## Ungulate Management in National Parks of the United States and Canada



Technical Review 12-05
December 2012

# Ungulate Management in National Parks of the United States and Canada 

## The Wildlife Society <br> Technical Review 12-05 - December 2012

## Citation

Demarais, S., L. Cornicelli, R. Kahn, E. Merrill, C. Miller, J. M. Peek, W. F. Porter, and G. A. Sargeant. 2012. Ungulate management in national parks of the United States and Canada. The Wildlife Society Technical Review 12-05. The Wildlife Society, Bethesda, Maryland, USA.

## Series Edited by

Theodore A. Bookhout

## Copy Edit and Design

Terra Rentz (AWB ${ }^{\circledR}$ ), Managing Editor, The Wildlife Society Jessica Johnson, Associate Editor, The Wildlife Society Maja Smith, Graphic Designer, MajaDesign, Inc.

## Cover Images

Front cover, clockwise from upper left: 1) Bull moose browsing on subalpine fir near Soda Butte Creek in Yellowstone National Park. Credit: Jim Peaco, National Park Service; 2) Bison in Stephens Creek pen in Yellowstone National Park. The Bison herds in Yellowstone are actively managed to maintain containment within park boundaries. Credit: Jim Peaco, National Park Service; 3) Bighorn sheep ram in Lamar Valley, Yellowstone National Park. Credit: Jim Peaco, National Park Service; 4) Biologists in Great Smokey Mountains National Park use non-lethal means, such as the use of a paintball gun depicted in this photo, to move elk from undesirable areas. Credit: Joseph Yarkovich; 5) National Park Service biologists Joe Yarkovich and Kim Delozier (now retired) working up an elk in Great Smokey Mountains National Park. Credit: Joseph Yarkovich; 6) Fencing protects willow (Salix spp.) and aspen (Populus spp.) from overgrazing by elk (Cervus elaphus) in Rocky Mountain National Park. Exclusion fences allow localized timber regeneration, but are only a temporary fix without long-term reduction of elk numbers. Credit National Park Service.

This report is copyrighted by TWS, but individuals are granted permission to make single copies for noncommercial purposes. To view or download a PDF of this report, or to order hard copies, go to:
wildlife.org/publications/technical-reviews.

# Technical Review Committee on Ungulate Management in National Parks of the United States and Canada 

Steve Demarais (Chair, CWB ${ }^{\circledR}$ )
Department of Wildlife, Fisheries, and
Aquaculture
Mississippi State University
P.O. Box 9690

Mississippi State, MS 39762 USA

## Lou Cornicelli

Minnesota Department of Natural Resources 500 Lafayette Rd.
St. Paul, MN 55155 USA

## Rick Kahn

Biological Resource Management Division
National Park Service
1201 Oakridge Dr. Suite 200
Fort Collins, CO 80525 USA

Evelyn Merrill (CWB ${ }^{\circledR}$ )
Department of Biological Sciences
University of Alberta
Edmonton, AB T6G 2E9 CA

## Craig Miller

Human Dimensions Research Program
Illinois Natural History Survey
Prairie Research Institute
University of Illinois
Champaign, IL 61820 USA

James M. Peek (CWB ${ }^{\circledR}$ )
Department of Fish and Wildlife Resources
University of Idaho
Moscow, ID 83844 USA
William F. Porter (CWB ${ }^{\circledR}$ )
Department of Fisheries and Wildlife
13 Natural Resources Building
Michigan State University
East Lansing, MI 48824 USA

Glen A. Sargeant
Northern Prairie Wildlife Research Center
U.S. Geological Survey

8711 37th Street SE
Jamestown, ND 58401 USA


The Wildlife Society
5410 Grosvenor Lane
Bethesda, MD 20814
P: 301.897.9770
F: 301.530.2471
www.wildlife.org
Promoting Excellence in Wildlife Stewardship through Science and Education

## Table of Contents

Foreword ..... vi
Acknowtedgements ..... vii
Executive Summary ..... viii
Purpose of National Parks ..... 1
Ungulates in Park Management Goals and Objectives ..... 7
Ungulate Conservation ..... 7
Conservation of Ecological Communities ..... 10
Disease and Parasite Management ..... 14
Visitor Experiences ..... 15
Conflicts with Other Agencies/Land Uses ..... 16
Ungulate Population Management Objectives ..... 19
Eradication ..... 19
Regulation at Low Density ..... 19
Regulation at High Density ..... 20
Alternatives to Ungulate Density ..... 20
Management Alternatives ..... 21
No Action ..... 21
Animal Removal ..... 22
Fertility Control ..... 29
Predator Management ..... 32
Redistribution ..... 33
Criteria for Selection of Management Strategies ..... 35
Enabling Legislation, Historical Context, and Naturalness ..... 35
Cost ..... 35
Animal Welfare ..... 36
Allowable Land Use ..... 36
Population Viability and Genetic Diversity ..... 37
Depredation ..... 37
Findings ..... 38
Literature Cited ..... 39

## Foreword



Bighorn sheep at Canyonlands National Park. Credit: Neal Herbert, National Park Service.

P
residents of The Wildlife Society (TWS) occasionally appoint ad hoc committees to study and report on selected conservation issues. The resulting technical review presents technical information and the views of the appointed committee members, but not necessarily the views of their employers.

This Technical Review focuses on management of ungulates in national parks of Canada and the United States. The review is copyrighted by TWS, but individuals are granted permission to make single copies for noncommercial purposes. All technical reviews are available in digital format on the TWS web page, www.wildlife.org, and additional copies may be requested from:

The Wildlife Society 5410 Grosvenor Lane, Suite 200
Bethesda, MD 20814
Phone: (301) 897-9770
Fax: (301) 530-2471
TWSAwildlife.org www.wildlife.org

## Acknowledgments



Pronghorn antelope in Yellowstone National Park. Credit: JR Douglass, National Park Service.

T
his report represents significant efforts by committed wildlife professionals serving the membership of The Wildlife Society. We acknowledge the support of TWS presidents in office during preparation of this report, including Presidents Bruce Leopold and Paul Krausman and Past Presidents Tom Ryder, Tom Franklin, and Dan Svedarsky. Members of The Wildlife Society Council Gary White and, especially, John McDonald provided comments and support. The Wildlife Society support staff, especially Christine Carmichael and Terra Rentz, provided encouragement, invaluable suggestions, and edits. This review was approved for development September 2009 by sitting President Bruce Leopold and approved
for publication in October 2012 by then- President Paul Krausman.

We received exceptional cooperation from people in various state, provincial, and national agencies across Canada and the United States. People within these agencies responded with requested information, and we specifically thank J. Powers with the National Park Service. We especially appreciate E. Leslie, K. Leong, M. Foley, and B. Frost with the National Park Service, J. Whittington and M. Bradley with Parks Canada, Mark Sherfy with the U.S. Geological Survey, and Bruce Stillings with the North Dakota Game and Fish Department for their critical reviews of the final draft.

## Executive Summary

Enabling legislation-that which gives appropriate officials the authority to implement or enforce the law-impacts management of ungulates in national parks of Canada and the United States (U.S.). The initial focus of such legislation in both countries centered on preserving natural and culturally significant areas for posterity. Although this objective remains primary, philosophies and practices have changed. A Canadian vision for ungulate management emerged during the latter half of the 20th century to protect and maintain or restore the ecological integrity of representative samples of the country's 39 distinct landscapes, and to include provisions for traditional hunting and fishing practices representative of past cultural impacts on the environment. The current ungulate management approach in the U.S. relies on natural (ecological) processes, as long as normal conditions are promoted and there is no impairment of natural resources. Emphasizing natural processes as the basis has been a challenge because ecosystem dynamics are complex and management is multi-jurisdictional. Additionally, natural regulation typically will not prevent ungulates from reaching and sustaining densities that are incompatible with preservation or restoration of native flora and fauna, natural processes, or historical landscapes.

Concern about ungulate impacts on woody vegetation and cascading effects on other flora and fauna has caused much deliberation over how active management is conducted. Management alternatives typically considered during park planning include no action, animal removal, fertility control, redistribution, and predator reintroduction. Problems such as human-conditioned animals, incomplete ecosystems, reductions in natural processes like wildfire, and loss of predators have implications that preclude a system-wide no-action approach to ungulate management in national parks.

Removals of ungulates from national parks have been controversial, and much of the debate has revolved around methods of removal. Disease issues limit the use of translocations as temporary solutions to abundance problems. Most ungulate removals from U.S. national parks have been accomplished by shooting. Public involvement in shooting has been controversial and limited by National Park Service (NPS) policies that do not allow hunting of native wildlife in national parks per se. Costs of shooting programs depend on costs of administration, payments to shooters, logistical challenges, methods of carcass disposal, and the degree of supervision by park management. Shooting programs modeled after public hunting programs (i.e., volunteers pay a modest fee, are not directly supervised, and retain carcasses for personal use) have been successful in the few instances where attempted.

Removal management can be successful only where a superintendent is interested in building a program based on science, is able to garner the resources to do the planning, and is willing to take political risks to achieve management goals. Fertility control has limited field application because of insufficient duration of effectiveness and the number of doses required, although recent increases in immunogenic capability (i.e., ability to stimulate antibody production) have improved these characteristics. Restoration of extant mammalian predators is limited by the small size of parks and complicated ecological and social issues. Range expansion or redistribution is only a short-term solution to overpopulation and has limited application.

Internal and external reviews of ungulate management in national parks during the 1980s and 1990s identified several problems. The management needs that were identified included clear statements of management goals and objectives; use of explicit
measures to objectively evaluate degradation of cultural or natural resources, including data on ungulate populations and vegetative communities; monitoring programs to measure change as management programs are implemented; and a clearly articulated plan for reviewing and adapting management as new knowledge is gained through time.

Our technical review reveals that NPS and Parks Canada are addressing these issues through leadership initiatives at park, regional, and national levels. We offer the following specific findings:

## Biological

1. Natural regulation within most national parks will not prevent ungulates from reaching and sustaining densities that are incompatible with preservation or restoration of native flora and fauna, natural processes, or historical landscapes. In such cases, controlled reduction programs may effectively reduce ungulate impacts.
2. Herbivory significantly influences park vegetation as ungulate density approaches biological carrying capacity. Monitoring vegetation and ungulate populations using clearly stated effectiveness measures can identify ecological consequences.
3. Flexible and adaptive ungulate management in the short- and long-term will be needed to account for imprecise population estimates and the dynamics of ungulate populations, park environments, and stakeholder interests.
4. Animal movement across park boundaries impacts both internal and external agency efforts to manage ungulate overpopulation.
5. Translocations have played a role in early efforts to regulate ungulate populations and to restore ungulates to previously occupied national parks. However, significant disease, ecological and social implications, and habitat limitations complicate future translocations.

## Social

1. Substantial progress has been made by national parks in managing ungulate overpopulation. Consideration of short- and long-term costs aids evaluation of potential management alternatives. Involving state and provincial wildlife agencies and other federal land management agencies in the decision-making process facilitates development of cost-effective methods to reduce or control ungulate populations.
2. There is a wide range of constituencies and opinions concerning ungulate management efforts in national parks, although typically these opinions have not been quantified scientifically during or after decision-making. Social science data can be an important part of the decision-making process by providing a more valid representation of public opinion than open meetings and written comments.
3. Educational programs on the technical issues of ungulate management would aid park superintendents and other decision-makers. Related educational programs explaining biological justifications and the effectiveness of alternatives would allow the general public and other stakeholders to provide informed input.
4. Well-informed specialists can provide critical input during the development of management policies and practices. Financial support is needed to provide technically-trained personnel to address information needs related to ungulate management, including wildlife biologists for ecological issues and specialists with human-dimensions training for social science issues.

# Purpose of National Parks 



National Park Service personnel deantler an elk in a trap in Yellowstone National Park in 1959. Credit: National Park Service,

## Enabling Legislation

Enabling legislation - that which gives appropriate officials the authority to implement or enforce the law -impacts resource management in many national parks in Canada and the U.S. Historically, the focus of national parks in both countries centered on preserving natural areas for posterity; although this objective remains primary, management philosophies and practices have changed.

Canada's first national park was created by the 1887 Rocky Mountains Park Act, which set aside Banff Hot Springs Reserve as a "public park and pleasure ground for the benefit, advantage, and enjoyment of the people of Canada" (Parks Canada 1997). The objective of Canadian national parks is "to protect representative natural areas in a system of national
parks that will encourage public understanding, appreciation, and enjoyment of this natural heritage and leave it unimpaired for future generations." By 1970, twenty national parks had been established in Canada without any formal plan. They represented a collection of special places created by heroic efforts, accidents of geography, or political opportunism and were set aside for a variety of purposes including to protect scenery for tourism, to provide regional recreation areas, to create wildlife sanctuaries, and to stimulate economic development. A vision for national parks that sought to protect a representative sample of each of Canada's 39 distinct landscapes, which are based on land and vegetation characteristics, was finally developed during the 1970s (Parks Canada 1997).

In addition to natural areas, nationally significant historic sites located in urban, rural, or wilderness settings are protected by National Historic Sites of Canada. The 800-plus historical sites range in size from a gravesite in Kingston, Ontario, to large cultural landscapes such as Nagwichoonjik in the Northwest Territories-a section of the Mackenzie River that flows through the Gwichya Gwich'in traditional homeland (Parks Canada 2000).

In 1974, the National Parks Act was amended to include provisions for traditional hunting and fishing practices. This amendment promoted the preservation of cultural landscapes and was based on archeological evidence of human activity in parks. However, the concern over eroding environmental quality of popular parks under strain of intensive human use led to convene the Panel on the Ecological Integrity of Canada's National Parks in 2000. From this effort sprang the Canada National Parks Act of 2000, which called for maintenance or restoration of ecological integrity. The concept of ecological integrity (EC) encompassed not only
composition and abundance of native species but rates of change and supporting processes, while remaining consistent with the early dedication of the parks, to be left "unimpaired," to "the people of Canada for their benefit, education, and enjoyment" (Campbell 2011).

Adopting EC as a management concept was an alternative to the "natural" concept espoused by the Leopold Report (1963) in the U.S.-a concept that presented the problem of how to define natural, given the long-involved human influences on ecological systems within North America. Since its formalization, EC has evolved from a scientific idea into a management approach that provides a rationale for when to use active management and restoration in park systems and that acknowledges that ecosystems are inherently dynamic and have a history of human disturbance and past management activities (Woodley 2010).

In the U.S., the national park system began in 1872 with Congress' establishment of Yellowstone National Park (Yellowstone) to serve as a public park for the benefit and enjoyment of the people (Haines 1974). The Organic Act of 1916 then established the NPS to manage parks and monuments to "conserve the scenery and natural and historical objects and wild life therein and provide for the enjoyment of the same by such means as will leave them unimpaired for the enjoyment of future generations." This dual responsibility of conservation and recreation has been recognized as a unique challenge to the NPS. Unlike other federal land management agencies, Congress allows the NPS to establish subunits that may act on specific objectives. For example, in 1950 Congress authorized the NPS to control elk by temporarily deputizing licensed hunters as park rangers in certain areas of Grand Teton National Park (Grand Teton).

NPS presently manages almost 400 properties of the following type:

- National Parks are large land or water areas with a diversity of natural resources and are typically closed to hunting.
- National Monuments are areas intended to preserve at least 1 nationally significant resource, are typically smaller than parks, and are also closed to public hunting.
- National Preserves are large land areas established for the protection of natural or cultural resources, and hunting is typically allowed as long as it does not impeded the purpose for establishment.
- National Lakeshores, Seashores, and Wild and Scenic Rivers specifically protect natural littoral areas, provide water-based recreation, and typically allow hunting.
- National Historic Sites include national battlefields and other culturally significant areas. They are variable in size and scope and are typically closed to hunting.
- National Recreation Areas often include large reservoirs that facilitate recreational activities. Management may include non-NPS agencies, and hunting is generally allowed.


## Management Philosophy

U.S. National Parks. - The history of ungulate conservation and management in U.S. parks is as old as the park system itself. Parks primarily protected ungulates from both anthropogenic and natural influences. For example, parks prohibited activities such as hunting, timber harvest, and livestock grazing, and engaged in predator control through the early 1900s.

George Wright was a forester and biologist who became an outspoken proponent of scientific wildlife conservation and management. In 1932, Wright and others wrote a seminal report on park wildlife that helped focus attention on issues such as predator management and wildlife habituation, and helped foster new policies favoring management of parks in a way that preserved natural conditions. However, Wright's untimely death in 1936 dramatically reduced national attention to wildlife management by the NPS.

A renewed interest in wildlife management during the 1960s led to the NPS-commissioned Leopold Report, which refocused national attention on how NPS managed wildlife resources (Leopold et al. 1963). The report recommended managing the national parks and monuments to preserve, or where necessary to recreate, the ecological scene as viewed by the first European visitors. The report has been interpreted by many, both within NPS and outside, as a mandate to promote natural processes and allow those processes to be the driving, and some might say sole, influence on park wildlife populations. However, the authors also noted a need to protect park habitats from damage caused by wildlife, particularly ungulates. During the mid-1960s to the mid-1990s, this second recommendation was largely ignored by NPS as it set a course for natural management.

The degree to which humans should interact with ecological processes is an important issue underlying ungulate management in national parks. As early as 1916, efforts were made to minimize human manipulation of parks so they might embody ecosystems encountered by the first European settlers (Wright 1992). However, most parks are too small to qualify as independent, fully functioning ecological units (Leopold et al. 1963). Ungulates and predators in particular face acute challenges because few parks are large enough to fully support their populations.

Leopold and others (1963) believed that it was not necessary to actively modify habitats in order to make them suitable for supporting relatively stable climax communities. However, in the absence of active management, climax communities within natural systems were being disrupted by unnatural elements such as feral burros in the Grand Canyon, or by fire suppression in areas where wildfire was common, such as Isle Royale National Park (Isle Royale) and Glacier National Park (Glacier). Thus, lack of active habitat management does not necessarily lead to a relatively stable climax community. However, climax communities and other natural process considerations are not always primary management concerns.

Park units that commemorate historic events typically are managed to present a picture (a stable vignette [Leopold et al. 1963]) and not to promote natural processes. This emphasis arises because features of landscapes may substantially influence visitors' perceptions and understanding of historic events. These parks are generally small, and both park lands and surrounding landscapes are heavily influenced by human activities. Maintaining or restoring features of historical landscapes is an explicit management goal in these areas.

The potentially contradictory practices of conserving natural and historical objects within national parks while allowing for their enjoyment by the public is codified in federal law and policy. For NPS, principle elements of this practice include the Organic Act of 1916, and the Management Policies and the Natural Resources Management Guidelines of the National Park Service (2006a). The piecemeal nature of enabling legislation combined with potentially contradictory goals within the Organic Act complicate management decisions, the ongoing conflict between motorized winter recreation and wildlife in Yellowstone.

From its inception, NPS has been charged with the dual responsibility of conservation and recreation. NPS has interpreted this charge to include
responsibility for both natural and cultural zones. In natural zones, the primary management objective originally was to "protect the natural resources and values in as natural a condition as possible while allowing for their enjoyment by current generations and ensuring their availability for future generations." In contrast, in cultural zones the primary management objective was to "protect and foster appreciation of the cultural resources; natural resource management actions are designed to support cultural resource management objectives (e.g., maintenance of a historical landscape)" (National Park Service 1991). Another difference in management objectives exists between different regions of the U.S. Parks in the eastern U.S. often focus on preserving cultural resources and portraying static images to visitors, whereas parks in the West emphasize natural resources preservation and the engagement of visitors in dynamic recreation. Where conflict occurs, NPS policy states that natural resource conservation takes precedence over recreational activities (National Park Service. 2006a).

Today, NPS policy emphasizes preventing impairment of park natural resources (E. Leslie, National Park Service, personal communication). This is supported by management plans put in place during the last 20 years which seek to: (1) prevent large-scale degradation of riparian areas (e.g., by elk in the Rocky Mountains), (2) ensure that native forests are able to regenerate (e.g., to support deer populations in parks of the eastern U.S.), (3) prevent widespread erosion and forest damage by nonnative species (e.g., nonnative feral pigs in Great Smokey Mountains National Park), and (4) manage grasslands in a conservative manner (e.g., to support elk populations in Theodore Roosevelt National Park [Theodore Roosevelt] and Wind Cave National Park [Wind Cave]).

The NPS is required to follow guidelines of the National Environmental Policy Act (NEPA) of 1969. Typically, this involves holding public hearings and meetings to both provide information to the public and solicit feedback. This format, however, fails
to provide the NPS with detailed scientific data gathered through accepted methods (e.g., random sample). Public input from such hearings can potentially yield feedback that overemphasizes some viewpoints and often fails to represent the interests of all stakeholders involved (Cornicelli and Grund 2011, Alessi and Miller 2012).

Issues surrounding ungulate management are often contentious and involve numerous stakeholders. Therefore, the NPS needs to have statistically sound data from social science research to help guide policy and management decision-making. To date, few social science research projects that examine public attitudes toward ungulate management in national park sites have been conducted (see, for example, Fulton et al. 2004, Fix et al. 2010). Increasing the quality and quantity of social science research will enhance the understanding of diverse public opinions toward ungulate management.

Parks Canada. - In Canadian national parks, Parks Canada works to maintain or restore ecological integrity. This means keeping ecosystems healthy and whole, a state where ecosystem biodiversity, structures, and functions are unimpaired and likely to persist (Parks Canada 1997). In fact, maintenance or restoration of ecological integrity is the first priority of the Parks Canada Minister in the list of all park management goals.

However, creating regional recreational areas is also an important goal of national parks, and Parks Canada manages national historic sites to preserve and recognize a location, person, or event that had a nationally significant effect on, or illustrates a nationally important aspect of, the history of Canada (Parks Canada 1997). Like national parks, national historic sites are designed to support recreation and be appreciated and enjoyed by the visiting public.

The separation between natural and cultural management objectives is not always clear cut. Human beings have left their mark on ecological communities across North America since Pleistocene times. Aboriginal peoples substantially
influenced the environment by exploiting wildlife and plants, introducing agriculture, and managing fire (Krech 1999). Anthropologists have debated whether NPS should maintain that aboriginal influence, ignore it, or tacitly prevent it (Krech 1999, Harkin and Lewis 2007, Braddock and Irmscher 2009, Rigal 2010). It is not as much of an issue in Canadian national parks where the concept of ecosystembased management accepts that humans form an integral part of these systems. For example, the ecosystems of Banff National Park (Banff) were modified and influenced by native peoples 10,000 years before the arrival of Europeans, and Banff is managed in a way that duplicates the influence of native burning and hunting, fire history, and predator-prey relationships that historically structured and maintained these ecosystems (Parks Canada 2011).

Furthermore, determining how to manage for conservation when prior conditions are uncertain can be difficult. For instance, it is not clear whether herbivores were as abundant as they are in some parks today, or whether they exerted as great an influence on plant communities. Ungulate densities may have been depressed, for example, by native hunting. Kelly (1997) concluded that aboriginal peoples occupying the central Mississippi River region around 1000 AD likely depleted large mammals near their camps. Geist (1996) wrote that Great Plains peoples depressed populations of bison (Bison bison) and elk (Cervus canadensis), and may have caused regional extinctions of moose (Alces alces). Krech (1999) wrote that aboriginal peoples in New England burned the woods in order to improve hunting conditions for white-tailed deer and other game. Elk were a secondary resource for Plains Indians, and regional patterns of harvest showed considerable variation (McCabe 2002).

Management Summary. - The current NPS approach to management can be thought of as one that emphasizes either natural/ecological processes or the preservation of prior conditions. An emphasis on ecological or natural processes has been the basis
for management of large parks where the goal is to help the visitor understand the natural ecosystem. However, educating visitors about natural ecosystems requires NPS to craft management policies that accommodate fluctuations that are inherent in dynamic ecosystems. The challenge is that ecosystem dynamics are complex, and the ability to convey that complexity to a visiting public is limited both by the ecological background of the public and by the short time each visitor spends in the park.

It is NPS policy that "whenever possible, natural processes will be relied upon to maintain native animal species and influence natural fluctuations in populations of these species" (National Park Service 2006a). The policy provides significant discretion to local managers, stating that "the Service may intervene to manage individuals or populations of native species only when such interventions will not cause unacceptable impacts to the populations of the species or to other components and processes of the ecosystems that support them" (National Park Service 2006a). Any removal must be done within the context of an approved action plan (Porter et al. 1994).

The effort to accommodate both the philosophical rationales and the practical realities of park management has resulted in management goals that seek to preserve both natural processes and stable vignettes in the U.S. and Canada. These goals often conflict and confound ungulate management. Culling elk in national parks and hunting migrating elk within park boundaries have been politically charged issues. In smaller parks in the eastern U.S., the primary objective was to protect and foster the appreciation of cultural resources. Even though deer threatened this objective by altering the vegetation structure and species composition inherent to the cultural resource, public support for managing these parks as natural areas remained strong. As with elk in western parks, the deer in eastern parks were responding to ecological conditions across a landscape much larger than
the parks themselves (Boyce 1991, Underwood and Porter 1997). Therefore, park management needed to include and coordinate with the sometimes fundamentally different objectives of the state and federal natural resource agencies managing these larger landscapes (Porter and Underwood 1999).

A brief review of NPS actions dealing with deer overabundance in eastern parks provides an example of the complex interactions between management practicalities and management philosophies. In the 1980s, NPS commissioned a series of studies to document deer densities and movements and their impacts on plant communities. NPS also studied alternative methods for controlling deer abundance. In particular, they explored the use of contraceptive vaccines to limit population growth and tested the idea that localized deer problems could be addressed using targeted removal of deer (Warren et al. 1993, McNulty et al. 1997, Aycrigg and Porter 1997). These studies showed promise but also identified important limitations in both vaccination and targeted removal.

A series of reviews of deer management by outside scientists included a special session at the 1991 North American Wildlife and Natural Resources Conference and a special section in the journal, Ecological Applications. A debate within the science community explored the ecological justifications for controlling deer populations and found little consensus (Underwood and Porter 1991, Warren 1991). NPS concluded that measurement difficulties made carrying capacity an inappropriate basis on which to justify management action (Porter 1991, Wagner et al. 1995, Underwood and Porter 1997).

The various reviews identified several shortcomings in NPS management of deer and made a series of recommendations. Parks needed: (1) clear statements of management goals and objectives, (2) explicit measures that could be used to objectively evaluate whether impairment of cultural or natural resources was occurring, (3) background data on deer populations and the park resources
deer were affecting, (4) a monitoring program to measure change as management programs were implemented, and (5) a clearly articulated plan for review and adaptation of management practices as new knowledge was gained through time.

None of these recommendations were surprising to an agency that had struggled with these issues during the 1980s, but the NPS faced several more immediate fundamental and systemic challenges. The Park Service was trying to reconcile its need to present the public with a static image of a historical scene le.g., the way the landscape looked during the battles at Gettysburg in July of 1863) with its need to protect the dynamic processes of natural ecosystems (Porter et al. 1994, Underwood and Porter 1997, Leong and Decker 2005).

Beginning in the mid-1990s and continuing to date, NPS confronted all of these issues through leadership initiatives undertaken at the regional and national levels. The NPS recognized the importance of conserving natural resources and integrated management objectives for natural resources into the general management plans for eastern parks. Parks were encouraged to monitor deer impacts on vegetation and to talk with external constituencies about how to manage deer.

At the Washington, D.C., level, NPS recognized that it needed to prepare environmental impact statements (EIS) for deer management and began developing background analyses on a range of deer management alternatives. The alternatives fell into 6 general classes: no management, fencing and repellents, trap and removal, predator restoration, fertility control, and lethal removal. The preferred alternative was a combination of actions but included significant reduction of deer populations through lethal removal via sharpshooting. NPS approached the EIS process with great care, and parks documented their efforts assiduously. As a result, each time a park was sued over deer management, the courts upheld NPS' authority to manage deer populations.

# Ungulates in Park Management Goals and Objectives 

## Ungulate Conservation

Legislation creating NPS units often does not specifically mention ungulates. In a rare exception, the enabling legislation for Grand Teton specifically authorized elk reduction using public hunters and mandated working with the Wyoming Game and Fish Department. When legislation does not specifically authorize hunting, NPS interprets the lack of authorization as a prohibition on hunting in national parks. Similarly, on national preserves, recreation areas, and seashores, NPS often does allow hunting even when legislation is not specific.

Another set of directions regarding ungulate management on NPS lands is contained in the Code of Federal Regulations (CFR) and contains both generalized regulations and park-specific regulations. For example, the CFR (36 CFR Chapter 1 2.2b4) states that "the laws of the state of Wyoming shall govern elk management as associated with formal reduction programs." This is quite specific because it stipulates the use of Wyoming Game and Fish Commission regulations, and also the inclusion of formal reduction programs in elk management. The CFR also confers significant general authority on park superintendents to prescribe additional terms and conditions on many of the general authorities outlined in the regulations.

Ecological Basis. - Having the maintenance of ecological integrity as the first management
priority within Canadian national parks appears to result in less resistance to the inclusion of herd reduction in ungulate management. For example, Parks Canada launched a program to reduce the number of ungulates in 1999 at Elk Island National Park (Elk Island) and has initiated a moose hunting program at Gros Morne and Terra Nova national parks. The goal of these programs was to restore a balanced consumption of the park's vegetation and to complement biological diversity (Parks Canada 2012).

NPS management policies provide management direction in instances where overarching laws and regulations are not specific (National Park Service 2006a). Direction on ungulate management tends to be broad and contains qualifiers such as "whenever possible natural processes will be relied upon to maintain native plant and animal species." Given this generalized direction in Federal statutes, regulations, and policies, and the significant authority granted to superintendents to use a wide range of discretion regarding wildlife management, it is difficult to claim that the U.S. has an overall national policy or direction for ungulate management. Past reviews of NPS wildlife management activities, from Wright in the 1930s, to the Leopold Report in 1963 (Leopold et al. 1963), to recent reviews in Ecological Applications (Wright 1999), have elicited changes in how the NPS manages ungulates. The Leopold Report in particular influenced development of the NPS philosophy to allow natural regulation of ungulates.

The concept of natural regulation, although never officially codified, nonetheless became the de facto management policy of NPS through the 1980s. In the mid-1990s, however, individual parks such as Rocky Mountain National Park (Rocky Mountain) in Colorado and Gettysburg National Military Park (Gettysburg) in Pennsylvania acknowledged that increases in elk and white-tailed deer populations, respectively, were negatively impacting park vegetation and, in Gettysburg, cultural areas as well. Both parks developed EIS that addressed their growing ungulate populations and the impacts the populations were causing. Both parks eventually implemented ungulate reduction programs. The rate at which individual parks began to develop and implement ungulate reduction programs increased dramatically through the 2000s, and numerous NPS units have started or completed formal EIS or environmental assessments to deal with ungulate management issues, predominantly overabundance.

Recent controversies over reductions in ungulates throughout the NPS system led the Service to begin, in 2011, the first internal review of ungulate management programs since the 1963 Leopold report. This system-wide assessment of ungulate management is expected to yield management recommendations that will be presented to the NPS director by late 2012.

Re-introduction to Historical Ranges. - With the widespread decline in ungulates in North America by the end of the 19th century, their reintroduction into vacant ranges became a key strategy for restoring native species in National Parks (Cahalane 1951). Reintroduction is the reestablishment of a species in an area that was once part of its historical range, but from which it has since been extirpated or become extinct (International Union for Conservation of Nature 1995). Today, we make a clear distinction between reintroduction, introduction, and translocation for conservation purposes (International Union for Conservation of Nature 1995). During the era of ungulate restoration, however, distinctions were not pronounced, and
rigorous guidelines for reintroductions have emerged only in the past 2 decades IInternational Union for Conservation of Nature 1995, Singer et al. 2000, Gates et al. 2010). As a result, past restoration efforts have often created problems for current management in national parks.

As the largest land mammal and the icon for the West, bison became a focus of early restoration efforts in national parks (Gates et al. 2010). Six free-ranging plains bison (B. b. bison)-descendants from Yellowstone bison-were shipped to Wind Cave in 1914 to supplement 14 individuals from the New York Zoological Society. During the same period, several hundred purebred bison from the privately owned Pablo-Allard herd in Montana were shipped northward to the newly created Elk Island in Canada (Fuller 2002). Two years later, all but about 48 of the animals were moved from Elk Island to a larger facility at Buffalo National Park (Buffalo) in Alberta. Bison in these two parks became core sources for plains bison reintroductions into native range across North America. At the same time, wood bison (B. b. athabascae) had been reduced to fewer than 300 animals in a remote area in the forested borderlands of Alberta and the Northwest Territories (Gates et al. 1992, 2001a). Introduction of plains bison into a previously wood bison dominated area in Wood Buffalo National Park (Wood Buffalo) in the late 1920s has had long-term implications for bison management in the park (Nishi et al. 2006).

Although bison restoration to public parks has occurred in the past, today bison exist largely on private lands. In 1970, about half of the restored bison in North America were in public herds located in national parks, wildlife refuges, and state wildlife areas (Shaw and Meagher 2000, Stephenson et al. 2001), but commercialization of bison on private and tribal lands has increased since the 1980s. Today, only $7 \%$ of the approximately 250,000 restored bison are managed primarily for conservation of the herd (Gates et al. 2010); thus there may be a lack of emphasis on maintaining genetic purity in the majority of cases. Of the 62 plains bison and 11
wood bison herds established for conservation, 9 bison herds exist in national parks in the U.S. and 5 in Canada.

Despite success in restoring many ungulate species since 1900, reintroduction efforts in parks have been complex and expensive, in part because few parks are large enough to sustain viable populations. For example, reintroduction of elk into Theodore Roosevelt took almost 3 years, required agreements among the U.S. Forest Service (USFS), the North Dakota Game and Fish Department (NDGF), and the National Park Service, and involved a lengthy public comment on the environmental assessment and negotiations with the Medora Grazing Association regarding compensation for elk-related damage. In 1985, 47 elk were finally reintroduced from Wind Cave into the south unit of Theodore Roosevelt. The population grew rapidly, and hay depredation complaints from ranchers adjacent to the park resulted in a call for a regional elk management plan (Sargeant and Oehler 2007). In 1993, the first elk roundup resulted in the transfer of animals to game reserves, zoos, and reservations, but 44 animals died in the process.

As the elk population expanded out of the park, NDFG instituted depredation hunts and NPS continued to relocate elk to tribal and state entities in North Dakota, South Dakota, and Kentucky. However, concern over chronic wasting disease (CWD) in the mid 1990s led to the suspension of relocation efforts. As a consequence, the elk population grew to more than 900 animals despite increased hunting opportunities outside of the park. Concern about the effects of sustained heavy grazing on the ecosystem, similar to that which has occurred in several other national parks in the West (e.g., Yellowstone, Rocky Mountain), led managers to invoke NEPA regulations to help identify the environmentally preferable alternative that best protects, preserves, and enhances historical, cultural, and natural resources.

Unlike elk and bison, whose post-restoration management has focused on population expansion, only $53 \%$ of 87 translocations of bighorn sheep (Ovis canadensis) before the 1980s resulted in persistent populations across their range (Leslie 1980). However, the existing population of desert bighorn sheep (O. c. nelsoni) in Canyonlands National Park that existed at the time of its establishment in 1964 increased as a result of protection from hunting, the phasing out of livestock grazing within the park, and the reduction of domestic sheep grazing on federal lands adjacent to the park. As this population grew, it became the source population to reestablish sheep populations in Arches and Capitol Reef National Parks, Glen Canyon National Recreation Area, and other areas in Utah. Successful sheep reestablishment requires the existence of available indigenous animal sources and their relocation into large patches of habitat with few to no domestic sheep (Singer et al. 2000).

The fragmented and isolated nature of bighorn sheep habitat requires consistent multi-agency collaboration for restorations. At Badlands National Park (Badlands), 22 Rocky Mountain bighorn sheep were introduced from Pikes Peak in Colorado in 1964 into a small enclosure in the Pinnacles area. The program was a cooperative effort between NPS and the South Dakota Department of Game, Fish, and Parks (SDGFP), with a goal to establish a captivebreeding program from which the species could be restored across its range (Hjort and Hodgins 1964). After several health-related difficulties, 14 sheep were released into the badlands ecosystem in 1967. Sheep were opportunistically monitored until 1987, followed by research initiated by SDGFP in 1991 and then perpetuated as a multi-agency federal program. Cooperation among state and federal agencies deteriorated (Bourassa 2001), and in 1996, Badlands established 2 subpopulations at Cedar Pass and Stronghold using sheep from Pinnacles. A lack of state support for the federal program hindered the program's progress, so Badlands integrated its effort into a long-term regional management plan for bighorn sheep (Bourassa 2001).

Early movement of animals among parks to supplement declining populations has often proved to have long-term implications for park management. Wood Buffalo was established in 1922 to protect the world's largest herd of $(\sim 1,500)$ free roaming wood bison (Soper 1941). The need to resolve a problem with the expanding bison herd in Buffalo at Wainwright led to the translocation of more than 6,000 plains bison into Wood Buffalo (Carbyn and Watson 2001, Fuller 2002). Parks Canada received criticism from both the U.S. and Canada for the translocation on the grounds that it would eliminate the wood bison subspecies, create hybrids not fit for the environment, and introduce diseases such as bovine tuberculosis.

Overall, the controversial translocation was successful. Despite some hybridization, Wood Buffalo bison remain genetically and morphologically distinct (Wilson and Strobeck 1999), and their conservation as part of the wood bison restoration effort is advocated by the Wood Bison Recovery Team (Gates et al. 2010). Forty-nine animals that were translocated from Wood Buffalo to Elk Island in the 1960s also carried diseases. A rigorous breeding and quarantine protocol for neonates subsequently eradicated bovine tuberculosis and bovine brucellosis at Elk Island, and the park has provided disease-free breeding stock for other restoration efforts.

## Conservation of Ecological Communities

The NPS's concern about ungulate impacts on vegetation has caused much deliberation over active management of deer in eastern parks and elk in western parks. The concern was a primary motivation for the review of wildlife policies in national parks by the Wagner committee in the 1990s (Wagner et al. 1995). Much of the debate about ungulate-vegetation interactions and active reductions of deer and elk populations has hinged on the concept of carrying capacity (Underwood
and Porter 1991, Warren 1991). Carrying capacity has proved to be an ecologically elusive concept, however. Original ideas about ungulate-plant systems, based on long-term constancy of carrying capacity and irruptive dynamics of ungulate populations, evolved to include the ideas of ecological and economic carrying capacities, as well as the concepts of frequent fluctuation of carrying capacity and centripetal dynamics (Caughley et al. 1987, McCullough 1997, Fryxell and Sinclair 2000).

Multiple working definitions of carrying capacity, combined with the lack of a clear method for measuring it, have made the concept too unwieldy to be practical for management in the national parks (Porter 1992, Porter et al. 1994). Consequently, the emphasis in eastern parks has shifted to documenting deer impacts on vegetation. These impacts are evaluated relative to efforts by NPS to manage vegetation to promote cultural and natural resources le.g., Final White-tailed Deer Management Plan and Environmental Impact Statement for Valley Forge National Historical Park). Even with this approach, NPS still faces the challenge of managing complex ecological processes to create specific conditions in natural and cultural features (Porter and Underwood 1999). These ecological processes are driven by a system of interacting components and feedback loops operating on multiple temporal and spatial scales. Browsing by white-tailed deer has a temporal effect because it alters the rate of forest development and the structure and composition of the plant community (West et al. 1981, Augustine and McNaughton 1998). Browsing also has a spatial effect, because the seasonal movements of deer have a profound impact on vegetation and some parks are too small to encompass these movements (Behrend et al. 1970, Tierson et al. 1985).

Studies at the Saratoga National Historical Park illustrate how deer density affects browsing impacts (Austin 1992, Underwood and Porter 1997). High deer density significantly slowed early forest development. Deer selectively removed many tree species, but clonal species such as dogwood (Cornus
spp.) persisted. Clonal species are more resilient to browsing than are species with independent stems, because they can reproduce vegetatively. Expanding clones prevent development of shade intolerant species but also serve as protective nurseries for shade tolerant species which eventually overtop the dogwood, but the process requires as many as 30 years (Austin 1992).

Browsing by deer can alter the species composition of eastern forests for extended periods. For example, losses of eastern hemlock (Tsuga canadensis) and white-cedar (Thuja occidentalis) in the Great Lakes region were partially attributed to excessive browsing by white-tailed deer (Alverson 1988, Alverson and Waller 1997). Densities exceeding 30 deer/km2 affect vegetative species composition (Tilghman 1989, Bratton and Kramer 1990, Stromayer and Warren 1997, Didion et al. 2009). A density of less than 8 deer/km2 in northern hardwood forests allowed a diversity of species to persist and created a diverse forest overstory (Kelty and Nyland 1981, Tilghman 1989).

Deer impact herbaceous vegetation and species richness declines when deer exceed 8 deer/km2 on the Allegheny National Forest (Redding 1995). Abundance of some endangered or threatened species (e.g., bluebead, Clintonia borealis) was inversely related to abundance of deer (Balgooyen and Walker 1995). Spring flora, such as trillium (Trillium grandiflorum), are impacted at deer population densities of 4-6 individuals/km2 (Anderson 1994, Knight 2003).

The spatial dimension of all of these impacts is complicated by the social organization and seasonal migration of deer. Even when deer densities are low on a regional basis, local impacts on vegetation can be substantial (e.g., Didier and Porter 2003). This variability occurs because of the concentration of deer social groups and non-uniform distribution of deer across the landscape (Mathews and Porter 1992, Aycrigg and Porter 1997, Campbell et al. 2004, Oyer and Porter 2004). Deer concentrations occur
more frequently in northern latitudes because of snow depth (e.g., Underwood 1990).

Predicting the impacts of herbivory in the West has been no less challenging than in the East, due partly to a philosophy in the western parks that has emphasized natural regulation and a hands-off approach (e.g., Cole 1971). Critics have argued that in the absence of wolves (Canis lupus), the natural regulation approach in the western parks was ill-conceived. Human-altered ecosystems, especially with respect to ungulates, limited the likelihood that natural regulation would occur, which was considered grounds for active management (Leopold et al. 1963). However, defining clear tests to determine whether ecosystems were actually beyond the bounds of natural regulatory processes proved unfeasible, and science was unable to provide practical guidelines for evaluating when intervention was warranted (Porter 1992). Yet, despite this larger debate, it was clear that ungulates were affecting vegetation.

Assessing the effects of ungulates on vegetation in western national parks has been an evolving challenge because of changing views on what regulates trophic dynamics. During the middle of the 19th century when ungulate populations were recovering in many western parks, the prominent view of vegetation management was in line with the "green world hypothesis": herbivores were not expected to modify plant resources because they were regulated by predators (Hairston et al. 1960, Pimm 1992, Polis 1999). Where natural predators such as wolves and cougars (Puma concolor) were extirpated, and hunting by native Americans and contemporary hunters was prohibited, culling and live removal of ungulates was justified to prevent animal starvation and ecosystem degradation (Stevens 1980). Thus, many of the early vegetation assessments practiced in parks, such as the Cole browse surveys (Cole 1963), used acceptable limits of vegetation removal adopted from range management. With the emergence of natural regulation as an NPS management policy in the
early 1970s, the view changed to one focusing on density-dependent feedback mechanisms between plants and herbivores that, in the end, were expected to result in either a stable or a dynamic equilibrium. A modified vegetative state from when herbivores were absent was viewed as a natural consequence of interactive plant-herbivore dynamics (Caughley 1979, Caughley and Lawton 1981). A potential complication was how humans had altered park systems, such as by limiting animal migrations or by aboriginals setting fires, such that natural feedback mechanisms would not function sustainably (Wagner 2006b).

The policy change was accompanied by considerable research addressing how large herbivores influenced plant community structure and ecosystem properties. The general view is that large herbivores influence plant community composition and functioning depending on movement patterns, degree of selective feeding, environmental conditions, and plant tolerances related to grazing history and physiological adaptations (Coughenour 1991, Frank and McNaughton 1992, Augustine and McNaughton 1998).

Feedback mechanisms work differently in grassland and forest ecosystems (Singer and Schoenecker 2003, Pastor et al. 2006). In grasslands of Wind Cave, Yellowstone, and Rocky Mountain, high populations of ungulates removed dead standing herbaceous material in the winter, thus reducing litter inputs and increasing bare ground. Herbivory increased nitrogen cycling and carbon fluxes by changing litter quality, stimulating nitrogen mineralization and retention, increasing carbon turnover, and adding readily available nitrogen from urine and feces to upper levels of the soil. These changes influenced below-ground organisms and soil processes that increased nitrogen availability to above-ground herbivores (Coughenour 1991, Frank and McNaughton 1992, Holland et al. 1992, Pastor et al. 1993, Merrill et al. 1994, Frank and Evans 1997, Frank et al. 2000, Detling 1998, Singer and Harter 1996, Singer et al. 1998, Zeigenfuss et al. 2002, Schoenecker et al. 2004, Frank et al. 2011).

In contrast, impacts of ungulates on woody vegetation were much more pronounced. In the forest communities at Isle Royale, non-migratory moose suppressed growth and survival of balsam fir (Abies balsamea) and deciduous trees (Risenhoover and Maass 1987, McInnes et al. 1992). In the boreal forest, selective browsing on deciduous plants provided a competitive advantage to coniferous species, thus facilitating forest succession (Pastor and Naiman 1992). However, at low moose density, browsing could stimulate shoot and leaf production by deciduous trees (Danell et al. 2003) and impede forest succession. Therefore, ungulates could stabilize or destabilize plant community structure, but in most situations they were likely to create oscillations in time or space (Pastor and Cohen 1997, Pastor et al. 2006). Where these cycles fall within the range of natural variability to which the system is adapted is unclear, but the conservation of processes, such as migratory behaviors, is likely to be critical.

Two woody species—aspen (Populus tremuloides) and willow (Salix spp.)—play important ecological roles (Knopf et al. 1988, Baker and Cade 1995, Naiman and Decamps 1997, Baril et al. 2011). Aspen and willow declined during the 1900s in Yellowstone, Rocky Mountain, and Banff (Gruell 1980, Houston 1982, Kay and Wagner 1994, Baker et al. 1997, Peinetti et al. 2002) concomitantly with increases in elk populations (Lubow et al. 2002). The relative importance of the effects of elk herbivory, climate change, fire (aspen), and hydrology (willow) and combinations of these factors on aspen and willow stands has been debated (Kay and Chadde 1992, Singer et al. 1994, White et al. 1998, Peinetti et al. 2002). Regeneration of aspen within long-term exclosures has been cited as evidence against climate change. A landscape-level resprouting of aspen after large fires allows aspen regrowth to outpace herbivory rates, but such an event has not occurred since the 1988 wildfires in Yellowstone, not even after prescribed burning in Banff and Jasper National Park (Jasper) (Romme et al. 1995, White et al. 1998, Beschta and Ripple 2007, Kauffman et al. 2010). In fact, burning actually may hasten impacts
under heavy browsing in some places (Kay and Wagner 1996, White et al. 1998).

Herbivory, hydrology, and flooding have interacted to impact willow communities since the 1930s. In Rocky Mountain, the decline of willow is associated with decreased complexity of river branching, loss of alluvial surface, and loss of beaver activity (Peinetti et al. 2002, Cooper et al. 2006). In both Yellowstone and Rocky Mountain, fall and winter herbivory stimulated woody biomass production and altered plant morphology (Kay and Chadde 1992, Singer et al. 1994, Peinetti et al. 2002, Gage and Cooper 2005, Cooper et al. 2006, Johnson et al. 2007, Bilyeu et al. 2008). Morphological changes included fewer, longer, and thicker shoots. Plant height was suppressed because of preferential browsing of shoots in the upper canopy, but not when water table levels were high (Bilyeu et al. 2008, lercek et al. 2010). Compensatory above-ground growth was hypothesized to have resulted in lower below-ground carbon allocation, which would influence competitive ability and survival of willow under dry conditions (Singer et al. 1994, Peinetti et al. 2002, lercek et al. 2010). Cumulatively, these studies indicate that elk reductions may not lead to rapid willow recovery lunless there are direct management inputs to restore the willow) because beaver (Castor canadensis) predation will fill the void. At the same time, some counter that the number of beavers in the 1920 s represented an unusually high number (Persico and Meyer 2009).

The return of wolves to U.S. and Canadian national parks has added to the ecological and management complexities because they can produce top-down trophic cascades. Reintroduction of wolves to Yellowstone in 1995-96 was associated with fewer elk and changes in elk selection patterns (Mao et al. 2005, Creel et al. 2005). These changes have been linked to reduced net N -mineralization in grasslands (Frank 2008) and willow and aspen recovery across the area, albeit not consistently (Kauffman et al. 2010, Kimble et al. 2011). Whether direct (numerical) or indirect (behavior-mediated) alteration of elk
herbivory by wolves (top down) is more or less important relative to environmental factors (bottom up) for structuring plant communities is unclear (Ripple et al. 2001, Fortin et al. 2005, Beyer et al. 2007, Christianson and Creel 2009, Kauffman et al. 2010). After wolves naturally recolonized at Banff, wolf avoidance of human activity resulted in wolf-mediated variation in herbivory (Hebblewhite et al. 2005, Hood and Bayley 2008, Baril et al. 2011). The extent to which humans play a similar role in other western parks remains to be seen, but is likely contingent on the spatial-temporal patterns in human development, vegetation types, and topographic relief (Ripple et al. 2001, Rogala et al. 2011).

Abundant ungulates may negatively impact populations of endangered ungulates when they share a common predator. Apparent competition describes such an indirect ecological interaction between two or more prey species and a shared predator, which has been increasingly linked to declines of prey species across taxa (DeCesare et al. 2009). Kinley and Apps (2001) posited that adult mortality by cougars within a declining population of endangered woodland caribou (Rangifer tarandus caribou) was sustained by the presence of abundant moose serving as an alternative prey. Gibson (2006) hypothesized that hyper-abundant alternative prey increased mortality by cougars within a population of endangered Sierra Nevada bighorn sheep (Ovis Canadensis sierrae).

The impacts of high densities of deer on vegetation have indirect impacts on other vertebrates.
Deer population densities of 8-25 deer/km2 in Pennsylvania damaged habitat and species richness of intermediate-canopy nesting songbirds (DeCalesta 1994). Excluding deer from certain areas increased populations of ground nesting and intermediate canopy bird species (McShea and Rappole 1997,2000 ). The mechanism by which this occurs is hypothesized to be the alteration of species composition and vegetation structure, as well as associated changes in food availability and nesting cover.

## Disease and Parasite Management

Enzootic diseases and parasites are present in park ecosystems. At the time Aguirre and Starkey (1994) summarized diseases in national parks in the mid-1990s, lungworm-pneumonia complex in bighorn sheep and epizootic hemorrhagic disease in white-tailed deer were among the most common diseases. Typically, NPS did not actively manage native species that were diseased or that had high parasite loads. For example, an infectious keratoconjunctivitis killed $60 \%$ of 500 bighorn sheep estimated to inhabit the Northern Range of Yellowstone. Although possible adverse humancaused impacts in the wake of the population crash were a concern, park management did not address the disease directly (Meagher et al. 1992).

The extent of disease management in national parks depends on perceived risks to the native ungulates within and outside the park, and the park's ecological, sociological, economic, and political context (Nishi et al. 2006). The NPS managed diseases only for the protection of endangered species and species of special concern for protection of populations in adjacent areas, or for public health reasons (Aguirre et al. 1995). NPS embraced a more contemporary view of disease management beginning in 2000 with the establishment of the Biological Resource Management Division which added wildlife health expertise to their staffing (E. Leslie, National Park Service, personal communication). Clinically ill animals could be removed under a categorical exclusion within NEPA, but control of healthy animals to prevent disease spread required preparation of an environmental assessment or EIS.

Focus on disease management for endangered ungulate species is now rare because few of these species currently exist in national parks, le.g., the Sonoran Pronghorn [Antilocapra americana sonoriensis] in Organ Pipe Cactus National

Monument), and disease is only one of many challenges to their continued persistence. In contrast, where national parks are reservoirs for disease that can be transmitted to livestock, management is based on the specifics of animal movement, the regional dependency of the economy on the livestock industry, and management feasibility and funding availability. In parks like Yellowstone, for example, bison management has been a balancing act between conserving natural migratory patterns, while contributing to regional disease management (Plumb et al. 2009). NPS also manages diseases that interfere with natural processes, that are not native, or that occur at an unnaturally high level due to human influences (E. Leslie, National Park Service, personal communication).

Some Canadian parks, like Elk Island, have had a long-standing tradition of managing disease. Testing for disease first began as part of the bison herd reduction program in the late 1920s. Bovine brucellosis was found late in the 1940s, and by the mid-1950s it appeared to be influencing calving rates and herd health (Blyth 1995). Initially, Parks Canada imposed a test and slaughter program and eventually included vaccination. The park was declared free of brucellosis in 1972, but testing continues (Nishi et al. 2002).

The continuing focus on disease management in Wood Buffalo is a classic example of coping with the legacy of past restoration decisions. Parks Canada considered translocating plains bison from a herd with bovine tuberculosis to Wood Buffalo. It was thought that the risk of moving the disease to Wood Buffalo could be minimized by pre-testing and moving mostly yearlings, but neither of these options was carried out (Fuller 2002). Since the introduction of plains bison into Wood Buffalo, 49\% of the bison have tested positive for tuberculosis and 31\% for brucellosis (Joly and Messier 2004). In 1990, a federal Environmental Assessment and Preview Process Panel recommended eradicating all bison from Wood Buffalo and restocking with disease-free bison from Elk Island (Federal

Environmental Assessment and Review Office 1990). The recommendation was unpopular with some conservationists and First Nations and was not followed. Over nearly 2 decades that followed, the lack of long-term vision, continuity, and full engagement of local communities kept the issue mired in inaction (Gates et al. 2001b, Nishi et al. 2006). Most current disease management to minimize the risk of spreading disease from Wood Buffalo comes from management outside of the park by the provincial governments. These entities conduct aerial surveillance of bison and use intensively regulated hunts to limit the opportunity of disease-free populations outside of the park from coming into contact with Wood Buffalo bison.

The emergence of CWD, now detected in 2 Canadian provinces and 17 states in the U.S., is likely the most broad-scale disease of cervids that the national parks have faced this century. However, uncertainty about the long-term impact of CWD on ungulate populations has lessened the urgency to take strong preventative measures. To date, CWD has not been detected in any of the 42 Canadian parks, although it is within 100 km of Riding Mountain in Saskatchewan and Elk Island in Alberta. Parks Canada's concerns currently focus on the effect that CWD might have on woodland caribou, a species at risk, as they move westward toward Jasper, Alberta, and how it might jeopardize Elk Island's reintroduction program across North America (Parks Canada 2008). As a result, Parks Canada is currently supporting provincial efforts rather than considering any direct management within the park units.

In the U.S., CWD is considered enzootic in Wind Cave and Rocky Mountain. At least 2 parks have initiated CWD planning, 3 parks have park-based CWD management plans, and CWD is a component of another park's management plan. Most jurisdictions believe CWD cannot be eradicated. Control measures such as herd reduction may impede the spread (Miller et al. 2008). Most parks have developed passive surveillance programs based on road kills and intend to remove animals with clinical signs
(White and Davis 2007). In areas of high ungulate densities where CWD might spread easily, disease management is only one consideration in addressing ungulate overabundance.

As federal agencies, Parks Canada and NPS are mandated to conserve their natural resources and ecological integrity despite frequent human visitation. In meeting these mandates, park managers face problems in disease management that stem not only from the legacy of the past and the political complexity of a park's context, but the uncertainty of the risks to park resources and visitors. Future directions in disease management in national parks are likely to move toward embracing the One Health concept, which is based on the premise that the health of people, animals, and our environment is inextricably interconnected. NPS is already exploring how this approach can be used to incorporate unified disease surveillance, an interdisciplinary response, and consensus guidance (One Health Commission 2011).

## Visitor Experiences

Wildlife plays an important role in providing visitors with a satisfying experience at national park sites, and viewing ungulates is an especially valued aspect of the visitor's experience. Visitors have expectations of seeing wildlife when they visit national parks and often base evaluations of their experience on whether these expectations were met. For example, Miller and Wright (1998) reported that visitors to Denali National Park and Preserve expressed greater levels of dissatisfaction when they did not see moose, than when other species were not seen. Large elk herds are perceived as positive attractions by visitors in western U.S. parks, and many visitors do not consider high ungulate populations a management problem (Fix et al. 2010, Davenport et al. 2002).

Visitors can interfere with feeding and other behaviors of wildlife species (Pedevillano and Wright
1986), and some interference results in physical contacts and injury to visitors or wildlife. However, visitors often do not recognize the impact of their activities on wildlife. Taylor and Knight (2003) reported that $50 \%$ of park visitors perceived their activities as not affecting wildlife and considered it acceptable to approach bison, antelope, and mule deer (Odocoileus hemionus) more closely than is considered a safe distance (the distance before which species exhibit defensive behaviors).

Visitor attitudes can sometimes conflict with management objectives for ungulate populations. However, park visitors are not the only stakeholders whose perceptions regarding ungulate management are of concern to managers; managers are concerned about resident attitudes as well. Fix et al. (2010) reported differences between Rocky Mountain visitors and Colorado residents in terms of the level of elk reduction that was acceptable to them in order to increase aspen and willow growth. Residents near parks, especially in the eastern U.S., have voiced concerns over NPS plans to regulate white-tailed deer. On the other hand, Fulton et al. (2004) reported that most residents near Cuyahoga Valley National Park supported efforts to employ lethal control to reduce the park's deer population.

Lethal management has often been opposed by vocal stakeholders. For example, managers at Valley Forge National Historical Park (Valley Forge) planned to significantly reduce deer within the park boundary using trained sharpshooters from the USDA Animal and Plant Health Inspection Service (National Park Service 2009b). Opposition efforts included a series of lawsuits and a court injunction during fall 2009 to stop the culling operation (Dale 2009). Animal rights organizations contended that coyotes should be allowed to naturally control the deer population in Valley Forge, and they have pursued court action to force park managers to prevent culling in favor of coyote predation (Gothard 2010).

Despite the high degree of contention at Valley Forge, investigation of visitor and resident acceptance of
management options, including lethal control, has been limited. Thus, undertaking further studies of public attitudes toward ungulate management in national parks is imperative.

## Conflicts with Other Agencies/Land Uses

NPS (2006a) policy requires consultation with other land management agencies when planning management or removal of native animals. Such agencies include other federal land management agencies, state wildlife management agencies, and tribal governments. The policy dictates that consultation will address: (1) the management of selected animal populations; (2) research involving the taking of animal species of interest to these agencies; and (3) cooperative studies and plans dealing with public hunting and fishing of animal populations that occurs across park boundaries.

Cooperative fish and wildlife management efforts by NPS are guided by the Department of the Interior policy 43 CFR Part 24 (Code of Federal Regulations 1983). The policy "reaffirms that fish and wildlife must be maintained for their ecological, cultural, educational, historical, aesthetic, scientific, recreational, economic, and social values to the people of the U.S.," and notes that resources are to be held in the public trust by governments for the benefit of present and future generations. Furthermore, the policy identifies the importance of cooperation between state and federal agencies and in being "good neighbors." There is also an acknowledgment that habitat is critical and species may rely on NPS lands seasonally.

Reintroductions. - A comprehensive planning process examining the feasibility of reintroducing elk to Theodore Roosevelt included formal meetings with the North Dakota Game and Fish Department in 1983, and a final environmental assessment was prepared in 1984. In 1985, 47 elk from Wind Cave were released at Theodore Roosevelt. High pregnancy rates and

Low mortality led to a rapidly increasing population, and an estimated 350 elk were in the park by 2003 (Sargeant and Oehler 2007).

The collaborative effort to reintroduce a native species was impressive, but the rate of population increase and issues resulting from high elk densities (e.g., disease concerns, habitat damage) has been problematic. By the early 1990s, NPS was receiving complaints from adjacent landowners regarding depredation from Theodore Roosevelt elk, but 2 relocations temporarily reduced the population prior to 2000. Relocations were halted upon discovery of CWD on some NPS units, so the elk management plan was revised to include shooting by park staff and volunteers (National Park Service 2010a).

Great Sand Dunes National Park is a park and preserve located in Colorado. Elk are common and protected from hunting in the park portion, but harvest is allowed in the preserve portion. The Colorado Division of Wildlife elk unit, Northern San Luis Valley Floor Plan, recommends that the population be minimized because of significant depredation concerns (Wagner 2006a). The expanding elk population at Great Sands (and the resulting spillover) has put the state agency in the difficult position of managing an elk population under the following conditions: 1) the federal lands have become an unregulated source of elk, 2) adjacent landowners are experiencing significant crop losses, and 3) recreational landowners who are not financially impacted by elk damage are in support of the growing elk populations. In essence, the state agency is incurring significant financial expense (crop damage payments) and diversion of staff time to address depredation and other private land issues.

A reintroduced gray wolf population increased to about 300 in the Greater Yellowstone Area; around 100 of these individuals inhabit Yellowstone. Evidence suggests that wolf depression of ungulate populations, particularly elk, has led to improvements in other species and habitats le.g., red
fox, beaver, small mammals, aspen, and willow). Elk comprise up to $90 \%$ of the wolf diet in Yellowstone, and the elk population has declined by $60 \%$ since the initial wolf releases (Smith et al. 2003), although drought and elk harvests adjacent to the park may have contributed to the decline. Although there are many positive attributes to a robust wolf population, the decline in the elk population is a cause of acrimony for some members of the public, including hunters. The Greater Yellowstone Area and Southwest Montana support approximately onehalf of Montana's annual elk harvest and elk hunter days afield, but since 2004 wolves are estimated to have taken more elk than hunters in the northern Yellowstone area (Hamlin and Cunningham 2009).

Disease Management. - Disease is a ubiquitous characteristic of any biological system. However, the greatest challenges for national parks have been when the disease lifecycle includes both park wildlife and domestic livestock. In these situations, park management is subject to both local and global pressures. For example, the Animal and Plant Health Inspection Service (APHIS) in the U.S. and the Canadian Food Inspection Agency are responsible for certifying states and provinces as having brucellosis disease-free status, which allows producers to export cattle to other states, provinces, and countries without prior testing. Domestic livestock managers have focused attention on national parks where wildlife is viewed as a reservoir for disease (Olsen 2010, Rhyan and Spraker 2010). In most instances involving diseases that affect both domestic and wild animals, multiagency and stakeholder task forces are formed as a part of regional management plans. However, in climates of uncertainty due to differences in values and mandates, policy directions for some parks can be complex and difficult to resolve (Rittel and Webber 1973).

Brucellosis was presumably transmitted to bison in Yellowstone by cattle that ranged in the park in the 1920s (Meagher and Meyer 1994). A test and slaughter program begun in the 1960s was quickly
eliminated because it was ineffective. Interactions between bison and cattle occur primarily when bison migrate outside Yellowstone to escape harsh winter conditions. The Interagency Bison Management Plan took over a decade to negotiate and began in 2000. In the plan, NPS, APHIS, the U.S. Forest Service, and the state of Montana prescribed measures to preserve the bison population while maintaining Montana's brucellosis-free status (Bidwell 2010). Response management is directed at hazing, hunting, or sporadic removals using a variety of means (U.S. Department of the Interior et al. 2008) that are based on bison movements and parturition (Jones et al. 2010, Geremia et al. 2011).

Recent outbreaks of brucellosis in states surrounding Yellowstone have redirected focus from bison to elk. Elevated brucellosis levels in elk have been associated with elk feeding grounds adjacent to Yellowstone in Wyoming and Idaho. The recent increased prevalence of brucellosis outside of the feeding grounds is attributed to increased elk density at the winter feeding grounds (Cross et al. 2010). As a result, management is now directed at lowering elk populations, but the program is constrained by limited hunting access on private lands.

In contrast to Yellowstone, Riding Mountain National Park (Riding Mountain) in Manitoba, Canada, is a small park considered to be an "ecological island situated amidst a sea of agriculture." Bovine tuberculosis was first confirmed in the park's elk in 1992 and in white-tailed deer in 2001 (Lees 2004, Nishi et al. 2006). Tuberculosis was routinely reported in cattle allowed to graze in Riding Mountain during the 1950 s and 1960s. To facilitate trade in 2003, the Canadian Food Inspection Agency established the Riding Mountain Eradication Area and gave it a BTB-Accredited Advanced status, whereas the rest of Manitoba was designated as disease-free. Concern over elk and deer from Riding Mountain infecting cattle herds outside of the park led to the development of a 5-year management and eradication plan by the Interagency Task Force Group for Bovine Tuberculosis. Because of the extensive


Over-populations of ecological keystone species, such as elk, deer and bison can negatively affect floral and faunal community dynamics. Here, excessive elk grazing limits aspen regeneration, which negatively impacts beaver and other vertebrate and invertebrate populations. Credit: National Park Service.
use of cattle pastures by Riding Mountain elk, management actions have included extensive elk testing, elk reduction via extended hunting seasons and wolf predation, prescribed burning inside of the park, laws to prevent baiting and its resultant unnatural aggregation of elk, and federal-provincial cost-share programs that provide barrier fences for baled hay (Nishi et al. 2006).

Hunting. - Most national parks do not allow hunting. The lack of hunting pressure on herds often leads to conflict between ungulates and adjacent landowners and residents in developed areas (e.g., Rocky Mountain), or habitat degradation within the national park. State and provincial wildlife agencies have recognized hunting as a tool to control ungulate over-population and acknowledge the need to manage populations at a scale larger than the park unit, but the lack of hunting in national parks often conflicts with the harvest management preferences of adjacent conservation partners.

# Ungulate Population Management Objectives 

Abundance, composition, and distribution manipulation is the defining feature of ungulate management. A prerequisite for the development of cogent management strategies is the translation of park purposes into objectives that establish clear expectations and a basis for evaluation.

Parks serve myriad purposes. Ungulate population objectives that are appropriate for one park may not be appropriate for others. Population objectives for U.S. parks have ranged from eradication to facilitation. Recent examples highlight variable and unique considerations that have contributed to this variability.

## Eradication

Although NPS policies encourage the presence-and even reintroduction-of native species on historical ranges, they also support eradication of feral and non-native ungulates that: (1) interfere with natural processes or perpetuation of natural features and habitats, (2) disrupt the accurate presentation of cultural landscapes, (3) damage cultural resources, (4) substantially hamper management of a park or adjacent lands, or (5) pose safety or health hazards (National Park Service 2006a).

Elk, mule deer, and feral pigs at Channel Islands National Park (Wakelee and Frisch 2010), feral goats and pigs at Hawai'i Volcanoes National Park (Hawai'i Volcanoes) (National Park Service 2011a), and exotic deer at Pt. Reyes National Seashore (National Park Service 2006b) exemplify circumstances that have led to population objectives of zero, or as
close to zero as possible. In each instance, nonnative ungulates were introduced prior to park establishment and have altered natural vegetation, with resultant adverse effects on native wildlife. Such effects were of particular concern at Hawai'i Volcanoes, where native plants were not adapted to grazing or browsing (National Park Service 2011a). Disease and competition with native tule elk (Cervus canadensis nannodes) and black-tailed deer (Odocoileus hemionus columbianus) were also priorities at Pt. Reyes, where non-native deer harbored both paratuberculosis and exotic lice that have elsewhere been implicated as a cause of mortality in mule deer (National Park Service 2006b).

## Regulation at Low Density

Elk were reintroduced to Theodore Roosevelt in 1985, encouraged by park policies to repatriate native species to historical ranges. The reintroduced elk achieved birth and survival rates that were among the greatest reported for the species and the population increased rapidly (Sargeant and Oehler 2007). Prior to 2002, NPS translocated excess elk to prevent the herd from exceeding approximately 400 animals.

Growing concern about CWD transmission led to the suspension of translocations in 2002, and the population increased to more than 900 by 2010, prompting the release of an elk management plan and EIS (National Park Service 2010a). The plan prescribed a 100-400 elk population objective, which was achieved during 2010-2012 by removing 868 elk. The upper limit was based on conservative projections from a park-specific forage allocation
model (Irby et al. 2002). Near the lower limit, grazing and browsing by elk are expected to have negligible effects on vegetation and other wildlife.

Conservative population objectives were deemed appropriate for Theodore Roosevelt because the park is embedded in a matrix of public and private lands that are managed primarily for livestock, agriculture, and oil production where early- and midsuccessional vegetation dominates. Conservative population objectives will protect late-successional vegetation in the park without jeopardizing elk persistence (National Park Service 2010a).

## Regulation at High Density

Whereas other parks referenced in this section were created for varied purposes rather than specifically for the benefit of ungulates, Wind Cave was dedicated expressly, though not exclusively, as a "permanent national range for a herd of buffalo" (37 Stat. 293). Population objectives for bison at Wind Cave reflect not only this distinction but also the special status of the Wind Cave bison population. Although bison currently number in the hundreds of thousands, approximately $95 \%$ are held in private herds managed for commercial production. Captive bison are generally excluded from conservation planning due to an uncertain heritage and history of selective breeding. In contrast, publicly owned conservation herds total fewer than 20,000 animals (Boyd and Gates 2006).

Genetic diversity of publicly owned bison herds was reduced by near extinction during the late 1800s (Boyd and Gates 2006). Of the 11 U.S. federally owned bison herds, only the Yellowstone and Wind Cave herds are believed to have not cross-bred with cattle (Halbert and Derr 2007). In addition, the Wind Cave population is the only one thought to be free of communicable diseases (e.g., brucellosis). These considerations amplify the conservation significance of Wind Cave bison. Bison management at Wind Cave reflects the park's mission (National Park Service 2006a). The NPS uses live capture and
translocation to regulate numbers but sustains a population of approximately 400 bison, the maximum number that is sustainable within the constraints imposed by available forage and competition with other herbivores.

Regulation at high density also appeals to those who perceive parks as sanctuaries, wherein action should be minimal, infrequent, and taken only to prevent imminent resource damage. However, regulation at high density may have unintended consequences. Grazing and browsing typically become dominant influences within park ecosystems well before resource limitations reduce herd survival or reproduction. Without a strong density-dependent response, significant resource impacts should be expected.

## Alternatives to

## Ungulate Density

In some parks, ungulates have reached such high densities that grazing and browsing have overwhelmed ecosystem influences, with undesirable consequences for plant community composition and structure. For common ungulates, those effects rather than ungulate populations themselves are often the principal focus of concern. In cases where undesirable effects on vegetation are already evident, establishing thresholds for action based on the status of indicator species may be advantageous, because vegetation can be measured more easily and accurately than ungulate density and can therefore more directly inform management priorities.

White-tailed deer management at Indiana Dunes National Lakeshore where excessive browsing threatened sensitive forbs, and at Catoctin Mountain Park where deer prevented tree seedling regeneration, exemplifies scenarios in which vegetation monitoring informed management decisions (National Park Service 2008a, 2009a). Thresholds for action were based on heights of selected forbs at Indiana Dunes and on tree seedling densities at Catoctin Mountain Park.

## Management Alterntatives



Bison (Bison bison) at Yellowstone Lake. Bison management is an ongoing need within the boundaries of Yellowstone National Park. Credit: Creative Commons.

## No Action

under NEPA, "no action" may refer to the continuation of existing management strategies. In practice, however, no-action alternatives for wildlife management in national parks typically minimize human intervention into ecosystem processes. However, national parks do not typically represent complete ecosystems (Leopold et al 1963), so habitat quality and
population demographics and health may be affected by factors external to the parks. Human influences may have been present for centuries and although their impacts on ungulates are difficult to estimate, they may well have been significant. This is readily acknowledged within policy statements of the Canadian national park system (Parks Canada 2011).

Efforts to minimize human interference with natural processes involving wild ungulates must be considered relative to scale. At the broadest
scale, nearly complete absence of management may occur in the largest parks, particularly those in Alaska, where the complement of predators and the processes affecting habitat are present. Particularly in tundra ecosystems where fire is not a factor, systems may be kept intact without much human effort. In taiga, where fire is present, efforts to manage the size, location, and frequency of fire occurrence affect ungulate habitat and therefore population distribution and dynamics.

At a medium scale-which includes most of the larger parks south of Alaska-some human influence will inevitably be present. Most parks are not complete ranges for larger ungulates, so populations often require more habitat than is available inside the park. One indirect human influence is predator-avoidance redistribution into areas where human occupation limits predator populations, such as occurs in Banff (Hebblewhite et al. 2005). Additionally, elk redistribute beyond the borders of Yellowstone during winter, where wolf predation is less intensive.

At the smallest scale, individual animals or groups of animals may occur in areas where humans commonly occur; these animals may pose risks to park visitors. Moose at Riley Creek developments in Denali and elk near Rocky Mountain and Buffalo are examples of conditioned animals that cause authorities to provide warnings and even to remove individuals on occasion.

The no-action alternative has had implications for ungulates in U.S. national parks. Prior to this policy, elk in Yellowstone were reduced through culling, wolves were not present, and brown bears (Ursus arctos) had been significantly reduced (Craighead et al. 1974). The no-action alternative was based on the assumption that bottom-up regulation of elk numbers was natural, and populations would fluctuate according to winter severity and forage supplies. Predation, the top-down regulation process, was considered superfluous to population density. Vegetative conditions were considered
a natural consequence of browsing pressure.
Subsequent to wolf restoration, elk have altered winter distribution, making more of the population available for hunting outside of the park. Elk have also changed their habitat use, indicating that predation is important (Ripple et al. 2001, Ripple and Beschta 2003, Smith et al. 2003). In contrast, long-term analysis of the Isle Royale wolf-moosevegetation complex suggests that more of the variation in moose population growth rates was explained by weather and forage-related processes than by wolf predation (Vucetich and Peterson 2004).

Given the long-term human presence in most systems, management of ungulates at some level would not be inimical to the goals of the national parks. However, the issues of conditioned animals, incomplete ecosystems, reductions in natural processes such as wildfire, and loss of predators have implications that preclude a system-wide no-action approach to ungulate management in national parks.

## Animal Removal

Historical Context.- Subsistence and market hunting decimated large mammal populations during European settlement of North America, which led to an initial national park emphasis on wildlife protection. Several parks also played an important role in ungulate conservation during the late 19th and early 20th centuries by providing source stock for restoration of native ungulates to historical ranges. Those translocations were the first coordinated removals of ungulates from U.S. national parks (Pritchard 1999).

Although other parks played a role, translocations of bison and elk from Yellowstone were the most influential within the U.S. By 1900, Yellowstone was home to the only free-ranging population of bison in the U.S. All existing plains bison derive from that population and 5 captive herds labout 130 individuals [Halbert and Derr 2007]); the only plains bison that
have not shown genetic evidence of cross-breeding with domestic cattle are related to Yellowstone stock (Dratch and Gogan 2010). More than 13,500 live elk were shipped from Yellowstone to 38 states, Canada, and Mexico (Robbins et al. 1982). Elk from Yellowstone were even used to repopulate areas that are now considered core elk range (e.g., Estes Park, Colorado [Robbins et al. 1982]; the Cascade and Blue Mountains of Washington [Couch 1935]].

Impacts on park vegetation by growing ungulate populations led to a shifting of priorities, from restoration to population control, during the 1920s. Vegetation impacts are reviewed in the section on "Conservation of Ecological Communities." Deteriorating range conditions at Yellowstone were attributed to elk and bison, whereas those noted at Rocky Mountain and Mount Olympus National Monument (now Olympic National Park [Olympic]) were attributed to mule deer and/or elk (Wright and Thompson 1935).

Removals for purposes of range management began around 1925: the translocation of mule deer from the Yosemite Valley to the Tuolumne Drainage, where deer had been nearly eradicated to control hoof-and-mouth disease, was one early example that still served a conservation purpose (Wright and Thompson 1935). Elsewhere, however, ungulate populations were recovering. Interest in surplus animals was dwindling because there were few ranges not already overstocked with wildlife and domestic animals (Cahalane 1943). Matters were further complicated by the growth of park ungulate populations and concomitant increases in the numbers of animals removed. Changing emphasis from conservation and restoration of ungulate populations to range management was therefore accompanied by a change in methods, from live capture and translocation to either live capture and slaughter or shooting. For example, the NPS began killing significant numbers of Yellowstone bison in 1925 (Meagher and Meyer 1994, Pritchard 1999, National Research Council 2002) and reduced elk numbers by about $80 \%$ at Wind Cave by 1932 (Lovaas 1973). After 1935, most elk removed from

Yellowstone were removed by shooting on their winter range (Houston 1982).

The magnitude of removals and the number of parks involved continued to increase as ungulate populations increased within and outside of parks. Removals from Rocky Mountain began during 1944 with the removal of 301 elk and 113 deer (National Park Service 2008b). At Wind Cave, state employees deputized by the NPS shot approximately 1,000 elk during the winters of 1953 and 1954 (Lovaas 1973). Removal of elk from Yellowstone peaked in 1962, when more than 4,000 were shot (Houston 1982, Robbins et al. 1982).

Changing national sentiment led to suspension of elk shooting at Wind Cave after 1957 (Lovaas 1973). Shooting within Rocky Mountain was discontinued in 1962 in favor of a winter hunt outside of the park (National Park Service 2008b). Shooting was most controversial at Yellowstone, where opposition culminated in congressional hearings (U.S. Senate 1967) and a new park policy of natural regulation, or minimal human intervention in ecological processes (National Park Service 2000, National Research Council 2002). Natural regulation ultimately became a national policy (National Park Service 1988, Soukup et al. 1999).

Natural regulation suggests that dynamics of park ungulate populations are influenced primarily by natural ecological processes that lead to predictable outcomes in the absence of human intervention. In fact, few experts expected natural processes to prevent elk populations from increasing in Yellowstone (Schullery 1997, National Research Council 2002, Sellars 2009), much less in smaller parks with less-complete assemblages of predators and prey.

Increasing populations meant that progressively greater removals were considered necessary in a growing number of parks. Considerations included special concerns associated with: (1) control of non-native species (e.g., mountain goats [Oreamnos americanus] at Olympic [Houston et al. 1991]; non-
native deer at Pt. Reyes National Seashore [Gogan et al. 2001, National Park Service 2006b]; introduced mule deer and elk at Channel Islands National Park [Wakelee and Frisch 2010]; feral goats in Hawaii [National Park Service 2011a]), (2) responsibilities associated with reintroductions of native species by the NPS (e.g., elk at Theodore Roosevelt ) (National Park Service 2010a), and (3) responsibility for the welfare of captive herds (e.g., bison at Badlands, Theodore Roosevelt, Wind Cave, and other national parks) (National Park Service 2006c).

Management of overabundant white-tailed deer has become a pervasive concern, affecting more than 50 U.S. parks in the northeastern U.S. by 2005 (Leong and Decker 2005). Many eastern parks exemplify circumstances that make ungulate management a complex, multijurisdictional issue. For example, many are relatively small; consequently, ranges of park deer are particularly likely to encompass surrounding agricultural lands or residential areas (e.g., Storm et al. 1989, Underwood et al. 1994). Movements of ungulates across park boundaries contribute to the evolution of diverse, and sometimes conflicting, stakeholder interests (e.g., in depredation control, hunting, and animal welfare [Porter and Underwood 1999]].

Matters are further complicated when policies and objectives are not complementary. For example, the NPS cannot simultaneously promote natural ecological processes and maintain the historical appearance of important cultural sites when the latter resulted primarily from human activity (Underwood and Porter 1997). Removals of white-tailed deer for purposes of population control have occurred at Gettysburg, Cuyahoga Valley National Park in Ohio (National Park Service 2006a), Catoctin Mountain Park in Maryland (National Park Service 2008a), Valley Forge in Pennsylvania (National Park Service 2009b), Rock Creek Park in the District of Columbia (National Park Service 2009c), and Indiana Dunes National Lakeshore (National Park Service 2009a).
Valley Forge provides a recent example of how eastern parks might engage reductions
of deer populations (National Park Service 2007a). Monitoring efforts showed no population regeneration occurring outside of deer exclosures beginning in 1995. An EIS completed at Valley Forge in 2008 stated the intent to reduce the deer population to support long-term preservation of native vegetation and to respond to a broader concern about CWD. Measurable target metrics included desired densities of deer and population regeneration. These targets were based on previous research and guidelines of the Pennsylvania Bureau of Forestry. The park plan built on the experience at Gettysburg and established a science team to oversee management that included the Pennsylvania Game Commission. Although Friends of Animals sued to prevent lethal removal of animals, the courts upheld the NPS management plans. Beginning in 2010, Wildlife Services removed 600 deer over 16 nights, donated more than $8,100 \mathrm{~kg}$ of deer meat to food banks, and tested 271 animals for CWDall were negative. The plan explicitly stated an adaptive management approach to the process and an independent, third-party observer commended NPS and Wildlife Services for their professionalism (National Park Service 2011b).

It is not clear that NPS can replicate Valley Forge successes in other parks. Leong and Decker (2005) interviewed 32 NPS resource managers throughout the northeastern U.S. They concluded that effective deer management in eastern parks requires an understanding of the uniqueness of each management environment, internal coordination, coordination with external stakeholders, effective planning efforts, and the availability of resources for staff and activities. Park managers are ultimately vested with decision making power (Leong and Decker 2005), so the ability of local managers to address these requirements is critical to deer management success in national parks.

The first challenge that superintendents face is having sufficient staff resources. Leong and Decker (2005) identified 3 elements crucial to planning for deer management:

1. Defining management objectives within the social and political, as well as ecological and economic, environment of the park,
2. Coordinating management within NPS, and
3. Coordinating management with external partners and constituencies.

Two essential planning points include defining impacts in clear and measureable terms and having a general management plan that includes deer. Communicating and coordinating planning for deer management with external partners and the many interest groups that emerge when deer management is proposed requires significant resource commitment by parks. Most of these duties are more appropriate for resource managers than for interpretive or enforcement staff. Although NPS regional and national offices offer assistance in planning and monitoring, and spearhead preparation of EIS, the coordination of all of this requires significant onsite individual attention. In parks like Gettysburg and Valley Forge that have resource managers, the planning and monitoring required years to put into place.

Although shooting was the predominant method of removal during the latter half of the 20th century, removal of live bison and elk from certain western parks (e.g., Badlands, Wind Cave, and Theodore Roosevelt) was a prominent exception made possible by: (1) open terrain that facilitated drive trapping and efficient handling of large numbers of animals, (2) demand for captive bison, and (3) renewed interest in the reintroduction of elk to unoccupied historical ranges, particularly in the eastern U.S. Such translocations enjoyed popular support and costs were typically borne by the agencies or organizations that received animals.

General Principles. - Removals of ungulates from national parks have been controversial, and much of the debate has revolved around removal methods. However, the methods are demographically
equivalent: effects on abundance and population composition depend only on the age structure, gender, and geographic distribution of removals. Moreover, removals that are representative of population composition and distribution reduce population density without directly affecting population structure.

Selective removals based on such factors as age, gender, distribution, or behavior affect population structure in ways that may serve strategic purposes. For example, adult females with relatively high reproductive value have been targeted to maximize effects on population growth rates; resultant effects on sex ratios were mitigated by preferential extrapark hunting of males (Frost et al. 1997, National Park Service 2010b). Spatially structured removals may be indicated when population subsets are not subject to the same controls le.g., extra-park hunting) or do not cause the same concerns (e.g., depredations, threats to public safety), and may minimize effects on extra-park ungulate hunting or viewing. For example, extra-park hunting was the leading cause of mortality for elk at Wind Cave (Sargeant et al. 2011), but elk residing in eastern reaches of the park rarely left and were effectively protected (National Park Service 2009d). At Banff since 2007, Parks Canada has focused removal efforts on the most habituated elk, resulting in measurable reduction in elk-human conflicts and an increase in the proportion of wary and migratory elk (J. Whittington, Parks Canada, personal communication).

In principle, an increasing population density will lead to competition for forage and induce compensatory reductions in survival. However, dietary and behavioral flexibility may enable ungulates to temporarily overcome these pressures. For example, density dependence was not evident for deer at Gettysburg and elk at Theodore Roosevelt (Frost et al. 1997, Palmer et al. 1997, Niewinski et al. 2006, Sargeant and Oehler 2007). Depensatory responses to population reductions are even possible. At Yellowstone, for example, survival of
adult elk declined with elk numbers because wolves maintained high kill rates and increasing proportions of the population were harvested by hunters outside of the park (White and Garrott 2005).

Implementation. - Two general classes of methodslive capture and shooting-have been used to remove ungulates from parks. Although these methods are demographically equivalent, details of implementation have often been controversial. Feasibility, costs, animal welfare, safety, and opportunities for disposal of animals have been critical considerations. Social acceptance and agency policy may impose additional limits; a method may be practical, economical, and humane, yet excluded from consideration by factors such as enabling legislation or public opposition.

Methods used to live-capture free-ranging ungulates target either individuals or groups. Techniques in the former class include net gunning, foot snaring, and chemical immobilization. The latter class includes methods such as drive traps and drop nets. Both classes have been used widely in national parks. However, capture of individual animals is labor intensive, so it has been used primarily for research and not on scales commensurate with population control. Removals of mountain goats from Olympic during the 1980s were a prominent exception, accomplished primarily via foot snares ( $n=233$ ), chemical immobilization ( $n=135$ ), and net gunning ( $n=69$ ), although drop nets also were used ( $n=182$ ). Operations were suspended in 1990 because live capture, though effective, was judged to pose unacceptable risks to personnel (Houston et al. 1994).

Group capture methods are of notable interest primarily because they have been used to expeditiously capture large proportions of bison or elk inhabiting several parks. For example, Theodore Roosevelt and Wind Cave currently use helicopters to herd bison into corral traps for translocation (National Park Service 2006c). Similar methods were used for elk prior to 2002, when cervid
translocations from the parks were suspended because of CWD.

During gathers, bison and elk have gradually been herded and directed by wing fences into corral systems modeled after livestock handling facilities. During 2009 to 2010, operational costs laircraft services, salaries, veterinary services, and supplies) averaged $\$ 125$ for 298 bison (approximately $92 \%$ of the population) captured in the North Unit of Theodore Roosevelt and \$185 for 277 bison (approximately $70 \%$ of the population) at Wind Cave. Gathers typically are accomplished in 2 to 4 days (M. W. Oehler, National Park Service, personal communication).

The efficiency of operations at Theodore Roosevelt and Wind Cave reflects the gregarious nature and tractability of bison and elk and has been facilitated by relatively open park landscapes. More generally, the time and effort required to capture ungulates varies among methods and species and is likely to depend strongly on factors such as animal abundance, habituation, density of vegetation, and ruggedness of topography. For example, costs of using drop nets to capture mountain goats in Olympic rose steeply, from approximately $\$ 400$ per goat in 1981 to $\$ 700$ per goat by 1984 , as densities were reduced and survivors became more dispersed and evasive (Houston et al. 1994).

Marginal costs (i.e., those above and beyond the costs of daily operation) also depend on factors such as agency policies and practices, staff availability, and the availability of existing infrastructure. The relatively low cost of capturing bison and elk at Theodore Roosevelt and Wind Cave, for example, would be much greater if it included full costs of administration and capture/handling infrastructure.

Live capture followed by humane destruction may be appropriate and expedient when disease or other circumstances preclude translocation. Capture and handling also pose variable and sometimes substantial risks of injury and death to the animals.

These risks tend to be much greater for some species than others. For example, direct drive trap mortality of bison and elk has been limited at Theodore Roosevelt and Wind Cave, but risks to elk increase substantially with handling time. In 1993, $16 \%$ of 176 elk captured at Theodore Roosevelt and quarantined for 90 days died prior to translocation. In contrast, only $1 \%$ of 298 elk captured and held for more than 11 days died in 2000 (National Park Service 2010a).

Hazardous environments and circumstances that require physical restraint, chemical immobilization, or extended handling periods may also elevate risks. At Olympic, for example, capture-related mortality of mountain goats increased from $9 \%$ to $19 \%$ when capture sites included more difficult terrain. Mortality resulted primarily from falls sustained during drug induction or when animals were netted (Houston et al. 1994). In some instances, effects of capture-related stress may not be immediately evident and may lead to increased risk of mortality after animals, particularly white-tailed deer, have been released (Spraker 1993, Beringer et al. 1996, Haulton et al. 2001). Translocation to unfamiliar surroundings may also dramatically increase risks of death from such causes as vehicle accidents and hunting (O'Bryan and McCullough 1985, Jones and Witham 1990, Beringer et al. 2002). Human tolerance and habitat suitability are now the primary factors limiting ungulate relocation. Awareness has grown of potential adverse consequences, particularly transmission of diseases and parasites, which likely will lead to even greater scrutiny of future translocations.

Most ungulate removals from U.S. national parks have been accomplished by shooting. Shooting free-ranging ungulates resolves several substantial limitations of live capture and translocation by eliminating capture and handling stress, the need to find relocation sites, and risks of spreading diseases or parasites. Stakeholders often perceive shooting to be less humane than live capture and translocation, and this perception has at times presented
challenges associated with public acceptance (Stout 1997). However, the preceding discussion of capture-related injuries and post-capture mortality highlights the fact that live capture is not without impacts on animal welfare.

Public involvement in shooting has been controversial (Pritchard 1999) but has largely been decided by NPS policies that currently do not allow hunting of native wildlife in national parks per se. However, the NPS can authorize hunting in other types of park units, such as national seashores and national preserves. Some enabling legislation specifically permits hunting as a park activity. For example, legislation that created Apostle Islands National Lakeshore directs park management to permit hunting, fishing, and trapping in accordance with appropriate state and federal laws (National Park Service 2007b).

Although recreational hunting is not allowed, NPS has used the public as volunteer shooters. In such instances, the volunteers do not get to keep the carcass of the harvested animal; instead, they are typically donated for the benefit of local entities. Contemporary examples include Grand Teton where enabling legislation provided for the use of licensed hunters to carry out population reduction programs, and Theodore Roosevelt where volunteers and park staff removed more than 800 elk during 2010 to 2012. Volunteer shooters supervised by NPS staff also removed feral goats from Hawai'i Volcanoes National Park (National Park Service 2011a) and elk from Rocky Mountain (National Park Service 2008b). Alternatives to public involvement have included shooting by employees of state or federal agencies le.g., elk at Wind Cave during the 1950s, white-tailed deer recently at Gettysburg and Valley Forge), and by NPS staff (e.g., elk at Yellowstone prior to 1967).

Costs of shooting programs depend on costs of administration, payments to shooters, logistic challenges, methods of carcass disposal, and degree of supervision by park management. In principle at least, shooting programs modeled after public hunting programs (i.e., volunteer shooters pay a
modest fee, are not directly supervised, and retain carcasses for personal use) could be self-sustaining. In practice, however, costs are variable. The cost of shooting white-tailed deer at Gettysburg by NPS personnel ranged from $\$ 88$ per animal ( $n=503$ deer) to $\$ 128$ per animal ( $n=355$ deer) during 1995 to 1997. However, these figures reflect more than 600 hours of assistance from volunteers (Frost et al. 1997). At Theodore Roosevelt, NPS staff and staff-supervised volunteers shot 868 elk during 2010 to 2012 for an average cost of $\$ 935$ per elk (National Park Service, Theodore Roosevelt, unpublished data). The much greater costs of removing elk at Theodore Roosevelt reflect both greater personnel costs associated with supervision of volunteers and greater costs of locating animals and removing carcasses.

Disposal of ungulate carcasses is an important component of any shooting program. To date, carcasses removed from U.S. national parks have been used principally for human consumption. Other options include leaving carcasses in place as carrion, using carcasses for animal feed, burial, or incineration. Numbers of carcasses involved and risks of disease transmission are key considerations that may affect selection of methods in the future.

Traditional Hunting. - Traditional recreational hunting generally is not practiced in U.S. and Canadian national parks. Exceptions in Canada include issuance of an order-in-council that allows hunting within a park (e.g., Pele National Park annual duck hunt during 1918 to 1989), and designated management situations that are designed to maintain ecological integrity (e.g., moose hunting in Gross Morne in 2010 to 2011). Within the U.S., the congressionally mandated elk reduction at Grand Teton uses licensed volunteer hunters deputized by NPS during the reduction. Within Canada, hunting is allowed for First Nations hunting on traditional grounds in many newly established national parks (e.g., Wood Buffalo). National parks in Alaska are governed largely by the Alaska Native Claims Act, and activities there are not typical of the remaining states.

Hunting is typically allowed on most other types of NPS units including seashores, recreation areas, scenic rivers, preserves, and monuments. Approximately $29 \%$ of NPS lands in the contiguous U.S. and $92 \%$ in Alaska is open to public hunting. In some NPS units, traditional hunting has been effective in controlling ungulate populations. Examples include both sport and subsistence hunting for moose and caribou in many parks and preserves in Alaska including Denali, Noatak, Gates of the Arctic National Park and Preserve, and Lake Clark. Eastern and Midwestern seashores and lakeshores such as Cape Cod, Cumberland Island, and Apostle Islands allow hunting of white-tailed deer under both NPS and state regulations. In these situations the harvest has precluded or limited (e.g., Apostle Islands) the need for alternative methods such as culling or immunocontraception to control white-tailed deer populations.

Hunting in U.S. national parks has been controversial. In the Organic Act of 1916, Congress declared that NPS "shall promote and regulate the use of the Federal areas known as National Parks ... to conform to the fundamental purpose of said parks ..., which purpose is to conserve the scenery and the natural and historic objects and the wild life <sic> therein and to provide for enjoyment ... by such means as will leave them unimpaired for ... future generations" (16 USC 1). Controversy has centered on interpretation and implications of the term "unimpaired." As will be detailed later in this document, ungulates have significantly impacted fauna, flora, and their associated ecological processes. The Organic Act makes no direct statements about whether or how hunting should occur in lands managed by NPS; rather, it has been subject to both court and agency interpretation over the past 95 years.

Current NPS policy states that: (1) "hunting shall be allowed in park areas where such activity is specifically mandated by Federal statutory law" and that (2) "Hunting may be allowed in parks where such activity is specifically authorized as a discretionary activity under Federal statutory law
if the superintendent determines that such activity is consistent with public safety and enjoyment, and sound resource management principles" (Code of Federal Regulations 2012). Basically, it states that hunting will be allowed only when Congress specifically takes action to affirm those activities. Although this particular federal regulation is fundamentally different from those used by the U.S. Forest Service, Bureau of Land Management, or Fish and Wildlife Service, legal action by the National Rifle Association to overturn it was dismissed by the U.S. District Court for the District of Columbia in 1986 (No.84-1348 Civil Action).

Traditional hunting, and possibly shooting programs, may impact the behavior of animals habituated to non-threatening human activity in national parks. Human habituation takes place when a wild animal becomes accustomed to what it perceives as nonthreatening human disturbances in its habitat. The degree of habituation can vary based on factors including variability in the behavior of individual animals or populations, species, location or type of disturbance, and the size of the group experiencing the disturbance. For example, in Yellowstone National Park, bison are nearly three times less likely to respond to human disturbances than elk (Borkowski et al. 2006). However, the degree of response to disturbances is similar-and increased at similar rates-among elk and bison when certain factors occurred. For example, if bison encounter humans on or near roads, they have a more severe response (i.e. fleeing and/or defensive behaviors) than if the encounter took place away from humanfrequented areas. In addition, Yellowstone bison and elk are less likely to respond negatively to the presence of humans in vehicles. However, when a person dismounts his vehicle, the animals are more likely to respond negatively (Borkowski et al. 2006).

Hunting also plays a variable role in the habituation of ungulates. For example, "the impact of hunting activity (when seasonal) on ungulates may vary depending on the level of exposure to humans in a non-threatening recreational context" (Stankowich
2008). Despite the vast number of factors that can alter an animal's level of habituation, flight responses in animals generally decrease in the presence of more dense human populations (Stankowich 2008).

Urban/Suburban Deer Management. - Wildlife managers have been challenged with the responsibility of managing white-tailed deer in urban and suburban areas for decades. Early research indicated a reluctance to implement lethal management techniques (Decker and Gavin 1987, Cornicelli et al. 1993). However, expansion of deer populations and their impacts have shifted stakeholder attitudes to one of general support for lethal techniques (Kilpatrick and LaBonte 2003, Fulton et al. 2004, Siemer et al. 2004, Stewart 2011).

Public safety and conflicts with other uses were initial concerns about hunting deer in urban/ suburban areas (Hansen and Beringer 1997). Although of obvious importance, the issue of public safety has been addressed thoroughly, and the literature addresses how to implement lethal control both safely and effectively (see Hansen and Beringer 1997, Kilpatrick and Walter 1999, Doerr et al. 2001 for a few examples). Typically, perceived safety concerns are addressed by more stringent shooting proficiency or additional oversight of hunters (Hansen and Beringer 1997, Kilpatrick et al. 1997, Kilpatrick and Walter 1999, Bies 2011). In a survey of state deer biologists, $85 \%$ ( 41 states surveyed) used managed archery hunts in urban and suburban areas (Urbanek et al. 2011). We can conclude that the use of hunting by a vast majority of state agencies (and indeed local units of government) would not be so widespread and prevalent were it not a safe and effective method in urban and suburban environments.

## Fertility Control

Opinions vary widely regarding when and how deer and elk populations should be controlled, with some ethical debate over the relative humaneness
of non-action compared to non-lethal and lethal approaches to population control. The general public perceives fertility control as more humane and morally acceptable than conventional methods of population control because it reduces birth rates instead of increasing mortality rates (Fagerstone et al. 2010). However, at Banff, Parks Canada found that stakeholders and the public clearly preferred humanely killing elk instead of fertility control (J. Whittington, Parks Canada, personal communication). Porton (2005) discussed the ethics of employing a decision-making process that includes determining which animals are the objects of concern-the animals that are lethally removed versus the remaining animals that benefit from the removal. All else being equal, if lethal removal and fertility control are similarly effective means of population control, yet fertility control uses financial resources that could otherwise be spent on activities that improve the wellbeing of the remaining animals, then which group of animals should have priority in the decision making process (Porton 2005)?

Asa and Porton (2005) reviewed reproductive control processes and the animal tissues that are targeted by various contraceptive methods. Most of the currently available chemical contraceptive methods interfere with the sequence of hormone production or release in order to control or impede specific reproductive events or processes (e.g., ovulation, spermatogenesis, fertilization, implantation).

Methods that employ steroids, such as estrogen and estrogen-progestin combinations, were investigated widely during the early years of contraception research (Fagerstone et al. 2010). More recently, norgestomet (progesterone approved for use in cattle) delivered in bio-bullets eliminated estrus behavior in 10 treated female black-tailed deer for one breeding season (Jacobsen et al. 1995) and inhibited breeding in 56 of 58 (97\%) female whitetailed deer for one breeding season (DeNicola et al. 1997). Food additives are effective at contraception under controlled conditions but are not applicable to field conditions for several reasons. Fagerstone and others (2010) concluded that use of steroid-hormone
based contraception in field situations requires repetitive application because the contraceptive is effective for only a short period of time, and also has some unsatisfactory food chain issues.

The future of contraception for deer and elk likely lies in development of long-lasting immuncontraceptive vaccines. Such vaccines use the animal's own immune system to produce antibodies against reproductive hormones or proteins on the egg or sperm (Fagerstone et al. 2010). A single dose of SpayVacTM immunocontraceptive vaccine, which contains porcine ZP encapsulated in liposomes, maintained high antibody titers and contraception in 41 female fallow deer (Dama dama) through 3 breeding seasons compared to the typical single year of effectiveness observed with other vaccines. Similarly, a shorter duration study of white-tailed deer showed that SpayVacTM immunocontraceptive vaccine, when inoculated only 30 days prior to the breeding season, provided complete contraception for 1 to 2 years (Locke et al. 2007). Fawns per female white-tailed deer treated with another variation of ZP vaccine averaged 0.17-0.34 compared to 0.691.08 for untreated females (Rutberg et al. 2004). With treatment of up to $90 \%$ of white-tailed deer on a 233ha study site, the population declined by an average of $7.9 \%$ per year, and rates of decline were even higher in following years when a higher proportion of females were treated (Rutberg et al. 2004). A disadvantage of porcine ZP immunocontraception (PZP), however, is that it causes vaccinated females to go through multiple estrus periods (Gray and Cameron 2010), which also stresses males because it causes them to endure an extended rutting season. PZP may also lead to late conception if antibody titers drop low enough, with subsequent stressful implications on the dam and her late-born fawns or calves.

The other main type of immunocontraceptive vaccine developed for use on deer and elk targets GnRH, a hormone that directly controls mammalian reproduction from its initiation in the brain (Fagerstone et al. 2010). Eliminating the stimulatory effects of GnRH causes a temporary non-surgical
castration in both males and females that lasts 1 to 4 years, depending on the dose given (Miller et al. 2004). An early study of the vaccine showed an $88 \%$ reduction in fawning by white-tailed deer. Effects from a newer formulation lasted 3 years in female elk, with efficacy generally declining over time (Powers 2011). The GnRH vaccine inhibits reproductive activity in general, which eliminates behavioral and stress-related problems associated with multiple estruses and the extended breeding seasons shown with ZP immunocontraception (Miller et al. 2004).

Gray and Cameron (2010) emphasized the urgent need to evaluate two potential evolutionary-level impacts of immunocontraception. The more significant issue is that immunocontraceptives may select for immuno-compromised individuals, because the treated animals that breed likely have a lower immune response to the contraceptive. Thus, successful breeders would produce offspring with a reduced immunological ability to fight off normal diseases. Another potential problem is the possible development of genetic resistance, similar to the response observed with other biological control agents.

The duration of the effectiveness of immunocontraceptives and the number of doses required for effectiveness limit field application. However, recent changes in the biochemical composition of vaccines have increased immunogenic capability (i.e., the ability to stimulate antibody production), allowing long-term effectiveness to be obtained with a single dose in white-tailed deer and elk (Gionfriddo et al. 2009, Miller et al. 2009, Powers 2011). A single vaccination against GnRH decreased subsequent pregnancy rates in adult female elk for 3 years post-treatment, and effectiveness declined from a high of $90 \%$ in year 1 to 12\% in year 4 (Powers 2011). Results with white-tailed deer have varied with different vaccine combinations. Some single-injection PZP vaccines combinations provided contraception rates of $80 \%$ for 5 years (Miller et al. 2009), but GonaCon Immunocontraceptive Vaccine Ithe commercial
name for a GnRH-based emulsion) decreased in effectiveness from $88 \%$ in year 1 to $47 \%$ in year 2 (Gionfriddo et al. 2009). Two long-term studies using PZP showed that contraception can reduce population size significantly.

Despite such studies, the usefulness of immunocontraceptives as a management tool depends on efficacy of the vaccine, accessibility of deer for treatment, and site-specific birth, death, immigration, and emigration rates (Rutberg and Naugle 2008). One logistical limitation is that, for long-lived species, many years must pass before natural mortality results in population density declines, unless mortality is artificially increased by lethal removal. Additionally, some hormone-based contraceptives have deleterious side effects such as cancer and other health-related concerns (Hutchins 2005).

Making general statements regarding the cost effectiveness of fertility management is difficult, because so many site-specific factors enter into the equation, especially accessibility of deer for treatment and local demographics (Rudolph et al. 2000). Depending on the contraceptive, the delivery system, and the accounting system used to calculate costs, estimates of contraceptive costs vary from $\$ 25$ to $\$ 500$, with much of the cost associated with personnel (Rutberg 2005, cited in Kirkpatrick 2007). Costs of reducing deer and elk populations by means of public hunting, which supplies free labor from hunters and potential revenue from license fees, will generally be more fiscally attractive than any contraceptive alternative (Kirkpatrick 2007). However, Kirkpatrick (2007) emphasized that monetary costs should always be compared to the full costs of actual alternative management strategies.

A briefing paper described recent NPS actions regarding fertility control with elk and deer (National Park Service 2010b). Fertility control is allowed by NPS Management Policies 2006 (Section 4.4.2.1) and Director's Order 77-4 and has been considered at numerous NPS facilities.

It has been used, however, only on native species on an experimental basis, on tule elk at Point $R$ eyes, and on white-tailed deer at Fire Island. Nonnative deer eradication at Point Reyes includes use of the GnRH immunocontraceptive GonaCon. A long-term evaluation project using GonaCon on female elk began in January 2008 at Rocky Mountain and ended in 2011.

## Predator Management

Extensive evidence exists to support the role of predators in limiting ungulate prey species (Gasaway et al.1983, 1992, Messier 1994, Ripple and Van Valkenburgh 2010). However, herbivore biomass will remain constant in the presence of carnivores only in systems where carnivores are present in adequate numbers to affect prey population dynamics (Wang et al. 2009). Predation by black bears (Ursus americanus), brown bears, cougars, and wolves have reduced populations of ungulates. Coyote (Canis latrans) predation can greatly reduce survival rates of white-tailed deer, but the facultative nature of their food habits make accurate predictions of impacts difficult in different regions or over time (Ballard 2011). High and additive neonatal mortality may occur even if productivity is high when predators are abundant, or when severe winter conditions or prolonged summer drought occurs (Ballard et al. 2001, Adams et al. 1995, Boertje et al. 2006).

Restoration of extant mammalian predators to national parks has been proposed as a management alternative to alleviate problems associated with ungulate overpopulation (Licht et al. 2010). However, a basic problem in restoring or maintaining larger mammalian predators in the national parks is that none of the parks in the lower 48 states is large enough to contain a viable predator population. Adjacent lands will have to be occupied by these predators if viable reproducing populations are the goal. Additionally, most national parks are not large enough to maintain naturally existing populations of these species at levels needed to exert the necessary pressures on ungulate prey to cause ecosystem
change. The unique case of Isle Royale illustrates how a small park of 544 km 2 where the moose population, though preyed on by wolves, is still able to alter vegetative composition to a less natural state (McLaren and Peterson 1994).

Fencing the national parks to prevent escape of large predators would be expensive and not likely tolerated by the public (Mech et al. 2010). Trimble and van Aarde (2010) reported serious ecological concerns over the fencing of Kruger National Park in South Africa, including influencing natural mechanisms of population control, restriction of animal movements in response to environmental changes such as fires and drought, and limitation of migration and genetic flow. Establishment of small populations of predators in a national park with the intent of intensively managing them and not restoring ecosystem processes may be feasible.

National parks serve as protected areas that are sources for expansion of populations to areas outside their boundaries. In areas where suitable habitat occurs outside, this can be a means to restore predators to areas where other means of restoring them are limited or absent. The expanding populations of wolves and grizzly bears from Yellowstone, Grand Teton, and Glacier exist within matrices of wilderness areas, national forests, and otherwise undeveloped lands. The expansion of Yellowstone grizzly bears outside of the park is the outstanding example (Schwartz et al. 2006). The reappearance of the black bear in Big Bend National Park from adjacent Mexico is another example. Wolves established outside Yellowstone and Glacier affect the number and distribution of elk, and depredate livestock. All of this was anticipated in the environmental assessments of the restoration effort (U.S. Fish and Wildlife Service et al. 2010). Similar experiences are documented for naturally restored predators at Banff (Hebblewhite et al. 2002, 2005).

Small populations of ungulates can be particularly vulnerable to reductions in numbers by predation. Isolated, small populations of desert bighorn sheep have been subject to heavy predation by cougars
in the past two decades, due to prolonged drought and reductions in mule deer populations (Kamler et al. 2002, Hall et al. 2004, Rominger et al. 2004, Bender and Weisenberger 2005, McKinney et al. 2006,). The ability of cougars to switch prey to domestic livestock, especially calves, and to bighorn sheep when mule deer populations decline, may explain declines in bighorn sheep in the 1990s (Kamler et al. 2002). Historically, cougar predation on bighorn sheep may have fluctuated along with changes in mule deer populations (Kamler et al. 2002), but predation on small isolated populations could significantly reduce numbers to levels that could jeopardize population persistence and require reductions in cougar numbers (Wehausen 1996). Provision of artificial water in sustaining both cougars and deer was also a factor in Arizona (Cain et al. 2008).

## Redistribution

Redistribution of animals involves their physical relocation by any one of several methods that vary in scale and intensity. The smallest scale alternatives include hazing of animals to keep them away from a specific site and diversion of animals away from areas of conflict by attracting them to an alternative site with supplemental feed. A potentially larger scale includes fencing to constrain animal access to certain areas. Still larger would include range expansion to allow additional population growth. Lastly, the most extreme scale for redistribution involves trans-locating animals to an entirely different location.

Hazing involves exploiting an animal's tendency to avoid areas with a perceived greater risk, typically accomplished using fear-provoking stimuli. Visual, auditory, and olfactory stimuli are most commonly used, and efficacy is improved by combining these methods. The main problem with fear-provoking stimuli is that animals soon learn that they pose no real threat and they become habituated to the stimuli. Thus, hazing is applicable only when redistribution is needed for a short period of several
days (Conover 2002). For example, hazing is included as part of a management alternative to facilitate movement of an appropriate number of elk off Wind Cave to make them susceptible to hunting mortality. Directed hazing at Wind Cave prior to the use of helicopters failed as a population control measure (Lovaas 1973). Experimental hazing of elk that were habituated to humans within Banff, through the use of humans or dogs, showed that such treatments could temporarily modify aspects of the behavior of moderately habituated elk (Kloppers et al. 2005).

A diversion program provides an alternative food source so that problem animals will consume the alternate food in lieu of an affected crop. The primary diversionary program for elk or white-tailed deer involves supplemental feeding, particularly during winter. Deer and elk respond to supplemental feed in a variety of ways, all of which tend to artificially increase density in the area where the food is offered (Conover 2002). For example, availability of supplemental feed within a 250-ha enclosure in Michigan increased reproductive rates that led to a 7 -fold increase in the density of whitetailed deer (Ozoga and Verme 1982). The increased population density makes diversion the least suited alternative for long-term problems that occur during a season when forage supplies are limited (Conover 2002). Greater density and frequency of animal-to-animal contact associated with supplemental feeding programs can increase infectious disease transmission in a population (Inslerman et al. 2006). For example, elk using winter supplemental feeding grounds in Wyoming have an average prevalence rate of brucellosis antibody titers that is 10 to 15 times higher than elk wintering on their native range (Dean et al. 2004).

The Wildlife Society's position statement, "Baiting and Supplemental Feeding of Game Wildlife Species," states that the practice of supplemental feeding should be evaluated carefully because it is often detrimental to wildlife resources. The Society's position includes encouraging fish and wildlife agencies to phase out supplemental feeding of wild ungulate populations and to manage populations
at levels compatible with the long-term carrying capacity of the habitat. Supplemental feeding of elk at Yellowstone was debated by leading conservationists in the early 1900s (Wolfe et al. 2002). Maintenance of artificially high elk densities by winter feeding at the National Elk Refuge may have led to habitat deterioration of summer range in Grand Teton and the southern part of Yellowstone (Beetle 1979, cited in Wolfe et al. 2002).

Fencing can be used to exclude deer or elk from access to alternative locations, although this approach generates several issues. A TWS technical review details the pros and cons of fencing as a management tool for ungulates (Demarais et al. 2002). When a wild ungulate is confined by the construction of a high fence, normal movement patterns including migration and dispersal are restricted, and exclusion from critical habitat types may impact population demographics and welfare. Increased disease susceptibility can be an important issue when wild ungulates are confined, especially under abnormally high confinement densities and the presence of supplemental feeding and watering structures (Samuel and Demarais 1993). Patterns of genetic variation may be altered by confinement as a consequence of altering the breeding structure, constricting the reservoir of genetic variation in the population, and blocking the infusion of new genetic material (Demarais et al. 2002).

The South Unit of Theodore Roosevelt is surrounded by a woven-wire fence just over 2 m high, but numerous naturally and specially designed crossings allow for movement of most wildlife, including elk (National Park Service 2010a). Wind Cave includes 11,450 ha that are enclosed by 2 to $2.5-\mathrm{m}$ high fencing with several gates that can be opened to encourage movement. Part of the preferred management plan at Wind Cave involves allowing some elk to leave the park during their normal spring movements and preventing their early fall return using supplemental fencing; these excluded elk would then be susceptible to hunting mortality on adjacent lands (National Park Service 2008c).

Range expansion is a short-term solution to overpopulation or may be used to resolve a specific deficiency in a habitat component le.g., when critical wintering habitat is not available on the original property). As a solution to overpopulation, range expansion has the same problem as supplemental feeding; overpopulation is alleviated only until the population grows and fills the new space to an equally overpopulated condition. Expansion of boundaries has been used several times to accommodate growing elk populations on NPS lands. The size of Wind Cave was more than doubled in 1946 to provide enough land to maintain viable populations of large mammals, and Grand Teton was enlarged in 1950 in part to accommodate increasing elk populations (Wolfe et al. 2002). Enlargement of boundaries was a strategy for Yellowstone during the 1920s, along with "killing predatory animals" and "feeding when necessary" (U.S. Department of the Interior 1917, cited in Wolfe et al. 2002).

Translocation of ungulates from national park lands has helped control densities within parks and has allowed ungulate reestablishment in previously extirpated areas. For example, from 1912 to 1967, more than 13,500 elk were trans-located from Yellowstone to 38 states, Canada, and Mexico (Robbins et al. 1982). Relocation of excess whitetailed deer is not a feasible option because potential relocation sites are already at carrying capacity (Asa and Porton 2005). Elk restoration projects continued into the 2000s in the eastern U.S. using western, non-NPS source populations, but a stringent health protocol was followed to minimize the potential for transfer of high-risk infectious agents such as CWD and bovine tuberculosis.

# Criteria for Selection of Management Strategies 

## Enabling Legislation, Historical Context, and Naturalness

The general topic of enabling legislation and the ways that it affects ungulate management in national parks in Canada and the U.S. is reviewed in the "Purposes of National Parks" section. Many areas managed by NPS and Parks Canada had enabling legislation that identified generally, and at times specifically, the activities allowed or forbidden on the property.

Gettysburg exemplifies the complexities encountered in addressing overabundant ungulate populations on historical and cultural sites that were established primarily for reasons other than natural resource conservation. Enabling legislation prohibited hunting or discharge of firearms within the park boundaries. Although deer were not present at the time of Gettysburg's creation, deer became a threat to vegetation regeneration by the 1980s. Lack of regeneration was problematic, because legislation mandated that the park be kept in the same condition as it existed during the Battle of Gettysburg in 1863 (Frost et al 1997, Storm et al. 1989, Vecellio et al. 1994). Other control measures were needed, because of the prohibition of recreational hunting by enabling legislation and the surrounding landscape matrix of suburban and commercial developments. After extensive public input and opposition, managers initiated a sharpshooting program to reduce the deer population. These problems are not unique to Gettysburg; similar issues surround overabundant
deer populations at Saratoga, Morristown, and Valley Forge national historical parks and numerous other parks in Canada and the U.S.

Discussion of the naturalness context of national parks can be exemplified by the creation of Yellowstone in 1876. Wright (1992) summarized the likely intent of the Yellowstone designation as being driven by a desire to preserve the "unique scenic wonders of the region, including the great geyser basins and the Grand Canyon of the Yellowstone River." The original act prohibited timber harvest and mining but did not afford protection to wildlife species. Wright (1992) posited that during this utilitarian time, there was no precedent for animal protection.

## Cost

All management strategies (e.g., culling, translocation, sterilization) involve complex interactions among NPS staff, the public, and the ungulate population in question. The long-term supporting data that must be collected prior to initiation of a planning process, the 3 to 5 year planning process required to develop management plans (as part of NEPA), and the inevitable lawsuits make the process costly, even before management actions are implemented (Leong and Decker 2005). The costs to implement ungulate management strategies on National Parks are significant and borne by taxpayers. Ultimately, those costs should represent a balance between the financial realities of declining budgets as measured against biological implications (Porter and Underwood 1999) and social considerations (Leong et al. 2006, Leong 2009).

The costs associated with ungulate population management in national parks vary widely by method. Given that the traditional method of managing ungulate populations (hunting) is generally not available, NPS has approached the problem by examining site-specific alternatives. For example, the Rocky Mountain elk reduction plan contained a range of management alternatives that included culling by NPS staff or volunteers and fertility control. The 20-year estimated costs of these alternatives ranged from $\$ 6.4$ million to $\$ 15.3$ million. Ultimately, NPS announced a plan to cull elk over a 20 -year period for an estimated $\$ 6$ million (Wildlife Management Institute 2009). Similarly, staff at Theodore Roosevelt examined several alternatives for a comparable problem and adopted the lowest cost alternative of using volunteer cullers. At Valley Forge, recurring deer management cost estimates ranged from a low of $\$ 56,000$ to $\$ 200,000$ for options that included lethal control to a high of $\$ 246,000$ to $\$ 1.16$ million for non-lethal actions (National Park Service 2009b).

Regulated hunting programs provide a costefficient method for state wildlife agencies to manage overabundant ungulate populations. Most agencies use hunting seasons and associated bag limits to keep ungulate populations in check both biologically and socially, and to generate revenue through license sales. Nationally, nearly 11 million individuals pursue big game and collectively spend an estimated $\$ 11.7$ billion dollars annually (U.S. Fish and Wildlife Service 2011). In urban areas, archery hunting is an alternative to firearm hunting and addresses public safety concerns (Messmer et al. 1997, Doerr et al. 2001).

Costs of hunting programs are highly influenced by the effort an agency puts into managing a program (e.g., oversight and supervision). Rural lands where firearm hunting is feasible could generate revenue from application and licensing fees; conversely, hunts that are staff-time intensive or require disease surveillance (e.g., CWD) would have increased costs. Properly structured hunting programs designed to
accomplish population objectives have the potential to bring in significant operating revenues while at the same time alleviating overabundance problems.

## Animal Welfare

Animal welfare and rights generate considerable concern among some stakeholders when considering ungulate management. Lawsuits based on animal welfare and rights temporarily halted management actions to control white-tailed deer on several NPS sites, most notably Valley Forge . A high deer population was threatening vegetation growth and regeneration in the park as well as in surrounding private lands (Lovallo and Tzilkowski 2003). The Valley Forge management plan called for significant reduction of the deer herd over a 4 -year period through use of trained sharpshooters. Opponents to herd reduction filed lawsuits to stop lethal control and suggested that natural methods, including coyotes, were sufficient to reduce the deer population, temporarily halting lethal control. After a federal judge rejected the last lawsuit, lethal control removed 600 deer between November 2010 and March 2011 (National Park Service 2011b).

## Allowable Land Use

Land use of national park lands is guided by enabling legislation for that unit or by policy guidelines. The NPS uses all available authorities to protect lands and resources within units of the NPS. The appropriate use of parks is embraced as a key to the enjoyment of the park system and is defined as "suitable, proper, or fitting for a particular park, or to a particular location within a park" (National Park Service 2006a). Any use must not have unacceptable impacts on park resources and values, and must not conflict with resource protection.

## Population Viability and Genetic Diversity

Bighorn sheep are among the most threatened ungulate on NPS lands. They inhabit fragmented landscapes, have low genetic heterozygosity (relative to other ungulates), and are highly vulnerable to diseases (e.g., pneumonia/lungworm complex). Populations throughout western national parks have declined through the 1990s and today exist at low numbers throughout their range. Although NPS management guidelines dictate restoration of native species, translocation projects are complex and expensive (Bleich 1990). Singer et al. (2000) provided an excellent review of a process to evaluate restoration of native bighorn populations. Indeed, the journal Restoration Ecology devoted an entire issue (volume 8[4S]) to the restoration of bighorn sheep populations.

Maintenance of genetic diversity is important for bison. Low levels of cattle introgression into bison herds have been reported, so conservation efforts should be focused on populations in which cattle genes have not been identified. Also, despite the fact that bison were nearly extirpated and current bison populations are small, no signs of inbreeding depression have been detected. Dratch and Gogan (2010) recommended attaining a metapopulation size of 1,000 animals or more with a sex ratio suitable for competition among breeding bulls, distributing remnant populations among a variety of sites, and developing more sophisticated techniques to measure bison genetics.

Mountain goats are a species of least concern, meaning they have a low risk of extirpation due to over-harvest or habitat loss or fragmentation (International Union for Conservation of Nature 2011). However, isolation of mountain goat populations has been reported in the Cascade region of Washington and throughout the fragmented mountain goat range, so genetic isolation and associated population reduction is possible (Shirk 2009).

## Depredation

Ungulates that inhabit NPS lands can cause landscape, agricultural, and livestock damage within surrounding properties. Well-documented problems are caused by elk at Rocky Mountain, Theodore Roosevelt, and Great Sand Dunes and by white-tailed deer throughout the eastern NPS units. Also notable are the conflicts between elk and bison in Grand Teton and Yellowstone. Both species have been implicated in spreading brucellosis to domestic cattle and causing agricultural losses on private land. At Grand Teton and the associated national elk refuge, a stakeholder-based process was undertaken collaboratively between NPS and the U.S. Fish and Wildlife Service to explore various EIS-based management alternatives. The resulting study highlighted the volatility of the issue and the disparity of opinions regarding how the populations should be managed (Koontz and Hoag 2005).

Ultimately, management of ungulates that spend a portion of their time on non-NPS lands falls under the jurisdiction of the relevant state agency. Typically, agencies manage depredation by focusing hunting efforts in areas where the problem occurs. However, this is not always effective because species become conditioned to avoid the areas of hunting pressure, thereby exacerbating the problem by redistributing themselves to other lands. At Theodore Roosevelt, elk avoided areas outside of the park during the hunting season (G. A. Sargeant, US Geological Survey, personal communication). The EIS for elk management at Theodore Roosevelt noted the interchange between NPS and other lands and the subsequent potential for depredation as populations increased (National Park Service 2010a). The NPS-preferred alternative of using volunteer shooters to reduce elk numbers in the park complements the state agency's attempts to modify hunt boundary and license numbers to reduce populations (and potential conflicts).

## Findings

nternal and external reviews of ungulate management in national parks during the 1980s and 1990s identified several issues. Needs included: clear management goals and objectives; use of explicit measures to objectively evaluate degradation of cultural or natural resources, including data on ungulate populations and vegetative communities; monitoring programs to measure change; and clearly articulated plans for reviewing and adapting management as new knowledge was gained.

Our review suggests NPS and Parks Canada are confronting these issues through leadership initiatives at the park, regional, and national levels. We offer the following findings:

## Biological

1. Natural regulation within most national parks is insufficient at controlling ungulate densities at levels that are compatible with preservation or restoration of native flora and fauna, natural processes, or historical landscapes. In such cases, controlled reduction programs may effectively reduce ungulate impacts.
2. Herbivory significantly influences vegetation as ungulate density approaches carrying capacity. Monitoring vegetation and ungulate populations using clear effectiveness measures can identify ecological consequences.
3. Flexible and adaptive ungulate management in the short- and long-term will be needed to account for imprecise population estimates and the dynamics of ungulate populations, park environments, and stakeholder interests.
4. Movement across park boundaries impacts both internal and external agency efforts to manage overpopulation.
5. Translocations have played a role in early efforts to restore ungulates to previously occupied national parks and regulate populations. However, significant disease, ecological and social implications, and habitat limitations complicate future translocations.

## Social

1. Substantial progress has been made in managing ungulate overpopulation. Consideration of shortand long-term costs aids evaluation of management alternatives. Involving state and provincial wildlife agencies and other federal land management agencies in the decision-making process facilitates development of cost-effective methods to reduce or control ungulate populations.
2. There is a wide range of opinions concerning ungulate management efforts in national parks, although typically these opinions have not been quantified scientifically during or after decisionmaking. Social science data is an important part of the decision-making process and provide a more valid representation of public opinion than open meetings and written comments.
3. Educational programs on the technical issues of ungulate management would aid decision-makers. Related programs explaining biological justifications and effectiveness of alternatives would allow the general public to provide informed input.
4. Well-informed specialists can provide critical input during management policies and practices development. Financial support is needed to provide technically-trained personnel to address management needs, including wildlife biologists for ecological issues and human-dimensions specialists for social science issues.

## Literature Cited

Adams, L. G., F. J. Singer, and B. W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584-594.

Aguirre, A. A., D. E. Hansen, E. E. Starkey, and R.G. Mclean. 1995. Serologic survey of wild cervids for potential disease agents in selected national parks in the United States. Preventive Veterinary Medicine 21:313-322.

Aguirre, A. A., and E. E. Starkey. 1994. Wildlife disease in United States national parks: historical and coevolutionary perspectives. Conservation Biology 8:654-661.

Alessi, M. G., and C. A. Miller. 2012. Comparing a convenience sample against a random sample of duck hunters. Human Dimensions of Wildlife 17:1-4.

Alverson, W. S. 1988. Forest to deer: edge effects in northern Wisconsin. Conservation Biology 2:348-358.

Alverson, W. S., and D. M. Waller. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280-297 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Anderson, R. C. 1994. Height of white-flowered trillium (Trillium grandiflorum) as an index of deer browsing intensity. Ecological Applications 4:104-109.

Asa, C. S., and I. J. Porton. 2005. Introduction. Pages xxv-xxxii in C. S. Asa, and I. J. Porton, editors. Wildlife contraception: issues, methods, and applications. Johns Hopkins University Press, Baltimore, Maryland, USA.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 88:43-53.

Austin, K. A. 1992. Gray dogwood (Cornus racemosa Lam.) as a refuge from herbivory in old fields of Saratoga National Historical Park, New York. Dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, USA.

Aycrigg, J. L., and W. F. Porter. 1997. Sociospatial dynamics of white-tailed deer in the central Adirondack Mountains, New York. Journal of Mammalogy 78:468-482.

Baker, B. W., and B. S. Cade. 1995. Predicting biomass of beaver food from willow stem diameters. Journal of Range Management 48:322-326.

Baker, W. L., J. A. Munroe, and A. E. Hessl. 1997. The effects of elk on aspen in the winter range in Rocky Mountain National Park. Ecography 20:155-165.

Balgooyen, C. P., and D. M. Walker. 1995. The use of Clintonia borealis and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. Natural Areas Journal 15:308-318.

Ballard, W. B. 2011. Predator-prey relationships. Pages 251-286 in D. G. Hewitt, editor. Biology and management of white-tailed deer. CRC Press, New York, New York, USA.

Ballard, W. B., D. Lutz, T. W. Keegan, L. H. Carpenter, and J. C. deVos, Jr. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29:99-115.

Baril, L. M, A. J. Hansen Andrew, R. Renkin, and R. Lawrence. 2011. Songbird response to increased willow (Salix spp.) growth in Yellowstone's Northern Range.
Ecological Applications 21:2283-2296.

Beetle, A. A. 1979. Jackson Hole elk herd: a summary after 25 years of study. Pages 259-262 in M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: ecology, behavior, and management. University of Wyoming, Laramie, USA.

Behrend, D. F., G. F. Mattfeld, W. C. Tierson, and J. E. Wilely, III. 1970. Deer density control for comprehensive forest management. Journal of Forestry 68:695-700.

Bender, L. C., and M. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33: 956-964.

Beringer, J., L. P. Hansen, J. A. Demand, J. Sartwell, M. Wallendorf, and R. Mange. 2002. Efficacy of translocation to control urban deer in Missouri: costs, efficiency, and outcome. Wildlife Society Bulletin 30:767-774.

Beringer, J., L. P. Hansen, W. Wilding, J. Fischer, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60:373-380.

Beschta R. L., and W. J. Ripple. 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Canadian Journal of Forest Research 37:1873-1885.

Beyer, H. L., E. H. Merrill, N. Varley, and M. S. Boyce. 2007. Willow on Yellowstone's Northern Range: evidence for a trophic cascade? Ecological Applications 17:1563-1571.

Bidwell, D. 2010. Bison, boundaries, and brucellosis: risk perception and political ecology at Yellowstone. Society and Natural Resources 23:14-30.

Bies, L. 2011. Policy concerns for urban hunts. Wildlife Society Bulletin 35:338-339.

Bilyeu, D., D. J. Cooper, and N. T. Hobbs. 2008. Water tables constrain height recovery on Yellowstone's Northern Range. Ecological Applications 18:80-92.

Bleich, V. C. 1990. Costs of translocating mountain sheep. Pages 67-75 in P. R. Krausman and N. S. Smith, editors. Managing wildlife in the southwest. Arizona Chapter of the Wildlife Society, Phoenix, USA.

Blyth, C. B. 1995. Dynamics of ungulate populations in Elk Island National Park. Thesis, University of Alberta, Edmonton, Canada.

Boertje, R. D., P. Valkenburg, and M. E. McNay. 2006. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474-489.

Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral Responses of Bison and Elk in Yellowstone to Snowmobiles and Snow Coaches. Ecological Applications 16:1911-1925.

Bourassa, M. A. 2001. Bighorn sheep restoration in Badlands National Park, South Dakota: lessons for cooperation. Pages 112-117 in D. Harmon, editor. Crossing boundaries in park management: proceedings of the 11th Conference on Research and Resource Management in Parks and on Public Lands. Canadian Cooperative Wildlife Health Centre 1996. Newsletter 4:4-6.

Boyce, M. R. 1991. Natural regulation of the control of nature? Pages 183-208 in R. B. Keiter and M. R. Boyce, editors. The Greater Yellowstone Ecosystem. Yale University Press, New Haven, Connecticut, USA.

Boyd, D. P., and C. C. Gates. 2006. A brief review of the status of plains bison in North America. Journal of the West 45:15-21.

Braddock, A.C., and C. Irmscher. 2009. A keener perception: ecocritical studies in American art history. University of Alabama Press, Tuscaloosa, USA.

Bratton, S. A., and E. A. Kramer. 1990. Recovery of live oak sprouts after release from browsing on Cumberland Island National Seashore, Georgia. Research on Mid-Atlantic Coastal Barrier Islands, December 1989. U.S. Department of Interior, National Park Service, and The Nature Conservancy, Nags Head, North Carolina, USA.

Cahalane, V. H. 1943. Elk management and herd regulation, Yellowstone National Park. Transactions of the North American Wildlife Conference 8:95-101.

Cahalane, V. H. 1951. A Program for restoring extirpated mammals in the National Park System. Journal of Mammalogy 32:207-210.

Cain, J. W., III, P. R. Krausman, J. R. Morgart, B. D. Jansen, and M. P. Pepper. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171.

Campbell, C.E. 2011. A century of Parks Canada: 19112011. University of Calgary Press, Alberta, Canada.

Campbell, T. A., B. R. Laseter, W. M. Ford, and K. V. Miller. 2004. Feasibility of localized management to control white-tailed deer in forest regeneration areas. Wildlife Society Bulletin 32:1124-1131.

Carbyn, L. N., and D. Watson. 2001. Translocation of plains bison to Wood Buffalo National Park. Pages 189-204 in D. S. Maehr, R. F. Noss, and J. Larkin, editors. Large mammal restoration: ecological and sociological challenges in the 21st century. Island Press, Washington, D.C., USA.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 2-8 in M.S. Boyce, editor. North American moose: ecology, behavior, and management. University of Wyoming Press, Laramie, USA.

Caughley, G., and J. H. Lawton. 1981. Plant-herbivore systems. Pages 132-166 in R. M. May, editor. Theoretical ecology: principles and applications. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Caughley, G. C., N. Shepherd, and J. Short. 1987. Kangaroos: their ecology and management in the sheep rangelands of Australia. Cambridge University Press, New York, New York, USA.

Christianson, D., and S. Creel. 2009. Effects of grass and browse consumption on the winter mass dynamics of elk. Oecologia 158:603-613.

Code of Federal Regulations. 1983. Department of Interior, fish and wildlife policy: state-federal relationships. lecfr.gpoaccess.gov/cgi/t>/text/text-id $x ? c=e c f r \& s i d=e a 583 e 757 c f 6399231 f 7 c 15071$ b58197 \&rgn=div5\&view=text\&node=43:1.1.1.1.24\&idno=43, accessed 6 May 2011).

Code of Federal Regulations. 2012. Title 36: parks, forests, and public property: lecfr.gpoaccess.gov/cgi/t/ text/text-idx?c=ecfr\&sid=aae1ee132b6f5aeec16b196 Obb75b1be\&rgn=div8\&view=text\&node=36:1.0.1.1.2.
0.1.2\&idno=36, accessed 6 May 2012).

Cole, C. F. 1963. Range survey guide, revised edition. Grand Teton National Park, Moose, Wyoming, USA.

Cole, G. F. 1971. An ecological rational for the natural or artificial regulation of native ungulates in parks. North American Wildlife and Natural Resources Conference 36:417-425.

Conover, M. 2002. Resolving human-wildlife conflicts: the science of wildlife damage management. Lewis Publishers, New York, New York, USA.

Cooper, D. J., J. Dickens, N. T. Hobbs, L. L. Christensen, and L. Landrum. 2006. Hydrologic, geomorphic, and climatic processes controlling willow establishment in a montane ecosystem. Hydrological Processes 20:1845-1864.

Cornicelli, L., and M. D. Grund. 2011. Assessing deer hunter attitudes toward regulatory change using selfselected respondents. Human Dimensions of Wildlife 16:174-182.

Cornicelli, L., A. Woolf, and J. L. Roseberry. 1993. Residential attitudes and perceptions toward a suburban deer population in southern Illinois. Transactions of the Illinois State Academy of Sciences 86: 23-32.

Couch, L. K. 1935. Chronological data on elk introduction into Oregon and Washington. The Murrelet 16:2-6.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology 28:71-82.

Craighead, J. J., J. R. Varney, and F. C. Craighead, Jr. 1974. A population analysis of the Yellowstone grizzly bears. Montana Forest and Conservation Experiment Station Bulletin 40. University of Montana, Missoula, USA.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387-3397.

Cross, P. C., E. K. Cole, A. P. Dobson, W. H. Edwards, K. L. Hamlin, G. Luikart, A. D. Middleton, B. M. Scurlock, and P. J. White. 2010. Probable causes of increasing brucellosis in free-ranging elk of the Greater Yellowstone Ecosystem. Ecological Applications 20:278-288.

Dale, M. 2009. Valley Forge deer hunt postponed. The Reporter. 25 December 2009. (www.thereporteronline.com/articles/2009/12/25/ news/doc4b32695579398375853238.txt, accessed 18 July 2011).

Danell, K., R. Bergstrom, L. Edenius, and G. Ericsson. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. Forest Ecology Management 181:67-76.

Davenport, M. A., W. T. Borrie, W. A. Freidmund, and R. E. Manning. 2002. Assessing the relationship between desired experiences and support for management actions at Yellowstone National Park using multiple methods. Journal of Park and Recreation Administration 20:51-64.

Dean, R., M. Gocke, B. Holz, S. Kilpatrick, T. Kreeger, B. Scurlock, S. Smith, E. T. Thorne, and S. Werbelow. 2004. Elk feedgrounds in Wyoming. Wyoming Game and Fish Department, Cheyenne, USA. (gf.state.wy.us/ downloads/pdf/elkfg83004.pdf, accessed 6 July 2011).

DeCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management 58:711-718.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2009. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13: 353-362.

Decker, D. J., and T. A. Gavin. 1987. Public attitudes towards a suburban deer herd. Wildlife Society Bulletin 15:173-180.

Demarais, S., R. W. DeYoung, L. J. Lyon, E. S. Williams, S. J Williamson, and G. J. Wolfe. 2002. Biological and social issues related to confinement of wild ungulates. Wildlife Society Technical Review 02-3. The Wildlife Society, Bethesda, Maryland, USA.

DeNicola, A. J., D. J. Kessler, and R. K. Swihart. 1997. Dose determination and efficacy of remotely delivered norgestomet implants on contraception of white-tailed deer. Zoo Biology 16:31-37.

Detling, J. K. 1998. Mammalian herbivores: ecosystemlevel effects in two grassland national parks. Wildlife Society Bulletin 26:438-448.

Didier, K. A., and W. F. Porter. 2003. Relating spatial patterns of sugar maple reproductive success and relative deer density in northern New York State. Forest Ecology and Management 181:253-266.

Didion, M., A. D. Kupferschmid, and H. Bugmann. 2009. Long-term effects of ungulate browsing on forest composition and structure. Forest Ecology and Management 258(supplement):S44-S55.

Doerr, M. L., J. B. McAninch, and E. P. Wiggers. 2001. Comparison of 4 methods to reduce white-tailed deer abundance in an urban community. Wildlife Society Bulletin 29:1105-1113.

Dratch, P. A., and P. J. P. Gogan. 2010. Bison conservation initiative: Bison Conservation Genetics Workshop: report and recommendations. Natural Resource Report NPS/NRPC/BRMD/NRR—2010/257. National Park Service, Fort Collins, Colorado, USA.

Fagerstone, K. A., L. A. Miller, G. Killian, and C. A. Yoder. 2010. Review of issues concerning the use of reproductive inhibitors, with particular emphasis on resolving human-wildlife conflicts in North America. Integrative Zoology 5:15-30.

Federal Environmental Assessment and Review Office. 1990. Northern diseased bison: report of the Environmental Assessment Panel. Environment Canada, Federal Environmental Assessment and Review Office Report 35. Minister of Supply Services Canada, Ottawa, Ontario, Canada.

Fix, P. J., T. L. Teel, M. J. Manfredo, and S. S. Boston. 2010. Assessing public acceptance of wildlife management trade-offs: a case study of elk and vegetation management in Rocky Mountain National Park, Colorado. Human Dimensions of Wildlife 15:405-417.

Fortin, E., H. L. Beyer, and M. S. Boyce, et al. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320-1330.

Frank, D. A. 2008. Evidence for top predator control of a grazing ecosystem. Oikos 117:1718-1724.

Frank, D. A., T. Depriest, K. McLauchlan, and A. C. Risch. 2011. Topographic and ungulate regulation of soil C turnover in a temperate grassland ecosystem. Global Change Biology 17:495-504.

Frank D. A., and R. D. Evans. 1997. Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238-2248.

Frank, D. A., P. M. Groffman, R. D. Evans, and B. F. Tracy. 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologia 123:16-121.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology 73:2043-2058.

Frost, H. C., G. L. Storm, M. J. Batcheller, and M. Lovallo. 1997. White-tailed deer management at Gettysburg National Military Park and Eisenhower National Historic Site. Wildlife Society Bulletin 25:462-469.

Fryxell, J. M., and A. R. E. Sinclair. 2000. A dynamic view of population regulation. Pages 156-174 in S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice Hall, Upper Saddle River, New Jersey, USA.

Fuller, W. A. 2002. Canada and the "buffalo" Bison bison: a tale of two herds. Canadian Field Naturalist 116:141-159.

Fulton, D. C., K. Skerl, E. M. Shenk, and D. W. Lime. 2004. Beliefs and attitudes toward lethal management of deer in Cuyahoga Valley National Park. Wildlife Society Bulletin 32:1166-1176.

Gage, E. A., and D. J. Cooper. 2005. Patterns of willow seed dispersal, seed entrapment, and seedling establishment in a heavily browsed montane riparian ecosystem. Canadian Journal of Botany 83:678-687.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kellyhouse, R. O. Stephenson, and D. G. Larson. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon with implications for conservation. Wildlife Monographs 120.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in Interior Alaska. Wildlife Monographs 84.

Gates, C. C., T. Chowns, and H. Reynolds, 1992. Wood buffalo at the crossroads. Pages in J. Foster, D. Harrison, and I. S. MacLaren, editors. Alberta: studies in the arts and sciences, special issue on the buffalo. 3:139-165. University of Alberta Press, Edmonton, Canada.

Gates, C. C., C. H. Freese, P. J. P. Gogan, and M. Kotzman, editors and compilers. 2010. American bison: status survey and conservation guidelines 2010. IUCN, Gland, Switzerland.

Gates, C. C., J. Mitchell, J. Wierzchowski, and L. Giles. 2001a. A landscape evaluation of bison movements and distribution in northern Canada. AXYS Environmental Consulting, Ltd.

Gates, C. C., R. O. Stephenson, H. W. Reynolds, C. G. van Zyll de Jong, H. Schwantje, M. Hoefs, J. Nishi, N. Cool, J. Chisholm, A. James, and B. Koonz, 2001b. National Recovery Plan for the wood bison (Bison bison athabascae). National Recovery Plan No. 21. Recovery of Nationally Endangered Wildlife (RENEW), Ottawa, Ontario, Canada.

Geist, V. 1996. Buffalo nation: history and legend of the North American bison. Voyageur Press, Stillwater, Minnesota, USA.

Geremia, C., P. J. White, R. L. Wallen, F. G. R. Watson, J. J. Treanor, J. Borkowski, C. S. Potter, and R. L. Crabtree. 2011. Predicting bison migration out of Yellowstone National Park using Bayesian models. PLoS ONE 6 e16848.

Gibson, L. 2006. The role of lethal control in managing the effects of apparent competition on endangered prey species. Wildlife Society Bulletin 34:1220-1224.

Gionfriddo, J. P., J. D. Eisemann, K. J. Sullivan, R. S. Healey, L. A. Millier, K. A. Fagerstone, R. M. Engeman, and C. A. Yoder. 2009. Field test of a single-injection gonadotropin-releasing hormone immunocontraceptive vaccine in female white-tailed deer. Wildlife Research 36:177-184.

Gogan, P. J. P., R. H. Barrett, W. W. Shook, and T. E. Kucera. 2001. Control of ungulate numbers in a protected area. Wildlife Society Bulletin 29:1075-1088.

Gothard, J. 2010. Coyotes could control Valley Forge deer population. The Examiner. 18 October. (www. examiner.com/rving-in-national/coyotes-could-control-valley-forge-deer-population, accessed 18 July 2011).

Gray, M. E., and E. Z. Cameron. 2010. Does contraceptive treatment in wildlife result in side effects? A review of quantitative and anecdotal evidence. Reproduction 139:45-55.

Gruell, G. E. 1980. Fire's influence on wildlife habitat on the Bridger-Teton National Forest, Wyoming. Volume 1. Photographic record and analyses. U.S. Forest Service Research Paper INT-235. U.S. Forest Service.

Haines, A. L. 1974. The Park Movement. Part III in A. L. Haines, editor.Yellowstone National Park: its exploration and establishment. (www.cr.nps.gov/ history/online_books/haines1/iee3a.htm, accessed 19 June 2012).

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 44:421-425.

Halbert, N. D., and J. N. Derr. 2007. A comprehensive evaluation of cattle introgression into U.S. federal bison herds. Journal of Heredity 98:1-12.

Hall, S. H, V. C. Bleich, and S. G. Torres. 2004. Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967-2002. Wildlife Society Bulletin 32:412-426.

Hamlin, K. L. and J. A. Cunningham. 2009. Monitoring and assessment of wolf-ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana statewide: Final Report. Montana Department of Fish, Wildlife, and Parks, Wildlife Division, Helena, Montana, USA.

Hansen, L. P., and J. Beringer. 1997. Managed controlled hunts to control white-tailed deer populations on urban public areas in Missouri. Wildlife Society Bulletin 25:484-487.

Harkin, M. E., and D. R. Lewis. 2007. Native Americans and the environment: perspectives on the ecological Indian. University of Nebraska Press, Lincoln, USA.

Haulton, S. M., W. F. Porter, and B. A. Rudolph. 2001. Evaluating 4 methods to capture white-tailed deer. Wildlife Society Bulletin 29:255-264.

Hebblewhite, M., D. H. Pletscher, and P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. Canadian Journal of Zoology 80:800-809.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135-2144.

Hjort, F. A., and R. A. Hodgins. 1964. Cooperative agreement between the National Park Service and the South Dakota Department of Game, Fish, and Parks for the reintroduction and management of bighorn sheep. National Park Service, Badlands National Park, South Dakota, USA.

Holland, E. A., W. J. Parton, J. K. Detling, and D. L. Coppock. 1992. Physiological responses of plantpopulations to herbivory and their consequences for ecosystem nutrient flow. American Naturalist 140:685-706.

Hood, G. A., and S. E. Bayley. 2008. The effects of high ungulate densities on foraging choices by beaver (Castor canadensis) in the mixed-wood boreal forest. Canadian Journal of Zoology 86:484-496.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. MacMillan Publishing Company, Inc. New York, New York, USA.

Houston, D. B., B. B. Moorhead, and R. W. Olson. 1991. Mountain goat population trends in the Olympic Mountain Range, Washington. Northwest Science 65:212-216.

Houston, D. B., E. G. Schreiner, and B. B. Moorhead. 1994. Mountain goats in Olympic National Park: biology and management of an introduced species. Scientific Monograph NPS/NROLY/NRSM-94/25. U.S. Department of the Interior, National Park Service, Olympic National Park. Port Angeles, Washington, USA.

Hutchins, M. 2005. Foreword. Pages ix-xvii in C. S. Asa, and I. J. Porton, editors. Wildlife contraception: issues, methods, and applications. Johns Hopkins University Press, Baltimore, Maryland, USA.
lercek, M. T., R. Stottlemyer, and R. Renkin. 2010. Bottom-up factors influencing riparian willow recovery in Yellowstone National Park. Western North American Naturalist 70:387-399.

Inslerman, R. A., J. E. Miller, D. L. Baker, R. Cumberland, P. Doerr, J. E. Kennamer, E. R. Stinson, and S. J. Williamson. 2006. Baiting and supplemental feeding of game wildlife species. Wildlife Society Technical review 06-1. The Wildlife Society, Bethesda, Maryland, USA.

International Union for Conservation of Nature. 1995. Guidelines for re-introductions. Prepared by the ICN/ SSC Re-introduction Specialist Group. IUCN, Gland, Switzerland, and Cambridge, United Kingdom.

International Union for Conservation of Nature. 2011. IUCN Red List of Threatened Species. Version 2011.2. (www.iucnredlist.org, accessed 17 December 2011).

Irby, L. R., J. E. Norland, J. A. Westfall, and M. A. Sullivan. 2002. Evaluation of a forage allocation model for Theodore Roosevelt National Park. Journal of Environmental Management 64:153-169.

Jacobsen, N. K., D. A. Jessup, and D. J. Kesler. 1995. Contraception in black-tailed deer by remotely delivered norgestomet ballistic implants. Wildlife Society Bulletin 23:718-722.

Johnson, D. B., D. J. Cooper, and N. T. Hobbs. 2007. Elk browsing increases aboveground growth of waterstressed willows by modifying plant architecture. Oecologia 154:467-478.

Joly, D. O., and F. Messier. 2004. Factors affecting apparent prevalence of tuberculosis and brucellosis in wood bison. Journal of Animal Ecology 7:623-631.

Jones J. D., J. J. Treanor, R. L. Wallen, and P. J. White. 2010. Timing of parturition events in Yellowstone bison Bison bison: implications for bison conservation and brucellosis transmission risk to cattle. Wildlife Biology 16:333-339.

Jones, J. M., and J. H. Witham. 1990. Post-translocation survival and movements of metropolitan white-tailed deer. Wildlife Society Bulletin 18:434-441.

Kamler, J. F., R. M. Lee, J. C. deVos, Jr., W. B. Ballard, and H. A. Whitlaw. 2002. Survival and cougar predation of translocated bighorn sheep in Arizona. Journal of Wildlife Management 66:1267-1272.

Kauffman, M., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91:2742-2755.

Kay, C. E., and S. Chadde. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. USDA Forest Service General Technical Report Intermountain 289:92-99.

Kay, C. E., and F. H. Wagner. 1994. Historical condition of woody vegetation on Yellowstone's Northern Range: a critical test of the natural regulation paradigm. Pages 151-169 in D. G. Despain, editor. Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem. U.S. Department of the Interior, National Park Service, Rocky Mountain Region, Yellowstone National Park, Wyoming, USA.

Kay, C. E., and F. H. Wagner. 1996. Response of shrubaspen to Yellowstone's 1988 wildfires; implications for natural regulation management. Pages 107-111 in J. Greenlee, editor. Proceedings of the Second Biennial Scientific Conference on the Greater Yellowstone Ecosystem. International Association of Wildland Fire, Fairfield, Washington, USA.

Kelly, L. S. 1997. Patterns of faunal exploitation at Cahokia. Pages 69-88 in T.R. Pauketat and T. E. Emerson, editors. Cahokia: domination and ideology in the Mississippian world. University of Nebraska Press, Lincoln, USA.

Kelty, N. J., and R. D. Nyland. 1981. Regenerating Adirondack northern hardwoods by shelterwood cutting and control of deer density. Journal of Forestry 79:22-26.

Kilpatrick, H. J., S. M. Spohr, and G. G. Chasko. 1997. A controlled deer hunt on a state-owned coastal reserve in Connecticut: controversies, strategies, and results. Wildlife Society Bulletin 25: 451-456.

Kilpatrick, H. J., and W. D. Walter. 1999. A controlled archery deer hunt in a residential community: cost, effectiveness, and deer recovery rates. Wildlife Society Bulletin 27: 115-123.

Kilpatrick, H. J., and A. M. LaBonte. 2003. Deer hunting in a residential community: the community's perspective. Wildlife Society Bulletin 31:340-348.

Kimble, D. S., D. B. Tyers, J. Robison-Cox, and B. F. Sowell. 2011. Aspen recovery since wolf reintroduction on the northern Yellowstone winter range. Rangeland Ecology Management 64:119-130.

Kinley, T. A., and C.D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158-164.

Kirkpatrick, J. F. 2007. Measuring the effects of wildlife contraception: the argument for comparing apples and oranges. Reproduction, Fertility, and Development 19:548-552.

Kloppers, E. L., C. C. St. Clair, and T. E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. Ecology and Society 10(1):31. (www.ecologyandsociety.org/vol10/iss1/ art31, accessed 10 July 2012).

Knight, T. M. 2003. Effects of herbivory and its timing across populations of Trillium grandiflorum (Liliaceae). Ecology 90:1207-1214.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100:272-284.

Koontz, L. M., and D. L. Hoag. 2005. Analyzing stakeholder preferences for managing elk and bison at the National Elk Refuge and Grand Teton National Park: an example of the disparate stakeholder management approach. U.S. Geological Survey, Open-File Report 2005-1224, Washington, D.C., USA.

Krech, S. 1999. The ecological Indian: myth and history. W. W. Norton, New York, New York, USA.

Lees, V. W. 2004. Learning from outbreaks of bovine tuberculosis near Riding Mountain National Park: applications to a foreign animal disease outbreak. Canadian Veterinary Journal 45:28-34.

Leong, K. M. 2009. The tragedy of becoming common: landscape change and perceptions of wildlife. Society and Natural Resources 23:111-127.

Leong, K. M., and D. J. Decker. 2005. White-tailed deer issues in NPS Units: insights from natural resource managers in the northeastern U.S. Human Dimensions Research Unit Publication Series no. 05-5. New

York State College of Agriculture and Life Sciences, Department of Natural Resources, Cornell University, Ithaca, New York, USA.

Leong, K. M., J. F. Forester, and D. J. Decker. 2006. Moving public participation beyond compliance: uncommon approaches to finding common ground. George Wright Forum 26:23-39.

Leopold, A. S., S. A. Cain, C. Cottam, I. N. Gabrielson, and T. L. Kimball. 1963. Wildlife management in the national parks. Transactions of the North American Wildlife Conference 28:27-45

Leslie, D. M., Jr. 1980. Remnant populations of desert bighorn sheep as a source for transplantation. Desert Bighorn Council Transactions 24:36-44.

Licht, D. S, J. J. Millspaugh, K. E. Kunkel, C. O. Kochanny, and R. O. Peterson. 2010. Using small populations of wolves for ecosystem restoration and stewardship. BioScience 60: 147-153.

Locke, S. L., M. W. Cook, L. A. Harveson, D. S. Davis, R. R. Lopez, N. J. Silvy, and M. A. Fraker. 2007. Effectiveness of Spayvac ${ }^{\circledR}$ for reducing white-tailed deer fertility. Journal of Wildlife Disease 43:726-730.

Lovaas, A. L. 1973. A cooperative elk trapping program in Wind Cave National Park. Wildlife Society Bulletin 1:93-100.

Lovallo, M. J., and W. M. Tzilkowski. 2003. Abundance of white-tailed deer (Odocoileus virginianus) within Valley Forge National Historical Park and movements related to surrounding private lands. Technical Report NPS/NERCHAL/NRTR-03/091. National Park Service, Washington, D.C., USA.

Lubow, B. C., F. J. Singer, T. L. Johnson, and D. C. Bowden. 2002. Dynamics of interacting elk populations within and adjacent to Rocky Mountain National Park. Journal of Wildlife Management 66:757-775.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691-1707.

Mathews, N. E., and W. F. Porter. 1992. Effect of social structure on genetic structure of free-ranging whitetailed deer. Journal of Mammalogy 74:33-43.

McCabe, R.E. 2002. Elk and Indians: then again. Pages 121-198 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

McCullough, D. R. 1997. Irruptive behavior in ungulates. Pages 69-98 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059-2075.

McKinney, T., T. W. Smith, and J. C. deVos, Jr. 2006. Evaluation of factors potentially influencing a desert bighorn sheep population. Wildlife Monographs 164.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555-1558.

McNulty, S. A., W. F. Porter, N. E. Mathews, and J. A. Hill. 1997. Localized management for reducing white-tailed deer populations. Wildlife Society Bulletin 25:265-271.

McShea, W. J., and J. H. Rappole. 1997. Herbivores and the ecology of forest understory birds. Pages 298-409 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

McShea, W. J., and J. H. Rappole. 2000. Managing abundance and diversity of bird populations through manipulation of deer populations. Conservation Biology 14:1161-1170.

Meagher, M., and M. E. Meyer. 1994. On the origin of brucellosis in bison of Yellowstone National Park, a review. Conservation Biology: 8:645-653.

Meagher, M., W. J. Quinn, and L. Stackhouse. 1992. Chlamydial-caused infectious keratoconjunctivitis in bighorn sheep of Yellowstone National Park. Journal Wildlife Diseases 28:171-176.

Mech, L. D., W. Ballard, E. Bangs, and B. Ream. 2010. Restricting wolves risks escapes. BioScience 60:485-486.

Merrill, E. H., N. L. Stanton, and J. C. Hak. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. Oikos 69: 231-240.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology 75:478-488.

Messmer, T. M., S. M. George, and L. Cornicelli. 1997. Legal considerations regarding lethal and nonlethal approaches to managing urban deer. Wildlife Society Bulletin 25: 424-429.

Miller, C. A., and R. G. Wright. 1998. Visitor satisfaction with public transportation services and wildlife viewing opportunities at Denali National Park and Preserve. Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho, Moscow, Idaho, USA.

Miller, L. A., J. Rhyan, and G. Killian. 2004. Gonacon™ ${ }^{\text {TM }}$ a versatile GnRH contraceptive for a large variety of pest animal problems. Vertebrate Pest Conference proceedings 21:269-273.

Miller, L. A., K. A. Fagerstone, D. C. Wagner, and G. J. Killian. 2009. Factors contributing to the success of a single-shot, multiyear PZP immunocontraceptive vaccine for white-tailed deer. Human-Wildlife Conflicts 3:103-115.

Miller, M. W., H. M. Swanson, L. L. L. Wolfe, F. G. Quartarone, S. L. Huwer, C. H. Southwick, and P. M. Lukacs. 2008. Lions and prions and deer demise. PLoS ONE 3 e4019 1-7.

Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28:621-658.

National Park Service. 1988. Management policies. U.S. Department of the Interior, Washington, D.C., USA. National Park Service. 1991. Natural resources management guidelines. U.S. Department of the Interior, Washington, D.C., USA.

National Park Service. 2000. Bison management plan for the state of Montana and Yellowstone National Park: final environmental impact statement. U.S.
Department of the Interior, National Park Service. Washington, D.C., USA.

National Park Service. 2006a. Management policies 2006. U.S. Department of the Interior, Government Printing Office, Washington, D.C., USA. (www.nps.gov/ policy/mp2006.pdf, accessed 6 May 2011).

National Park Service. 2006b. Point Reyes National Seashore non-native deer management plan: protecting the seashore's native ecosystems: final environmental impact statement. U.S. Department of the Interior, National Park Service, Point Reyes National Seashore. Point Reyes Station, California, USA.

National Park Service. 2006c. Bison management plan: Wind Cave National Park. U.S. Department of the Interior, National Park Service, Wind Cave National Park, Hot Springs, South Dakota, USA.

National Park Service. 2007a. General management plan and environmental impact statement record of decision. (parkplanning.nps.gov/document.cfm?p arkID=284\&projectID=11314\&documentID=20852, accessed 4 June 2012).

National Park Service. 2007b. Wildlife management plan and environmental assessment for harvestable species. U.S. Department of the Interior, National Park Service, Apostle Islands National Lakeshore, Bayfield, Wisconsin, USA.

National Park Service. 2008a. Final white-tailed deer management plan/environmental impact statement: Catoctin Mountain Park. U.S. Department of the Interior, National Park Service, Catoctin Mountain Park, Thurmont, Maryland, USA.

National Park Service. 2008b. Elk and vegetation management plan, Rocky Mountain National Park, Colorado: final environmental impact statement. U.S. Department of the Interior, National Park Service, Rocky Mountain National Park, Estes Park, Colorado, USA.

National Park Service. 2008c. Final elk management plan and environmental impact statement. U.S. Department of the Interior, National Park Service, Washington D.C., USA.

National Park Service. 2009a. Indiana Dunes National Lakeshore draft white-tailed deer management plan/ environmental impact statement. U.S. Department of the Interior, National Park Service, Indiana Dunes National Lakeshore, Porter, Indiana, USA.

National Park Service. 2009b. Final white-tailed deer management plan/environmental impact statement for Valley Forge National Historic Park. U. S. Department of the Interior, National Park Service, Valley Forge National Historic Park, King of Prussia, Pennsylvania, USA.

National Park Service. 2009c. Rock Creek Park draft white-tailed deer management plan/environmental impact statement. U.S. Department of the Interior, National Park Service, Rock Creek Park, Washington, D.C., USA

National Park Service. 2009d. Wind Cave National Park final elk management plan/environmental impact statement. U.S. Department of the Interior, National Park Service, Hot Springs, South Dakota, USA.

National Park Service. 2010a. Theodore Roosevelt National Park elk management plan/final environmental assessment. U.S. Department of the Interior, National Park Service, Theodore Roosevelt National Park, Medora, North Dakota, USA.

National Park Service. 2010b. Fertility control and sterilization. Biological Resource Management Division briefing paper, September. National Park Service, Washington, D.C., USA.

National Park Service. 2011a. Hawai'i Volcanoes National Park draft plan/environmental impact
statement for protecting and restoring ecosystems by managing non-native ungulates. National Park Service, Hawai'i County, Hawai'i, USA.

National Park Service. 2011b. White-tailed deer management: Valley Forge National Historic Park initiates the second year of deer management during winter 2011-2012. (www.nps.gov/vafo/parkmgmt/ white-tailed-deer.htm, accessed 1 May 2012).

National Research Council. 2002. Ecological dynamics on Yellowstone's Northern Range. National Academy Press. Washington, D.C., USA.

Niewinski, A. T., T. W. Bowersox, and R. J. Laughlin. 2006. Vegetation status in selected woodlots at Gettysburg National Military Park pre and post whitetailed deer management. U.S. Department of Interior, National Park Service Technical Report NPS/NER/ NRTR-2006/037. National Park Service, Washington, D.C., USA.

Nishi, J. S., C. Stephen, and B. T. Elkin. 2002. Implications of agricultural and wildlife policy on management and eradication of bovine tuberculosis and brucellosis in free-ranging wood bison of northern Canada. Annals of the New York Academy of Sciences 969:236-244.

Nishi, J. S., T. Shury, and B. T. Elkin. 2006. Wildlife reservoirs for bovine tuberculosis (Mycobacterium bovis) in Canada: strategies for management and research. Veterinary Microbiology 112:325-338.

Nishi, J. S. 2010. A review of best practices and principles for bison disease issues: Greater Yellowstone and Wood Buffalo areas. Wildlife Conservation Society and American Bison Society, American Bison Society Working Paper No. 3., Bronx, New York, USA.

O'Bryan, M. K., and D. R. McCullough. 1985. Survival of black-tailed deer following relocation in California. Journal of Wildlife Management 49:115-119.

Olsen, S. C. 2010. Brucellosis in the United States: role and significance of wildlife reservoirs. Vaccine 28: Suppl. 5 F73-F76.

One Health Commission. 2011. The National Park System, a living laboratory for one health. Newsletter 4:7-8.

Oyer, A. M., and W. F. Porter. 2004. Localized management of white-tailed deer in the central Adirondack Mountains, New York. Journal of Wildlife Management 68:257-265.

Ozoga, J. J., and L. J. Verme. 1982. Physical and reproductive characteristics of a supplementally fed white-tailed deer herd. Journal of Wildlife Management 46:281-301.

Palmer, W. L., G. L. Storm, R. Quinn, and W. M. Tzilkowski. 1997. Profiles of deer under different management and habitat conditions in Pennsylvania. Pages 151-163 in W. J. McShea, J. H. Rappole, and H. B. Underwood, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Parks Canada. 1997. National Parks system plan, third edition. Parks Canada. (www.pc.gc.ca/eng/docs/v-g/ nation/nation2.aspx, accessed 19 April 2012). Parks Canada. 2000. National historical sites of Canada system plan.

Parks Canada. (www.pc.gc.ca/eng/docs/r/system-reseau/sites-lieux1.aspx, accessed 20 April 2012).

Parks Canada. 2008. Proceedings of the Parks Canada workshop on the management of CWD: a first step toward developing approaches to manage chronic wasting disease in the National Parks of the prairie region. College of Veterinary Medicine, Saskatoon, Saskatchewan, Canada.

Parks Canada. 2011. Banff National Park of Canada: ecosystem management and ecosystem models. (www.pc.gc.ca/pn-np/ab/banff/plan/gestionmanagement/plan8b.aspx, accessed 22 April 2012).

Parks Canada. 2012. Elk Island National Park: 4.0 managing for ecological integrity. (www.pc.gc.ca/pn-np/ab/elkisland/plan/plan4,-d-,0.aspx, accessed 24 April 2012).

Pastor J., and Y. Cohen. 1997. Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. Theoretical Population Biology 51:165-179.

Pastor, J., Y. Cohen, and T. Hobbs. 2006. The role of large herbivores in ecosystem nutrient cycles. Pages 289-325 in K. Danell, R. Bergström, P. Duncan, and J. Pastor, editors. Large mammalian herbivores, ecosystem dynamics, and conservation. Cambridge University Press, Cambridge, United Kingdom.

Pastor, J., B. Dewey, R. J. Naiman, P. F. Mcinnis, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467-480.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist 139:690-705.

Pedevillano, C., and R. G. Wright. 1986. The influence of visitors on mountain goat activities in Glacier National Park, Montana. Biological Conservation, 39:1-11.

Peinetti, H. R., M. A. Kalkhan, and M. B. Coughenour. 2002. Long-term changes in willow spatial distribution on the elk winter range of Rocky Mountain National Park (USA). Landscape Ecology 17: 341-354.

Persico, L., and G. Meyer. 2009. Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park, Wyoming. Quaternary Research 71:340-353.

Pimm, S. L. 1992. The balance of nature? University of Chicago Press, Chicago, Illinois, USA.

Plumb, G. E., P. J. White, M. B. Coughenour, and R. L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. Biological Conservation. 142: 2377-2387.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86:3-15.

Porter, W.F. 1991. White-tailed deer in eastern ecosystems: implications for management and
research in national parks. Natural Resources Report NPS/ NRSUNY/NRR-91/105. National Park Service, Denver, Colorado, USA.

Porter, W. F. 1992. Burgeoning ungulate populations in national parks: is intervention warranted? Pages 304-312 in D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Press, New York, New York, USA.

Porter, W. F., M. A. Coffey, and J. Hadidian. 1994. In search of a litmus test: wildlife management in the U.S. national parks. Wildlife Society Bulletin 22:301-306.

Porter, W. F., and H. B. Underwood. 1999. Of elephants and blind men: deer management in the U.S. national parks. Ecological Applications 9:3-9.

Porton, I. J. 2005. The ethics of wildlife contraception. Pages 3-16 in C. S. Asa, and I. J. Porton, editors. Wildlife contraception: issues, methods, and applications. Johns Hopkins University Press, Baltimore, Maryland, USA.

Powers, J. 2011. Reproductive, behavioral, and first generation effects of gonadotropin releasing hormone vaccine in female rocky mountain elk (Cervus elaphus nelson). Dissertation, Colorado State University, Fort Collins, USA.

Pritchard, J. A. 1999. Preserving Yellowstone's natural conditions. University of Nebraska Press. Lincoln, Nebraska, USA.

Redding, J. A. 1995. History of deer population trends and forest cutting on the Allegheny National Forest. Pages 214-224 in Proceedings of the 10th Northcentral Hardwood Conference. U.S. Forest Service Technical Report NE-197. U.S. Forest Service, Morgantown, West Virginia, USA.

Rhyan, J. C., and T. R. Spraker. 2010. Emergence of diseases from wildlife reservoirs. Veterinary Pathology 47:34-39.

Rigal, L. 2010. Beyond "The trouble with wilderness." American Quarterly 62:989-999.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184:299-313.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's Northern Range. Biological Conservation 102:227-234.

Ripple, W. J., and B. Van Valkenburgh. 2010. Linking top-down forces to the pleistocene megafaunal extinctions. BioScience 60:517-526.

Risenhoover, K. I., and S. A. Maass. 1987. Influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research 17:357-364.

Rittel, H. W. J., and M. M. Webber. 1973. Dilemmas in a general theory of planning. Policy Sciences 4:155-69.

Robbins, R. L., D. E. Redfearn, and C. P. Stone. 1982. Refuges and elk management. Pages 479-507 in J. W. Thomas and D. E. Toweill, editors. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. Ecology and Society 16:16. (dx.doi.org/10.5751/ES-04251-160316, accessed 31 July 2012).

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. Journal of Wildlife Management 68: 993-999.

Romme, W. H., M. G. Turner, L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in northern Yellowstone National Park. Ecology 76:2097-2106.

Rudolph, B. A., W. F. Porter, and H. B. Underwood. 2000. Evaluating immunocontraception for managing suburban white-tailed deer in Irondequoit, New York. Journal of Wildlife Management 64:463-473.

Rutberg, A. T. 2005. Deer contraception: what we know and what we don't. Pages 23-42 in A. T. Rutberg, editor. Humane wildlife solutions. Humane Society Press, Washington, D.C., USA.

Rutberg, A. T., and R. E. Naugle. 2008. Population-level effects of immunocontraception in white-tailed deer (Odocoileus virginianus). Wildlife Research 35:494-501.

Rutberg, A. T., R. E. Naugle, L. A. Thiele, and I. K. M. Liu. 2004. Effects of immunocontraception on a suburban population of white-tailed deer Odocoileus virginianus. Biological Conservation 116:243-250.

Samuel, W. M., and S. Demarais. 1993. Conservation challenges concerning wildlife farming and ranching in North America. Transactions of the North American Wildlife and Natural Resources Conference 58: 445-447.

Sargeant G.A., and M. W. Oehler. 2007. Dynamics of newly established elk populations. Journal of Wildlife Management 71:1141-1148.

Sargeant, G. A., D. C. Weber, and D. E. Roddy. 2011. Implications of chronic wasting disease, cougar predation, and reduced recruitment for elk management. Journal of Wildlife Management 75:171-177.

Schoenecker, K. A., F. J. Singer, L. C. Zeigenfuss, D. Binkley, and R. S. C. Menezes. 2004. Effects of elk herbivory on vegetation and nitrogen processes. Journal Wildlife Management 68: 837-849.

Schullery, P. 1997. Searching for Yellowstone: ecology and wonder in the last wilderness. Houghton Mifflin Company, Boston, Massachusetts, USA.

Schwartz, C. C., M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Sellars, R. W. 2009. Preserving nature in the national parks. Yale University Press. New Haven, Connecticut, USA.

Shaw, J. H., and M. Meagher. 2000. Bison. Pages 447-466 in S. Demarais and P. R. Krausman, editors. Ecology and management of large mammals in North America. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.

Shirk, A. J. 2009. Mountain goat genetic structure, molecular diversity, and gene flow in the Cascade Range, Washington. Thesis, Western Washington University, Bellingham, Washington, USA.

Siemer, W. F., T. B. Lauber, L. C. Chase, D. J. Decker, R. J. McPeake, and C. A. Jacobson. 2004. Deer/elk management actions in suburban environments: what will stakeholders accept? Pages 228-237 in W. W. Shaw, L. K. Harris, and L. Vandruff, editors. Proceedings of the 4th International Urban Wildlife Symposium on Urban Wildlife Conservation, 1-5 May 1999, Tucson, Arizona, USA.

Singer, F. J., V. C. Bleich, and M. A. Gudorf. 2000. Restoration of bighorn sheep metapopulations in and near western National Parks. Restoration Ecology 8:14-24.

Singer F. J., and M. K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecological Applications 6:185-199.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone northern winter range. Journal of Range Management 47:435-443.

Singer, F. J., and K. A. Schoenecker. 2003. Do ungulates accelerate or decelerate nitrogen cycling? Forest Ecology and Management 181:189-204.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin 26:375-390.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. Bioscience 53:330-340.

Soper, J.D. 1941. History, range, and home life of the northern bison. Ecological Monographs 11:347-412.

Soukup, M., M. K. Foley, R. Hiebert, and D. E. Huff. 1999. Wildlife management in U.S. national parks: natural regulation revisited. Ecological Applications 9:1-2.

Spraker, T. R. 1993. Stress and capture myopathy in artiodactylids. Pages 481-488 in M. E. Fowler, editor. Zoo and wild animal medicine: current therapy 3. W. B. Saunders Company, Philadelphia, Pennsylvania, USA.

Stankowich, T. 2008. Ungulate flight responses to human disturbances: a review and meta-analysis. Biological Conservation. 141:2159-2173.

Stephenson, R. O., S. C. Gerlach, R. D. Guthrie, C. R. Harington, R. O. Mills, and G. Hare. 2001. Wood bison in late Holocene Alaska and adjacent Canada: paleontological, archaeological and historical records. Pages 124-158 in S. C. Gerlach and M. S. Murray, editors. People and wildlife in northern North America: essays in Honor of R. Dale Guthrie. BAR International Series 944. British Archaeological Reports, Oxford, United Kingdom.

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park: a 10-year study. NPS Report ROMO-N-13. Rocky Mountain National Park, Estes Park, Colorado, USA.

Stewart, C. M. 2011. Attitudes of urban and suburban residents in Indiana on deer management. Wildlife Society Bulletin 35: 316-322.

Storm, G. L., R. H. Yahner, D. F. Cottom, and G. M. Vecellio. 1989. Population status, movement patterns, habitat use, and impact of white-tailed deer at Gettysburg National Military Park and Eisenhower National Historic Site, Pennsylvania. U.S. National Park Service Technical Report NPS/NRTR-89/043. U.S. Department of the Interior, National Park Service, Washington, D.C., USA.

Stout, R. 1997. Urban Missourians' opinions about white-tailed deer management in St. Louis and Kansas City. Public Profile 1-97, Missouri Department of Conservation, Jefferson City, USA.

Stromayer, K. A., and R. J. Warren. 1997. Are overabundant deer herds in the Eastern United States creating alternative stable states in forest plant communities? Wildlife Society Bulletin 25:227-234.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions.
Ecological Applications 13:951-963.

Tierson, W. C., G. F. Mattfeld, R. W. Sage, Jr., and D. F. Behrend. 1985. Seasonal movements and home ranges of white-tailed deer in the Adirondacks. Journal of Wildlife Management 49:760-769.

Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in Northwestern Pennsylvania. Journal of Wildlife Management 53:524-532.

Trimble, M. J., and R. J. van Aarde. 2010. Fences are more than an issue of aesthetics. BioScience 60: 486. Underwood, H. B. 1990. Population dynamics of whitetailed deer in a fluctuating environment. Dissertation, State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA.

Underwood, H. B., K. A. Austin, W. F. Porter, R. L. Burgess, and R. W. Sage, Jr. 1994. White-tailed deer and vegetation at Saratoga National Historical Park. Technical report NPS/NARROSS/NRTR/95-28. U.S. Department of the Interior, National Park Service, Washington, D.C., USA.

Underwood, H. B., and W. F. Porter. 1991. Values and science: white-tailed deer management in eastern national parks. Transactions of the North American Wildlife and Natural Resources Conference 56: 67-72.

Underwood, H. B., and W. F. Porter. 1997. Reconsidering paradigms of overpopulation of ungulates: whitetailed deer at Saratoga National Historical Park. Pages 185-198 in W. J. McShea, H. B. Underwood, and J. H. Rappole, editors. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA.

Urbanek, R. E., K. R. Allen, and C. K. Nielsen. 2011. Urban and suburban deer management by state wildlife-conservation agencies. Wildlife Society Bulletin 35: 310-315.
U.S. Department of the Interior, National Park Service, and U.S. Department of Agriculture, Forest Service, Animal and Plant Health Inspection Service, and the State of Montana, Department of Fish, Wildlife, and Parks, Department of Livestock. 2008. Adaptive
adjustments to the interagency bison management plan. Yellowstone National Park, Mammoth, Wyoming, USA. (ibmp.info/Library/2008\ IBMP\  Adaptive\%20Management\%20Plan.pdf, accessed 10 July 2012).
U.S. Fish and Wildlife Service. 2011. Deer Hunting in the United States: demographics and trends. Addendum to the 2006 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. (wsfrprograms.fws. gov/Subpages/NationalSurvey/NatSurveyIndex.htm, accessed 21 June 2012).
U.S. Fish and Wildlife Service, Nez Perce Tribe, National Park Service,Montana Fish, Wildlife, and Parks, Blackfeet Nation, Confederated Salish \& Kootenai Tribes, Idaho Fish and Game, and USDA Wildlife Services. 2010. Rocky Mountain wolf recovery 2009 interagency annual report (C. A. Sime, and E. E. Bangs, editors). U.S. Fish and Wildlife Service, Ecological Services, Helena, Montana, USA.
U.S. Senate. 1967. Hearings before a Subcommittee of the Committee on Appropriations, Nineteenth Congress First Session, on elk population, Yellowstone National Park. Washington, D.C., USA.

Vecellio, G. M., R. H. Yahner, and G. L. Storm. 1994. Crop damage by deer at Gettysburg Park. Willdife Society Bulletin 22:89-93.

Vucetich, J. A. and R. O. Peterson. 2004. The influence of top-down, bottom-up, and abiotic factors on the moose (Alces alces) population of Isle Royale. Proccedings of The Royal Society Biological Sciences 271:183-189.

Wagner, C. 2006a. Elk data analysis unit plan E-55. Northern San Luis Valley Floor. Colorado Division of Wildlife, Monte Vista, Colorado, USA. (wildlife.state.co.us/SiteCollectionDocuments/ DOW/Hunting/BigGame/DAU/Elk/E55DAUPlan_ NorthernSanLuisValleyFloor06.pdf, accessed 13 September 2011).

Wagner, F. H. 2006b. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. Oxford, United Kingdom.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and H. Salwasser. 1995. Wildlife policy in the U. S. national parks. Island Press, Washington, D.C., USA.

Wakelee, D. W., and S. A. Frisch. 2010. Implications of hunting in Channel Islands National Park. Pages 111-116 in S. Weber, editor. Rethinking protected areas in a changing world: proceedings of the 2009 GWS Biennial Conference on Parks, Protected Areas, and Cultural Sites. The George Wright Society, Hancock, Michigan, USA.

Wang, G., N. T. Hobbs, S. Twombly, R. B. Boone, A. W. Illius, I. J. Gordon, and J. E. Gross. 2009. Density dependence in northern ungulates: interactions with predation and resources. Population Ecology 51:123-132.

Warren, R. J. 1991. Ecological justification for controlling deer populations in eastern national parks. North American Wildlife and Natural Resources Conference 56:56-66.

Warren, R. J., R. A. Fayrer, L. I. Muller, L. P. Willis, and R. B. Goodloe. 1993. Research and field application of contraceptives in white-tailed deer, feral horses, and mountain goats. USDA National Wildlife Research Center Symposium: contraception in wildlife management. University of Nebraska-Lincoln, Lincoln, Nebraska, USA.

Wehausen, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471-479.

West, D. C., H. H. Shugart, and D. B. Botkin. 1981. Forest succession: concepts and application. SpringerVerlag, New York, New York, USA.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin 26:449-462.

White, P. J., K. M. Proffitt, L. D. Mech, S. B. Evans, J. A. Cunningham, and K. L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy 91:827-837.

White, P. J., and R. A. Garrot. 2005. Yellowstone's ungulates after wolves: expectations, realizations, and predictions. Biological Conservation 125:141-152.

White, P. J., and T. Davis. 2007. Chronic wasting disease planning for an inevitable dilemma. Yellowstone Science 15:8-10.

Wildlife Management Institute. 2009. Park Service begins culling elk in Rocky Mountain National Park. (www.wildlifemanagementinstitute.org/index. php?option=com_content\&view=article\&id=332\%3Ac ulling-elk\&Itemid=95, accessed May 1, 2012).

Wilson, G. A., and C. M. Strobeck. 1999. Genetic variation within and relatedness among wood and plains bison populations. Genome 42:483-496.

Wolfe, M. L., J. F. Kimball, Jr., and G. T. M.
Schildwachter. 2002. Refuges and elk management. Pages 583-615 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

Woodley, S. 2010. Ecological integrity and Canada's National Parks. The George Wright Forum 27:151-160.

Wright, G. M., J. S. Dixon, and B. H. Thompson. 1932. Fauna of the National Parks of the United States, Series 1 and 2. U.S. Government Printing Office, Washington, D.C., USA.

Wright, G. M., and B. H. Thompson. 1935. Wildlife management in the national parks. Fauna of the national parks of the United States 2. United States Government Printing Office, Washington, D.C., USA.

Wright, R. G. 1992. Wildlife research and management in the national parks. University of Illinois Press, Champaign, Illinois, USA.

Wright, R. G. 1999. Wildlife management in the National Parks: questions in search of answers. Ecological Applications 9:30-36.

Zeigenfuss, L. C., F. J. Singer, S. A. Williams, and T. L. Johnson. 2002. Influences of herbivory and water on willow in elk winter range. Journal Wildlife Management 66:788-795.

The Wildlife Society
5410 Grosvenor Lane
Bethesda, MD 20814
P: 301.897.9770
F: 301.530.2471
www.wildlife.org
Promoting Excellence in Wildlife Stewardship through Science and Education

