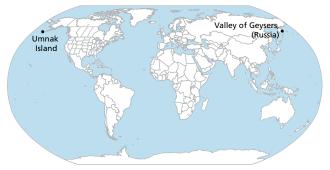
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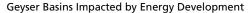
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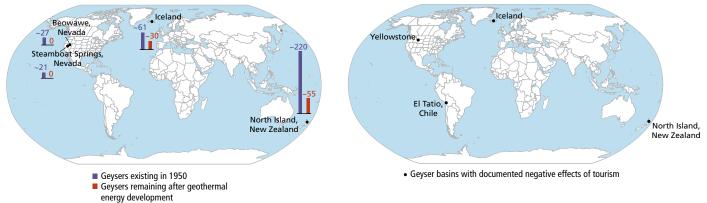
Human Impacts on Geyser Basins

The "Crystal" Salamanders of Yellowstone Presence of White-tailed Jackrabbits Nature Notes: Wolves and Tigers Geyser Basins with no Documented Impacts





Geyser Basins Impacted by Tourism



Impacts to geyser basins from human activities. At least half of the major geyser basins of the world have been altered by geothermal energy development or tourism. Courtesy of Steingisser, 2008.

Yellowstone in a Global Context

IN THIS ISSUE of *Yellowstone Science*, Alethea Steingisser and Andrew Marcus in "Human Impacts on Geyser Basins" document the global distribution of geysers, their destruction at the hands of humans, and the tremendous importance of Yellowstone National Park in preserving these rare and ephemeral features. We hope this article will promote further documentation, research, and protection efforts for geyser basins around the world. Documentation of their existence is essential to their protection.

In her article, Sarah McMenamin describes some unusual salamanders living in the park. The discovery of their translucent color sparked excitement about physiological—rather than genetic—differences caused by environmental factors. Their manifestation is made possible by the environmental diversity Yellowstone provides.

We also report on the status and distribution of whitetailed jackrabbits in Yellowstone in response to a study that claimed they had been extirpated from the park. As they have since the park's establishment, jackrabbits continue to persist in the park in a small range characterized by arid, lower elevation sagebrush-grassland habitats. With so many species in the world on the edge of survival, the confirmation of the jackrabbit's persistence is welcome.

The Nature Note continues to consider Yellowstone with a broader perspective. Shannon Barber-Meyer, who did her PhD work in Yellowstone on elk calf mortality (see issue 13:3), describes her new experiences as the Tiger Conservation Program Officer for the World Wildlife Fund. She considers the similarities and differences between Yellowstone and India's Corbett National Park as well as between wolves and tigers.

We hope you enjoy the issue.

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on the cover, left to right: Blotched tiger salamander, S. McMenamin. White-tailed jackrabbit, Bob Weselmann. Steamboat Geyser, NPS photo.



A blotched tiger salamander.

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NEWS & NOTES

Science Panel Reviews Lake Trout Suppression Program

In late August, Yellowstone National Park invited 15 fisheries scientists from around the country to attend a conference at Chico Hot Springs designed to critically review the park's lake trout suppression program. The conference was also attended by 35-40 interested participants from state agencies, nonprofit groups, universities, and several federal agencies including the National Park Service, U.S. Geological Survey, and U.S. Fish and Wildlife Service. The park tasked the science panel to (1) evaluate the effectiveness of the current program, (2) review emerging technologies that could possibly be employed for lake trout suppression, and (3) make recommendations for the future direction of the program. The science panel overwhelming agreed that the Yellowstone Lake Yellowstone cutthroat trout population is in serious trouble, but that suppression efforts could restore this population to healthy levels. They stated that efforts to date, while certainly slowing the lake trout population growth rate, have not been substantial enough to collapse that population. Consequently, the

cutthroat trout population remains in peril. They strongly stated that very little time remains to turn the situation around and immediate action to increase suppression efforts should be taken. Increased monitoring and evaluation of the population status of both the cutthroat trout and lake trout should also be undertaken. Finally, although several emerging technologies show promise for future use in reducing lake trout populations, none currently exist that could replace direct removal efforts. Long range plans, however, should include further research in these areas.

A report with complete findings of the science panel, including strengths and weaknesses of the current program and specific recommendations to the park, is expected in 2009.

Passing of Robert J."Bob" Murphy

Bob was born May 18, 1918, in Geraldine, Montana. He attended Bozeman schools and graduated from Gallatin County High School in 1937. He worked in Yellowstone National Park while attending Montana State College in Bozeman from 1938 to



Members of the science panel hear discussion on lake trout suppression.



Former ranger Bob Murphy.

1941. He served as a ranger in Yellowstone from 1941 to 1957. He went on to a distinguished career in the National Park Service, serving as a district ranger of Glacier National Park (NP), as chief ranger at Theodore Roosevelt NP and Wind Cave NP, as superintendent of Death Valley NP and later, in 1968, as superintendent of Lassen Volcanic NP. He was awarded the Meritorious Service Award by the Secretary of the Interior for outstanding service. After retiring from the park service in 1977, Bob and his wife Alice lived in Paradise Valley, Montana. Bob liked exploring Yellowstone country on horseback and enjoyed writing. He authored Bears I Have Known, relating 20 years of experiences with bears, and Desert Shadows, an account of the arrest and investigation of the Charles Manson family in Death Valley, which took place during Bob's tenure there.

Yellowstone National Park Recognizes Bob Smith

On September 30, 2008, Superintendent Suzanne Lewis recognized Dr. Robert B. Smith for his many years of dedicated service to Yellowstone National Park.

Bob Smith began his career with the U.S. Fish and Wildlife Service,

mapping fish habitats and streams around Yellowstone Lake. His studies of the effects of the 1959 Hebgen Lake earthquake focused interest on earthquakes and fault systems. Appointed to the faculty of the University of Utah in 1967, Bob began his geophysics career in Yellowstone. He has supervised more than 40 research and monitoring projects in Yellowstone and Grand Teton national parks and published 94 related papers.

As importantly, Bob has performed work that helps the National Park Service (NPS) educate the public about Yellowstone's dynamic geology. He is a coordinating scientist with the Yellowstone Volcano Observatory, assists park interpreters through training sessions and field trips, and works with journalists and television producers to get the stories right.

Bob, his students, and his staff are highly sensitive to the need to protect Yellowstone's environment and resources. The installation of seismic monitoring and GPS stations was acutely sensitive to these needs, and done respectfully with minimum disruption. Superintendent Lewis expressed the NPS's appreciation for Bob's contribution to the body of knowledge about Yellowstone's geological environment and we thank him for his continued efforts on the park's behalf.

Bob was also recently honored with the NPS Intermountain Region's Natural Resource Research Award. He was cited for his research, including studies of earthquakes and volcanism and their impact on Yellowstone and Grand Teton national parks, and for providing the NPS with "foundational knowledge of the dynamics of the Yellowstone volcano, the park's extraordinarily high heat flow, and its potential catastrophic future." He was also nominated for the national award.

RM-CESU 2008 Project Award Goes to Park Cooperators

The Rocky Mountains Cooperative Ecosystem Studies Unit (RM-CESU) awards program was established in 2007 as a way for federal agencies to recognize outstanding accomplishments by academic institutions and students. Emily Yost, currently working at Yellowstone National Park, and Ben Baldwin of Utah State University (USU) received this award for 2008. They were nominated by Judy Visty of the Continental Divide Research Learning Center, Rocky Mountain National Park, for their work "Improving Science Communication for



Dr. Robert B. Smith and Yellowstone National Park Superintendent Suzanne Lewis.

Multiple Parks and Networks: Summer 2006 through Summer 2008." This nomination recognizes a large number of products created by Emily benefiting 11 parks over the last two years. During this time, Emily and Ben worked under six different task agreements between the National Park Service (NPS) and USU with a focus on communicating science information to a variety of audiences, both internal and external to the NPS.

Emily began her contributions as a Tehabi intern, which grew into a Research Associate position. During this time, she authored text for websites, fact sheets, and communication plans, and edited task agreements. Altogether, Emily was directly involved in more than 120 communication products. Beyond the breadth and number of items, Visty noted that Emily has been an important agent of change as she moved between the Greater Yellowstone Science Learning Center, Glen Canyon National Recreation Area, Sand Creek Massacre National Historic Site, Rocky Mountain National Park, Learning Center of the American Southwest, and the Rocky Mountain Network. Emily has shared approaches she developed or observed during her journey and has introduced park-based employees to methods being implemented in other locations.

One common thread in all of Emily's products has been a clarity of writing over a wide variety of subject matters. For example, she has summarized and translated into plain language technical reports on such varied subjects as bighorn sheep, prehistoric resources, historic structures, prescribed fire, bats, and lake and river use.

Ben Baldwin was recognized for his steady support of parks and ongoing mentorship of Emily. Emily consults him frequently for guidance on projects. Ben's professional interest is in helping young students develop resource careers. Emily is just one of the many students he has influenced,



Emily Yost, Jim Burchfield (RM-CESU executive committee chair), and Ben Baldwin.

making him an asset within the CESU network.

Emily continues to work with Ben and contribute to NPS science communication efforts through a RM-CESU agreement. She currently provides technical assistance to the Greater Yellowstone Science Learning Center, Yellowstone National Park, the Learning Center of the American Southwest, and the Greater Yellowstone Network.

2008 MacArthur Award Goes to Dr. Monica Turner

The MacArthur Award is given by the Ecological Society of America to an established ecologist in mid-career for meritorious contributions to ecology, in the expectation of continued outstanding ecological research. The 2008 recipient was Monica Turner, an ecology professor at the University of Wisconsin–Madison who has conducted research in Yellowstone since 1988.

Monica Turner first visited Yellowstone National Park in 1978, when she worked at Old Faithful as a ranger-naturalist through the Student Conservation Association. That formative summer confirmed her decision to become an ecologist. After completing a BS in Biology from Fordham University, she earned a PhD in Ecology from the University of Georgia. As a graduate student, she worked as a summer intern with the NPS in Washington, D.C.; she conducted her doctoral research in Virgin Islands National Park and Cumberland Island National Seashore.

With her collaborators and students, her research has addressed the effects of fire on vegetation, carbon and nitrogen dynamics, movement patterns and habitat use by elk, interactions between fire and bark beetles, and implications of climate change. She was a member of the National Research Council committee that evaluated ungulate management in Yellowstone (*Ungulate Dynamics on Yellowstone's Northern Range*, 2002, National Academy Press).



Dr. Monica Turner spoke at The '88 Fires: Yellowstone and Beyond conference in 2008.

Turner is an acknowledged international leader within landscape ecology. This growing discipline addresses the dynamics of large, spatially complex ecological systems. Turner has built principles of landscape ecology through her work on a remarkable variety of systems, including coastal barrier islands, the Pacific Northwest, the southern Appalachians, the Wisconsin River floodplain, the lake-rich Northern Highlands of Wisconsin, and the Greater Yellowstone Ecosystem. Her contributions to pragmatic, real-world problem solving must also be noted.

Turner has been and continues to be a conceptual innovator, topmost communicator, and most effective interpreter in landscape ecology. She is generous with her ideas and enthusiasm, and she is widely known as an excellent teacher, mentor, and public speaker. She is a truly exceptional scientist.

Errata

In Yellowstone Science issue 16(3), we reported that Ralph Taylor had won the Intermountain Region's Hartzog Award for Outstanding Volunteer Service. We regret that we incorrectly identified Hartzog's first name as Charles.

The award is named for George B. Hartzog, Jr., who served as the 7th Director of the National Park Service for nine years, from January 1964 until December 1972. He established the Volunteers-In-Parks program in 1970.

Hartzog accomplished much toward three major goals as director: to expand the system to save important areas before they were lost, to make the system relevant to an urban society, and to open positions to people who had not previously had much access to them, especially minorities and women. He operated in the style of first NPS Director, Stephen Mather, in gaining the cooperation of members of Congress.

Hartzog passed away on June 27, 2008, at the age of 87.

The '88 Fires: Yellowstone and Beyond Conference

by Emily Yost

AST FALL, fire professionals returned to the Greater Yellowstone Area where, in 1886, the first federal public land firefighting efforts took place. Managers were joined by scientists from September 22-27, 2008, at The '88 Fires: Yellowstone and Beyond conference held in Jackson Hole, Wyoming, at the Snow King Resort. This meeting served as the 9th Biennial Scientific Conference on the Greater Yellowstone Ecosystem and was cosponsored by the International Association of Wildland Fire. This event marked the 20th anniversary of fires that covered 1.4 million acres of the Greater Yellowstone Area and other large fires that occurred in the West that year. The fires were the focus of much attention and sparked dialogue about land managers' approach to and understanding of fire in wildland areas. The primary themes of the conference were lessons learned from the fires and how management and fires are likely to change in the future. Among the approximately 450 attendees were agency managers, scientists, and university researchers and students from the U.S. and other countries, and many who participated in the '88 firefighting efforts. Presenters focused on ways the '88 fires and their aftermath continue to shape fire management and science. Speakers often framed their lessons learned with personal accounts from the summer's experience.

The conference began with an evening of stories from managers who were in Yellowstone during the interagency effort in the park. On Tuesday morning Chuck Bushey, president of the International Association of Wildland Fire, welcomed the attendees. Colin Campbell, deputy superintendent of Yellowstone, delivered



Jackson Hole, Wyoming | September 22-27, 2008

Superintendent Suzanne Lewis' opening remarks underscoring the scientific, social, economic, and historic significance of the Yellowstone fires. The welcome began with a tribute to the two firefighters who died in the aftermath of the fires, Donald Kuykendall and Edward Hutton.

More than 140 presentations and discussions were given throughout the week in addition to the keynote speeches. Session topics covered fire behavior, ecology, modeling, and history; weather; fire management and policy focussing on suppression, fuels, operations, safety, and planning; global trends in carbon, invasive species, and climate change; interagency cooperation; cultural and social perceptions of fire and human interactions with fire; and, lastly, a panel discussion on criminal liability.

Keynote session topics extended beyond the Greater Yellowstone Area and speakers reflected on their experiences and the future of fire management. Bob Barbee, superintendent of Yellowstone during the '88 fires, spoke about the fires as a character-building experience and catalyst to focus on the fundamental role of fire in natural systems, including the limitations of its use as a management tool. Barbee noted that "nature is not always a gentle hostess, [but] she never fails to be an inspiring teacher."

Orville Daniels, retired forest supervisor of the Lolo National Forest, spoke about his experience and lessons learned from supervising the Canyon Creek Fire in the Bob Marshall Wilderness during the summer of '88. Even though Daniels had been a pioneer of prescribed fire in U.S. Forest Service wilderness in the early 1970s, he called the Canyon Creek Fire his "baptism" in wildfire management. He said it was a humbling experience that underscored the importance of adapting to change quickly. Daniels also advised the fire community to be cohesive and that it will need new mechanisms to develop fire policy for wilderness areas: "I fear that the challenges of the future are going to make it hard for us to make the same kind of progress that we've made in the past if we don't have some kind of systems approach ... [to] policy setting."

Former Director of the Yellowstone Center for Resources John Varley addressed the portrayal of the '88 fires by the media, noting that there were few environmental reporters at the time and that the regional media did a good job of covering the event. Professor Cathy Whitlock of Montana State University spoke about fire history, echoing and expanding on Daniels's comment on the importance of fire history. Whitlock reviewed data analyses, the history of humans and fire, and climate change. Professor Monica Turner of the University of Wisconsin–Madison spoke of the opportunity the '88 fires provided to study the effects of a large, infrequent disturbance in an ecological system minimally affected by humans, which led to new insights about the nature, mechanisms, and importance of change to a system.

The Wednesday afternoon plenary session focused on fire management challenges. Anthony Westerling, assistant professor at the University of California-Merced, spoke about the changing climate and its role in increasing wildfires in the western U.S. Mike Flannigan, senior research scientist with the Canadian Forest Service, offered a Canadian perspective and suggested adaptations the fire community might adopt such as strategic planning for landscape management and sustainable forests, increased research on the social aspects of wildland fire, and international cooperation. Steve Frye of the Montana Department of Natural Resources and Conservation spoke about changes in large fire management since the '88 fires and as "unusual" fires become more common. The expanding expectations of fire managers now include social aspects and the increased use of large equipment. This session was followed by discussions about the role of organizational learning and developing future fire professionals.

Andy Hansen, professor at Montana State University, gave a presentation on the changes in the landscape and how



John Varley gives his plenary address.



Bob Barbee, former Yellowstone superintendent, and Orville Daniels, retired Lolo National Forest supervisor, gave the Tuesday morning keynote, "I Was There."

these changes affect biodiversity. He suggested that fire management needs to be tailored to local conditions within regions and across the country. Forest Service Region One Deputy Director of Fire, Aviation, and Air George Weldon spoke about the history of fires in the Greater Yellowstone Area and urged the agency to recognize that suppressing fires in fire-dependent ecosystems is not a sustainable management practice. Weldon also said that we can create fire-smart landscapes, inform the public about what the Forest Service can do to protect homes in wildland areas, have a common vision of how people will protect their homes, work with locallevel planners, and increase our ability to manage long-duration events.

The final keynote speakers gave capstone presentations on fire science and management. Professor Tom Swetnam, Director of the Laboratory of Tree-ring Research at the University of Arizona, spoke about climate change and future megafires, noting that if we act now with urgency, purpose, and wisdom, we can adapt to the coming changes and reduce the worst impacts. Tom Zimmerman, Program Manger of Wildland Fire Management Research, Development, and Application at the Forest Service's Rocky Mountain Research Station, indicated that as the fire environment changes, we will need a common message and to be flexible and responsive to change.

Norm Christensen, professor and

founding dean of the Nicholas School of the Environment at Duke University, gave the closing banquet speech on Friday evening. He covered over 100 years of changes in the U.S. public's and land managers' views of fire, reminding the group that most of the changes in managers' understanding of fire during the 1970s and 1980s were "totally invisible to the person on the street." The '88 fires were a "watershed" event that increased public awareness by demonstrating the role of disturbance on large landscapes and the remarkable resilience of ecosystems in general. Looking to the future, Christensen noted, "Megafires repeatedly confirm the fallacy of the assertion that fires can be excluded from the ecosystem without consequences.... Fire management will at once become more compelling and more daunting." Christensen remembered the "Ten Standard Firefighting Orders" written in 1957 that were based on lessons learned from tragic fires. He provided a contemporary version for managers, incorporating the lessons learned from the past 20 years. He concluded, "Be humble, manage adaptively."

Numerous sponsors and partners contributed to *The '88 Fires: Yellowstone and Beyond* conference. The next *Yellowstone Science* issue will be devoted to the conference. The proceedings, by Tall Timbers Research Station, will be available in 2009.

Human Impacts on Geyser Basins

ASSAS FROM THE

Alethea Steingisser and W. Andrew Marcus

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Given the state of the state of

This article places the remarkable geyser activity of Yellowstone within a global context, examines human impacts to geyser basins worldwide, and examines historical and potential future impacts to thermal features in Yellowstone from tourism and possible geothermal development outside the park. This article is based on a master's thesis in geography completed at the University of Oregon in 2006.

Data

NPS PHOTO

There are few global, systematic accounts of human impacts to geysers and other geothermal features; most research is site specific. T. Scott Bryan provided a synthesis of global geyser basin distribution and human impacts as an appendix in his guidebooks, *The Geysers of Yellowstone* (1991, 1995). Donald White, known for his research on geothermal resources and geyser basins in particular, also documented global impacts of geothermal development on geyser basins (1967, 1968, 1979, 1988, 1992). This article expands on the contributions made by Bryan, White, and others to provide a historical summary of geyser basins as a global resource that has been altered by various types of human activities.

In addition to a literature review, research in this article comes from many wonderful hours absorbed in the archives at the Yellowstone National Park Heritage and Research Center in Gardiner, Montana, and the National Park Service (NPS) library and photo archives at Harpers Ferry, West Virginia. Additional geyser information and historical photos were found through the Geyser Observation and Study Association, a nonprofit organization dedicated to the collection and dissemination of information about geysers.

Geysers and Their Controls

Geothermal regions occur where heat from Earth's interior rises and creates phenomena such as volcanoes, geysers, and hot springs. While volcanic features are generally spread over relatively large areas associated with plate boundaries and hot spots, hydrothermal areas (where heated water rises to the surface to create springs and geysers) are more limited in extent due to local-scale controls on subsurface heat flow, water availability, and pressure. Fournier (1989) describes these controls in Yellowstone in detail.

The difference between geysers and hot springs is the presence or absence of pressure. Pressure is controlled by a variety of factors including rock type and configuration of the

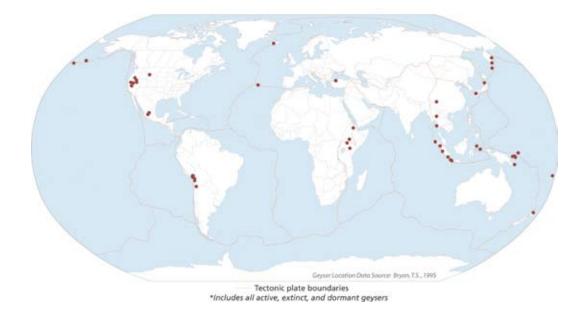


Figure 1. Global distribution of geysers (Steingisser 2006: adapted from Bryan 1995). The number of geysers at these locations is uncertain because geysers can disappear and reappear over time.

underground passage through which the heated water passes on its way toward the surface. If the water can flow freely toward the surface, it bubbles out as a hot spring. Alternatively, if there is enough pressure to prevent the water from rising easily to the surface, it may eventually burst to the surface in an eruption.

Because the geologic and hydraulic components responsible for geysers are so precisely balanced, there may be significant natural variability in the temperature, discharge, periodicity, or eruptive characteristics of individual features within a basin. In many cases, the behavior or characteristics of a feature change with no identifiable cause. In other examples, natural events such as earthquakes, volcanic eruptions, and landslides have created changes in multiple features simultaneously. For example, the 7.1 magnitude Hebgen Lake earthquake outside of Yellowstone in 1959 caused major changes in geothermal features throughout the park. The discharge of many hot springs greatly increased while others were nearly drained. Geysers erupted that had never before been recorded. In many thermal features throughout the park, the temperature increased and their waters became murky with sediment (Marler 1964).

Thermal features such as hot springs, geysers, fumaroles, and mud pots can assume characteristics of one another on a monthly, yearly, or decadal scale. Geysers are the most rare of these forms and occur in close proximity to other geothermal features, although the degree of inter-connectedness between geothermal features is still poorly understood.

Global Distribution of Geysers

Globally, there are at least 40 locations where geyser activity has been documented, but geysers are now extinct in many of those locations. Figure 1 shows these locations as reported by Bryan in 1995. Even in the few sites where geysers have been carefully documented, enumeration at any scale is problematic if not impossible because geysers are inherently unstable both temporally and spatially. Historical and contemporary accounts often disagree about the number of features. The definition of what constitutes a geyser rather than a boiling spring may change from one observer to the next, the length of field observations may vary, and access can be difficult. There is, however, general agreement in the contemporary literature regarding those areas that historically have contained significant numbers of geysers. Figure 2 shows geyser counts for the eight historically largest geyser basins, for which reasonably high quality data are available on geyser distributions and associated human impacts. Although precise counts are elusive because of the nature of geysers, all sources agree that Yellowstone has more geysers than any other thermal area in the world.

Human Impacts to Geysers

Historical Use of Geothermal Resources

It is believed that human use of geothermal resources may date as far back as the Paleolithic period, but concrete evidence only dates to 8,000 to 10,000 years ago, as exemplified by archeological finds near hot springs in North America. The first written evidence of human use of hydrothermal basins dates to the twelfth century BC, when the Etruscans established urban centers such as Bolsena, Populonia, and Saturnia near geothermal sites to extract hydrothermal minerals such as sulfur, kaolin, and travertine for export to foreign markets. Bathing in thermal springs was also highly valued for spiritual and therapeutic reasons and is still popular today. Historical use of hydrothermal basins was mostly confined to hot springs, due in part to the great abundance of hot springs relative to the very few geyser basins worldwide. More importantly, historical use of thermal features was limited to those found at Earth's surface. It was not until the Industrial Revolution in the nineteenth century that technological development and increasing demand for electricity inspired a new use for geothermal resources: energy production.

Geothermal Energy Development

Even though geothermal energy comprises less than 1% of total global energy production and only 4% of total renewable energy use (IEA 2007), geothermal energy prospecting and development has had a greater impact on geyser basins worldwide than any other human activity. Globally, at least eight geyser basins have lost all or most of their natural geyser activity due to geothermal energy development (Bryan 1995), while several others are threatened by potential development from geothermal leases on site or in adjacent areas. Because of the lack of long-term documentation of geysers in many locations, the exact number of individual features that have been altered or destroyed is uncertain.

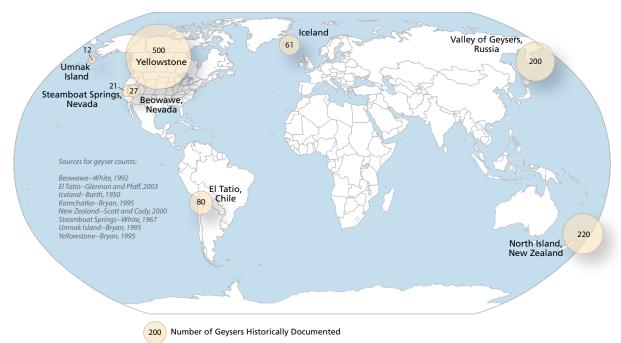
Damage to geysers and springs from geothermal energy development results from drilling into the subsurface hydrothermal reservoir. Drill holes created to extract heated groundwater and steam create new channels that rob geysers and springs of water and heat needed to sustain pressure. Geysers often stop erupting or erupt less frequently and with less volume, and springs dry up. Although the first use of geothermal energy for electric generation occurred in 1904, geothermal energy production was initially concentrated in vapor dominated reservoirs that contain relatively large amounts of steam. Development where geysers were located did not occur until the 1950s, when there was a shift toward the use of geothermal systems that contain an abundant supply of heated groundwater relatively close to the surface. These systems were less expensive to develop, easier to find due to obvious geothermal activity at the surface, and more abundant worldwide (Duffield and Sass 2003, Rinehart 1980).

Tourism

Geysers and hot springs have also been impacted by human activities related to tourism, such as vandalism and infrastructure development. Throwing objects into geysers, whether to induce eruptive activity or simply for "good luck," can change the delicate balance of water pressure and circulation (in essence, plugging the vent), resulting in alteration or cessation of the feature's natural activity. Rocks, sticks, clothing, coins, and numerous other items have been pulled from geyser vents. The circulation change can also change the water temperature, harming microbial algae mats that require specific temperatures.

Development of tourist facilities such as roads, structures, walkways, and paths in thermal areas has undoubtedly damaged some features, although these infrastructure impacts are poorly documented. While these impacts do not often alter entire geyser basins, they are responsible for impacting individual features.

Figure 2. The number of geysers historically documented in select geyser basins (Steingisser 2006). Geyser counts include active, dormant, and extinct geysers, and do not imply that all were active simultaneously. Geyser counts at a location can vary. The counts shown here are based on the sources cited in the figure.



Location	Ahered by geothermal energy development	Documented negative effects of tonrism	Geysers historically documented	Geysers lost due to human activities	Percent of geysers lost
Yellowatone	No	16	500	*	i.
Beowawe (Nevada)	Yes		27	27	100
Steamboat Spring (Nevada)	Yor	4	21	21	100
Ummak Island (Alaska)	*	9	12	*	
New Zeiland	Yes	The	220	165	35
Iceland	Yes.	Yes	61	30	49
El Tatio (Chile)		View	80		
Valley of Geysers (Russia)	*	*	200		-8.

Table 1. Geyser counts and summary of human impacts to geysers.

* No data available

Global Summary of Impacts

Half of the major areas containing geysers have been hydrologically altered by geothermal energy development, and individual springs and geysers at four or more locations have been altered as a result of tourism (Table 1). The Valley of the Geysers on the Kamchatkan Peninsula and the geysers on Umnak Island in Alaska have sustained few, if any, impacts due to their relatively remote locations, while the geyser basins of New Zealand and Iceland were severely altered due to their location in areas where substantial populations needed energy resources. New Zealand has suffered the loss of more geysers than anywhere else in the world. The exact number of features altered at most locations is uncertain, owing to the dynamic nature of geysers and lack of long-term documentation.



Waimangu Geyser, the largest geyser ever documented in terms of height and volume, formed in 1900 near Mt. Tarawera in New Zealand. It became extinct in 1904 as a result of landslide materials blocking its vent. (A. Shepherd, 1903. Printed with permission of the Museum of New Zealand Te Papa Tongarewa, #C.016361).

New Zealand. The geyser basins of New Zealand once contained the third largest concentration of geysers in the world. More than 20 geothermal areas are located in the Taupo Volcanic Zone on the North Island, five of which (Wairakei, Orakeikorako, Rotorua, Waimangu, and Waiotapu) have contained geyser activity. It is estimated that more than 220 geysers existed in these basins as recently as the 1950s. By the 1990s only 55 geysers remained, with many losses due to geothermal resource development (Scott and Cody 2000).

The withdrawal of geothermal fluids for electricity production in the Wairakei basin resulted in the extinction of all geysers (about 70), loss of approximately 240 hot springs (Scott and Cody 2000), and ground subsidence of 14 meters, the largest ever recorded for any type of fluid withdrawal including gas and oil (Allis 2000). At Orakeikorako, nearly 70 geysers and 200 hot springs were flooded by the creation of Lake Ohakuri in 1961 when the Waikato River was dammed for hydroelectric power production (Environment Waikato Regional Council 2006).

The exploitation of geothermal resources at Rotorua began in the 1920s, primarily to pipe geothermal water through homes and businesses for heating. By 1980 more than 500 geothermal wells were producing electricity. The increased fluid withdrawals, combined with a long-term decrease in precipitation, caused many geysers to stop erupting, while others showed the largest decreases in activity seen in 140 years. Government regulations later forced the closure of many wells to protect the remaining geysers. Some geysers have reverted back to their former state while others show sporadic recovery and many remain dormant (Allis and Lumb 1992, Scott and Cody 2000). Several geysers in Rotorua were soaped to induce eruptions for tourist displays, and channels and dams were also built around thermal features to manipulate geyser activity (Cody and Lumb 1992, Rinehart 1980). Other geysers were lost as a result of natural activity. Waimangu Geyser, the largest geyser ever documented in terms of height and volume, formed in 1900 and became extinct in 1904 as a result of landslide materials blocking its vent (Hunt et al. 1994).

El Tatio, Chile. El Tatio has so far been spared large-scale geothermal development, in part because of its remote location in the Chilean Andes. The Chilean government drilled six exploratory wells and seven production wells between 1969 and 1974, but the project was soon abandoned and no studies on impacts to thermal features were undertaken. El Tatio has since become a tourist destination, albeit not a developed one. There are no designated roads or walkways, nor is there a management system in place. Human impacts observed by Glennon and Pfaff (2003) were relatively minor and included objects thrown into springs and geysers and tire marks on thermal features.

Iceland. Being a volcanic island, Iceland lacks fossil fuel energy reserves and depends almost entirely on geothermal energy and hydropower. The primary use of geothermal resources is for space heating; 87% of Iceland's 280,000 residents live in homes with geothermal heat (Ragnarsson 2003). Prior to exploitation, approximately 60 geysers existed in scattered basins, mostly on the western side of the island (Barth 1950). There are no specific studies, at least in the English language, that document the disappearance of geysers in Iceland. There is evidence that geysers were soaped and fitted with pipes to induce eruptions (Barth 1950, Nielsen 1937), but it is uncertain if these actions had any long-term effects on geyser activity. Bryan (1995) indicates that most of the thermal features in the Reykir geyser basin have been destroyed by geothermal drilling, and that many of the individual features scattered across the island are gone as well. Iceland now has fewer than 30 active geysers.

Valley of Geysers, Russia. Reports by Russian scientists indicated that there were more than 20 geysers present in the Valley of the Geysers on the Kamchatkan Peninsula when they first explored it in 1941. Bryan observed at least 200 geysers during field research in 1991. The area has not been commercially developed for tourism or energy development and is protected as part of the Kronotsky Nature Preserve, which encompasses an area approximately equal in size to Yellowstone. Access in the past was difficult, expensive, and usually undertaken only by ecotourism-related travel companies. As such, the Valley of Geysers thermal features are not believed to have been altered by human activity (Bryan 1995). However, in June 2007, a massive landslide buried some of the features under as much as 60 meters of debris and dammed the nearby Geysernaya River. The flooding from the river has turned much of the valley into a lake, silencing many of the remaining geysers. The ramifications of this natural disruption have not yet been fully evaluated.

United States. In the U.S., the shift from dry steam to hydrothermal reservoirs for geothermal energy production in the 1950s resulted in increased exploration of hydrothermal systems. By 1965, the drilling of exploratory wells had caused the loss of all natural geyser activity at Beowawe and Steamboat Springs in Nevada, the two largest geyser basins in the U.S. outside of Yellowstone (White 1967, 1992). The Geyser Bight Geothermal Area on Umnak Island in the Aleutian Islands is part of one of the hottest and most extensive areas of thermal springs in Alaska (Motyka et al. 1993) and is the only geyser location in the United States other than Yellowstone that has not been altered by geothermal resource development. Geyser Bight has been spared mainstream tourism and geothermal development due to its remote location. However, research funded by the U.S. Department of Energy concluded that the region would make an excellent site for geothermal energy development for industries wishing to site themselves in the Aleutians (Motkya et al. 1993, Nye et al. 1990). In Yellowstone a small number of geysers have stopped functioning as a result of tourism-related activities, as described below, but there is potential for greater damage if geothermal development occurs outside the park boundaries.

Yellowstone's Geothermal Landscape

Although Native Americans were aware of Yellowstone's geyser basins, the first Euro-American reports of the region surfaced in the late 1820s when American trappers moved into the Yellowstone region. Few Americans believed trapper and mountain man Jim Bridger's tales of hot water and steam shooting up out of the ground, but his stories inspired the Folsom-Cook-Peterson expedition to investigate and finally confirm his stories by 1869. The following year, a party led by Henry Washburn became the first white men to "discover" the Upper Geyser Basin and Old Faithful. In 1871, Congress funded the first official government expedition, which was led by Ferdinand Hayden, head of the U.S. Geological and Geographical Survey of the Territories. Hayden had the foresight to invite artist Thomas Moran and photographer William Henry Jackson, who provided the first visual representations of the Yellowstone region. Hayden's scientific observations and catalogues, combined with Jackson's and Moran's artwork, inspired Congress to set aside Yellowstone as the world's first national park in 1872. The creation of the park to protect the unique thermal



An eruption of Yellowstone's Beehive Geyser.

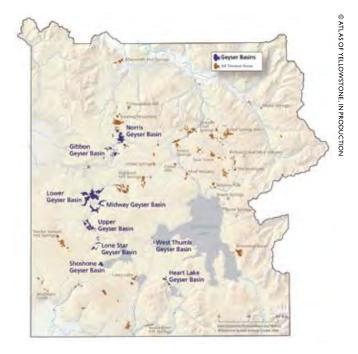


Figure 3. Yellowstone contains more than 11,000 thermal features and perhaps as many as 500 historically documented geysers, more than any other geothermal region in the world. There are at least 100 thermal areas in the park, with geysers documented in nine of them.

features within its boundaries also protected it from the direct large-scale geothermal energy development that later altered or destroyed the natural activity of many of the world's large geyser basins. It is now known that Yellowstone contains more than 11,000 thermal features (Rodman, pers. comm., 2008) and as many as 300 to 500 historically documented geysers (Heasler, pers. comm., 2008), more than any other geothermal region in the world. Data supplied by the Yellowstone Center for Resources Spatial Analysis Center show approximately 100 thermal areas within the park (Fig. 3), nine of which are known to contain geysers. These data do not include the numerous thermal features beneath Yellowstone Lake.

There is remarkable diversity within and among the nine geyser basins. For example, Norris Geyser Basin has evidence of the oldest thermal activity in Yellowstone, dating back at least 12,000 and possibly up to 150,000 years. It is also home to Steamboat Geyser, currently the tallest geyser in the world, and Black Growler fumarole, which holds the record for the highest surface temperature recorded in the park (138°C) (White et al. 1988). The Upper Geyser Basin is home to Old Faithful, which may be the most well-known geyser in the world and certainly in the U.S. It is also thought to contain up to 200 active geysers, more than any other single geyser basin in Yellowstone and perhaps the world (Bryan 1995).

Six of Yellowstone's geyser basins (Norris, Gibbon, West Thumb, Lower, Upper, and Midway geyser basins) are

developed for mainstream tourism with easy access by roads and trails. The Lone Star, Shoshone, and Heart Lake basins are only accessible via backcountry travel. The Congressional act of drawing a line around a piece of land unknowingly protected Yellowstone's thermal features from large-scale geothermal resource development, but exposed them to tourism-related impacts. With approximately three million visitors per year, the struggle between protecting Yellowstone's thermal features while allowing access for public enjoyment is constant.

Human Impacts to Yellowstone's Geyser Basins

Human impacts in Yellowstone's geyser basins are those that have resulted from tourism in the park. The following examples, which include historical accounts of alteration to individual geothermal features, are intended to provide a basis for understanding potential impacts in other geothermal locations, not a complete listing of all features that have been damaged in Yellowstone. Future geothermal development just outside the park also poses a potential threat to Yellowstone's thermal features.

Impacts from Tourism

Vandalism, as we now consider it, has been a problem since the first park visitors, employees, and researchers arrived. Although the 1872 Yellowstone National Park Act reserved two million acres "as a public park or pleasuring ground for the benefit and enjoyment of the people," there were no institutional structures in place for managing the park. Even though park visitation was low at first (approximately 500 per year until 1896), acts of vandalism were pronounced enough that Superintendent Nathaniel Langford's assistant remarked in 1873 that "the parapets of sinter surrounding the 'Castle' and 'Old Faithful' and the 'Bee Hive' [geysers] have been much defaced by visitors to the park" (Bartlett 1985). Souvenir hunters broke up geyser formations and carved their names in thermal features, damage that still occurs today (Magoc 1999). The high demand for Yellowstone souvenirs inspired entrepreneurs to put horseshoes and bottles in hot spring formations so they would become encrusted with travertine.

Both visitors and park officials attempted to induce eruptions by throwing soap down geyser vents, a practice that is thought to have originated at Chinaman Spring in the Upper Geyser Basin as early as 1885 (Whittlesey 1988). A concessioner using the spring's natural agitation to launder clothing apparently induced an eruption by adding soap to the mix, throwing clothing all over the landscape (Bryan 1995). Once tourists learned that soap could induce eruptions, sales of soap skyrocketed and toilet soap from the hotels was in constant short supply. When park geologist Arnold Hague heard these rumors, he conducted his own experiments using both soap and lye, "which proved so satisfactory that I continued my investigations throughout the season on many of the hot springs and geysers in the principal basins." In a letter dated September 6, 1888, Hague describes how this practice benefited park photographer F. Jay Haynes by producing eruptions at times with the best lighting, clouds, and wind rather than at the whim of the geysers' schedule. However, Hague was unsuccessful in his attempt to induce Giant Geyser to erupt:

... In the "Giant" geyser, which, at the time of my experiments, had not played for several months, I was able to cause most violent agitation and the throwing out of water, but nothing that could be called a genuine eruption. People familiar with the behavior of the "Giant" before an eruption, but ignorant of what I had done, believed the geyser was ready to resume its former activity.

Throwing objects into geysers and hot springs has been a problem since Yellowstone's early days and has been a major cause of irreversible damage that continues to threaten to the park's thermal features. Frank Carpenter, who visited the park in 1877 from Radersburg, Montana, described what happened after his party dropped their clothing into Old Faithful:

...the next instant, with a rush and a roar she "goes off" and the clothes, jackets, rags, etc., mixed in every conceivable shape, shoot up to a distance of a hundred feet or more and fall with a splash in the basins below. The water subsides and we fish out the clothing which we find nice and clean as a Chinaman could wash it with a week's scrubbing.

The party then gathered up nearby items and continued their experiment:

...we collect an immense quantity of rubbish and drop it into the crater. We have filled it to the top with at least a thousand pounds of stones, trees, stumps, etc.... the earth begins to tremble...and away go rocks, trees and rubbish to a height of seventy-five or eighty feet in the air.

These types of activities are now known to cause tremendous and often irreversible damage to geyser systems. Objects introduced into thermal features disrupt circulation and pressure within the system and can result in permanent alteration or cessation of the feature's natural activity.

After the Army was given responsibility for protecting park resources in 1886, thermal features continued to be vandalized. O'Brien (1999) comments that the focus was more on accommodating visitors than on protecting park resources during this time. The creation of the NPS in 1916 by the NPS Organic Act enunciated the primary goals of park management, whose mission was "to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." This mission was to be accomplished by staffing the parks with personnel who would participate in all aspects of park management. However, correspondence by Yellowstone personnel during the 1940s and 1950s indicates the severity of the ongoing problem and the methods used to reduce vandalism and reverse its effects. Park geologist George Marler (1946) stated:

... To name all the thermal features where vandalism is in evidence would be a cataloguing of most of the pools, springs and geysers in the Upper, Midway and Lower Basins. Just as a slowly advancing delta destroys the lake, just as certainly continually man-added debris will destroy the pools, springs and geysers of Yellowstone....

...granting he comprises but one percent or less of the traveling public, still this army of thousands is spreading a pestilence which if unchecked will produce a vastly different Yellowstone a few generations hence....

Geothermal features suffered heavily from vandalism during the summer of 1946, when the end of the war brought increased visitation (Condon n.d.). Marler's strong sentiments are due in part to his responsibility for cleaning debris out of thermal features in 1946, when he twice removed rocks weighing more than 40 pounds from the vent of Turban Geyser. In 1947, he reported hauling 55 wheelbarrows full of rocks and debris from springs and geysers in addition to a large tree from Emerald Pool, stating that "the culprits had resorted to considerable labor to drag this tree to the pool and shove it in."

Superintendent Fred Johnston tried to prevent vandalism by educating the public. He submitted Chief Naturalist



Ole Anderson's coating racks on the Mammoth Terraces provided visitors with souvenirs encrusted in travertine, photo ca. 1895.



So many items had been thrown into Morning Glory Pool that it was called "the garbage can" by park staff in the 1950s. Although it was cleaned out several times (above right), the spring's temperature changed due to materials blocking its vent.

David Condon's essay, "Invaluable Natural Assets in Yellowstone National Park Suffer from Vandalistic Acts" to the park's regional director, urging publication in the mass media. Condon described how one pebble tossed into a spring or geyser, when multiplied by hundreds or thousands, can cause permanent damage or complete destruction of geysers and springs.

Despite the efforts of park management, numerous features have been damaged by vandalism. Morning Glory Pool, in the Upper Geyser Basin, is perhaps the most notorious damaged feature within the park. Before the highway was diverted away from Morning Glory in 1971, its easy access and high popularity caused the spring to be the receptacle for large quantities of objects, including coins, rocks, logs, bottles, and clothing. Many efforts were made to remove items from the spring, but the continual addition of material clogged the vent, perhaps enough to lower the spring's temperature and allow the growth of algae. The color of the pool changed to a deeper blue because of bacterial growth, and its scalloped edges were destroyed (Bryan 1995, Whittlesey 1988). Yellowstone Park geologist Henry Heasler (2008) notes that the temperature of Beauty and Chromatic pools (located in the same general area as Morning Glory) also dropped, but as a result of natural causes. As such, it is unclear whether the temperature change in Morning Glory was natural, a result of vandalism, or a combination of both factors.

Minute Geyser in Norris Geyser Basin may be the most vandalized geyser in the park. During the late nineteenth century, it erupted once per minute, sometimes up to 40 feet high. A stagecoach stop located there sometime later encouraged passengers to throw coins and other items into the vent (Whittlesey 1988). When new roads were constructed, Minute Geyser remained relatively close to the main access road and was continually vandalized. In 1935, a park naturalist noted, "I found about 10 boulders ranging up to the size of a man's head, almost completely filling the smaller of the two openings." By 1969 the vent was clogged with rocks that were cemented in place by the spring's mineral waters (White et al. 1988), causing the geyser's eruptive activity to shift to a side vent. Minute Geyser's activity became irregular and it erupted only a few feet. Another Norris Basin feature, Ebony Geyser, also became highly irregular due to vandalism that clogged its vent (Bryan 1995).

Handkerchief Pool, in the Black Sand Basin, was wellknown for its ability to suck down items of clothing and spit them back up in a few minutes, scrubbed and clean. Its activity ceased in 1926 as a result of a log shoved into its vent. Nonetheless, visitors continued to throw objects into the pool. When the pool was first cleaned in 1929, more than one and a half bushels of debris were removed, including handkerchiefs, coins, more than 100 hair pins, nails, bolts, a horseshoe and other various items. In 1950, George Marler cleaned the spring,



Debris removed from Morning Glory Pool, 1950.



Now inactive, Handkerchief Pool was a visitor favorite because of its ability to suck down handkerchiefs and eject them washed and clean.

removing the log and gravel that had washed into the spring. Although water flowed once again into the pool, it was forever changed by the long period of inactivity during which algae mats encroached on its rims (Whittlesey 1988, Bryan 1995).

There is little doubt that park development such as road building, subsurface utility emplacement, and the construction of boardwalks has affected thermal features. Many roads are located next to or directly on top of geothermal areas. There is, however, little information on the impacts of development on specific features except for the personal communications of George Marler and U.S. Geological Survey employee Robert Fournier. Beehive's Indicator, a small geyser located a few feet from Beehive Geyser, commonly erupted immediately before activity at Beehive Geyser began, until its vent became plugged with sand and gravel in 1953. Marler, who attributed the plug to altered drainage patterns caused by boardwalk construction that diverted runoff from Giantess Geyser, attempted to clean out the debris. Bryan described Beehive's Indicator as active but irregular in the mid-1990s. Marler also noted that a road had been built over the base of the Great Fountain Geyser, much of



Steaming pavement after the 1959 Hebgen Lake earthquake, Fountain Paint Pots area, Yellowstone National Park.



Aerial view of the Upper Geyser Basin, 1968. Development of facilities such as roads, structures, walkways, and paths in thermal areas has probably damaged some thermal features.

which had been physically "hacked away" and removed during the construction process "despite extensive, suitable, adjacent terrain."

Fournier worked closely with park maintenance staff, advising them on issues regarding hot spring activity. In a 1971 letter to Superintendent Jack Anderson, Fournier identified issues that presented maintenance problems and offered solutions that would minimize damage to thermal features. In particular, he noted the futility of building roads atop active springs. The chemical-rich water and release of carbon dioxide gas eventually breaks down the pavement above the spring, a fact made evident by the 1959 Hebgen Lake earthquake. In his correspondence, Fournier referred to road deterioration resulting from spring activity in the Chocolate Pot area. He suggested designing a drainage system made of coarse gravel that would preserve the spring's natural activity but allow the water to drain to the edge of the roadbed. He also suggested covering the gravel with plastic sheeting to vent the gases away from the road.

Although the full extent of impacts resulting from tourism is poorly documented, these examples indicate that public access to thermal features, especially popular ones, can create significant problems. It is probable that intentional acts of vandalism by park visitors represent only a very small minority of Yellowstone's visitors, and that the great majority of visitors engage with the park in a manner that promotes preservation. However, damage to Yellowstone's thermal features at any scale must be addressed and prevented because the damage is often irreversible. The effects of vandalism have been alleviated to some degree by aggressive public education campaigns that include roving interpretive rangers, signs, and information published in the park newspaper about how vandalism damages thermal features (Taylor 2005). Additionally, dedicated volunteers such as Ralph Taylor, president of the Geyser Observation and Study Association, perform surface cleaning of thermal features during the heavy summer tourist season as well as monitor geyser activity.

Potential Impacts from Geothermal Energy Development

While vandalism and in-park developments have altered individual features within Yellowstone, potential impacts from external threats may pose the greatest risk to the park's hydrothermal systems. Two known geothermal resource areas (KGRAs), Island Park and Corwin Springs, are located adjacent to park boundaries (Figure 4). The potential for geothermal development in these areas poses a risk because the hydrologic connections between the KGRAs and park features are poorly understood (U.S. Forest Service and Bureau of Land Management 1979, Sorey 1991). After the Geothermal Steam Act of 1970 opened federally-owned portions of the KRGAs to geothermal leasing, more than 200 applications were filed for locations in Island Park, but none were approved because of concerns about the effect on the park of extracting subsurface fluids there. Amendments to the Geothermal Steam Act in 1984 banned federal geothermal development in the Island Park KRGA. However, leases for 25,000 acres of state and private land were granted, and potential geothermal development from these leases still threatens park resources (Harting and Glick 1994).

In 1986 the Church Universal and Triumphant drilled a geothermal well near Corwin Springs, only 8 km from the park boundary and 14 km from Mammoth Hot Springs, sparking an outcry by the NPS and conservation groups. The well significantly reduced the flow of LaDuke Hot Springs, located adjacent to the well site. This drilling and other concerns regarding resource development adjacent to national parks resulted in the Geothermal Steam Act amendments of 1988 that gave the Secretary of the Interior the right to turn down a lease application if it was "reasonably likely to result in a significant adverse effect on a significant thermal feature within a unit of the National Park System." The amendment also specified that there would be no further development or geothermal leasing at Corwin Springs until the U.S. Geological Survey and NPS conducted a study on the hydrologic connections and possible impacts of development on Yellowstone's thermal features. The study later found that there was a possible hydrologic connection between Mammoth Hot Springs and the Corwin Springs KGRA, but determined that limited development could continue at LaDuke Hot Springs without adversely affecting Yellowstone's thermal features

(Sorey 1991). In 1992, the moratorium on geothermal development at Corwin Springs KGRA expired, so potential harm to Yellowstone's thermal features could still result if large-scale development occurs. More legislation was introduced in 1994 to protect Yellowstone's thermal features, particularly the Old Faithful Protection Act, which would ban geothermal development within 15 miles of the park boundary, but it failed to pass in the Senate (Harting and Glick 1994).

A major milestone in the protection of Yellowstone's thermal features was the signing of the Montana–NPS Water Compact in 1994. The compact allows Yellowstone and Glacier national parks and Big Hole Battlefield National Monument to retain all federally reserved water rights based on the year of each park's establishment. The compact also addresses the protection of Yellowstone's unique hydrothermal systems. This was accomplished by designating a Controlled Groundwater Area located just north and west of the park that has potential hydrologic connections with Yellowstone's thermal features (Amman et al. 1995, Custer et al. 1994). The compact restricts hot and cold groundwater withdrawals and geothermal development within this area to prevent adverse effects to Yellowstone's thermal features.

The NPS has only limited water rights agreements with Yellowstone's other two bordering states, Idaho and Wyoming. Idaho has granted Yellowstone all reserved water rights, but the

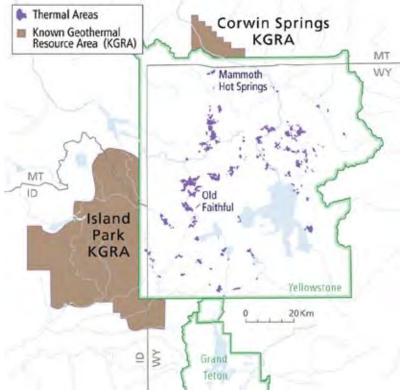


Figure 4. There is currently no geothermal development at Corwin Springs or Island Park. If future development occurs, it could threaten Yellowstone's unique geothermal features.

agreement does not specifically address waters with possible geothermal connections. Wyoming has only settled rights for a small portion of the park and has no agreements that address geothermal resources (Harting and Glick 1994).

Conclusions

This research illustrates how vulnerable geyser basins are to the effects of human activities. At least half of the major areas around the world that contain geysers have been impacted to varying degrees by human activities and countless minor thermal features have been lost. Those that remain are potentially threatened by growing populations, tourism, increasing development, the growing demand for energy, and the relative ease by which geothermal energy is developed. Even thermal features in Yellowstone are potentially endangered by geothermal energy development along park boundaries and by tourism in the park, despite the fact that the park has had protected status since 1872. As the analysis of Yellowstone has suggested, preservation-oriented management and public education can perhaps relieve some of these negative effects, but we need to be increasingly vigilant and aggressive in protecting these rare and special features.

This review indicates the tremendous need for widespread monitoring of geothermal resources in order to monitor existing resources and assess human impacts. Unfortunately, many geyser basins of the world have not been carefully inventoried nor are they monitored to help protect them from potentially destructive future impacts.

Yellowstone has perhaps the most aggressive inventory and monitoring program of any large geothermal region in the world. Yellowstone's Thermal Inventory Project has employed ground survey crews each summer since 1998. These crews have surveyed more than 11,000 thermal features. The project was designed to inventory Yellowstone's thermal features spatially using Geographic Information Systems and contains sampling data about acidity and temperature.

Congress funded geothermal monitoring projects for Yellowstone in 1996 and 2005, resulting in strategies that greatly improved monitoring efforts. Yellowstone scientists monitor and assess geothermal activity through indicators such as chloride flux measurements in streams draining thermal areas, groundwater inventories, and thermal remote sensing. Yellowstone is also engaged in cutting-edge geothermal monitoring studies, including isotope and environmental tracers of thermal water to determine flowpaths, groundwater flow characteristics as determined from shallow wells, heat flow of hydrothermal areas from airborne thermal infrared imaging, and geochemical studies of hydrothermal basin-scale convective heat flow (Heasler, pers. comm., 2008). These multiple methods of data collection, monitoring, and assessment provide the baseline data necessary to detect change due to natural and anthropogenic causes, but they can be labor intensive and are often costly.

In addition, Yellowstone staff are actively involved in protecting thermal features on a daily basis. Interpreters educate visitors and also warn them of improper actions. Law enforcement rangers aggressively protect thermal areas and park maintenance staff work to minimize impacts to thermal features from infrastructure development.

Much of the problem with protecting geysers around the world lies in the difficulty of measuring and quantifying a dynamic system whose origins lie beneath Earth's surface. Insufficient documentation creates problems for protection because it is difficult to protect something that one does not know about. People in many areas have failed to recognize the fragility of these features, their rarity, and the need to protect them for future generations. This research documents and explains changes due to geothermal energy and tourist development, but it does not discuss the human values associated with the landscape that ultimately direct the path to protection or development. These aesthetic, cultural, spiritual, ecological, and economic values will ultimately determine how much effort is expended on geothermal protection, development, and monitoring. Yellowstone National Park is thus the most critical area in the world for protecting geothermal resources into the future because of the tremendous number of features within its boundaries and the park's international prominence in helping the public develop a deeper appreciation for geothermal features, their scarcity, and their fragility.

Note: One of the problems we faced in compiling this research was the paucity of scientific literature on geysers outside of Yellowstone. Many of these areas are poorly documented in English language publications. T. Scott Bryan, in his popular book *The Geysers of Yellowstone*, relies on personal travels, records, and anecdotal accounts to generate a global map of locations where geyser activity has been reported historically. In many cases, Bryan was the only documentation we found.

Acknowledgements

We would like to thank many contributors to this work. The initial inspiration for this research came from a speech by then Yellowstone Center for Resources Director John Varley given to the Annual Meeting of the Greater Yellowstone Coalition outlining the rarity of geysers, the lack of data on non-Yellowstone geysers, and the tremendous need to protect Yellowstone's geothermal features. James E. Meacham provided guidance on content and graphics in this article. Ann Rodman and Carrie Guiles from the Spatial Analysis Center at Yellowstone National Park as well as other National Park Service staff provided data and invaluable information about Yellowstone and also helped to fact check the data for the Yellowstone maps. Yellowstone National Park Geologist Henry Heasler reviewed the article and offered important insights. Communications with T. Scott Bryan and members of the Geyser Observation and Study Association (www.gosa.org) and the Geyser email listserver offered information, advice, and references. The dedication of all these individuals to understanding and protecting geothermal features the world over and in Yellowstone in particular provided the inspiration for this work.

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Literature Cited

Allis, R. G. 2000. Review of subsidence at Wairakei Field, New Zealand. *Geothermics* 29(4-5):455-478.

- Allis, R. G., and J. T. Lumb. 1992. The Rotorua Geothermal Field, New Zealand: Its physical setting, hydrology, and response to exploitation. *Geothermics* 21(1–2):7–24.
- Amman, D., B. Cosens, and J. Specking. 1995. Negotiation of the Montana-National Park Service Compact. *Rivers* 5(1):35–45.

Barth, T. F. W. 1950. Volcanic geology, hot springs and geysers of Iceland. Carnegie Institute of Washington, Washington D.C.

- Bartlett, R. A. 1985. Yellowstone: A wilderness besieged. University of Arizona Press, Tucson, 437 pp.
- Bryan, T. S. 1991. The geysers of Yellowstone. University Press of Colorado, Niwot, 299 pp.
- Bryan, T. S. 1995. The geysers of Yellowstone. University Press of Colorado, Niwot, 463 pp.
- Cody, A. D., and J. T. Lumb. 1992. Changes in thermal activity in the Rotorua Geothermal Field. *Geothermics* 21(1–2):215–230.

Condon, D. n.d., noted as probably 1946–47. Invaluable natural assets in Yellowstone National Park suffer from vandalistic acts. Yellowstone National Park Archives, Box 151, file 732-06.5.7 pp.

- Custer, S. G. et al. 1994. Two strategies for Yellowstone National Park hydrothermal protection in light of scientific uncertainty. In R. A. Marston, and V. R. Hasfurther, (eds.), Effects of human-induced changes on hydrologic systems. American Water Resources, Association, Bethesda, MD, pp. 821–830.
- Duffield, W. A., and J. H. Sass. 2003. Geothermal energy: Clean power from the earth's heat, U.S. Geological Survey circular 1249. U.S. Geological Survey, Menlo Park, pp. 36.
- Environment Waikato Regional Council http://www.ew.govt.nz/enviroinfo/geothermal/index.htm> Accessed 3 March, 2006.
- Fournier, R. O. 1989. Geochemistry and dynamics of the Yellowstone National Park hydrothermal system. *Annual Review of Earth*
- and Planetary Sciences 17:13–53. Glennon, J. A., and R. M. Pfaff. 2003. The extraordinary thermal activity of El Tatio Geyser Field, Antofagasta Region, Chile. GOSA Transactions, VIII:31–78.
- Harting, A., and D. Glick. 1994. Sustaining Greater Yellowstone: A blueprint for the future. Greater Yellowstone Coalition, Bozeman, 1994.
- Heasler, H., C. Jaworowski, and D. Susong. 2004. A geothermal monitoring plan for Yellowstone National Park. Yellowstone National Park, Wyoming. 22 pp.
- Hunt, T. M., R. B. Glover, and C. P. Wood. 1994. Waimangu, Waiotapu, and Waikite geothermal systems, New Zealand: Background and history. *Geothermics* 23(5/6):379–400.
- International Energy Agency. 2007. Renewables in global energy supply: An IEA fact sheet. Paris, France, pp. 34. Available at http://www.iea.org/textbase/papers/2006/renewable_fact-sheet.pdf>.
- Magoc, C. J. 1999. Yellowstone: The creation and selling of an American landscape, 1870–1903.
 University of New Mexico Press, Albuquerque, 266 pp.
- Marler, G. D. n.d. Memorandum to the Superintendent, Yellowstone National Park on "Misuse of the Hot Springs."
- Marler, G. D. 1946. Vandalism in the geyser basins. Yellowstone National Park Archives Pamphlet-Geology-Hydrothermal-General YNP-Thermal.

- Marler, G. D. 1964. Effects of the Hebgen Lake Earthquake of August 17, 1959 on the hot springs of the Firehole Geyser Basins, Yellowstone National Park. US Geological Survey Professional Paper, 435-Q:45.
- Motyka, R. J., C. J. Nye, D. L. Turner, and S. A. Liss. 1993. The Geyser Bight Geothermal Area, Umnak Island, Alaska. *Geothermics* 22(4):301– 327.
- Nielsen, N. 1937. Renewed activity of the Great Geyser. The Geographical Journal, 89:5, pp. 451–454.
- Nye, C. J., R. J. Motyka, D. L. Turner, and S. A. Liss. 1990. Geology and geochemistry of the Geyser Bight Geothermal Area, Umnak Island, Aleutian Islands, Alaska. Department of Energy Report ID:12742-1. Obtained from <http://www.osti.gov/energycitations/servlets/ purl/6193109-4EODc1/native/6193109.pdf> Accessed 7 May, 2006.
- O'Brien, B. R. 1999. Our national parks and the search for sustainability. University of Texas Press, Austin, 246 pp.
- Ragnarsson, Á. 2003. Utilization of geothermal energy in Iceland. Proceedings of the International Geothermal Conference, Reykjavík, pp. 7. Obtained from http://jardhitafelag.is/papers/ PDF_Session_10/S10Paper123.pdf> Accessed 12 March, 2006.
- Rinehart, J. S. 1980. Geysers and geothermal energy. Springer-Verlag, New York, pp. 223.
- Scott, B. J., and A. D. Cody. 2000. Response of the Rotorua geothermal system to exploitation and varying management regimes. *Geothermics* 29(4–5):573–592.
- Sorey, M. L. 1991. Effects of potential geothermal development in the Corwin Springs Known Geothermal Resources Area, Montana, on the thermal features of Yellowstone National Park. 91-4052, U.S. Geological Survey, Menlo Park.
- Steingisser, A. 2006. Losing steam: a multi-scale historic analysis of human impacts on geyser basins. M.S. thesis, University of Oregon.
- Taylor, R. 2005. Report on VIP activity, summer 2005. Internal report from Ralph Taylor to National Park Service supervisory staff. Obtained electronically through personal communication, May 2006.
- U.S. Forest Service and Bureau of Land Management. 1979. Final environmental impact statement of the Island Park Geothermal Area, Idaho, Montana, Wyoming. Washington. EPA 800061; FS-800061. 280 pp.
- White, D. E. 1967. Some principles of geyser activity, mainly from Steamboat Springs, Nevada. *American Journal of Science*, 265:641–684.
- White, D. E. 1968. Hydrology, activity and heat flow of the Steamboat Springs thermal system, Washoe County, Nevada. US Geological Survey Professional Paper, 458-C:108.
- White, D. E. 1979. Memorandum. Effects of geothermal exploitation on natural geysers, specifically with respect to Whakarewarewa, New Zealand. 26 February, 1979. YNP Archives.
- White, D. E., R. A. Hutchinson, and T. E. C. Keith, 1988. The geology and remarkable thermal activity of Norris Geyser Basin, Yellowstone National Park, Wyoming. US Geological Survey Professional Paper, 1456:84.
- White, D. E. 1992. The Beowawe Geysers, Nevada, before geothermal development. US Geological Survey Bulletin, 1998:25.
- Whittlesey, L. H. 1988. Yellowstone place names. Montana Historical Society Press, Helena, 178 pp.

Biodiversity and the "Crystal" Salamanders of Yellowstone



Sarah K. McMenamin



IODIVERSITY 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

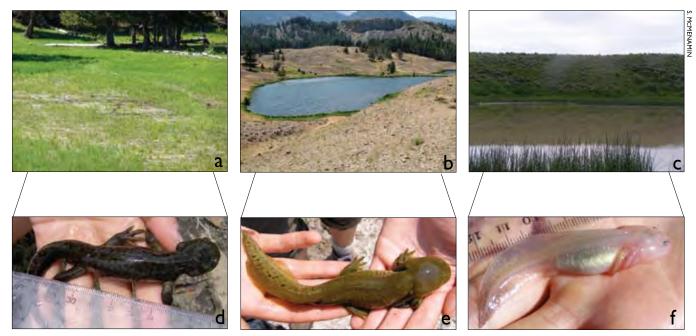


Figure I. Habitat-phenotype relationships in tiger salamanders. Ephemeral wetlands (a) support rapidly metamorphosing populations (d). Permanent ponds and fishless lakes (b) can support adults as well as reproductively mature paedamorphs (e); extremely murky ponds (c) support "crystal" juvenile populations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



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.

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.



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



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.

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.

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



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

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.

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.

— YS

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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 land-scapes. 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.



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

HITE-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, whitetailed 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



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

Mad as a March Hare

The Facts about White-tailed Jackrabbits

HITE-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).



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)

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. Whitetailed 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 I 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.

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 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 covote 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 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



Jackrabbit tracks are regularly found at low arid elevations.

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 georeferenced 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

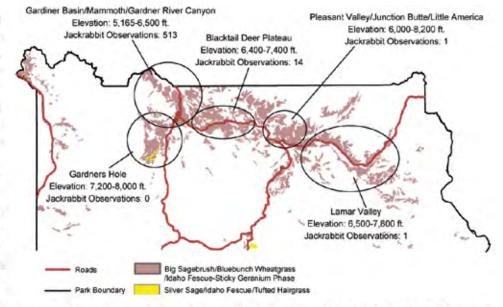


Figure I. Concurrence of vegetation, elevation, and jackrabbit distribution in Yellowstone.

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 midas 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

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

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 Whengeass	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%	6	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%

"Grassland mosaic covering large mudflows near the north emrance.

Sagebrush-grassland Area	Elevation (fr/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	14
Pleasant Valley/Junction Butte/Little America Flats	6.000-8,200 / 1,829-2,499	0/1 ^b
Blackxail 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

^aJackrabbit observation was at 2,000 meters (6,560 fr)

^bBones 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 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, pelagewhite 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.

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,

Table 3. Observations of white-tailed	jackrabbits in zones of	f differing annual	precipitation.
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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	12%
14-16 / 35.6-40.6	16,512	1%	342	64%
16-18 / 40.6-45.7	43,834	2%	16	5%
18-20 / 45.7-50.8	48,507	2%	1	<196
20-30 / 50.8-76.2	512,298	23%	4	196
30-40 / 76.2-101.6	628,006	29%	0	0%
40-50 / 101.6-127	483.517	22%	0	0%0
50-60 / 127-152.4	266,867	12%	0	0%i
60-70 / 152.4-177.8	149,075	2%	D	0%
70-80 / 177.8-203.2	40,709	2%	0	0%6
Total	2,195,448	100%	533	100%

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

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 whitetailed 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 I. 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

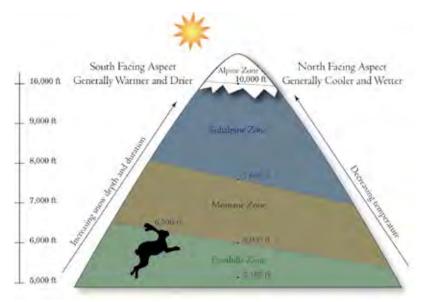


Figure 2. Jackrabbit distribution in the life zones of Yellowstone.

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 habi-

tats 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 sagebrushgrassland habitats of Yellowstone.

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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? Whitetailed 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 I. 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. Blacktailed 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. I. 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 I. 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

TO 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 life-time 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.

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 km²) is much larger than

Corbett (~520 km²) 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 km². 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



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

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 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

"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."

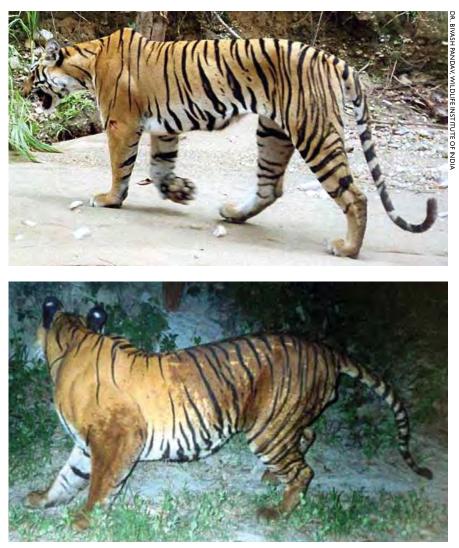
the King cobra and python. I would be remiss if I didn't mention some of Corbett's notable birds such as the great pied hornbill, the khalij pheasant, and the Himalayan griffon.

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 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 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. 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, nongovernmental 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, capturemark-recapture studies can be used to estimate population abundance, density, home range size, reproduction, and survival without ever having to



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

physically capture or mark the tigers. Yellowstone wolf research could be a lot easier if wolves had just evolved with unique stripe patterns!

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,



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.

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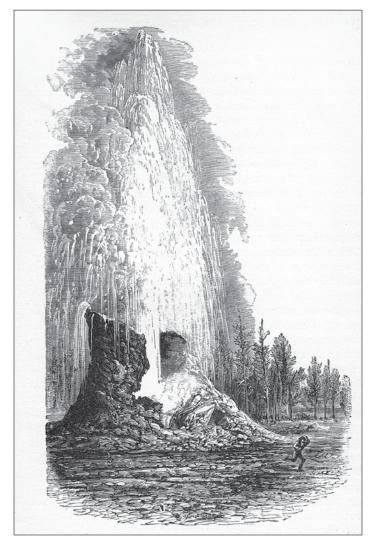
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FROM THE ARCHIVES





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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