcasses.

We believe that the arid, sagebrush-grassland habitat types in the park that occur at elevations below 1,980 m (6,500 ft) and receive less than 40 cm (16 in) of annual precipitation provide a good representation of the current distribution of white-tailed jackrabbits in the park (Fig. 2). If this distribution accurately represents suitable jackrabbit habitat in the park, then very little (<1% or approximately 18,676 acres) of the park is likely suitable for jackrabbits. The winter snow accumulation and snow persistence above 1,980 meters likely inhibits occupancy at higher elevations of the park. The lowest elevation areas of the park may represent the upper limits of jackrabbit range in this region.

We concur with several points Berger made in the *Oryx* paper. These include: (1) an appreciation of historical conditions is crucial to understanding functional relationships, (2) lacking information about historical conditions makes it difficult to determine whether current systems function ecologically like past ones, and (3) a bottom-up approach to reintroduction of extirpated species may result in the establishment of dynamic ecological processes that were intact prior to extirpation (Berger 2008a). Although jackrabbits are not as popular or studied as other fauna, they continue to persist—apparently as they have for some time—relatively unnoticed, within a very small suitable range in the arid, lower elevation sagebrush-grassland habitats of Yellowstone. YS

Acknowledgments

We would like to thank J. Gerdes, J. Jerla, and L. Finn for help in locating rare books and other archival material containing historical information on the abundance and distribution of white-tailed jackrabbits in the park. Shortly after reports that jackrabbits had been extirpated from the park appeared in the national press, D. Stahler, B. Crabtree, B. Weselmann, B. Fuhrmann, B. Suderman, J. Brodie, M. Weeks-Condon, T. McEneaney, K. McEneaney, M. McAdam, P. Petroff, D. Swanke, G. Spoto, D. Chapman, M. Breis, T. Blackford, J. Waller, C. Lang, T. Patton, E. Williams, N. Bishop, and D. Herring reported their recent sightings of jackrabbits in the park, the Gardiner Basin, and Paradise Valley. Thanks to these individuals, we were able to collect more than 500 sightings of jackrabbits, their sign, and their road-killed carcasses within a few months of the jackrabbit's reported extirpation. M. Yochim, T. Lindstrom, and B. Suderman quickly reported the presence of road-killed jackrabbits so that we could obtain tissue samples for DNA analysis. T. Wyman collected the road-killed carcasses. S. Mills provided DNA analysis without charge. C. Guiles assisted with GIS analysis of the data.

Literature Cited

Bailey, V. 1936. The mammals and life zones of Oregon. *North American Fauna* 55:1–416.

Barnosky, E. H. 1994. Ecosystem dynamics through the past 2000 years as revealed by fossil mammals from Lamar Cave in Yellowstone National Park, USA. *Historical Biology* 8:71–90.

Bear, G. D. and R. M. Hansen. 1966. Food habits, growth, and reproduction of white-tailed jackrabbits in southern Colorado. Technical Bulletin 90. Colorado State University of Agriculture Experiment Station, Fort Collins, Colorado, USA.

Berger, J. 2008a. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. *Oryx* 42 (1):1–4.

Berger, J. 2008b. Extant or extinct? White-tailed jack rabbits and Yellowstone's food web. *Oryx* 42 (2):176.

Berger, J. 2008c. Read the full story before commenting on hares. *Billings (MT) Gazette*, February 25.

Berger, J., K. Murray Berger, P. F. Brussard, R. Gibson, J. Rachlow, and A. Smith. 2006. Where have all the rabbits gone?: Summary and recommendations from a workshop held in Grand Teton National Park, September 23–24, 2005. Wildlife Conservation Society, Bronx, New York.

Brodrick, H. J. 1954. Wild animals of Yellowstone National Park. Yellowstone Interpretive Series, Number 1. Yellowstone Library and Museum Association. Yellowstone National Park, Wyoming.

Brown, M. 2008a. Neither hide nor hare found in Yellowstone. Associated Press, February 25.

Brown, M. 2008b. Egg on the face. Associated Press, March 6.

Despain, D. G. 1990. Yellowstone vegetation: Consequences of environment and history in a natural setting. Boulder, Colorado: Roberts Rinehart Publishers.

Dubke, R. T. 1973. The white-tailed jackrabbit in Wisconsin. Final Report, Pittman/Robinson Study 106, Project W-1741-R-8. Madison: Wisconsin Department of Natural Resources.

Fautin, R. W. 1946. Biotic communities of the Northern Desert Shrub biome in western Utah. *Ecological Monographs* 16 (4):251–310.

Fisher, C., D. Pattie, and T. Hartson. 2000. Mammals of the Rocky Mountains. Washington: Lone Pine Publishing.

Flinders, J. T., and J. A. Chapman. 2003. Black-tailed jackrabbit (*Lepus californicus* and Allies). In Wild mammals of North America: Biology, management, and conservation, 2nd ed., ed. G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, 126–146. Baltimore, Maryland: John Hopkins University Press.

Flinders, J. T., and R. M. Hansen. 1972. Diets and habitats of jackrabbits in northeastern Colorado. Science Series 12. Colorado State University Range Science Department, Fort Collins, Colorado.

Forsyth, A. 1999. Mammals of North America: Temperate and arctic regions. Ontario: Firefly Books.

Hall, E. R., and K. R. Kelson. 1959. The Mammals of North America, vol. 1. New York: Ronald Press.

Halfpenny, J. C. 2008. Jackrabbit tracking survey, Old Yellowstone Road, Gardiner to Reese Creek. A Naturalist's World, Gardiner, Montana.

Halfpenny, J. C., and L. Marlow. 2008. Jackrabbit tracking survey, Old Yellowstone Road, Gardiner to Reese Creek, March 14 and 15, 2008. A Naturalist's World, Gardiner, Montana.

Johnson, K. A., and R. L. Crabtree. 1999. Small prey of carnivores in the Greater Yellowstone Ecosystem. In Carnivores in ecosystems: The Yellowstone experience, ed. T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva. New Haven, Connecticut: Yale University Press.

Joyner, N. F. 1929. The prairie hare. *Yellowstone Nature Notes* 6(3), March 1. Yellowstone National Park, Wyoming.

Kershaw, L., A. Mackinnon, and J. Pojar. 1998. *Plants of the Rocky Mountains*. Washington: Lone Pine Publishing.

Kline, P. D. 1963. Notes on the biology of the jackrabbit in Iowa. In *Proceedings from the Iowa Academy of Science* 70:196–204.

Lechleitner, R. R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. *American Midland Naturalist* 60 (1):145–55.

Lim, B. K. 1987. *Lepus townsendii. Mammalian Species* 288:1–6.

Lowery, J. C. 2006. The tracker's field guide: a comprehensive handbook for animal tracking in the United States. Helena, Montana: Falcon Guide.

Ludlow, W. 1876. Report of a reconnaissance from Carroll, Montana Territory on the Upper Missouri, to the Yellowstone National Park, and return, made in the summer of 1875. U.S. Army, Chief Engineer, Department of Dakota. Appendix NN of the Annual Report of the Chief of Engineers for 1876. U.S. Government Printing Office, Washington, D.C.

McEneaney, T. 1988. Birds of Yellowstone. Boulder, Colorado: Roberts Rinehart Publishers.

Murie, A. 1940. Ecology of the coyote in the Yellowstone. Fauna of the National Parks of the United States Bulletin No. 4. National Park Service, Washington D.C.

Murie, O. J. 1935. Food habits of the coyote in Jackson Hole, Wyoming. U.S. Department of Agriculture Bulletin 362. Washington, D.C.

Orr, R. T. 1940. The rabbits of California. Occasional Papers of the California Academy of Sciences 19. San Francisco, California.

Skinner, M. P. 1926. The Yellowstone Nature Book. Roosevelt Field Naturalist, Roosevelt Wild Life Forest Experiment Station. A.C. McClurg and Company, Chicago, Illinois.

Smith, R. L. 1974. Ecology and field biology, 2nd ed. New York: Harper and Row.

Streubel, D. 1989. Small mammals of the Yellowstone ecosystem. Boulder, Colorado: Roberts Rinehart.

Nature Notes

Wolves and Tigers: Reflections of Yellowstone in Corbett National Park, India

PHOTO BY DR. SHANNON BARBER-MEYER, WORLD WILDLIFE FUND–US

Shannon Barber-Meyer

Piercing out of the wild jungle shine the tiger's eyes. The white and black facial ruff is strikingly brilliant against the shadows. The massive orange body can just barely be seen crouching down on the forest floor under the dense vegetation. I hold my breath. In a flash like a compressed spring suddenly released—the tiger leaps in one swift move and disappears into the green. The tiger's growl signals its new hiding place. We drive up the dusty path to a small pond flanked by thick jungle flora. Everyone points excitedly—the tiger must be approaching. I haul myself up and out the vehicle window while holding onto the roof rack. I get my camera ready for a once in a lifetime close-up shot of the tiger. Without a sound the tiger emerges from the near impenetrable forest cover and pads just beyond the pond less than 50 meters from me—I'm frozen—my arm doesn't move to take the picture—my jaw drops. I suddenly remember to breathe and almost unconsciously utter "whoa." The tiger's pace is regal—it isn't slow—but it isn't running—it is in command. I feel as though I've just watched a giant ship passing on the ocean waters with everything reeling in its wake.

I FOUND MYSELF IN Corbett National Park (Corbett) spotting my first wild tigers this past April while traveling for my new job with the World Wildlife Fund (WWF) and TRAFFIC (the wildlife trade monitoring network of WWF and International Union for Conservation of Nature). Corbett is located in the foothills of the Himalayas in the northern Indian state of Uttarkhand. Visiting Corbett was part of my larger trip throughout the entire Terai Arc Landscape, which stretches from India's Yamuna River in the west to Nepal's Bagmati River in the east. This landscape is one of the last remaining strongholds for tigers but portions of this tigerland face dire threats—mainly habitat degradation and destruction and the poaching of tigers and their prey. By traveling the entire length of the Terai, I was able to get a first hand view of where these threats are greatest and how tiger habitat and prey densities vary throughout the landscape. These details inform strategic conservation intervention measures and help determine what monitoring methods for live tigers and their prey are best suited for certain areas.

During my brief visit to Corbett, I often found myself comparing it with my experiences in Yellowstone National Park (Yellowstone), where I spent almost three years conducting my PhD research. Yellowstone, established in 1872, was the first park of its kind in the world, while Corbett, created in 1936, was the first national park on the Asian mainland. The Asian park went through several name changes before being christened in the mid 1950s after Jim Corbett, an Indian-born hunter and conservationist who wrote *Jungle Lore* and *Man-Eaters of Kumaon* and helped with the establishment and marking of the park's boundaries. While Yellowstone was originally set aside as a protected area largely for its geological resources, Corbett was protected as a game reserve by the then British government. Protection is the main focus of Corbett's management, while habitat and water management and ecotourism are other areas of attention. Yellowstone (~8,987 km^2) is much larger than Corbett (~520 km^2) although Corbett National Park is only one part of the Corbett Tiger Reserve which, including the surrounding wildlife sanctuary, reserve forests, and buffer zone lands, has a total size of ~1,318 km^2. Akin to *Yellowstone Science*, Corbett was the first national park in India to have its own in-house magazine; it is published in both English and Hindi.

The famous Project Tiger, India's ambitious tiger conservation program, was launched from Corbett in 1973. The project initially created nine tiger reserves based on a "core-buffer" strategy, which focuses on a strictly protected core area surrounded by areas less restricted to human access and use called a "buffer zone." Originally, Project Tiger was funded by India's central government. Later, various Indian states shared the expenses. Additionally, the WWF has supported Project Tiger over the years by providing funds, equipment, expertise, and literature worth $1 million. Project Tiger's main successes include the creation of 27 tiger reserves, increased research activities, intensified protection and ecodevelopment, and support of voluntary village relocation from the core areas of reserves. Although tigers disappeared (likely due to poaching) from one of the reserves, Sariska, India has taken steps to bring the tiger's roar back by translocating a male and female tiger there during 2008. Because India was successful in protecting Sariska's habitat from human encroachment, it remained available for tiger relocation. South Asia is one of the most densely populated regions in the world. Only through holistic habitat management plans that explicitly incorporate and manage humans will tigers thrive in the wild.

Similar to Yellowstone, Corbett boasts a wide variety of topography and vegetation: mountains, expansive sal forests, shrub-covered forest floors, and—my favorite for wildlife viewing—lush grasslands where elephants romp in the distance, hog deer march, chital (spotted deer) prance, otters dart, and wild boar scurry. Just like the famous Yellowstone River, the Ramganga supplies Corbett's flora and fauna with essential water. I was lucky to spot the famed Golden Mahseer (a huge carp-like fish) from the bluffs overlooking the precious fresh water.

Like Yellowstone, Corbett is known for its large predator suite, being home to the tiger, leopard, leopard cat, jungle cat, golden jackal, sloth bear, and the Himalayan black bear. In addition to the herbivores already mentioned, Corbett also has sambar, barking deer, and ghoral (a goat-like animal). Unlike Yellowstone however, Corbett also maintains resident populations of large reptiles, including two crocodilian species (gharial and mugger) and snakes like the King cobra and python. I would be remiss if I didn't mention some of Corbett's notable birds such as the great pied hornbill, the khalij pheasant, and the Himalayan griffon.

One of the most interesting contrasts I found related to park closures. While Yellowstone closes most roads to automobile travel during the winter because of snowfall, Corbett is completely closed to visitation from June 15 to November 15 due to the monsoon season. It only reopens after park crews have actually rebuilt roads that wash away each year during the heavy rains. Imagine having to wait for roads to be rebuilt in Yellowstone rather than just waiting for the snowplow to come through!

Recreational opportunities differ vastly between the parks as well. While a typical Yellowstone visitor may enjoy a long day hike through the backcountry followed by a nice sleep in a tent, a visitor to Corbett is not even allowed to get outside of their car unless they are in specially marked areas or inside designated fenced-off areas protected from wildlife such as elephants, tigers, and leopards. A tragic incident that led to the death of David Hunt, a British ornithologist, by a tiger in the late 1980s led the authorities of Corbett to take such a step. In addition, visitors are not allowed to drive from 11 a.m. to 3 p.m. This is intended to give the wildlife a rest from the pressure of visitors tracking them down in vehicles eager for a once-in-a-lifetime viewing. Just because you can't drive during the afternoon doesn't mean you can't do any wildlife watching. Like many other Asian reserves, Corbett has machan towers situated throughout the park for elevated wildlife watching, but once you go up, you can't come down until the afternoon driving hours commence, so you better bring sunscreen and lunch. I was treated to a magical sight while up the machan—a tiger escaping the mid-day heat by soaking in the Ramganga River for almost two hours. By sunset, all visitors must have either left the park or be in the fenced areas to lodge for the night. The wildlife fun does not end once you are locked inside; just as in Yellowstone, visitors can enjoy educational presentations during the evenings. It is also a great time to swap wildlife stories and—if you had a lucky day—add your tiger sighting to the running tally on the chalkboard.

"Not unlike the Yellowstone visitors who eagerly rise before the dawn to catch a glimpse of a wolf, nearly everyone who comes to Corbett wants to see a tiger."

Not unlike the Yellowstone visitors who eagerly rise before dawn to catch a glimpse of a wolf, nearly everyone who comes to Corbett wants to see a tiger. These iconic predators draw visitors from all over the world. In many ways, however, Corbett's tigers are very different from Yellowstone's wolves. For starters, the tigers weren't reintroduced; they've been constant residents since long before the park was established. Tigers and wolves also differ strikingly in their hunting habits.

DR. SHANNON BARBER-MEYER, WORLD WILDLIFE FUND–US

While leopard scats are often found containing Hanuman langur fur, these primates are not a frequent component of the tiger's main diet.

Tigers are ambush and stalk predators, whereas wolves are coursers that will sort a herd and take the most vulnerable prey. While wolves are famous for their families, tiger "families" do not often exist. Usually, a male tiger will maintain a territory that encompasses several tigresses and a tigress is left to raise the cubs on her own. Although Yellowstone wolves breed primarily during the winter, tigers breed year round. One similarity, however, is that tigers communicate in many of the same ways as wolves, such as scent marking and vocal communication.

Similar to Yellowstone, Corbett Tiger Reserve researchers include members of the government, non-governmental organizations, and universities. Because of the unique Yellowstone wolf situation where wolves can be seen almost every day, research can be conducted simply by observing them. This method, however, can't provide answers to all of the questions researchers ask, so other techniques are employed such as radio collaring, scat DNA analyses, and kill site investigations. Because tigers occupy a much different habitat (thicker vegetation) than the Yellowstone wolves and have more solitary and secretive behaviors (in part because they are ambush predators), tigers are not usually observable for long periods each day as Yellowstone wolves often are. While techniques such as collaring and scat DNA analyses are also used on tigers, camera trapping, where a camera is set up on each side of a trail or other high tiger-traffic area, is much more common. The cameras are self-triggered by large moving objects so that a picture is captured of each side of a tiger passing along the trail. In this way the tiger is "marked" or identified because of its unique stripe pattern, similar to our fingerprints. Using the tiger's natural markings and remote cameras, capture-mark-recapture studies can be used to estimate population abundance, density, home range size, reproduction, and survival without ever having to physically capture or mark the tigers. Yellowstone wolf research could be a lot easier if wolves had just evolved with unique stripe patterns!

DR. BIVASH PANDAV, WILDLIFE INSTITUTE OF INDIA

Camera traps along the southern boundary of Corbett Tiger Reserve identify two distinct tigers based on their differing stripe patterns, 2006.

While most tiger photo "matches" are done manually by researchers, software is being developed to enable automated tiger-stripe pattern matching. Programs are also being created that will take a photographic image of a flat tiger pelt (for example, pelts seized from poachers or smugglers of illegal tiger parts) and generate an image of how the pelt would have looked on a live tiger so it could be matched to the image obtained from a camera trap. This innovative link will facilitate stronger anti-poaching enforcement by determining from where individual poached and smuggled tigers originate.

As a sign of wolf recovery, northern Rocky Mountain gray wolves were officially removed from the federal list of endangered species in 2008 (though this decision was recently reversed, at least for the time being). However, unlike tigers, the gray wolf has never been a globally threatened species. Tigers are globally endangered and some populations are critically endangered. The next listing category beyond critically endangered is extinct. An analysis published in the journal *Bioscience* in 2007 by Eric Dinerstein and colleagues revealed that tigers occupy only 7% of their historical range and,

DR. SHANNON BARBER-MEYER, WORLD WILDLIFE FUND–US

An ex-poacher demonstrates the types of snares used to kill tigers in Indonesia.

even more alarming, since 1995 occupied tiger range declined by 40%. In 2008 the Indian government released a tiger population estimate of around 1,400, a number that is dramatically lower than previous estimates and puts the world's total wild tiger population at around 4,000. Similar to wolves, the main threat to tiger persistence is conflict with humans. Livestock depredation often results in retaliatory or even preemptive killing. In many areas throughout their range, tigers are also poached to supply the illegal markets for pelts, traditional medicines containing tiger components, and meat. Alarmingly, during the same month as my visit, the Tiger Protection Task Force (the anti-poaching patrol staffed by ex-army personnel and supported by Corbett management funds) found 39 illegal traps made of nylon rope intended to catch tiger prey species like wild boar, sambar, and chital.

Both direct and indirect human impacts on tigers result from the 92 villages (about 66,000 people and 44,000 livestock) located within two to three kilometers of Corbett Tiger Reserve. Although it is illegal to chop down trees in India except on a plantation, people reduce the forage, shade, and cover for native ungulates by harvesting wood branches for fuel, and grass and leaves for livestock feed, and by grazing livestock in areas that force direct competition with native tiger prey. Neither of these activities is allowed inside Corbett but the nearby buffer zones are susceptible to these threats. In order to minimize these human impacts, the Field Director of Corbett is making considerable efforts to increase community support by organizing free educational visits with the best nature guides for the relocated villagers. Many of the nature guides in the park were trained in a special program to provide tangible ecotourism benefits to local communities by educating unemployed youth in natural history, visitor management, and park interpretation. The services provided by these nature guides give Corbett staff more time to focus on management activities.

As in Yellowstone, the large scale impact of climate change is a concern in Corbett and for tigers across their range. The importance of seasonal water availability will become increasingly critical as resident tigers search for reliable water sources during the long, hot dry season. However, like wolves in Yellowstone, tigers will persist in Corbett if the park maintains a high level of community support through incentives, ecotourism benefits, alternative livelihoods, and depredation compensation programs, and through effective management which includes the dual responsibilities of managing the resource as well as the humans—mitigating visitor impacts and preventing illegal activities. Yellowstone is the crown jewel of the U.S.'s conservation efforts. Because of India's conservation efforts, Corbett National Park similarly stands as one of the last strongholds of wild tigers. YS

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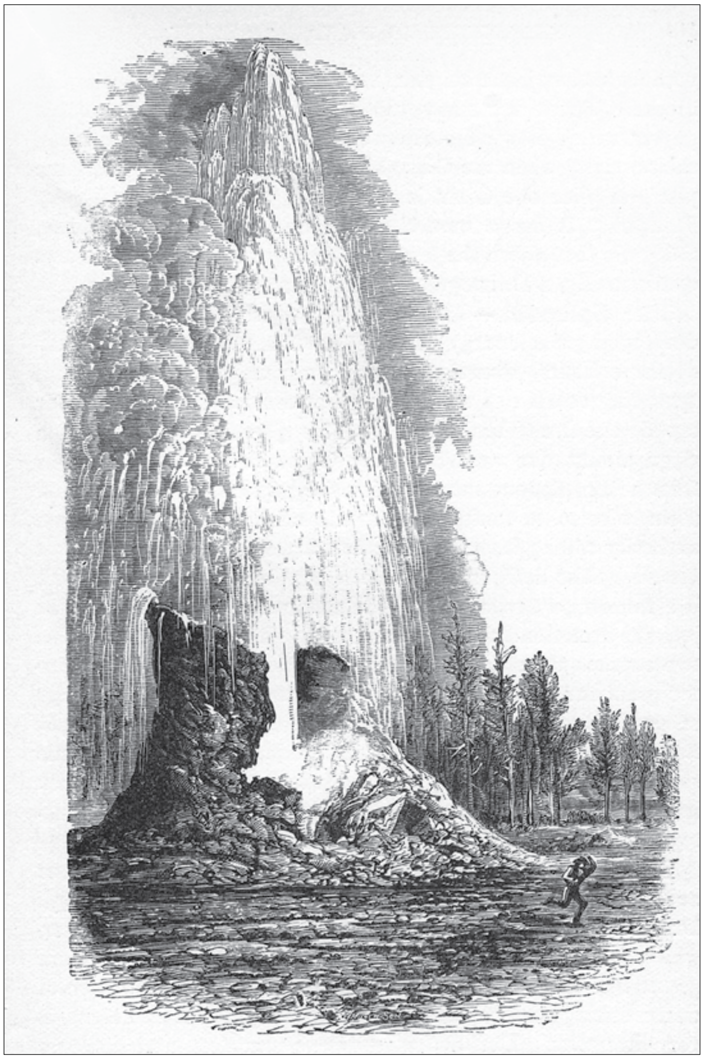
PHOTO COURTESY OF THE AUTHOR

Shannon Barber-Meyer received her PhD in 2006 from the University of Minnesota after conducting research in Yellowstone National Park on the survival and mortality of elk calves following wolf restoration. Her dissertation findings were recently published in *Wildlife Monographs* with co-authors Drs. L. David Mech (U.S. Geological Survey) and P.J. White (National Park Service, Yellowstone). She now works as the Tiger Conservation Program Officer for the World Wildlife Fund – US and TRAFFIC. So far her tiger work has taken her to Cambodia, Thailand, Malaysia, Indonesia, India, Nepal, and China.

From the Archives



An engraving of "Giant Geyser in Action" from the *Official Guide to Yellowstone National Park, Containing Routes, Rules and Regulations* by E. Heinemann and A. Demarest, W.C. Riley Publisher, St. Paul, 1889. p. 107.

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In this issue

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A postcard printed by Frank Jay Haynes of the Haynes Studio in 1910 depicting the eruption of Giant Geyser.

In the next issue, *Yellowstone Science* reports on the 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem: *The '88 Fires: Yellowstone and Beyond*.

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