

wilderness

Where the Wild Things Are: A Research Agenda for Studying the Wildlife-Wilderness Relationship

Michael K. Schwartz, Beth A. Hahn, and Blake R. Hossack

We explore the connection between US designated wilderness areas and wildlife with the goal of establishing a research agenda for better understanding this complex relationship. Our research agenda has two components. The first, “wildlife for wilderness,” considers the impact of wildlife on wilderness character. Whereas studies show that wildlife is important in both the perception and actual enhancement of wilderness character, the context and particulars of this relationship have not been evaluated. For instance, is knowing that a rare, native species is present in a wilderness area enough to increase perceptions of naturalness (an important wilderness quality)? Or does the public need to observe the species or its sign (e.g., tracks) for this benefit? The second part of our research agenda, “wilderness for wildlife,” considers the types of research needed to understand the impact of wilderness areas on wildlife and biodiversity conservation. Several studies show the effect of one area being designated wilderness on one wildlife species. Yet, there has been no research that examines how the networks of wilderness areas in the National Wilderness Preservation System (NWPS) are used by a species or a community of species. Furthermore, we found no studies that focused on how the NWPS affects ecological or trophic interactions among species. We hope that by providing a research agenda, we can spur multiple lines of research on the topic of wildlife and wilderness.

Keywords: ecoregions, National Wilderness Preservation System, stewardship, wildlife, wilderness, wilderness character

Public perception of the relationship between wildlife and wilderness has drastically changed over the past century. The public attitude toward wilderness in the early 1900s can be characterized by Theodore Roosevelt (1893, p. xiii) in “The Wilderness Hunter,” where the “wilderness” is a force to challenge oneself against.

In hunting, the finding and killing of the game is after all but a part of the whole. The free, self-reliant, adventurous life, with its rugged and stalwart democracy; the wild surroundings, the grand beauty of the scenery, the chance to study the ways and habits of the woodland creatures—all these unite to give the career of the wilderness hunter its peculiar charm. The chase is among the best of all national pastimes; it cultivates

that vigorous manliness for the lack of which in a nation, as in an individual, the possession of no other qualities can possibly atone.

Wildlife in the wilderness setting was to be hunted, not necessarily for food, but for the chase. Wilderness was a place to shape American character. Testing oneself against wildlife within wilderness provided for character-shaping adventures (Callicott and Nelson 1998). This utilitarian perspective of both wildlife and wilderness has been called both anthropocentric and ethnocentric (Callicott 2000), yet was certainly dominant among a segment of American society at the beginning of the 20th century. Even by the midcentury, wilderness advocates such as Aldo Leopold suggested that “Public wilderness areas are essentially a means for allowing the more virile and primitive forms of outdoor recreation to survive” (Leopold 1992, p. 138). This primitive form of recreation extolled hunting to such a degree that Leopold suggested that the Gila Wilderness formally be named the “Gila National Hunting Grounds” (Huggard 2001).

The utilitarian interpretation of wilderness is in sharp contrast to the view ex-

Received May 23, 2015; accepted February 10, 2016; published online March 17, 2016.

Affiliations: Michael K. Schwartz (michaelkschwartz@fs.fed.us), National Genomics Center for Wildlife and Fish Conservation, USDA Forest Service, Missoula, MT. Beth A. Hahn (beth_hahn@nps.gov), Aldo Leopold Wilderness Research Institute. Blake R. Hossack (blake_hossack@usgs.gov), Aldo Leopold Wilderness Research Institute.

Acknowledgments: We thank the organizers of the National Wilderness Conference for hosting the Wildlife and Wilderness symposium from which this article was created. We thank Sean Parks for his work on wolverine modeling and James Tricker for his guidance on wilderness representation by ecosystem. We also thank Susan Fox for encouraging us to work on this topic and Peter Landres for providing comments on an early draft of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

pounded on by a different US President, Lyndon B. Johnson. On signing the Wilderness Bill and the Land and Water Conservation Fund Bill on Sept. 3, 1964 Johnson (1964, p. 1033) stated,

This is a very happy and historic occasion for all who love the great American outdoors, and that, needless to say, includes me. The two bills that I am signing this morning are in the highest tradition of our heritage as conservators as well as users of America's bountiful natural endowments.... I believe the significance of this occasion goes far beyond these bills alone. In this century, Americans have wisely and have courageously kept a faithful trust to the conservation of our natural resources and beauty.... The wilderness bill preserves for our posterity, for all time to come, 9 million acres of this vast continent in their original and unchanging beauty and wonder.

President Johnson's statement captures an American public viewpoint that shifted from considering wilderness from the practical purpose for building character and providing resources to areas that are being maintained for conservation and preservation of the elements within them (Kolb et al. 1994, Callicott 2000). The conservation perspective extended to wildlife protection, as Johnson noted in this same landmark speech:

Action has been taken to keep our air pure and our water safe and our food free from pesticides; to protect our *wildlife*; to conserve our precious water resources.

Despite President Johnson's strong remarks suggesting that wilderness had a function to protect wildlife, there is very little mention of wildlife in the Wilderness Act (16 USC 1131-1136) itself. In fact, the word "wildlife" is only used three times in the Wilderness Act: two times in reference to the National *Wildlife* Refuges, and a third time to acknowledge the shared jurisdiction of the Federal Government and States:

Nothing in this Act shall be construed as affecting the jurisdiction or responsibilities of the several States with respect to wildlife and fish in the national forests.

There is no mention of the aim of protecting, conserving, or preserving wildlife in the Wilderness Act. Moreover, the Wilderness Act allows for actions with direct impacts on wildlife populations (e.g., hunting and fishing regulated by state agencies), as well as indirect impacts (e.g., continuance of livestock grazing in areas where it was already established before wilderness designation). Thus, the Wilderness Act cannot be thought of as a biodiversity, wildlife, or en-

dangered species law as there is no language within the Wilderness Act that mandates wildlife or biodiversity protection. It took nearly 9 more years before the US Congress passed comprehensive legislation aimed to protect endangered species and ecosystems (i.e., Endangered Species Act of 1973 [ESA], although there had been prior individual acts protecting specific taxa or more limited in scope such as the Lacey Act of 1900, the Migratory Bird Conservation Act of 1929, the Bald Eagle Protection Act of 1940, the Marine Mammal Protection Act of 1972, or the Endangered Species Preservation Act of 1966).

The Wilderness Act also does not speak directly to wilderness *research*. Although influential figures such as Aldo Leopold called wilderness "a base-datum of normality, a picture of how healthy land maintains itself" (Leopold 1941, p. 3), the use of wildernesses for reference conditions or baseline assessment was not included in the text of the Wilderness Act. The closest the Wilderness Act comes to noting wilderness' significance to wildlife research is in the "definitions" section. Wilderness is defined as follows (*italics ours*):

A wilderness, in contrast with those areas where man and his own works dominate the landscape, is hereby recognized as an area where the earth and its community of life are untrammelled by man, where man himself is a visitor who does not remain. An area of wilderness is further defined to mean in this Act an area of undeveloped Federal land retaining its primeval character and influence, without permanent improvements or human habitation, which is protected and managed so as to preserve its natural conditions and which (1) generally appears to have been affected primarily by the forces of nature, with the imprint of man's work

substantially unnoticeable; (2) has outstanding opportunities for solitude or a primitive and unconfined type of recreation; (3) has at least five thousand acres of land or is of sufficient size as to make practicable its preservation and use in an unimpaired condition; and (4) *may also contain ecological, geological, or other features of scientific, educational, scenic, or historical value.*

Notwithstanding public perception regarding the intent of the Wilderness Act to have areas set aside as bellwethers, the National Wilderness Preservation System (NWPS) cannot be thought of as formal means of establishing a research baseline for nature.

Wildlife and wildlife research are not central to the Wilderness Act, yet the topics of wildlife and wilderness are complexly intertwined and often understudied. With the 50th anniversary of the Wilderness Act celebrated in September 2014, we look toward a research agenda for the next 50 years of wilderness research. Although each wilderness will have its own unique matters to be addressed, we can broadly group questions into two categories, which form the basis of our wilderness-wildlife research agenda: How important is wildlife for wilderness character? and How does the existence and maintenance of wilderness character in an individual wilderness area or the network of many wilderness areas affect wildlife (Figure 1)? By "wilderness character" we mean the "combination of biophysical, experiential, and symbolic ideals that distinguishes wilderness from all other lands" defined by the qualities of (1) untrammelled, (2) natural, (3) undeveloped, and (4) opportunities for solitude or a primitive and unconfined type of recreation, as expressed in the Wilderness Act (Landres 2004, p. 9). Untrammelled is a

Management and Policy Implications

This article establishes a multiscale research agenda to help set the stage for research examining wildlife and wilderness. Our research agenda distinguishes the effects that wildlife has on wilderness character versus the impact that wilderness character has on wildlife populations, species, and communities. We consider both parts of this research agenda of equal importance. Understanding how wildlife contributes to wilderness character is essential to the legal mandate to preserve it. Managers are increasingly faced with decision tradeoffs in managing for both wildness and naturalness within wilderness through proposals such as assisted migration, wildlife reintroductions, and supplementations. Well-crafted social science can help with these policy decisions. The second prong of our research agenda examines how wilderness character affects wildlife. It encourages studies that go beyond the effect of one wilderness on one species. There has been increased perception in the policy and management arena that protection of one patch is inadequate for species protection and that management of the entire landscape matrix, across multiple jurisdictions and management plans, is critical for conservation. Our research agenda advocates research that understands the role of the network of wilderness areas in biodiversity conservation.

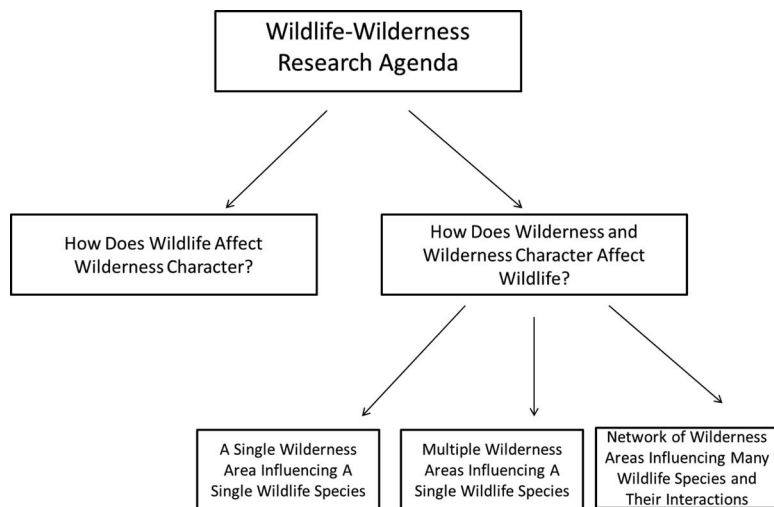


Figure 1. Schematic diagram showing the proposed research agenda for studying the wildlife-wilderness interaction.

word unique to the wilderness literature and can be defined as “unhindered and free from intentional actions of modern human control or manipulation” (Landres et al. 2015, p. 10–11), whereas “natural” is the quality that is “preserved when there are only indigenous species and natural ecological conditions and processes, and may be improved by controlling or removing nonindigenous species or by restoring ecological conditions.” (Landres et al. 2015, p. 11).

Wildlife for Wilderness

It is often assumed that wildlife influences the perception of wilderness character. Certain indigenous wildlife species—such as grizzly bears (*Ursus arctos horribilis*), caribou (*Rangifer tarandus*), and gray wolves (*Canis lupus*)—suggest wilderness (Hendee and Mattson 2009). Senses of the natural qualities of wilderness character are often associated with encountering wildlife in wilderness. Yet, active management for wildlife in wilderness may degrade the qualities of wilderness character (Knapp et al. 2001, Landres et al. 2001, 2015). Encountering a water capture device used to subsidize rare wildlife populations in arid environments may impact perceptions of wilderness by degrading the untrammeled and undeveloped qualities of wilderness character (*Wilderness Watch v. US Fish and Wildlife Service* 2010).

In this research agenda, we consider a hierarchical approach for conducting studies to investigate the effect of wildlife on wilderness character, starting with the fundamental question, “How important is wildlife for wilderness character?” The Wilderness Act emphasizes not only the end goal (e.g., im-

proving natural components by maintaining wildlife populations) but also the means of achieving this action (e.g., implementation methods). If wildlife is found to be only marginally important for the perception of naturalness then there is no need to degrade other wilderness qualities to enhance wildlife populations for the sake of maintaining wilderness character. Alternatively, if wildlife substantially increases the perception of naturalness, then there may be reasons to degrade other wilderness qualities to achieve this goal. Kammer (2013) suggests that restoring wildlife populations in wilderness is a commendable goal to achieve naturalness, but that this goal is secondary to the intent of the Act, which is to keep areas free from human control. Others have argued that the natural quality that wildlife brings to Wilderness is essential to maintaining wilderness character (*Wilderness Watch v. US Fish and Wildlife Service* 2010) and is equal to managing for other qualities of wilderness character (Landres et al. 2015; see Cole and Yung 2010 for this full debate). Understanding the relationship between wildlife and wilderness character should influence management standards and guidelines used to implement wilderness management (achieve naturalness) under the Wilderness Act. Without adequate research on this topic, wilderness managers must assume the importance of wildlife for enhancing wilderness character.

Public perceptions of wildlife in wilderness areas were evaluated during surveys conducted in 1994–1995 and 2000 (Cordell et al. 2003). Respondents were asked to

describe their perception of various wilderness benefits. In 1994–1995, “protection of wildlife habitat” ranked as the second of 14 most important benefits, but in 2000, it ranked third of 14 behind “protecting water quality” and “protecting air quality.” Despite dropping from second to third, there was an increase of 9.2% in respondents suggesting that wildlife habitat protection was “extremely” or “very important.” Similarly, “protection of endangered species” ranked fifth of 14 benefits in both time frames (Cordell et al. 2003). Cordell et al. (2003) demonstrated that the public perceives a value of wilderness for wildlife, but this does not specifically address the question, “How important is wildlife for the public’s perception of wilderness?” Watson et al. (2015) conducted a survey of wilderness visitors ($n = 635$) to Sequoia and Kings Canyon National Parks, where they asked visitors to identify the relative importance of different characteristics in defining wilderness character. The survey characteristic “a place without non-native animals” ranked 15th of 19 in defining wilderness character. We believe research is vital to understanding how wildlife affects wilderness character.

Our initial question “How important is wildlife for wilderness character?” and the existing studies treat all wildlife encounters equally, but the range of possible answers is more nuanced. For instance, the perception of the natural quality of wilderness may vary with different types of wildlife, such as seeing a threatened, endangered, or socially important species, a charismatic or flagship species, or an invasive species. Viewing a native wolverine (*Gulo gulo*) in the John Muir Wilderness in California, where none have been seen for nearly a century (Moriarty et al. 2009) may be perceived differently from seeing an introduced brook trout (*Salvelinus fontinalis*) or feral pig (*Sus scrofa*). Similarly, different user groups (e.g., hunters versus hikers) may respond differently to seeing Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), black bears (*Ursus americanus*), or moose (*Alces alces*) in a wilderness area. We would like to see the National Survey on Recreation and the Environment or a similar instrument ask more comprehensive questions about how different categories of wildlife are perceived by different user groups and how these various categories influence wilderness experiences.

Wildlife viewing is only one way to experience wildlife. There are many ways to be influenced by wildlife encounters in wilder-

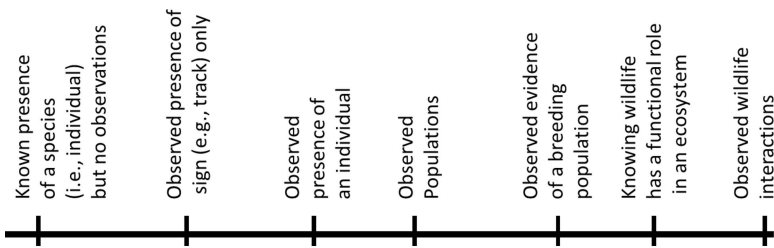


Figure 2. Schematic diagram of a gradient of perception of a wildlife species in a wilderness area. The left portion of the bar represents the cases in which there is no direct human-wildlife interaction, whereas on the right are situations in which not only is wildlife playing a functional role in the ecosystem but also this interaction is observed.

ness (Figure 2), and future surveys could examine what specifically about wildlife influences wilderness experience. Wildlife experience ranges from simply knowing a species is present without witnessing it (left side of Figure 2) to knowing that wildlife is present as a functional component of the ecosystem (right side of Figure 2). For example, it may be enough for some wilderness users to know that lynx (*Lynx canadensis*) exist in the Bob Marshall Wilderness to increase their perception of the natural quality of wilderness character, whereas others may need to see tracks or the actual animal to receive benefits. Similarly, perceptions of the untrammeled and natural qualities of wilderness character may be heightened by seeing bands of native bighorn sheep (*Ovis canadensis*) in the Frank Church-River of No Return Wilderness, Idaho, whereas others may have similar perceptions of wilderness character from seeing only signs (e.g., tracks or feces). Future surveys could examine the specific influences of wildlife on the wilderness experience, which would provide managers with a target of how to preserve wilderness character. We extol surveys that ask the question “How important is wildlife for wilderness character?” However, more informative questions would be, “How important is wildlife for perceptions of the natural quality of wilderness character,” or “How important is wildlife for perceptions of the untrammeled quality of wilderness character?” The ideal would be a survey that could ascertain the relative importance of various wildlife experiences, by different user groups in influencing each quality of wilderness character.

A research agenda for understanding the role of wildlife in wilderness needs to investigate public attitudes about the range of acceptable wildlife management actions at large landscape scales to improve the natural quality of wilderness. Ecosystems within wilderness areas are not static, nor are wildlife

populations. Wilderness is influenced by events occurring outside of individual wilderness areas and at temporal and spatial scales much larger than even the largest network of wilderness areas. Changes in regional fire regimes, elimination of source populations of wildlife outside of wilderness, spread of disease, climate change, and drought occur at spatial scales larger than a wilderness area. Yet these forces affect species compositions and demographics of wildlife within wilderness. Most notably, climate change can lead to changes in species compositions in wilderness due to idiosyncratic species responses to shifts in temperature or precipitation (Thuiller et al. 2005, Dobrowski et al. 2013). The reverse is also true: actions within wilderness areas may affect wildlife on surrounding lands both positively and negatively. What is the role of wilderness managers in offsetting large-scale, human-induced change?

Managers are also increasingly faced with decision tradeoffs in managing for both untrammeled and naturalness within wilderness through proposals such as assisted migration, predator control, wildlife reintroductions, and supplementations. Kammer (2013) suggests that managing with restraints and leaving areas “beyond humans’ manipulative reach” takes primacy, but what happens when human-induced change is at the scale of the climate or ecosystem? Watson et al. (2015) explored the topic of managing effects beyond the scale of an individual wilderness. Wilderness visitors to Sequoia and Kings Canyon National Park supported the reintroduction of extirpated native species and the removal of nonnative species to support native species recovery but did not support potential intervention actions to mitigate the effects of climate change. A research agenda for the next 50 years would be incomplete without further examining this issue, which involves diverse scientific, legal, and ethical issues. There is

an ongoing, robust debate about ecological restoration actions in wilderness related to species, habitats, and ecological processes (reviewed in Cole and Yung 2010). We would like to see more human dimensions-oriented studies to help inform this debate.

Wilderness for Wildlife

The second prong of our wildlife and wilderness research agenda considers how wilderness influences wildlife. Management for primeval character, the minimization of human activity, and the emphasis on maintaining natural conditions has often benefited fish and wildlife populations (Kershner et al. 1997, Mittermeier et al. 2003, Hendee and Mattson 2009). For example, the reclamation of old logging roads can reduce human interactions and contact with wildlife, improving the survival of threatened species (Cole et al. 1997, McLellan et al. 1999). Yet the influence of wilderness character on wildlife is beyond the management of a single wilderness area. Research at multiple temporal and spatial scales is crucial and should include the effects not only of wilderness designation or improved wilderness character on a single species but also on how species interact in ecological communities.

A literature search revealed a paucity of published research on how federal wilderness designation or wilderness character affects species’ population growth, vital rates (e.g., survival), or extinction risk. Searches of academic databases (e.g., Google Scholar, Web of Science, *Journal of Wildlife Management*, and *Conservation Biology*) for the terms “wilderness” and “wildlife” or “fish” produced many published papers, but almost exclusively where the term “wilderness” is broadly defined and used as a descriptor of a landscape. Most papers did not differentiate between a federally designated wilderness that adheres to a strict set of laws and rules, and large remote areas that are descriptively called wilderness. Of the few studies that occurred in federally designated wilderness, most were autecological studies of one species in one wilderness (e.g., Koehler and Hornocker 1977, Etchberger et al. 1989, Papouchis et al. 2001, Rominger et al. 2004, Wasser et al. 2004, Fraser et al. 2005, Schoenecker et al. 2015). For example, Etchberger et al. (1989) found that human disturbance and the presence of habitat where fire had been excluded were responsible for a decrease in the range size of bighorn sheep from 79.5 to 17.0 mile² within Pusch Ridge Wilderness, Santa Catalina Moun-

tains, Arizona. Other autecological studies described changes in animal behavior (Walker and Marzluff 2015) with unknown implications for fitness (e.g., Titus and VanDruff 1981). In addition to studies that use wilderness as a general term or were limited to autecological examinations of species in a single wilderness, several studies speculated on the responses of wildlife to wilderness designation based first on principles of wildlife and conservation biology (e.g., Mech et al. 1988). These studies assume that the designation of an area as wilderness affords protection for conserving species. Yet, few studies have explicitly evaluated the role of wilderness in wildlife conservation.

We contend that it is important to collect data on wildlife in wilderness for several reasons. First, there are specific wildlife issues related to particular wilderness areas (e.g., Davidson and Knapp 2007, Burger et al. 2012). Rominger et al. (2004) studied cause-specific mortality of translocated bighorn sheep in the Wheeler Peak Wilderness in northern New Mexico. They found that high mountain lion (*Puma concolor*) predation, encouraged by the encroachment of woody vegetation used for stalking cover and increased food subsidies from cattle operations, was the probable cause of the enhanced mortality. Equipped with this knowledge, wilderness managers can discuss the tradeoff between vegetation management, issuing of grazing permits, and the management goal to have bighorn sheep in the area.

Second, we cannot assume that biological, evolutionary, and geographic understandings from outside of wildernesses apply within wildernesses. The emphasis on unmanipulated landscapes may present different evolutionary pressures (called “unnatural selection”) to wildlife populations within wilderness compared with those outside these areas. Harvesting wildlife is allowed in most US federal wilderness areas but may be limited in some locations because of access or because they are part of a National Park that disallows hunting. Coltman et al. (2003), Allendorf and Hard (2009), and Douhard et al. (2015) showed that human harvest of desirable wild animals (e.g., large body size in fish or large horns and antlers in some mammals) can change gene frequencies responsible for the trait in the population. To be considered unnatural selection, it is important that this is genetic change and not plasticity or acclimation (i.e., change that is nongenetic and not heritable). For

example, the extensive harvest of cod (*Gadus morhua*) off Georges Bank produced “fisheries-induced evolution,” where the age and size at maturity of cod dramatically declined in association with harvest pressure. This is due to a genetic change in the population (e.g., unnatural selection) as the trait has not shifted back after tighter fishing regulations and stock recovery (Olsen et al. 2004). Similarly, Coltman et al. (2003) showed that the average horn length of bighorn sheep declined at Ram Mountain, Alberta, Canada, as a result of the heavy harvest of rams with genes that strongly contributed to horn growth. Wilderness areas can be remote and given their undeveloped mandate are often used less by sportsmen. National Parks, which do not allow hunting (with some notable exceptions) may also act as reservoirs where natural selection can dominate over unnatural selection. The difference may be that National Parks, which encourage development for the enjoyment of people, may be selecting for other behaviors or traits (e.g., reduced fear of humans or increased movement rates) (Ciuti et al. 2012). By minimizing unnatural selection, wilderness can preserve the natural selection process that acts on wild populations and these genetic outcomes.

Last, it is not only evolutionary pressures that may be different in wilderness areas; habitat use and behavior of a species may be altered in wilderness. This may be especially true of species that are sensitive to development or degradation of other elements of wilderness character. Without directly studying how wildlife uses wilderness, we make assumptions about habitat use based on observed behavior and distributions outside of wilderness that may be incomplete (McKelvey et al. 2008, Schwartz et al. 2015).

Given that there are important reasons to study wildlife in wilderness, why is there such a paucity of studies measuring the role of wilderness in biodiversity and wildlife conservation? We believe this probably results from several contributing factors. The most obvious is that wilderness areas can be difficult to access (Oelfke et al. 2000): systematic surveys are complicated by the lack of roads and other developed infrastructure (i.e., wilderness is defined as “an area of undeveloped federal land”). This leads to increased cost associated with accessing many wilderness locations to collect data. Second, the enacting wilderness legislation does not prioritize using wilderness areas as a scientific baseline for assessing change (see above). This

means that wilderness managers may rank other activities over scientific data collection in a landscape not dominated by humans. Third, regardless of the size or accessibility of a wilderness, many research tools conflict with prohibited uses because equipment is mechanized, requires semipermanent or permanent installations, or degrades the untrammelled, natural, or undeveloped qualities of wilderness character (Franklin 1987, Landres et al. 2015). A common tool used to study habitat use of mammals is a radio or satellite collar placed on an individual animal. It is often perceived that capturing wildlife degrades the untrammelled quality of wilderness character, whereas the presence of the satellite collar on an animal degrades the undeveloped quality of wilderness character (Landres et al. 2015). This can lead to tension between wildlife biologists trying to collect data and wilderness managers trying to preserve wilderness character by minimizing trammeling actions and effects on the natural quality of wilderness character (Schwartz et al. 2011). This tension may hinder interest of wildlife researchers to work in wilderness. Schwartz et al. (2011) show that new nonintrusive and noninvasive research tools (e.g., noninvasive genetic sampling and stable isotope analysis) can substantially reduce conflict and make wildlife work in wilderness more feasible. Fourth, there is the perception that we can effectively extrapolate information on wildlife from outside of wilderness areas to inform decisions within wilderness. As we described above, there are biological reasons why habitat selection, behavior, and genetic composition may be different inside versus outside wilderness. Last, there is the untested hypothesis that wilderness buffers wildlife populations against declines; thus, research in these areas is less critical. This argument erroneously contends that active management is not allowed in wilderness; therefore, there is limited use of information obtained on wildlife in these areas.

Studies on the effect of wilderness on wildlife also may be limited because wilderness is not an ecological variable. Displaying the centroids of the congressionally reserved wilderness areas of the United States on the Omernik (1987) Level 1 and Level 3 Ecoregions of the contiguous United States demonstrates the range of ecosystems and landscapes represented by wildernesses (Figures 3 and 4). Simply stated, not all wildernesses are the same; they are in different ecoregions (Figure 3), have different landscape config-

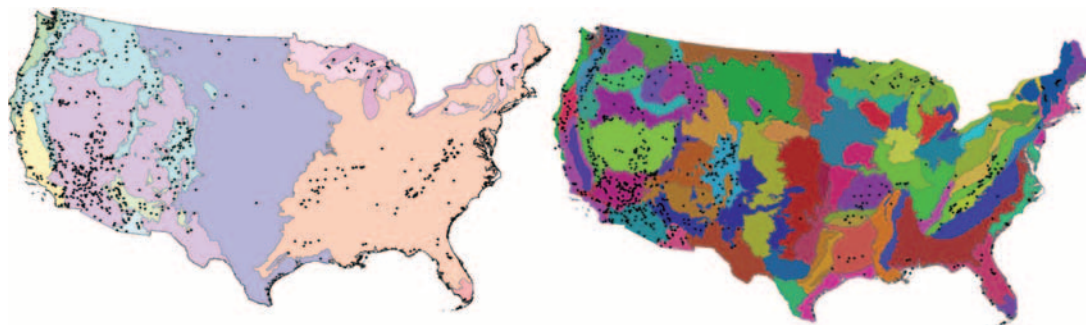


Figure 3. Centroids of the congressionally reserved wilderness areas of the United States plotted on Omernik (1987) Level 1 (left) and Level 3 (right) Ecoregions of the contiguous United States. This figure illustrates the range of Level 1 and Level 3 Ecoregions represented by wilderness areas.

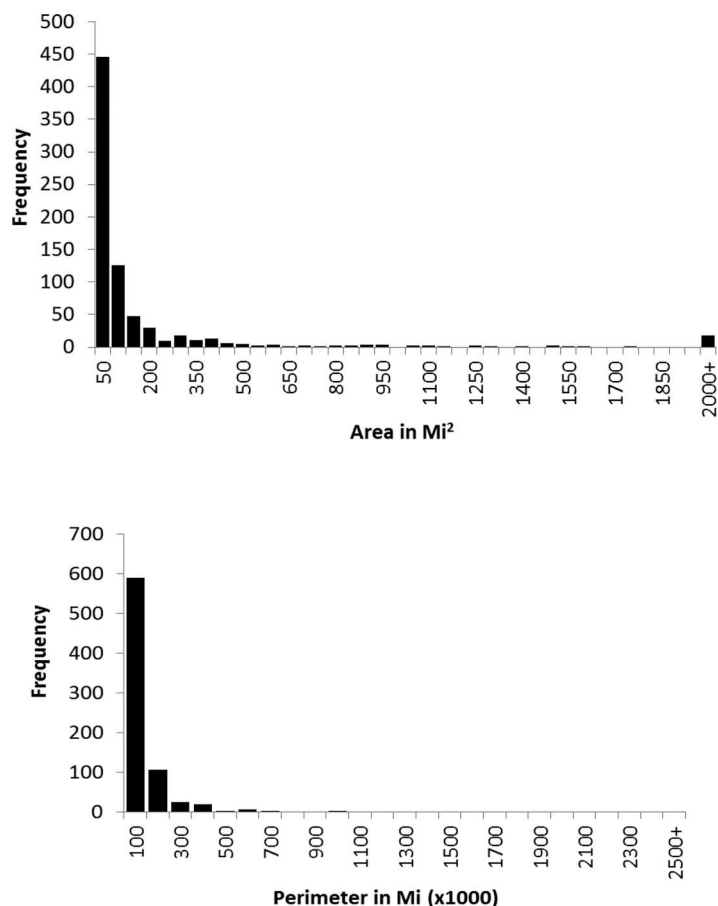


Figure 4. Plot of the distribution of wilderness areas by size (top) and edge or perimeter (bottom). (Data are from www.wilderness.net; last accessed Sept. 1, 2014).

urations (Figure 4), and differ on a suite of ecological variables (Dietz et al. 2015). Size, in terms of area and perimeter of wildernesses, vary as well (Figure 4) and need to be considered along with other landscape shape metrics in the design of studies that consider wildlife in wilderness. Wilderness, while a legally and socially important construct, is not necessarily a biological or landscape characteristic meaningful to wildlife (see also Graber 1983). We encourage comprehensive studies that stratify by ecoregion, size,

edge, and other landscape variables and then ask how wilderness protection acts on critical demographic or genetic parameters associated with a species. Given the large number of federally designated wilderness areas in the United States (762), this type of stratification is possible.

To advance wilderness-wildlife research, we recommend studies conducted on multiple spatial and ecological scales. We encourage the wildlife biology community to go beyond one wildlife species-one area

questions and ask how networks of wildernesses are used by a species (a one-to-many relationship). We also encourage questions on how networks of wilderness areas are being used by a community of species, studying the species themselves, the community, and the interspecific interactions (many-to-many relationship) (Figure 1). In our review, we found no studies that focused on how the NWPS or any portion of this network affects biological diversity, nor have we found studies on how the NWPS affects ecological interactions among trophic levels. Rizzari et al. (2015) identified different trophic interactions among species within marine protected areas versus outside of these areas where fishing is allowed. We encourage similar studies within versus outside of wilderness areas.

We explored our own data to demonstrate the kinds of questions that can be asked with existing information once placed in a wilderness context. Copeland et al. (2010) showed that wolverines, a rare mustelid in the contiguous United States, are dependent on snow for denning. Thus, their distribution can best be predicted by where snow is present in the spring (April 24–May 15). Spring snow not only predicts locations year-round but also gene flow of wolverines across a large space (Squires et al. 2007, Schwartz et al. 2009, Parks et al. 2013). In the Rocky Mountains, 28% of wolverine habitat, as mapped by the spring snow association, is in federally designated wilderness areas. Climate change is predicted to reduce spring snow cover and thus the distribution of wolverines (McKelvey et al. 2011). Considering a multiple wilderness-to-single species relationship, we can ask how important will the NWPS (i.e., a network of wilderness areas) become for wolverines in the future given climate change? Using the McKelvey et al. (2011) climate predictions, we project

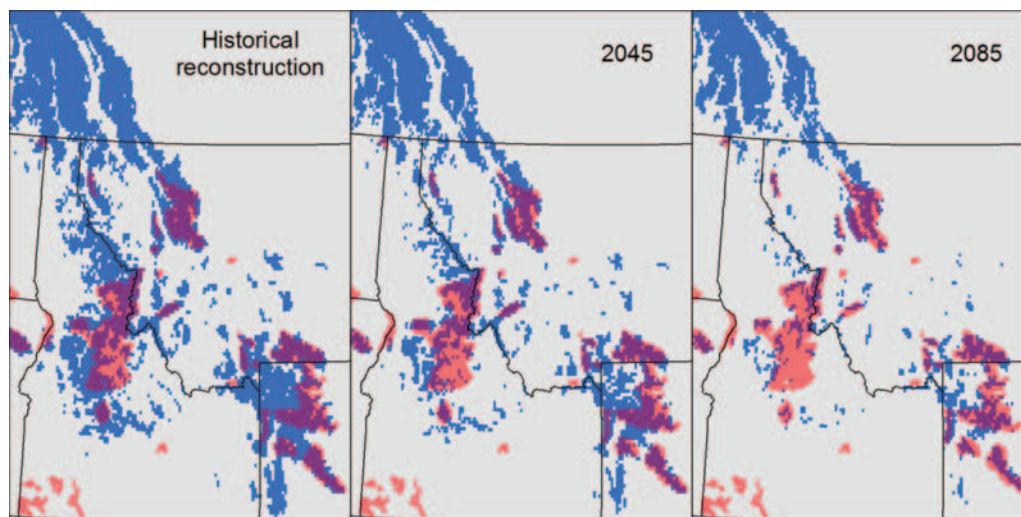


Figure 5. The increasing importance of wilderness habitat to wolverine in the contiguous United States given the climate change projections detailed in McKelvey et al. (2011) for the contemporary time period (historical reconstruction), 2045, and 2085. The area in blue is correlated to wolverine den detections and snow present in the spring. Wilderness areas are shown in red. Areas where wolverine detections overlap with wilderness areas are shown in dark red.

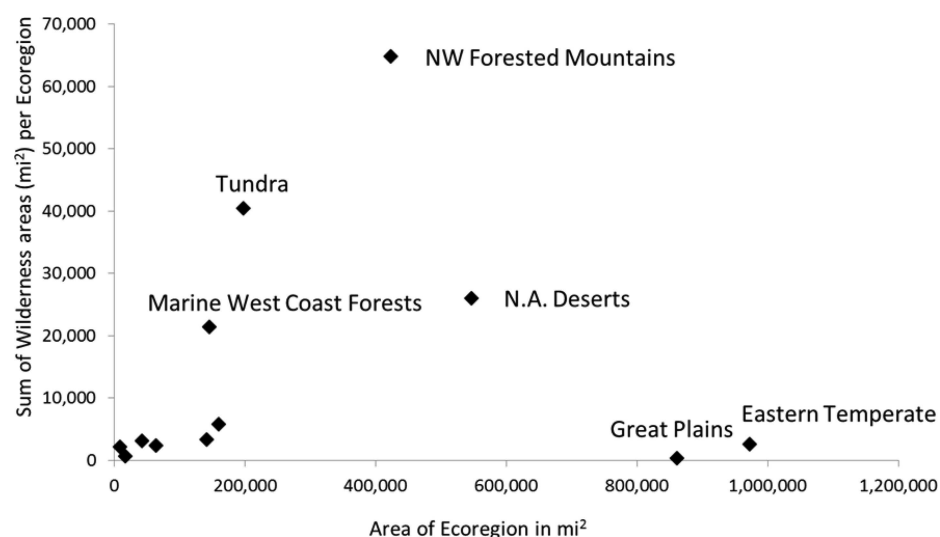


Figure 6. The sum of wilderness area per ecoregion compared with the total area of the ecoregion (using Omernik 1987 Level 1 Ecoregions). The cluster of points in the lower left quadrant of this figure are the Northern Forests, Tropical Wet, Temperate Sierras, Southern Semiarid Highlands, Taiga, and Mediterranean California Ecoregions. N.A. Deserts is an abbreviation for North American Deserts and NW Forested Mountains is an abbreviation for Northwestern Forested Mountains.

that by 2045, 35% of wolverine habitat in the Rocky Mountains will be in wilderness, and by 2085, 45% of wolverine habitat will be in wilderness. If we include areas used for dispersal (e.g., Schwartz et al. 2009), the NWPS becomes even more important for wolverine persistence in the contiguous United States, providing important climate refugia for this species over time (Figure 5).

We urge wildlife biologists to work with biogeographers to understand the gaps in wildlife habitat protection in the United States. The amount of wilderness area pro-

ected per ecoregion compared with the total area of the ecoregion indicates that not all areas are equally represented (Dietz et al. 2015, Aycrigg et al. 2016). Proportionally more northwestern forested mountains are protected than even North American deserts, despite the large total area of deserts in the NWPS (Figure 6). Similarly, eastern temperate ecoregions are widespread, but proportionally underrepresented as an ecotype in the NWPS. This may translate to vulnerability of entire suites of wildlife species not adequately represented or protected by wil-

derness areas. Recent analyses that have included other types of land protection have identified similar gaps in biodiversity conservation protection (Jenkins et al. 2015). We recommend that wildlife researchers explore the impact of the NWPS as a whole in conserving wildlife and biodiversity, especially in light of climate change and other large human-driven stressors.

Last, our wildlife-wilderness research agenda encourages going beyond correlation and conducting studies to understand the mechanistic relationship between qualities of wilderness character and wildlife. We recommend studies on how the qualities of wilderness character (natural, solitude, undeveloped, and untrammeled) affect wildlife or wildlife interactions. For instance, there are qualities of wilderness character that directly influence the ecology of a species and can be quantified. That is, there may be common mechanisms that impact both wilderness character and wildlife simultaneously, such as the presence of roads. To find these common variables, we can begin by examining a relationship between the components of wilderness character and a population's growth rate or fitness components (e.g., survival of juveniles or number of offspring produced in a lifetime). Is the population response (either growth rate or fitness) relatively impervious to development in a wilderness area and sensitive to naturalness (Figure 7)? Imagine, for example, populations of mountain yellow-legged frogs (*Rana muscosa*) in the Sierra Nevada of California. It is well established that human use in and near

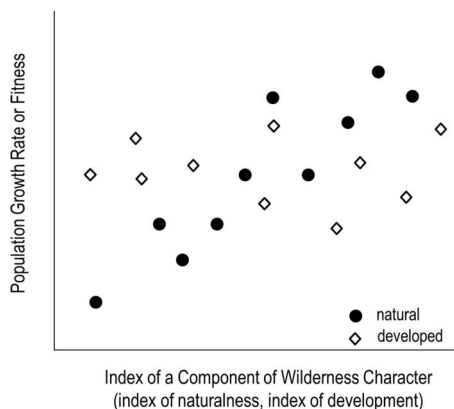


Figure 7. Schematic diagram showing possible research avenues that go beyond examining the impact of one wilderness area on one population of wildlife for one species. This diagram shows a hypothetical relationship between an index of two components of wilderness character (naturalness and developed) and either a population's growth rate or a fitness measure (e.g., survival of juveniles or number of offspring produced in a lifetime). In this hypothetical example, the population response (either growth rate or fitness) is relatively impervious to levels of development in a wilderness area, whereas it is sensitive to an index of naturalness.

streams can negatively affect the survival and recruitment of eggs and larvae, as well as impact the survival of adults (US Fish and Wildlife Service 2012). Similarly, nonnative trout introductions into previously fishless lakes have drastically reduced the geographic range of many amphibian species (Knapp et al. 2007). If we evaluated population growth rate relative to an index of naturalness and an index of development for multiple wilderness areas, we can determine whether species are responding more to one type of wilderness character versus another (Figure 7). This approach provides an understanding of mechanisms needed for biodiversity and wildlife conservation in association with wilderness protection.

Conclusions

We wrote this article surrounding the 50th anniversary of the Wilderness Act with the hopes of establishing a multiscale research agenda to help set the stage for the wilderness-wildlife research for the next 50 years. Our research agenda distinguishes the effects that perceptions of wildlife have on wilderness character versus the impact that wilderness character has on wildlife populations, species, and communities. Both parts

of this research agenda are of equal importance in our estimation. Understanding how perceptions of wildlife contribute to wilderness character is essential to the legal mandate to preserve it. Not all wildernesses started out as pristine, untouched landscapes, but rather many have been recently designated and are only now beginning to be dominated by dynamic, natural processes. Restoring naturalness may mean facilitating the recovery of threatened or endangered species. Even just the known presence of rare species can increase the perception of the natural quality of wilderness quality. We support rigorous social science studies that investigate how different types of human-wildlife experiences influence wilderness character.

Our research agenda also examines how wilderness character affects wildlife by encouraging studies that go beyond the effect of one wilderness on one wildlife species. We hope that future studies examine how the NWPS, a network of wilderness areas, influences one species or an entire ecological community. Over the past decades, there has been increased perception in the wildlife and conservation biology arena that protection of one patch is often inadequate for protection of one species and that management of the entire landscape matrix, across multiple jurisdictions and management plans, is critical for conservation (Bailey 2007). Our research agenda supports this concept and pushes research that explores wilderness in the context of global biodiversity conservation.

Literature Cited

- ALLENDORF, F.W., AND J.J. HARD. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proc. Natl. Acad. Sci. USA* 106 (Suppl. 1): 9987–9994.
- AYCRIGG, J.L., J. TRICKER, R.T. BELOTE, M.S. DIETZ, L. DUARTE, AND G.H. APLET. 2016. The next 50 years: Opportunities for diversifying the ecological representation of the National Wilderness Preservation System. *J. For.* 114(3):396–404.
- BAILEY, S. 2007. Increasing connectivity in fragmented landscapes: An investigation of evidence for biodiversity gain in woodlands. *For. Ecol. Manage.* 238:7–23.
- BURGER, J., L.J. NILES, R.R. PORTER, A.D. DEY, S. KOCH, AND C. GORDON. 2012. Migration and over-wintering of Red Knots (*Calidris canutus rufa*) along the Atlantic Coast of the United States. *Condor* 114:302–313.
- CALLICOTT, J.B. 2000. *Contemporary criticisms of the received wilderness idea*. P. 24–31 in *Wilderness science in a time of change conference. Vol. 1: Changing perspectives and future directions*, 1999 May 23–27, Missoula, MT, Cole, D.N., S.F. McCool, W.A. Freimund, and J. O'Loughlin (comps.). USDA For. Serv., Proc. RMRS-P-15-VOL-1, Rocky Mountain Research Station, Ogden, UT.
- CALLICOTT, J.B., AND M.P. NELSON (EDS.). 1998. *The great new wilderness debate*. Univ. of Georgia Press, Athens, GA. 712 p.
- CIUTI, S., T.B. MUHLY, D.G. PATON, A.D. McDEVITT, M. MUSIANI, AND M.S. BOYCE. 2012. Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc. London B. Biol. Sci.* 279(1746):4407–4416.
- COLE, D.N., AND L. YUNG (EDS.). 2010. *Beyond naturalness: Rethinking park and wilderness stewardship in an era of rapid change*. Island Press, Washington, DC. 304 p.
- COLE, E.K., M.D. POPE, AND R.G. ANTHONY. 1997. Effects of road management on movement and survival of Roosevelt elk. *J. Wildl. Manage.* 61:1115–1126.
- COLTMAN, D.W., P. O'DONOGHUE, J.T. JORGENSEN, J.T. HOGG, C. STROBECK, AND M. FESTA-BIANCHET. 2003. Undesirable evolutionary consequences of trophy hunting. *Nature* 426:655–658.
- COPELAND, J.P., K.S. MCKELVEY, K.B. AUBRY, A. LANDA, J. PERSSON, R.M. INMAN, J. KREBS, ET AL. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): Do climatic constraints limit its geographic distribution? *Can. J. Zool.* 88:233–246.
- CORDELL, H.K., M.A. TARRANT, AND G.T. GREEN. 2003. Is the public viewpoint of wilderness shifting? *Int. J. Wild.* 9:27–32.
- DAVIDSON, C., AND R.A. KNAPP. 2007. Multiple stressors and amphibian declines: Dual impacts of pesticides and fish on yellow-legged frogs. *Ecol. Applic.* 17:587–597.
- DIETZ, M.S., R.T. BELOTE, G.H. APLET, AND J.L. AYCRRIGG. 2015. The world's largest wilderness protection network after 50 years: An assessment of ecological system representation in the US National Wilderness Preservation System. *Biol. Conserv.* 184:431–438.
- DOBROWSKI, S.Z., J. ABATZOGLOU, A.K. SWANSON, J.A. GREENBERG, A.R. MYNSBERGE, Z.A. HOLDEN, AND M.K. SCHWARTZ. 2013. The climate velocity of the contiguous United States during the 20th century. *Global Change Biol.* 19:241–251.
- DOUHARD, M., M. FESTA-BIANCHET, F. PELLETIER, J.M. GAILLARD, AND C. BONENFANT. 2015. Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecol. Applic.* 26(1):309–321.
- ETCHBERGER, R.C., P.R. KRAUSMAN, AND R. MAZAIKA. 1989. Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. *J. Wildl. Manage.* 53:902–907.
- FRANKLIN, J.F. 1987. Scientific use of wilderness. P. 42–46 in *Proc. National Wilderness Research Conference: Issues, state-of-knowledge, future directions, 1985 July 23–26, Fort Collins, CO*, Lucas, R.C. (comp.). USDA For. Serv., Gen. Tech. Rep. INT-220, Intermountain Research Station, Ogden, UT. 22 p.
- FRASER, J.D., S.E. KEANE, AND P.A. BUCKLEY. 2005. Prenesting use of intertidal habitats by

- piping plovers on South Monomoy Island, Massachusetts. *J. Wildl. Manage.* 69:1731–1736.
- GRABER, D.M. 1983. Rationalizing management of natural areas in national parks. *George Wright Forum* 3(4):48–56.
- HENDEE, J.C., AND D.J. MATTSO. 2009. Wildlife in wilderness: A North American and international perspective. P. 308–334 in *Wilderness management: Stewardship and protection of resources and values*, 4th ed., Hendee, J.C., and C. Dawson (eds.). Fulcrum Publishing, Golden, CO.
- HUGGARD, C.J. 2001. America's first wilderness area: Aldo Leopold, the Forest Service, and the Gila of New Mexico, 1924–1980. P. 133–179 in *Forests under fire: A century of ecosystem mismanagement in the Southwest*, Huggard, C.J., and A.R. Gomez (eds.). Univ. of Arizona Press, Tucson, AZ.
- JENKINS, C.N., K.S. VAN HOUTAN, S.L. PIMM, AND J.O. SEXTON. 2015. US protected lands mismatch biodiversity priorities. *Proc. Natl. Acad. Sci. USA* 112(16):5081–5086.
- JOHNSON, L.B. 1964. Remarks upon signing the Wilderness Bill and Land and Water Conservation Fund Bill. In 1963–64 (in two books): *Containing the public messages, speeches, and statements of the President*. US Government Printing Office, Washington, DC. 1709 p.
- KERSHNER, J.L., C.M. BISCHOFF, AND D.L. HORAN. 1997. A comparison of population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and non-wilderness streams in the Uinta Mountains. *N. Am. J. Fish. Manage.* 17:1134–1143.
- KAMMER, S. 2013. Coming to terms with wilderness: The Wilderness Act and the problem of wildlife restoration. *Environ. Law* 43:83–124.
- KNAPP, R.A., P.S. CORN, AND D.E. SCHINDLER. 2001. The introduction of nonnative fish into wilderness lakes: Good intentions, conflicting mandates, and unintended consequences. *Ecosystems* 4:275–278.
- KNAPP, R.A., D.M. BOIANO, AND V.T. VREDENBURG. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). *Biol. Conserv.* 135:11–20.
- KOEHLER, G.M., AND M.G. HORNOCKER. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *J. Wildl. Manage.* 41: 500–505.
- KOLB, T.E., M.R. WAGNER, AND W.W. COVINGTON. 1994. Concepts of forest health: Utilitarian and ecosystem perspectives. *Soc. Am. For.* 92:10–15.
- LANDRES, P. 2004. Developing indicators to monitor the “outstanding opportunities” quality of wilderness character. *Int. J. Wildl.* 10:8–12.
- LANDRES, P., C. BARNS, S. BOUTCHER, T. DEVINE, P. DRATCH, A. LINDHOLM, L. MERIGLIANO, N. ROEPER, AND E. SIMPSON. 2015. *Keeping it wild 2: An updated interagency strategy to monitor trends in wilderness character across the National Wilderness Preservation System*. USDA For. Serv., Gen. Tech. Rep. GTR-340, Rocky Mountain Research Station, Fort Collins, CO. 114 p.
- LANDRES, P., S. MEYER, AND S. MATTHEWS. 2001. The Wilderness Act and fish stocking: An overview of legislation, judicial interpretation, and agency implementation. *Ecosystems* 4:287–295.
- LEOPOLD, A. 1941. Wilderness as a land laboratory. *Living Wildl.* 6:3.
- LEOPOLD, A. 1992. *The River of the Mother of God and other essays by Aldo Leopold*. Univ. of Wisconsin Press, Madison, WI. 400 p.
- McKELVEY, K.S., K.B. AUBRY, AND M.K. SCHWARTZ. 2008. Using anecdotal occurrence data for rare or elusive species: The illusion of reality and a call for evidentiary standards. *BioScience* 58:549–555.
- McKELVEY, K.S., J.P. COPELAND, M.K. SCHWARTZ, J.S. LITTELL, AND K.B. AUBRY. 2011. Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecol. Applic.* 21:2882–2897.
- McLELLAN, B.N., F.W. HOVEY, R.D. MACE, J.G. WOODS, D.W. CARNEY, M.L. GIBEAU, W.L. WAKKINEN, AND W.F. KASWORM. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *J. Wildl. Manage.* 63:911–920.
- MECH, L.D., S.H. FRITTS, G.L. RADDE, AND W.J. PAUL. 1988. Wolf distribution and road density in Minnesota. *Wild. Soc. Bull.* 16: 85–87.
- MITTERMEIER, R.A., C.G. MITTERMEIER, T.M. BROOKS, J.D. PILGRIM, W.R. KONSTANT, G.A. DA FONSECA, AND C. KORMOS. 2003. Wilderness and biodiversity conservation. *Proc. Natl. Acad. Sci. USA* 100:10309–10313.
- MORIARTY, K.M., W.J. ZIELINSKI, A.G. GONZALES, T.E. DAWSON, K.M. BOATNER, C.A. WILSON, F.V. SCHLEXER, K.L. PILGRIM, J.P. COPELAND, AND M.K. SCHWARTZ. 2009. Wolverine confirmation in California after nearly a century: Native or long-distance immigrant. *Northw. Sci.* 83:154–162.
- OELFKE, J.G., R.O. PETERSON, J.A. VUCETICH, AND L.M. VUCETICH. 2000. Wolf research in the Isle Royale Wilderness: Do the ends justify the means? P. 246–251 in *Wilderness science in a time of change conference. Vol. 3: Wilderness as a place for scientific inquiry; 1999 May 23–27; Missoula, MT*. USDA For. Serv., Proc. RMRS-P-15-VOL-3, Rocky Mountain Research Station, Ogden, UT.
- OLSEN, E.M., M. HEINO, G.R. LILLY, M.J. MORGAN, J. BRATTEY, B. ERNANDE, AND U. DIECKMANN. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* 428:932–935.
- OMERNIK, J.M. 1987. Ecoregions of the conterminous United States. *Ann. Assoc. Am. Geogr.* 77:118–125.
- PARKS, S.A., K.S. McKELVEY, AND M.K. SCHWARTZ. 2013. Effects of weighting schemes on the identification of wildlife corridors generated with least-cost methods. *Conserv. Biol.* 27:145–154.
- PAPOUCHIS, C.M., F.J. SINGER, AND W.B. SLOAN. 2001. Responses of desert bighorn sheep to increased human recreation. *J. Wildl. Manage.* 65:573–582.
- RIZZARI, J.R., B.J. BERGETH, AND A.J. FRISCH. 2015. Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs. *Conserv. Biol.* 29:418–429.
- ROMINGER, E.M., H.A. WHITLAW, D.L. WEYBRIGHT, W.C. DUNN, AND W.B. BALLARD. 2004. The influence of mountain lion predation on bighorn sheep translocations. *J. Wildl. Manage.* 68:993–999.
- ROOSEVELT, T. 1893. *The wilderness hunter: An account of the big game of the United States and its chase with horse, hound, and rifle*. G.P. Putnam's Sons, New York. 306 p.
- SCHOENECKER, K., M.K. WATRY, L. ELLISON, G. LUIKART, AND M.K. SCHWARTZ. 2015. Estimating bighorn sheep (*Ovis canadensis*) abundance using noninvasive sampling at a mineral lick within a National Park Wilderness Area. *West. N. Am. Nat.* 75:181–191.
- SCHWARTZ, M.K., W. BLOCK, AND J. SANDERLIN. 2015. Manage habitat, monitor species. P. 128–156 in *Wildlife habitat conservation: Concepts, challenges, and solutions*, Morrison, M.L., and H.A. Mathewson (eds.). John Hopkins Univ. Press, Baltimore, MD.
- SCHWARTZ, M.K., J.P. COPELAND, N.J. ANDERSON, J.R. SQUIRES, R.M. INMAN, K.S. McKELVEY, K.L. PILGRIM, L.P. WAITS, AND S.A. CUSHMAN. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology* 90:3222–3232.
- SCHWARTZ, M.K., P.B. LANDRES, AND D.J. PARSONS. 2011. Wildlife scientists and wilderness managers finding common ground with non-invasive and nonintrusive sampling of wildlife. *Int. J. Wildl.* 17:4–8.
- SQUIRES, J.R., J.P. COPELAND, T.J. ULIZIO, M.K. SCHWARTZ, AND L.F. RUGGIERO. 2007. Sources and patterns of wolverine mortality in western Montana. *J. Wildl. Manage.* 71:2213–2220.
- THUILLER, W., S. LAVOREL, AND M.B. ARAÚJO. 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecol. Biogeogr.* 14:347–357.
- TITUS, J.R., AND L.W. VANDRUFF. 1981. Response of the common loon to recreational pressure in the Boundary Waters Canoe area, Northeastern Minnesota. *Wildl. Monogr.* 79: 3–59.
- US FISH AND WILDLIFE SERVICE. 2012. 5 year review for Mountain yellow-legged frog (*Rana muscosa*). *Fed. Regis.* 67 FR 44382.
- WALKER, L.E., AND J.M. MARZLUFF. 2015. Recreation changes the use of a wild landscape by corvids. *Condor* 117:262–283.
- WASSER, S.K., B. DAVENPORT, E.R. RAMAGE, K.E. HUNT, M. PARKER, C. CLARKE, AND G. STENHOUSE. 2004. Scat detection dogs in wildlife research and management: Application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. *Can. J. Zool.* 82:475–492.
- WATSON, A., S. MARTIN, N. CHRISTENSEN, G. FAUTH, AND D. WILLIAMS. 2015. The relationship between perceptions of wilderness character and attitudes toward management intervention to adapt biophysical resources to a changing climate and nature restoration at Sequoia and Kings Canyon National Parks. *Environ. Manage.* 55:1–11.
- Wilderness Watch v. US Fish, and Wildlife Service*, 629 F.3d 1024 (9th Cir. 2010).