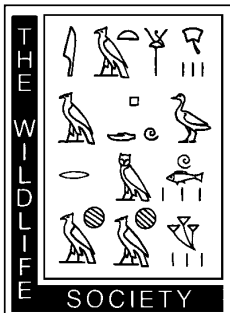


Biological and Social Issues Related to Confinement of Wild Ungulates



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BIOLOGICAL AND SOCIAL ISSUES RELATED TO CONFINEMENT OF WILD UNGULATES

The Wildlife Society

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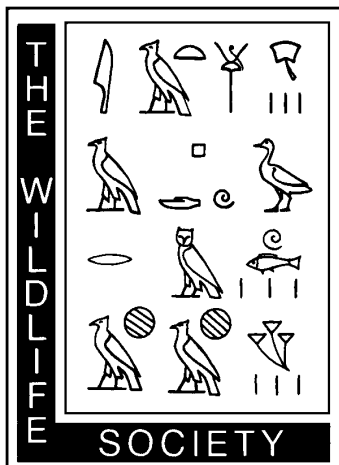
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Foreword

Presidents of The Wildlife Society occasionally appoint ad hoc committees to study and report on selected conservation issues. The reports ordinarily appear in 2 related series called either Technical Review (formerly "White Paper") or Position Statement. Review papers present technical information and the views of the appointed committee members, but not necessarily the views of their employers. Position statements are based on the review papers, and the preliminary versions ordinarily are published in *The Wildlifer* for comment by Society members. Following the comment period, revision, and Council's approval, the statements are published as official positions of The Wildlife Society.

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SYNOPSIS

Commercial demand for hunting and for sale of live ungulates and their products has prompted the growth of a commercial industry that raises non-domesticated native ungulates within managed properties. These properties vary in size, management intensity, and product, but typically include fencing designed to control animal movements. Animals often are confined to fulfill management goals related to population management for harvest and commercial production of live animals or their products (e.g., venison, velvet, semen). The rapid expansion in number and acreage of fenced properties throughout North America has prompted a need for a review of the biological and social issues related to these management practices. In this report we review the primary biological and social issues directly and indirectly associated with confinement of wild ungulates, defined as all hoofed mammals.

Fencing is used to control movement of animals to improve population-level management effectiveness and for commercial production of live animals or their products. Fences used to confine ungulates have various names representing either the type of fence or the reason for confinement, such as high fence or game fence. The most typical high fence consists of 2.4-m-high net wire. The extensive use of high fences began in Texas in the 1930s, but has expanded to other states and provinces in recent years. For example, in Wisconsin there are 947 high-fenced facilities containing 35,000 captive cervids—deer and elk.

Biological issues related to confined ungulates include behavioral impacts on target species, diseases associated with confinement, genetic impacts of confinement and shipment across natural ranges, habitat impacts, and impacts on non-target species. The goal of high-fence construction is to modify animal movement patterns. While most animals adapt to such a change, exclusion from critical or migratory habitats may impact survival or production. The migration patterns of free-ranging animals may be disrupted if high fences surround critical migratory range or block migratory corridors. Fences can reduce egress of animals and facilitate control of ungulate density, sex ratio, and age structure to improve local management effectiveness. Some fenced populations do not receive harvest rates sufficient to control population density, resulting in overpopulation. Infectious diseases are a concern when transmission is increased at high densities, when host animals are subjected to nutritional or environmental stressors, and when animals of different species and sources are mixed. The risk of disease transmission between captive and free-ranging animals depends upon the management circumstances (e.g., fencing, geography, etc.), the likelihood of direct or indirect contact between the captive and free-ranging species, and the routes of transmission of any given pathogen. Chronic wasting disease (CWD), bovine tuberculosis (TB), and meningeal worm are of most concern to wildlife managers. Control or eradication of CWD is extremely difficult given the long incubation period, absence of practical

antemortem diagnostic tests, an extremely resistant infectious agent possibly leading to environmental contamination, and limited knowledge of the mode of transmission. Management currently involves quarantine or depopulation of captive CWD-affected herds, significant population reduction of wild populations, and banning translocation and artificial feeding of cervids in the endemic areas. In the absence of complete information, the public health concerns about CWD remain important. Bovine tuberculosis in farmed cervids has been a serious problem in North America since the 1980s and has been the subject of a state–federal eradication program. The genetic impacts of enclosed populations and the mixing of genetically distinct populations is unclear. If escapees breed with free-ranging natives, there could be dilution of unique genetic stocks and reduced fitness. The potential impact of escapees would be proportional to the number, survival, and reproductive success of escaping animals and the severity of selective disadvantage for any maladaptive traits. The long-term genetic effects of intensive management strategies within enclosures are unknown. Vegetative diversity and ecological health decline when ungulate populations are allowed to exceed habitat carrying capacity. However, ecological health within fenced habitats may increase when improved effectiveness of population control is combined with habitat management and regulation of livestock grazing pressure.

Social issues related to confined ungulates include ownership of wildlife resources, hunter ethics, the public perception of hunting, commercialization and domestication of wild animals, and ecological stewardship. The North American system of wildlife management is based on the premise that endemic wildlife belongs not to individuals but to the people of the state, and responsibility for managing that wildlife is entrusted to the governmental regulatory agency. The application of the “public trust doctrine” to wildlife is deeply rooted in history, beliefs, and court opinions. Defining sportsmanship and describing a satisfactory hunter ethic for modern conditions have been controversial. A “canned” hunt describes a situation in which the client pays to kill a specific type of animal under conditions where the probability of failure is greatly reduced. We consider this type of practice unethical. This activity could be used by anti-hunters in their attempts to sway public opinion against hunting. Efforts are needed to improve the management, practice, and image of hunting. A major impetus for expansion of the game farm and hunting industries in North America has been agricultural diversification. There are 4 primary products in the game farm industry: meat, velvet, breeding stock, and shooter bulls. The venison and velvet market niche is limited and mostly filled by foreign producers. The market for breeding stock has been impacted by a United States Department of Agriculture declaration of CWD as an animal health emergency and state actions related to CWD. Wildlife managers recently have begun to discuss the ethics of wildlife management as practiced in the modern world. Professional wildlife managers should encourage ecological stewardship as the basis for management actions.

INTRODUCTION

Commercial demand for hunting and for sale of live ungulates and their products has prompted an expansion of a commercial industry that raises non-domesticated native ungulates within managed properties. These properties vary in size, management intensity, and product, but typically include fencing designed to control animal movements. The rapid expansion in number and acreage of fenced properties throughout North America and the activities associated with these facilities has generated a variety of biological and social issues at state, national, and international levels.

Fencing as a management tool has been described as existing along a “corral continuum” (Stedman 1998). On the least intensive end of this continuum are properties where the fencing simply encloses large areas of natural habitat with the objective of improving effectiveness of “traditional” population management, such as manipulation of density, sex ratio, and age structure. On the most intensive end of the continuum are properties where fencing is used to manipulate genetic composition within small breeding pens using controlled breeding or artificial insemination. Brood stock must be obtained, which requires private ownership, sale, and shipment of animals among breeding facilities. To facilitate record keeping, animals are clearly marked using livestock ear tags or freeze branding. At this most intensive end, pens are too small and animal density is too high to allow natural provision of habitat requirements, so husbandry must fulfill nutritional requirements by providing full-ration feed and water. Infectious diseases are a concern whenever animals are maintained at high densities, and shipment of diseased or exposed animals among facilities is problematic.

Our primary objective is to review the important biological and social issues associated directly and indirectly with confinement of non-domesticated, native ungulates. Biological issues include behavioral impacts on target species, diseases associated with confinement, genetic impacts of confinement and shipment across natural ranges, habitat alteration, and unintended effects on non-target species. Social issues include ownership of wildlife resources, recreational ethics related to fair chase and “canned hunts,” the public perception of hunting, commercialization and domestication of wild animals, and ecological stewardship within the wildlife profession.

Our secondary objective is to include a discussion of the implications of non-domesticated, native ungulate confinement on our natural resources.

OVERVIEW OF FENCING

High fences may be used in conjunction with intensive ungulate management to prevent egress of animals and to

increase effectiveness of actions to manipulate density, sex ratio, and age structure by limiting animal movement between properties. High fences control access to older-aged males, some of which have been afforded protection from earlier harvest. If harvest rates are adequate, increased control results in ungulate densities lower than surrounding properties. However, some fenced populations do not receive harvest rates sufficient to control population density, resulting in overpopulation. Ungulates may also be confined for commercial production of venison, hide, velvet, hard antler, or breeding purposes. In some jurisdictions, specialized fencing requirements are used to minimize contact between confined and free-ranging populations.

The acreage included within high fenced enclosures varies dramatically. Enclosure size varies from one-acre breeding pens up to population-level management enclosures of 30,000 to 40,000 acres. Generally, the smaller holdings generate the most significant biological and social issues.

In a 2001 survey, 58 American states and Canadian provinces documented the extent and circumstances associated with construction of ungulate enclosures (K. M. Hunt, Department of Wildlife and Fisheries, Mississippi State University, unpublished data). Fencing was allowed in 49 of 58 (85%) responding states–provinces, but 27 of those had some restrictions relating to the practice. Nine of 58 (15%) states–provinces forbade enclosures through a law or agency regulation. Of those forbidding enclosures, 3 states–provinces “grandfathered” enclosures remaining from the period before regulation. Fencing of free-ranging ungulates was not allowed in 43 of 58 (74%) responding states–provinces. Of the 15 (26%) states–provinces that allowed enclosure of free-ranging ungulates, 11 (71%) considered the enclosed animals to be public property even after being enclosed. In 3 of the 4 states–provinces where animals became private property, the enclosure owners were required to pay compensation to the state or province for the enclosed animals. A detailed list of 2002 state regulations related to chronic wasting disease are available from the Michigan Department of Natural Resources at <http://www.schmitts@michigan.gov> (S. M. Schmidt, Michigan Department of Natural Resources, personal communication).

Physical Characteristics

Fences used to confine ungulates have various names representing either the type of fence or the reason for the confinement. A partial list includes high fence, game fence, elk (proof) fence, and deer (proof) fence.

The most typical high fence is 2.4-m-tall, 12-gauge or greater woven wire fence with vertical stays placed at 15-cm

intervals and 17 evenly spaced horizontal wires creating a 15-cm × 15-cm mesh. The woven wire often attaches to and is suspended from a heavier gauge, high tensile wire running between posts. The most common posts are round, pressure-treated wood, 15 cm in diameter or greater, and, depending upon soil conditions, buried 1–2 m deep. Pipe greater than 2.5 cm in diameter may also be used as posts. Occasionally, steel posts are alternated with wooden posts. Corners and stress points are braced. Gates are designed with similar height and mesh characteristics to the fence. Fences may be buried to prevent movement of predators under the fence.

An available variation of the woven wire fence is to stagger the mesh diameter. The spacing of horizontal wires is variable and creates a fence with the lower 1.25 m composed of, in ascending order, 8 × 18-cm, 10 × 18-cm, and 13 × 18-cm mesh sizes. Smaller mesh sizes lower on the fence exclude predators and confine neonates. Fences confining valuable white-tailed deer are frequently extended to 3 m by adding 2 smooth, high tensile wires above the 2.4-m woven wire, with the added benefit of protecting the fence from falling vegetation.

Other fence designs are becoming more common (Palmer et al. 1985). Electric fencing is often attractive because maintenance costs are lower. High tensile wire fences with 5–9 horizontal wires are used in some locales. Low fences may be used to confine non-jumping ungulates such as pronghorn and blackbuck antelope.

Double fencing (i.e., 2 parallel 2.4-m or higher fences situated 2–3 m apart) is required by some regulatory agencies when confining ungulates in situations where escape or direct contact with wild animals would pose significant adverse consequences.

Distribution

The extensive use of high fences to restrict ungulate movements began in Texas in the 1930s as a way to confine exotic wildlife (J. Cooke, Texas Parks and Wildlife Department, personal communication). Under Texas law, exotics are considered livestock and fencing limits their movement onto neighboring properties. The number of exotic species and individuals confined within high fences in Texas has increased steadily; the most recent survey showed that high fences confined 118,000 individuals from 71 exotic species (Traweek 1995). The exotic species most commonly confined in high fences were axis deer, blackbuck antelope, and fallow deer. Roughly 1,000 properties in Texas are high fenced, with the total area confined by fence estimated to be 1.6 million ha, confining about 200,000 whitetails or 4.6% of the statewide white-tailed deer population (E. L. Young, Texas Parks and Wildlife Department, unpublished data).

Some fenced areas exceed 8,000 ha (S. J. Williamson, Wildlife Management Institute, personal observation).

Fencing of ungulates has increased greatly in recent years. Mississippi contains a minimum of 65 high-fenced enclosures and most were constructed within the last 10 years; small, private breeding pens are not allowed (L. E. Castle, Mississippi Department of Wildlife, Fisheries, and Parks, personal communication). In Wisconsin there are 947 high-fenced facilities containing 35,000 captive cervids. Of these fenced facilities, 575 contain 17,500 white-tailed deer, 272 contain 10,815 elk, 43 contain 4,480 red deer, 17 contain 149 reindeer, and 40 contain 2,333 exotics such as fallow deer (T. Hauge, Wisconsin Department of Natural Resources, personal communication). From 1994 to 1998 in Michigan, the numbers of captive deer and elk have grown 50% and 100%, respectively, with 21,000 deer and 2,600 elk enclosed in 1998 (Coon et al. 2002). Most enclosures in Michigan are relatively small, with 76% less than or equal to 8 ha (20 ac, Coon et al. 2002).

BIOLOGICAL ISSUES

Behavioral Impacts

Movements and Home Range

When a wild ungulate is confined by the construction of a high fence, movement patterns within the animal's daily or seasonal home range may be altered. Construction of a high fence may also exclude wild ungulates from important habitats located within the fence. While most animals will quickly adapt to such a change, exclusion from critical habitat types may impact survival or production.

In some areas, periodic droughts cause ungulates to wander widely in search of forage or water supplies (Urness 1981, Cooke 1993). Movements would be limited during drought conditions in South Texas today due to the proliferation of high fences (J. Cooke, Texas Parks and Wildlife Department, personal communication). In the northern United States and Canada, periodic severe winter weather causes ungulates to move to winter ranges where forage is most readily available, or where vegetation buffers snow depth. Winter ranges are not static (Kelsall 1969, Nelson and Mech 1986) and weather patterns determine which ranges are chosen within a season, or between years. High fences likely limit the ability of individuals to seek alternate home ranges in times of climatic stress.

Ungulate home range size varies with population dynamics, environmental factors, and habitat quality. Wild ungulates home ranges are frequently extensive (e.g., Demarais et al. 2000), so that only the largest high-fenced areas could possibly provide all components of a typical home range. In

Michigan, for example, 76% of ungulate enclosures were <8.1 ha in size (Coon et al. 2000). Most high-fence operations, therefore, must provide supplemental food and/or water for the confined animals. The negative consequences associated with supplemental feeding, including disease transmission, ungulate overabundance, societal disapproval, and threats to human health and safety, are highlighted in Williamson (2000).

Dispersal and Migration

Ungulate population dynamics regularly include dispersal by young animals. Where habitat quality is patchy, dispersal distances may be significantly greater than norms presented here. Yearling male white-tailed deer typically disperse from 3 to 10 km from natal ranges (Demarais et al. 2000). Black-tailed deer move 12–15 km (Bunnell and Harestad 1983). Elk may move hundreds of kilometers when dispersing (Adams 1982). Moose calves distanced themselves from their mothers by an average of 14.8 km (Labonte et al. 1998). High fences, almost without exception, curtail normal dispersal patterns. A high fence in New York with 5 openings that allowed deer to move in and out of the enclosure delayed emigration of yearling male white-tailed deer (Nielsen et al. 1997).

Seasonal migrations of ungulates may be quite extensive, depending upon the species. White-tailed deer in Michigan, for example, moved an average of 8 km between summer and winter ranges (Van Deelan et al. 1998). High fences exclude confined animals from migratory ranges located outside of the fence. High fences may also disrupt migration patterns of free-ranging animals if high fences surround critical migratory range or block important corridors used by ungulates to access migratory ranges. In Wyoming, for example, a landowner blocked the migration pathway of a pronghorn herd with a fence, resulting in excessive winter mortality (H. Harju, Wyoming Game and Fish Department, personal communication). The fence design was subsequently altered to allow pronghorn to cross.

Habitat Impacts

Confining ungulates for wildlife management purposes is an extremely intensive and costly management technique. On properties where reduced ungulate density is a management goal, such as on 2 Texas Parks and Wildlife Department management areas, vegetative diversity within high fenced areas may be greater than habitats outside the fence. However, on those properties with higher ungulate densities, vegetative conditions within the enclosure may be reduced.

Within high fences, the interacting effects of confinement, high ungulate density and supplemental feeding, result in ungulate populations that can quickly exceed carrying

capacity. Vegetative diversity and ecological health decline in areas where ungulate populations are allowed to exceed carrying capacity (Miller et al. 1992, Stromayer and Warren 1997, Miller and Wentworth 2000). Impacts of exceeding carrying capacity are not limited to ungulates. Excess herbivory has been shown to affect other species of wildlife that feed, nest, roost, or hide in lower canopy levels or dense grasses (Casey and Hein 1983, deCalesta 1994, McShea 1997). Many confined ungulate populations existing today subsist on overbrowsed or overgrazed ranges and supplemental nutrition is provided.

Vegetative diversity may be significantly higher inside high fences designed to limit ingress of animals into areas practicing density control through hunting. Many high fenced ranches in Texas could serve as demonstration areas for sustainable management of healthy white-tailed deer populations and native vegetation. Managed stands of native “brush” in southern Texas can rarely be improved upon as deer habitat and high fences help managers control the level of herbivory on native forages. When combined with habitat management and regulation of grazing pressure by domestic livestock, high-fenced ranches enclose some of the most ecologically diverse areas in Texas (S. J. Williamson, Wildlife Management Institute, personal observation).

Impacts on Non-ungulate Species

Few studies have documented impacts to other species of wildlife from high fences. Most small to medium-sized mammals can move under, through, or over high fences, except when high fence designs are employed specifically to deny access to predators (i.e., 8-cm +/- mesh sizes with the bottom buried). Clevenger et al. (2001) found that black bears, grizzly bears, and cougars easily climbed and crossed a 2.4-m-high fence designed to keep ungulates off highways in British Columbia. Coyotes frequently crossed by crawling underneath the gaps in the fence created by uneven topography (Clevenger et al. 2001). High fences rarely confine or exclude javelinas in South Texas (S. J. Williamson, Wildlife Management Institute, personal observation).

Birds are not confined by a high fence designed to confine ungulates, but may be susceptible to collisions with the fence. Baines and Summers (1997) and Catt et al. (1994) documented mortality of woodland grouse in Scotland caused by collisions with wire mesh fences designed to exclude red deer from forestry plantations.

Diseases and Parasites Associated with Confinement

Disease often tops the list of issues related to wild ungulate farming and ranching from the perspective of the wildlife manager (Samuel and Demarais 1993). Disease issues have

been reviewed by Miller and Thorne (1993), and most are still valid. Managers of domestic and wild species have concerns about infectious diseases. Depending on circumstances, infectious diseases may impact animal agriculture due to direct morbidity and mortality and associated lost productivity and economic costs. Disease may result in restrictions on trade involving movement of animals or animal products possibly carrying pathogens, and some diseases may have public health implications. Additionally, disease may influence local populations directly (for example, outbreaks of hemorrhagic disease), and concerns about translocating pathogens may impact movement of wild ungulates for restoration and translocation purposes (e.g., testing requirements imposed on animals crossing jurisdictional lines, animal sourcing). Finally, questions may arise about the safety of venison for human consumption.

In general, most free-ranging and captive ungulates are healthy. However, infectious diseases are a concern whenever animals are maintained at high densities, thus facilitating transmission of pathogens. High density populations may also be subjected to nutritional, environmental, or social stressors, which may reduce immunocompetence (Griffin 1989). When animals of different species and from various sources are mixed, exposure of naive individuals to pathogens may increase their disease risk. When these circumstances occur in confined wild ungulates, there may be risks to free-ranging ungulates. The risk of transmission of diseases from captive ungulates to free-ranging ungulates (and potentially from free-ranging ungulates to captive ungulates) depends upon the management circumstances (e.g., fencing, geography, etc.), the likelihood of direct or indirect contact between the captive and free-ranging species, and the routes of transmission of any given pathogen. Some pathogens may occur in geographically limited populations of free-ranging ungulates; however, good management practices dictate that introduction of new pathogens into wild populations should be avoided. Our focus is on diseases of cervids and highlights those diseases that have the greatest potential to impact free-ranging ungulates in North America.

Chronic Wasting Disease

Chronic wasting disease (CWD) of cervids is a transmissible spongiform encephalopathy (TSE), which has similarities to several diseases of humans (kuru, Creutzfeldt-Jakob Disease [CJD], and variant CJD) and animals (bovine spongiform encephalopathy or BSE ["mad cow disease"] and scrapie of domestic sheep). These diseases apparently are caused by proteinaceous agents called prions that are devoid of nucleic acids (Prusiner 1982).

Chronic wasting disease recently was reviewed (Williams and Miller 2002). It was first recognized in the late 1960s as

a clinical syndrome among captive mule deer at wildlife research facilities in northeastern Colorado (Williams and Young 1992). In 1977 CWD was determined to be a spongiform encephalopathy by microscopic examination of brains from affected animals (Williams and Young 1980). Shortly afterward, CWD was recognized among captive mule deer at a wildlife research facility in southeastern Wyoming; animals had been exchanged between the Colorado and Wyoming facilities over the years. Diagnosis of CWD in Rocky Mountain elk from these same facilities followed (Williams and Young 1982).

In 1981, CWD was recognized in a free-ranging elk in Colorado (Spraker et al. 1997). Subsequently, it was found in free-ranging elk in Wyoming and in free-ranging mule deer and white-tailed deer in both states. The known distribution of CWD in free-ranging cervids has expanded rapidly in recent years. It occurs endemically in southeast Wyoming and northeast Colorado (Miller et al. 2000) and portions of the panhandle of Nebraska (B. Morrison, Nebraska Game and Parks Commission, personal communication). It was recently diagnosed in deer in southwestern Wisconsin (T. Hauge, Wisconsin Department of Natural Resources, personal communication), southern New Mexico (K. Mower, New Mexico Game and Fish Department, personal communication), western Saskatchewan, western South Dakota (R. Fowler, South Dakota Department of Game, Fish and Parks, personal communication), and on the western slope of the Rocky Mountains in Colorado (M. W. Miller, Colorado Division of Wildlife, personal communication). The source of CWD in free-ranging deer in Nebraska may have been a game farm with CWD-positive animals (B. Morrison, Nebraska Game and Parks Commission, personal communication) and there may be a link between elk farms with CWD in Saskatchewan and CWD in free-ranging deer. Studies are ongoing to understand the epidemiology of these situations and to determine the degree of infection in the local free-ranging deer populations. Many states and provinces are currently conducting surveillance in populations of free-ranging deer and elk and over the last few years thousands of cervids have been tested and found negative for CWD.

Within the last 5 years, CWD has become a disease of considerable concern within the captive cervid industry in North America after its diagnosis in elk on game farms in Saskatchewan and South Dakota during 1996 and 1997, respectively. This was followed by recognition of CWD in elk on game farms in Nebraska, Oklahoma, Colorado, and Montana, and most recently in Kansas (L. Creekmore, United States Department of Agriculture, personal communication). The presence of CWD has led to quarantine and/or slaughter of elk herds. The number of animals involved is large; over 8,000 privately owned elk in

Saskatchewan and 1,600 elk in Colorado have been or are scheduled for depopulation. Chronic wasting disease in the commercial elk industry forced the United State Department of Agriculture to declare CWD an animal health emergency (USDA 2001a) in order to obtain funding for indemnity to compensate owners of elk slaughtered to control CWD in the industry. A federal CWD management program for the captive cervid industries is currently being developed.

The origin of CWD within the captive cervid industry is not known and there are currently no known direct epidemiologic links to the free-ranging cervids in Wyoming, Colorado, or Nebraska. Chronic wasting disease in free-ranging cervids predates recognition of the disease in the captive elk industry. The epidemiology of CWD in the commercial cervid industry in North America is being investigated and the geographic extent will become better known as federal, state, and provincial control and monitoring programs are instituted.

Only 3 species of Cervidae are known to be naturally susceptible to CWD: mule deer, white-tailed deer, and Rocky Mountain elk. Subspecies of these cervids probably are also naturally susceptible, as was demonstrated by diagnosis of CWD in a black-tailed deer resident in a CWD endemic facility (Williams and Young 1980). Of concern to the captive cervid industry is the likelihood that other subspecies of *Cervus elaphus* (red deer, Manitoba elk, tule elk) also are susceptible to CWD.

Domestic livestock are not known to be naturally susceptible to CWD. A few cattle, sheep, and goats have resided in research facilities with CWD for prolonged periods without developing the disease. Three of 13 cattle developed CWD following intracerebral inoculation with an incubation period of between 24 and 27 months (Hamir et al. 2001). Cattle exposed to CWD agent via oral or contact routes remain healthy approximately 50 months post-inoculation, but these studies are planned to continue for a total of 10 years.

The specific routes of transmission of CWD are unknown. There is no evidence that CWD is a food borne disease associated with rendered ruminant meat and bonemeal, as was the case in BSE (Wilesmith et al. 1988). Occurrence of the disease among captive deer and elk, many of which were acquired from the wild, and field and model data provide strong evidence of lateral transmission (Williams and Young 1992; Miller et al. 1998, 2000). Maternal transmission may also occur; however, this has not been definitively determined. The epidemiology of CWD in free-ranging cervids is actively under study (Spraker et al. 1997, Conner et al. 2000, Miller et al. 2000, Gross and Miller 2001).

Lymphoid tissues associated with the digestive tract (tonsil, cervical lymph nodes, Peyer's patches, mesenteric and

ileocecal lymph nodes) of affected deer and elk contain PrP^{res} (Sigurdson et al. 1999, Williams and Miller 2000), thus alimentary tract shedding may also occur in CWD. The TSE agents are extremely resistant in the environment (Brown and Gajdusek 1991); pasture contamination has been suspected of being the source of prions in some outbreaks of sheep scrapie (Greig 1940, Pálsson 1979). Observations strongly suggest fence-line contact and/or environmental contamination as the source(s) for the CWD agent (Williams et al. 2000). Concentration of deer and elk in captivity or in the wild by artificial feeding may increase the likelihood of transmission between individuals.

Modeling studies indicate lateral transmission among free-ranging cervids is necessary to maintain CWD at the prevalence observed in the endemic areas. The models also suggest that CWD has been present in free-ranging populations for >30 years (Miller et al. 2000). Maternal transmission may occur, but this route of transmission alone when used in the model was not adequate to maintain the disease at observed levels (Miller et al. 2000).

Currently there is no validated diagnostic for CWD that can be used on a large scale on live animals. However, because PrP^{res} can be detected in lymphoid tissues early in the incubation period before the animals are showing clinical signs (Sigurdson et al. 1999), biopsy of tonsil and use of immunohistochemistry has promise in a research setting (Williams et al. 2002, Wolfe et al. 2002). This testing requires that the animal be anesthetized to obtain the biopsy; thus, this technique is not suited to testing of large numbers of animals.

There is no known treatment for animals affected with CWD and it is considered 100% fatal once clinical signs develop. If an affected animal develops pneumonia, treatment with antibiotics might prolong the course of illness, but will not alter the fatal outcome.

Control of CWD is problematic. Designing methods for control or eradication of CWD is extremely difficult in the face of long incubation periods, subtle early clinical signs, absence of practical antemortem diagnostic tests, the extremely resistant infectious agent, possible environmental contamination, and our lack of understanding of the mode of transmission. Management currently involves quarantine or depopulation of captive CWD-affected herds. Two early attempts to eradicate CWD from captive cervid facilities failed; the cause of the failure was not determined, but residual environmental contamination following facility clean-up was possible (Williams and Young 1992). Management of premises after depopulation for CWD remains controversial. It is not known if these premises could pose a risk to free-ranging cervids. The United States

Department of Agriculture has developed a proposed program for management and eradication of CWD from the captive cervid industry (United States Department of Agriculture 2001b).

Management of CWD in free-ranging animals is even more problematic (Gross and Miller 2001). Long-term active surveillance to determine distribution and prevalence of CWD has been instituted to assist in evaluating changes over time and the effect of management intervention. Translocation and artificially feeding cervids in the endemic areas has been banned in an attempt to limit range expansion and to decrease transmission of CWD. Localized population reduction in areas of high CWD prevalence is being conducted on an experimental basis in Colorado (M. W. Miller, Colorado Division of Wildlife, personal communication) and on a 374-square-mile CWD eradication zone in Wisconsin (Wisconsin Department of Natural Resources 2002). Simulation modeling suggested that selective culling for CWD control must be initiated when prevalence is very low (<0.01%) to be effective in eliminating CWD (Gross and Miller 2001).

No cases of human disease have been associated with CWD and a recent World Health Organization consultation stated that CWD is not currently known to affect humans (World Health Organization 2000). Investigation of several cases of Creutzfeldt-Jakob disease in young people in the United States who had hunted or consumed venison did not reveal a link to CWD (Belay et al. 2001). However, in the absence of complete information and in consideration of the similarities of animal and human TSEs, the public health concerns remain one of the reasons why CWD is important for wildlife managers.

The question of commercial marketing of elk carcasses from CWD-exposed animals for venison is being examined. Following slaughter or depopulation of elk from herds with CWD, brains are tested by immunohistochemistry. Test negative animals have been passed for human consumption in some states, while in other states all carcasses from depopulated animals have been destroyed. The Centers for Disease Control and Prevention (E. Belay, Centers for Disease Control and Prevention, personal communication) have recommended that carcasses from CWD-exposed herds not go into the commercial venison market because of lack of "informed consent" on the part of consumers. The presence of CWD in captive and free-ranging cervids is a serious wildlife management problem. Indemnity for depopulated cervids has just been made available in the United States and is being used to compensate owners of affected herds in Canada. Guidelines for management of captive herds with CWD are being developed by federal,

state, and provincial animal health officials in consultation with the affected industries, public health officials, wildlife management agencies, nongovernmental organizations, and the public.

Implications for free-ranging populations of deer and elk are significant. Deer and elk should not be translocated from CWD-endemic areas. Surveillance programs are expensive for wildlife management agencies. The impacts of the disease on the population dynamics of deer and elk are not currently known. Modeling suggests that CWD could detrimentally affect populations of mule deer (Miller et al. 2000, Gross and Miller 2001), though effects on free-ranging elk are much less likely.

Bovine Tuberculosis

Bovine tuberculosis (TB) is a bacterial disease caused by *Mycobacterium bovis*. It has a relatively wide host range, including humans, domestic animals, and wildlife. Because of public health concerns, as well as the economic impact of the disease in domestic cattle, bovine tuberculosis has been the subject of a state-federal eradication program involving the United States Department of Agriculture, state departments of agriculture, and the cattle industry for many years. Bovine tuberculosis is nearly eradicated from domestic cattle and game-farm cervids in the United States.

Bovine tuberculosis in game-farmed cervids became a serious problem in North America during the 1980s (Stumpff 1982, Miller et al. 1991, Essey 1992b, Rhyan et al. 1992, Thoen et al. 1992, Haigh and Hudson 1993, Whiting and Tessaro 1994). After a gap of less than 10 years without a recognized outbreak of TB in elk, the disease was identified in game-farm elk imported to Canada that originated from Montana (Essey 1992a). This recognition resulted in Canada closing the border to importation of cervids from the United States and extensive testing of captive elk and deer in herds across Canada and the United States.

Control of the disease was difficult because of lack of government compensation programs at adequate market value for elk that were killed. Several states lost tuberculosis-free status when cattle became infected from contact with elk (Essey 1992a) or other cervids, resulting in considerable hardship to livestock producers in affected states. Game-farm cervids are now included in the Cooperative State-Federal Bovine Tuberculosis Eradication Program in the United States using the Uniform Methods and Rules for the Eradication of Tuberculosis in Cervidae.

Surveillance of free-ranging wild animals in areas adjacent to one affected game farm detected *M. bovis*-infected mule

deer and coyotes (Rhyan et al. 1995, Whipple et al. 1997). Subsequent surveillance has not detected persistence of *M. bovis* in wildlife in this area. Bovine tuberculosis is not currently known to be present in populations of free-ranging elk in the United States (Williams et al. 1995), but it occurs in a herd of elk in Manitoba.

There are relatively few examples of maintenance of TB in populations of free-ranging wild ungulates (Clifton-Hadley and Wilesmith 1991, Clifton-Hadley et al. 2001). Sporadic cases of TB were reported in the earlier part of the century in white-tailed deer (Schmitt et al. 1997); these cases were thought to have been directly due to transmission from affected cattle to wild ruminants. At that time, TB was relatively common in cattle herds and populations of wild ruminants were generally low, thus decreasing the likelihood that the disease would be maintained as self supporting infections within populations of free-ranging ungulates. However, under conditions of increased wild ruminant density, TB can be a significant problem.

Bovine tuberculosis was reported in elk, bison, and moose from Elk Island National Park, Alberta, in the 1950s, but was not maintained among those species following population reduction (Corner and Connell 1958). It is, however, maintained in populations of free-ranging red deer and elk in New Zealand (O'Neil and Pharo 1995, Clifton-Hadley et al. 2001). The presence of TB in free-ranging white-tailed deer in Michigan is a serious problem.

Currently, TB is endemic in a dense white-tailed deer population in northern Michigan (Schmitt et al. 1997). The disease was perpetuated among these deer by the practice of winter feeding that greatly concentrated the deer, thereby increasing the rate of transmission. It has resulted in significant changes in how these animals are managed and has brought public health and agricultural agencies, as well as the Michigan DNR, into the business of disease management of free-ranging species. Considerable personnel and monetary resources are currently being expended in Michigan for surveillance and management, with eradication of the disease in free-ranging white-tailed deer the goal. The consequences of establishment of TB in additional free-ranging cervid populations would be serious (Thorne et al. 1992, Schmitt et al. 1997).

The clinical signs of TB in elk and red deer have been reviewed (Clifton-Hadley and Wilesmith 1991). Diagnosis of mycobacterial infection may be difficult (Clifton-Hadley and Wilesmith 1991, Rhyan et al. 1992, Rhyan and Saari 1995). Culture and identification of *M. bovis* is required for definitive diagnosis of TB.

None of the antemortem diagnostic tests are completely reliable in individual animals, but they are useful for

detecting infected herds (Haigh and Hudson 1993). Diagnosis of *M. bovis* infection in game-farm cervids is by skin testing (single cervical test, comparative cervical test). These tests are conducted by an accredited veterinarian and require a 3-day holding period between injection and evaluation of the test. Some additional tests are approved for use in game-farm elk, depending on the state or province.

Bovine tuberculosis is transmitted primarily by the respiratory route. An infected animal coughs and expels bacteria and exudates in an aerosol. If a susceptible animal inhales the bacteria, colonies may form in the lung. High densities of animals increase transmission between infected and susceptible animals. Exposure may also occur orally from consumption of forage and feed contaminated with the bacteria, in which case, the bacteria probably first infects the tonsils or lymph nodes associated with the digestive tract. Concentration of animals around feeding troughs probably facilitates both aerosol and oral transmission (Clifton-Hadley and Wilesmith 1991). Calves may become infected by nursing dams shedding the bacteria in milk associated with lesions in the mammary glands.

The organism has a thick, protective, waxy outer coating and hence is relatively resistant in the environment. Organisms survive protected in feces for months, but under conditions of exposure to sunlight (ultraviolet light), such as on open pastures, fluctuations in temperature, and desiccation, the organism may only remain viable for days or weeks (Mitscherlich and Marth 1984, Jackson et al. 1995).

Though predators and scavengers serve as significant reservoirs of bovine tuberculosis in the United Kingdom, where European badgers are important (Clifton-Hadley et al. 1993, 2001), and New Zealand, where brush tailed possums and feral ferrets are free-ranging reservoir species (Morris and Pfeiffer 1995, Clifton-Hadley et al. 2001), no such wild reservoir is considered significant in North America. Wolves, coyotes, raccoons, black bear, and bobcat (Tessaro 1987, Whipple et al. 1997, Bruning-Fann et al. 1998, 2001) may become infected, presumably via consumption of carcasses of tuberculous ungulates.

Humans are susceptible to TB, though it is not nearly as common in humans as tuberculosis caused by *Mycobacterium tuberculosis*. Some humans in contact with game-farmed elk became infected and skin-tested positive (Fanning 1992, Stumpff 1992).

Meningeal Worm

Meningeal worm (*Parelaphostrongylus tenuis*) belongs to a small group of lungworms that are associated with connective tissues of the central nervous system and

musculature of Cervidae. The biology of this parasite recently has been reviewed by (Lankaster 2001). Its usual definitive host is white-tailed deer. Meningeal worm is found throughout the deciduous forests of eastern North America and has not been recorded west of approximately 105° W. longitude. Intermediate hosts are terrestrial snails and slugs.

Meningeal worm is relatively innocuous in white-tailed deer, but it can cause a serious neurologic disease in many domestic and wild ungulates. Neurologic disease has been observed in naturally or experimentally infected caribou (Anderson and Strelive 1968), elk (Carpenter et al. 1973, Samuel et al. 1992), fallow deer (Pybus et al. 1992), moose (Anderson 1964), mule deer (Tyler et al. 1980), bighorn sheep (Pybus et al. 1996), pronghorn antelope (Anderson and Prestwood 1981), llama (Rickard et al. 1994), domestic sheep (Pybus et al. 1996), and domestic goats (Anderson and Strelive 1972).

Diagnosis of meningeal worm infection is by examination of feces for first-stage larvae using some version of the Baermann technique. The larvae of *P. tenuis* have a dorsal spine (dorsal-spined larvae). Recently developed techniques may assist in diagnosing *P. tenuis* infection by blood tests (enzyme-linked immunosorbent assays, Bienek et al. 1998, Ogunremi et al. 1999), but these have not been fully validated or used in the field.

Because larval shedding may be intermittent, experiments suggest that infected elk could go undetected by currently used diagnostic techniques (Welch et al. 1991). Samuel et al. (1992) successfully infected white-tailed deer with elk-origin larvae, proving that transmission from elk to deer is possible.

Treatment of white-tailed deer with ivermectin (an anthelmintic) is not effective in removing adult *P. tenuis*. The drugs may induce temporary cessation of larval shedding in deer feces (Kocan 1985, Samuel and Gray 1988), resulting in false negative fecal examinations. Thus, requirements for fecal examinations to detect *P. tenuis* infection for the purposes of excluding infected animals need to take the possibility of ivermectin treatment causing false negative results into consideration.

For meningeal worm to become established in a new area, first-stage larvae in feces of a definitive cervid (white-tailed deer or elk) must reach local terrestrial gastropods and develop to the infective stage. The snails and slugs must then be ingested by suitable ungulate hosts. Only a few gastropods are important intermediate hosts for meningeal worms (Lankaster and Anderson 1968, Lankaster and

Samuel 1998); several of these are widely distributed across western North America, where *P. tenuis* does not occur.

The risk of accidental introduction of *P. tenuis* to susceptible ungulate populations in western North America through movement of deer and elk has generated considerable concern and controversy (Samuel 1987, Samuel et al. 1992, Miller and Thorne 1993). Meningeal worm could become established in western North America if the parasite were introduced in areas where there are populations of white-tailed deer, appropriate gastropod intermediate hosts, and conditions suitable for survival of the worms.

Paratuberculosis

Paratuberculosis, also called Johne's disease, is a bacterial disease primarily affecting the digestive tract of cattle, caused by *Mycobacterium avium paratuberculosis*. All bovids and cervids are considered susceptible to infection and disease caused by this bacterium (Williams 2001). This organism, which is distantly related to *M. bovis* (the cause of TB), also is quite resistant in the environment. It may persist in soil for a year or longer (Mitscherlich and Marth 1984), but it is relatively sensitive to exposure to ultraviolet radiation from sunshine, drying and high temperatures. Under natural conditions, it probably remains viable less than a year in the environment.

Chiodini et al. (1984) reviewed general features of paratuberculosis in ruminants and a more recent review covers the disease in small ruminants and deer (Stehman 1996). It is a disease with primary effects on the intestinal tract. High densities of susceptible animals contribute to transmission of this infection. The incubation period is prolonged and may take years. Thus, young animals are seldom clinically affected, though they may be infected, and the disease is primarily observed in mature animals.

Paratuberculosis has been reported in many species of wild ruminants (Williams and Spraker 1979, Chiodini et al. 1984), but in North America it is only known to be endemic in a herd of tule elk in California (Jessup et al. 1981), in a small population of Key deer in Florida (C. Quist and V. Nettles, Wildlife Health Associates, Incorporated, personal communication), and in several herds of bighorn sheep and mountain goats in one area of Colorado (Williams et al. 1979). Paratuberculosis has been maintained in tule elk at Point Reyes National Seashore, California (Jessup et al. 1981), for at least 20 years (Cook et al. 1997). These elk probably contracted the disease via contact with pastures contaminated by dairy cattle infected with *M. avium paratuberculosis* (Jessup et al. 1981). Rocky Mountain elk are susceptible to experimental infection by the oral route (Williams et al. 1983a), but clinical disease has not been

observed in free-ranging elk other than at Point Reyes. This disease is of concern in the game farming industry, where it exists (Gilmour 1984, Griffin 1988, Haigh and Hudson 1993, Power et al. 1993), but the prevalence in North America is not known.

Diagnosis of paratuberculosis in the live animal is difficult, as is true of many mycobacterial diseases (Thoen and Haagsma 1996). There are several types of blood tests (ELISA tests, complement fixation tests, immunodiffusion tests) that measure antibody production and other blood tests (lymphocyte blastogenesis tests) that detect cell-mediated immunity. However, none of these tests are ideal and false negative and false positive results are possible. Culture of feces for the bacteria is a definitive method of diagnosis. This method is useful on a herd basis, but it lacks sensitivity in individual animals because of sporadic shedding of the organism in the feces of subclinically infected individuals. There are newer tests for detection of *M. avium paratuberculosis*, including radiometric detection (Collins et al. 1990, Cook et al. 1997) and molecular techniques (de Lisle and Collins 1995, Thoen and Haagsma 1996), but none are completely satisfactory.

Environmental conditions and animal behavior play a role in maintenance of this organism in free-ranging populations. The bacterium survives best under humid conditions with reduced exposure to sunlight (ultraviolet radiation). Thus, paratuberculosis is seldom a problem in dry, high-elevation environments. Because the organism is shed in feces, and transmission is via ingestion, behavior which concentrates animals, especially at a young age, will potentiate transmission of the organism.

The presence of paratuberculosis in herds of free-ranging wild ruminants is a management problem for several reasons. This disease may be fatal in a small percentage of animals, with a great many other animals having subclinical infections. These subclinical animals may shed the organism into the environment, thus serving as a reservoir of the organism for other susceptible animals. The biological effect of subclinical infection on individual animal performance is not known for wild species, but paratuberculosis is considered economically significant in domestic livestock. Herds of wild ungulates with paratuberculosis are usually not considered suitable as source herds for relocations, though quarantine protocols have been developed in an attempt to manage growing tule elk populations with paratuberculosis by transplantation. The presence of paratuberculosis in free-ranging ungulates causes conflicts with agricultural interests. The prevalence of paratuberculosis in captive cervids is not known.

A controversy exists as to the zoonotic potential of paratuberculosis. Some researchers have reported evidence linking *M. paratuberculosis* with Crohn's disease of humans (Chiodini and Rossiter 1996, El-Zaatari et al. 2001), but other researchers do not believe there is an association between these conditions (Van Kruiningen 1999). Even if such a relationship was confirmed, the possibility that humans would contract this disease from contact with wild ungulates or their feces seems unlikely.

Diseases of Lesser Concern

Diseases of less concern are thus categorized due to low likelihood for transmission from confined to free-ranging ungulates. The consequences of transmission, should it occur, probably would be less serious than for the previously discussed diseases.

Cervid adenoviruses. The importance and distribution of adenoviruses in cervids is currently unknown. A large outbreak of adenoviral hemorrhagic disease in California among free-ranging black-tailed and mule deer in the 1990s resulted in death of thousands of animals (Woods et al. 1996). Since then, sporadic cases of adenoviral infection have been diagnosed in captive moose and white-tailed deer elsewhere in North America. The epidemiology of cervid adenoviruses is poorly known but the virus (or viruses) is probably much more widely distributed than is currently recognized both among free-ranging and captive cervids. Based on an understanding of the epidemiology of adenoviruses in domestic livestock, it is likely that many animals may be exposed to the virus and only under stressful conditions is overt disease manifested.

Transmission is probably via direct contact and aerosol. There are no commercial diagnostic tests currently available for cervid adenoviruses. Humans and domestic livestock are not known to be susceptible to cervid adenoviruses. Methods to reduce direct contact between free-ranging cervids and alternative livestock would decrease the potential for transmission of cervid adenoviruses from captive to free-ranging cervids or vice-versa.

Cerebrospinal elaphostrongylosis. The biology of these nematode parasites has been reviewed by Lankaster (2001). These are close relatives of meningeal worm (*P. tenuis*). These worms are considered exotic to North America or are only found in geographically limited areas on this continent. Though there is considerable confusion over the taxonomy of these parasites, *E. cervi* is considered to be a parasite of red deer and moose and *E. rangiferi* is naturally found in caribou and reindeer. *Elaphostrongylus rangiferi* was introduced into Newfoundland, Canada, with reindeer originating in Scandinavia and is now established in free-

ranging caribou. *Elaphostrongylus cervi* is a common parasite of red deer and was introduced from Europe into New Zealand when those animals were imported and released. Imported infected red deer have been detected in quarantine facilities in Canada.

In general, these parasites are innocuous worms that live in the skeletal muscles, but occasionally they cause disease in the lung, brain, and spinal cord when they migrate, which may lead to death of the normal host, as well as aberrant hosts such as domestic livestock and other species of cervids. The life cycle of the parasite involves slugs and snails as intermediate hosts. Diagnosis of infection is by examination of the feces for larvae but determination of the species is difficult unless the adult worm is recovered. This is similar to the difficulties encountered when diagnosing *P. tenuis*. Larvae may not always be found in the feces of infected animals because shedding may be low and intermittent, thus repeated testing is required. In addition, treatment with some anthelmintics will reduce larval production for a short time, but will not kill the adult worms, thus false negative diagnostic results may occur when testing fecal samples.

Giant liver fluke. The giant liver fluke *Fascioloides magna* is a natural parasite of white-tailed deer and elk, but it may infect many wild and domestic hosts. Pybus (2001) recently reviewed the biology of this parasite. It provides one of the earliest known examples of introduction of an exotic parasite with translocation of the host, when elk were introduced from North America to Italy in 1865. Since that local introduction, the giant liver fluke has spread into many areas of Europe, causing disease in native wildlife and domestic livestock. When found in high numbers, especially in an abnormal host, the worm can produce extensive lesions in the liver, which may result in death. Intermediate hosts are various aquatic snails, thus the distribution of this parasite is dependent upon adequate habitat (wetlands) to support the snail hosts in adequate numbers. In normal hosts, the parasites form cysts in the liver and eggs are expelled through the bile ducts and out into the environment with the feces. However, in abnormal hosts, including cervids other than elk and white-tailed deer, and in domestic livestock, particularly domestic sheep, the parasites continue to migrate in the liver, which may result in significant impairment of liver function, economic loss due to condemnation of livers at slaughter, and even death.

Malignant catarrhal fever. Malignant catarrhal fever (MCF) is caused by 2 bovid herpesviruses: ovine herpesvirus 2, the cause of “North American” or “sheep-associated” MCF, and alcephine herpesvirus 1, the cause of “African” or “wildebeest-associated” MCF. African form MCF is

considered an exotic disease in North America and African antelope that could be hosts to MCF viruses are regulated in most jurisdictions and are not found on game farms. Clinical MCF occurs in domestic cattle, bison, and cervids, though the species vary in their degree of susceptibility. The epidemiology of ovine herpesvirus 2 infection is still being studied, but it appears that transmission of the virus primarily occurs in association with lambing and contact with neonatal lambs. The potential for other members of the subfamily Caprinae to transmit ovine herpesvirus 2 is not clear. The role that wild ungulates play is far from understood (Li et al. 1996), and white-tailed deer may actually harbor their own MCF herpesvirus (Li et al. 2000). Cervids are usually considered “dead-end hosts” and there is no direct evidence that these species are capable of transmitting the virus.

Septicemic pasteurellosis. Septicemic pasteurellosis in wild ruminants is caused by several serotypes (A:2, A:3,4, B:1, B:3,4) of the bacterium *Pasteurella multocida* (Miller 2001). Disease results when bacterial infection involves the blood; damage to multiple organs follows and results in rapid death. Outbreaks of septicemic pasteurellosis have caused death of elk on the National Elk Refuge, Wyoming (Franson and Smith 1988), and other feedgrounds in Wyoming, and sporadic cases have occurred elsewhere. Septicemic pasteurellosis also occurs in domestic and wild bovids, but the species and serotype of the bacteria varies in different species. Septicemic pasteurellosis is sometimes incorrectly confused with “hemorrhagic septicemia,” which is an infection caused by certain serotypes of *P. multocida* and is considered an exotic disease in North America. Unapparent infection is probably common and the bacterium probably resides in the throat and tonsils. Outbreaks of septicemic pasteurellosis are associated with environmental stress, such as severe winter weather in situations of high density, which facilitates transmission among animals. Transmission is by direct contact and aerosol transmission.

Because the bacterial serotypes that cause septicemic pasteurellosis are probably widely distributed in both free-ranging cervids and confined ungulates and the occurrence of the disease appears to be directly related to environmental conditions and stresses, risk reduction includes managing animals to reduce stress.

Rangiferine brucellosis. Brucellosis caused by *Brucella abortus* (bovine brucellosis) is not known to occur among captive wild ungulates in North America. However, *Brucella suis* biotype 4 causes brucellosis in some populations of free-ranging caribou and reindeer in parts of Alaska and Canada. Thorne (2001) reviewed features of rangiferine brucellosis. Like *Brucella abortus*, the

bacterium is transmitted from an affected animal to a susceptible animal via contact with aborted fetuses, placenta, fluids, and reproductive tract exudates. Cervids other than reindeer and caribou are susceptible to infection, and there is some experimental evidence that rangiferine brucellosis may be fatal in moose. There are no reports of rangiferine brucellosis being maintained in populations of cervids other than *Rangifer*. However, other cervids will develop antibodies that cross-react on serologic tests for bovine brucellosis, which may cause confusion.

Currently Unidentified Diseases and Exotic Diseases

It is important to realize that not all potentially serious pathogens and diseases of captive and free-ranging ungulates have been identified. New diseases (due either to new or newly recognized pathogens or to new species affected by pathogens because of changes in host range) are being found in diagnostic laboratories throughout North America with regularity and it is frequently not possible to predict if these new pathogens or new host-pathogen relationships will have significant impact on populations of wild animals or how we manage them. Obviously, managing for unknown pathogens is nearly impossible. Thus, it becomes very important to maintain disease surveillance in populations of captive, as well as free-ranging, species and to guard against artificially mixing populations of wild ungulates.

In addition, wild ungulates are susceptible to many highly infectious diseases of domestic animals that are classified as exotic by the USDA or CFIA in Canada. It is important to note that foreign animal diseases could affect wild ungulates. For example, wild ungulates in North America are susceptible to foot and mouth disease virus. Introduction of a foreign animal disease into free-ranging ungulates could have devastating effects on wildlife and agricultural industries.

Genetic Diversity and the Management of Wild Ungulates

The intensive management of wild ungulates commonly involves one or more of the following: the establishment of game-proof enclosures, translocations of different genetic stocks, and selective harvest. These actions may affect population demographics and census size and also the patterns of genetic variation as a consequence of altering the breeding structure, reducing the number of breeding individuals, constricting the reservoir of genetic variation in the population, and blocking the infusion of new genetic material. This review describes genetic variation and how it is measured, as well as important population genetic concepts relevant to the confinement and intensive management of wild ungulates. These topics include: effective population size, genetic drift and founder effects, genetic bottlenecks, inbreeding, gene flow and dispersal,

effects of habitat fragmentation and dispersal barriers, hybridization and genetic introgression, outbreeding depression, effects of selective harvest, and the dilution of unique genetic stocks.

Genetic Variation in Natural Populations

Genetic variation in natural populations is present at many different levels, but is typically referred to at the individual or population basis. Heritable genetic mutations are the ultimate source of genetic variation, while recombination results in new arrangements of existing genetic material (Hartl and Clark 1997). Individual genetic variation is usually described by the percentage of loci at which the individual is heterozygous, while population genetic variation is characterized by percentage of polymorphic loci, number of alleles per locus, or expected heterozygosity assuming Hardy-Weinberg equilibrium (Nei 1973, Lacy 1997). Some genetic variation between individuals and populations is quantifiable by phenotypic differences, but much individual and population genetic variation must be visualized at the molecular level by comparing protein or DNA sequences (Falconer and Mackay 1996).

Individual traits, such as developmental stability, growth rate, metabolic efficiency, fertility, survival, and disease resistance, are probably influenced by heterozygosity (Allendorf and Leary 1986, Falconer and Mackay 1996). Thus, population genetic variation is important for long-term persistence of a population in the face of environmental change (Lande 1988). The likelihood of population extinction is influenced by genetic diversity, as evidenced by the high probability of extinction in genetically depleted populations, as well as the association between population genetic diversity and variables which induce extinction (Nunney and Campbell 1993). Our knowledge of genetic variation in natural populations has increased rapidly during the past 3 decades, primarily due to the development of easily identifiable genetic markers and automated analysis techniques. Modern population genetics focuses on understanding the origin, maintenance, and function of genetic variation in natural populations.

Natural populations differ in the level of genetic variability, as well as in the frequency and types of alleles present. Large mammalian taxa exhibit patterns of genetic variation on both broad and fine geographic scales, even when populations are apparently contiguous. Allozyme variation is associated with geographic location in white-tailed deer (*Odocoileus virginianus*, Smith et al. 1984, Sheffield et al. 1985, Carr et al. 1986, Gavin and May 1988, Karlin et al. 1989). There also is evidence that white-tailed deer populations are genetically subdivided on a microgeographic (<8-km²) scale (Sheffield et al. 1985, Kennedy et al. 1987).

Genetic differentiation or subdivision over short geographic distances has been documented in many large mammals, including moose (*Alces alces*, Chesser et al. 1982), mule deer (*O. hemionus*, Cronin et al. 1991), and mouflon (*Ovis gmelini*, Petit et al. 1997). Geographic patterns of genetic variation also vary temporally (Scribner et al. 1997), probably due to demographic and environmental stochasticity.

Effective Population Size

Census size is an important factor determining population genetic variation, but the effective population size (N_e) actually governs the maintenance or loss of genetic variation (Wright 1931, Nei 1987). Effective population size is a complex concept that is usually described as the number of breeding individuals in a population. In reality, N_e for wildlife species is often much smaller than predicted due to fluctuating census and family size, sex ratio, mating system, migration, genetic drift, and other stochastic variation (Wright 1931, Nei 1987).

Genetic Drift, Founder Effect, and Bottlenecks

Another important factor influencing population genetic variation is genetic drift (Wright 1931). Genetic drift is a random process by which allele frequencies fluctuate between generations. Since the alleles present in the offspring generations are a sample of alleles present in the parental generations, the allele frequencies are affected by sampling variation between generations, with sampling variation increasing as the number of parents decreases (Falconer and Mackay 1996). These random fluctuations of allele frequencies are more severe in small populations, where the effect is intensified by unequal reproductive success among the few breeding individuals (Hedrick and Miller 1992). Since all individuals do not contribute equally to reproductive effort, some individuals substantially impact the genetic composition of subsequent generations, while others have little or no contribution. The long-term survival and fitness of small populations is threatened because genetic drift becomes more important than natural selection in their evolution (Lacy 1997).

Two situations where genetic drift may have a large influence on population genetic diversity are founder events and bottlenecks. The founder effect results from establishment of a new population by a small number of individuals (Nei 1987). A bottleneck occurs when a previously large population undergoes a severe reduction in size (Nei et al. 1975, Nei 1987). The genetic structure of the new population is dependent on the genetic variation in the founding individuals and their offspring. In each case, N_e is small and genetic variability is usually decreased in the new population. The effects of the genetic bottleneck may be

long-lived, especially if population size remains small after the bottleneck, because new genetic variation will not accumulate for many generations. For example, species that have undergone known historical bottlenecks typically have little diversity within the major histocompatibility complex (MHC), a genetic system important in disease recognition and resistance. Contemporary populations of Przewalski's horse and Arabian oryx (*Oryx leucoryx*) were founded from <20 individuals and have little MHC diversity (Hedrick et al. 1999, 2000). A population bottleneck predating moose range expansion into North America contributed to low MHC diversity in present European and North American moose populations (Mikko and Andersson 1995). The MHC locus diversity in South African bontebok (*Damaliscus pygargus pygargus*), which underwent 2 severe population bottlenecks, was far less than in non-bottlenecked blesbok (*D. p. phillipsi*, Van Der Walt et al. 2001). Fitzsimmons and Buskirk (1997) found lower allozyme heterozygosity and fewer alleles per locus in 3 of 4 reintroduced bighorn sheep populations compared to the source population. The founding populations were small ($8 > n > 69$) and N_e remained low for 10–20 years post release.

Inbreeding

As population size decreases or populations become subdivided, inbreeding (mating between related individuals) is more likely to occur. Inbreeding increases the probability of 2 alleles at a locus being identical by descent from a common ancestor (Lacy 1997). An increase in the amount of inbreeding decreases heterozygosity, and individuals are more likely to become homozygous for deleterious recessive allele combinations, which are present at low frequencies (therefore rarely expressed) in large, random-mating populations (Falconer and Mackay 1996). Inbreeding depression effects that reduce survival have a greater effect on population extinction probability than on effects that reduce fecundity (Mills and Smouse 1994). Although inbreeding, even at low levels, probably has a greater effect on populations with low growth rates (Mills and Smouse 1994), inbreeding effects on fitness may be tolerable when inbreeding is gradual over time (Falconer and Mackay 1996). This is because there is opportunity to rid deleterious homozygous recessive alleles from the genome through selection (Falconer and Mackay 1996).

Most of our knowledge of inbreeding effects (e.g., reduced fitness and population viability) comes from laboratory animals and domestic livestock, but inbreeding probably affects wild populations similarly (Lacy 1997). Ralls et al. (1979) documented significantly greater juvenile mortality in inbred captive ungulates than in non-inbred captives. Fetal growth, maternal weight, and fetal number are positively associated with allozyme heterozygosity in white-tailed deer

(Cothran et al. 1983, Johns et al. 1996). Multilocus heterozygosity also is correlated to other traits presumably related to individual fitness in white-tailed deer (Smith et al. 1982, Chesser and Smith 1987). Birth weight and neonatal survival are positively correlated with genetic variation in harbor seals (*Phoca vitulina*, Coltman et al. 1998). Coulson et al. (1998) observed heterosis (or "hybrid vigor") where mean allele length divergence at microsatellite loci was positively correlated with birth weight and neonatal survival in red deer, which they attributed to population mixing. Further research revealed sex-dependent differences in juvenile survival associated with inbreeding and outbreeding in red deer (Coulson et al. 1999). Inbreeding depression also affects lifetime breeding success in both male and female red deer (Slate et al. 2000). Inbred Soay sheep (*Ovis aries*) were more vulnerable to intestinal parasites and experienced reduced survival (Coltman et al. 1999).

Gene Flow and Dispersal

Some form of genetic exchange is necessary to link subpopulations and provide a continual source of new genetic material. Individuals which emigrate or disperse from one population into another will introduce their genetic material into the new population if they reproduce. This exchange of genetic material between populations is known as gene flow. Intrapopulation gene flow results in similarity of nuclear alleles and mtDNA haplotypes within a population. Subdivided populations experience reduced gene flow and an increased probability that the patterns of genetic variation will diverge (Honeycutt et al. 1999).

Gene flow is important in maintaining genetic variation in wild ungulate populations since the absence of gene flow would result in genetic substructuring due to social and behavioral factors. This is because individuals within populations may associate and disperse in nonrandom fashion or form social units based upon philopatry or coordinated dispersion of related individuals (Chesser 1991). A typical pattern in large mammals is female philopatry, which may subdivide populations along matrilineal lines (Chesser 1991, Cronin et al. 1991, Mathews and Porter 1993, Mathews et al. 1997). For example, female white-tailed deer commonly are found in matrilineal groups composed of adult females, several generations of female offspring, and juvenile male offspring (Hawkins and Klimstra 1970, Hirth 1977, Mathews and Porter 1993, Mathews et al. 1997). Male dispersal acts to maintain gene flow between these population subdivisions. Yearling male white-tailed deer disperse from their natal groups and may establish new home ranges that are quite distant (Hawkins et al. 1971, Kammermeyer and Marchinton 1976, Nelson and Mech 1984, Dusek et al. 1989). Male white-tails also tend to expand their home ranges during the rut (Tierison et al.

1985), which increases the number of breeding opportunities with different matrilineal lines and facilitates gene flow. An example of the importance of gene flow to diversity is Rocky Mountain bighorn sheep populations, where mtDNA diversity was maintained through metapopulation dynamics despite drastic reduction in census size and continuity of subpopulations (Luikart and Allendorf 1996).

Barriers to dispersal or factors affecting dispersal distance, such as high fences, can limit gene flow (Honeycutt 2000). Geography, climate, and habitat features may isolate populations and cause genetic divergence, contributing to population substructuring and partitioning of genetic variation. For example, island populations of white-tailed deer have significantly less genetic variation than mainland populations (Ellsworth et al. 1994a). Travis and Keim (1995) observed genetic differentiation between mule deer populations separated by the Grand Canyon in Arizona, and Cronin (1991) detected genetic differentiation between mule and black-tailed deer populations separated by the North American Cascade mountain range.

Artificial Dispersal Barriers

The genetic effects of artificial barriers to gene flow, such as enclosures, are difficult to predict because empirical documentation of the genetic effects of enclosures is lacking. However, habitat fragmentation and population isolation affect genetic variation in free-ranging populations, many of which are larger than enclosed populations. Habitat loss and fragmentation threaten genetic diversity of Asian wild cattle and buffalo species due to both isolation and reduction in census size (Heinen and Srikosamatara 1996). Gonzalez et al. (1998) documented genetic differentiation based on mtDNA sequences in populations of Pampas deer (*Ozotoceros bezoarticus*), which have been subdivided by habitat fragmentation since 1900. O'Ryan et al. (1998) demonstrated a significant relationship between genetic variation and population size in African buffalo (*Synercus caffer*) on fragmented game reserves using microsatellite markers. Luikart and Allendorf (1996) concluded that patterns of historic gene flow between Rocky Mountain bighorn sheep populations were affected by habitat fragmentation. Lee et al. (1994) observed greater mtDNA diversity in pronghorn antelope (*Antilocapra americana*) from Yellowstone National Park than in 28 other populations due to habitat preservation and robust historical census size in the Yellowstone population. Large genetic distances between contemporary gray wolf (*Canis lupus*) populations are the result of recent habitat fragmentation and reduced population size (Wayne et al. 1992). Old World wolves, with greater population dispersion, exhibit greater mtDNA subdivision than New World wolves (Wayne et al. 1992). In contrast, coyotes (*C. latrans*), which recently expanded their

range, do not display genetic differentiation, probably due to extensive gene flow (Wayne et al. 1992).

Unlike habitat fragmentation, game fencing is an intentional barrier to gene flow. For example, net-wire fencing ≥ 2.5 m in height effectively restricts ungulate movements when properly maintained (McCullough 1979, Woolf and Harder 1979, Ozoga and Verme 1982). An enclosure of this type is essentially impermeable to immigration and emigration and may have the characteristics of a population bottleneck and/or founder event. Unless the enclosed area encompasses thousands of hectares, yearling males may not be able to disperse far enough from their natal group to avoid inbreeding with close relatives. Males breeding within the same matriline for several generations would produce offspring with successively higher inbreeding coefficients. Enclosures also may alter the population breeding structure by concentrating individuals or influencing social structure. This occurs in white-tailed deer, whose normal breeding system involves pursuit and courtship of individual females by males (Hirth 1977). This breeding system probably results in a large male effective population size in natural populations which have balanced sex ratios and age structure. However, a single or small number of socially dominant males may monopolize breeding in enclosures, reducing the overall effective population size (DeYoung et al. 2002). Captive breeding facilities and other small, artificially enclosed populations are thus vulnerable to loss of genetic variation and viability (Honeycutt 2000).

Hybridization and Genetic Introgression

Hybridization may be described as mating between species, subspecies, or populations which differ genetically, while introgression occurs when there is genetic interchange between populations which hybridize via backcrossing of the hybrid offspring into either or both ancestral populations (Rhymer and Simberloff 1996). If population size is reduced, population genetic integrity becomes especially vulnerable to hybridization and introgression.

The genetic integrity of many Asian wild cattle and buffalo species is threatened due to hybridization with domestic ungulates (Heinen and Srikosamatara 1996). Expansion of exotic zebu cattle (*Bos indicus*) in western Africa, aided by advances in veterinary medicine and destruction of tsetse fly (*Glossina* spp.) habitat, threatens the genetic purity of trypanosomiasis-resistant taurine cattle (*B. taurus*, MacHugh et al. 1997). European bison (*B. bonasus*), North American bison (*B. bison*), and yak (*Bos grunniens*) show contemporary or historical genetic signatures of hybridization with domestic cattle (Polzheim et al. 1995, Schaller and Wulin 1996, Ward et al. 1999). Ward et al. (1999) found domestic cattle mtDNA haplotypes in 6 of 15

North American bison populations and 5.2% of all bison examined. Goodman et al. (1999) documented a hybrid zone in Scotland between native red deer (*Cervus elaphus*) and introduced Japanese sika deer (*C. nippon*). Where the 2 species are sympatric, up to 40% of individuals possess introgressed alleles. Though hybridization occurs at a low rate, substantial genetic introgression has taken place in the 30 years since sika and red deer became sympatric (Goodman et al. 1999). Lehman et al. (1991) documented coyote introgression into gray wolf populations in the north central U.S. and Canada due to recent expansion of coyote populations caused by changes in forest ecosystems associated with agriculture. Other studies also have documented coyote introgression into gray wolf (Wayne et al. 1992), red wolf (*C. rufus*), and eastern Canadian wolf (*C. l. lycaon*) populations (Wilson et al. 2000).

White-tailed deer (*O. v. texanus*) are expanding into areas of western Texas occupied by mule deer (*O. h. crookii*) due to invasion of woody species, which creates favorable habitat for white-tails (Wiggers and Beasom 1986). Early research indicated that the occurrence of mule deer–white-tailed deer hybrids in western Texas deer populations varied from 0 to 24% (Stubblefield et al. 1986). Carr and Hughes (1993) documented substantial hybridization between the 2 species in western Texas, with gene flow occurring predominantly from mule deer into white-tailed deer. Cronin (1991) observed introgressive hybridization of mtDNA from mule (*O. h. hemionus*) and black-tailed deer (*O. h. columbianus* and *O. h. sitkensis*) into white-tailed deer (*O. virginianus*) and widespread interbreeding of mule and black-tailed deer where the 2 species overlap.

Though the narrow zones of introgression may not threaten the genetic integrity of declining mule deer or expanding white-tailed deer populations in western Texas (Derr 1991), displacement of mule deer with white-tails and hybrids is symptomatic of ongoing habitat loss for mule deer (Wiggers and Beasom 1986). The reduced population size of mule deer may result in lost economic opportunities for private landowners in these regions (Carr et al. 1986, Stubblefield et al. 1986). In addition, there is genetic evidence for introgression of black-tailed deer (*O. h. columbianus*) genes into endangered Columbian white-tailed deer (*O. v. leucurus*) in the Pacific Northwestern United States (Gavin and May 1988). The patchy distribution of small Columbian white-tailed deer populations within a continuous distribution of black-tailed deer may presage dilution of the Columbian white-tail genome (Gavin and May 1988).

Outbreeding Depression

Outbreeding depression is a phenomenon similar to hybridization, which may occur when genetic stocks from

different ecotypes interbreed (Templeton 1986). The hybrid progeny have reduced fitness due to differences in chromosome number, phenotype, or interacting gene complexes (Honeycutt 2000). An extreme example of outbreeding depression occurred during the restocking of ibex (*Capra ibex*) in Czechoslovakia. Ibex in the source populations, Turkey and the Sinai, bred at different times than the native ibex and resulting hybrids produced offspring during winter, driving the population to extinction (Templeton 1986). Captive white-tailed deer in Mississippi of northern lineage and northern-crosses experienced reduced survival versus southern deer, primarily due to hemorrhagic disease and pneumonia (Jacobson and Lukefahr 1998). Even where hybrids are not viable and genetic introgression does not occur, threatened populations receive no benefit from reproductive effort wasted on offspring that are not viable (Rhymer and Simberloff 1996), especially in species of *k*-selected large mammals where there is significant parental investment in few offspring.

Harvest

Harvest, which is essentially a form of artificial selection, is another factor influencing population genetic variation. Harvest plans may affect patterns of within- and between-population genetic diversity by altering population demographics, breeding structure, and N_e , especially under male-biased harvest (Ryman et al. 1981). Population genetic variation may quickly be reduced under some harvest regimes, and the effect is largely independent of population size (Ryman et al. 1981). Fitzsimmons et al. (1995) found positive correlations between horn volume and allozyme heterozygosity in bighorn sheep. The authors hypothesized that selective removal of large-horned males may decrease genetic variation and result in loss of fitness in small insular bighorn populations. Likewise, allozyme heterozygosity was positively correlated to antler size in white-tailed deer (Smith et al. 1982, Scribner et al. 1989, Scribner and Smith 1990). Harvest selection criteria based on antler size for young white-tails substantially decreased cohort antler size in some Mississippi deer populations (Strickland et al. 2001). Thelen (1991) suggested that certain elk harvest plans could affect population antler characteristics. Long-term differences in harvest plans between Himalayan tahr (*Hemitragus jemlahicus*) populations in New Zealand affected spatial distribution of sex and age classes (Forsyth 1999). Ellsworth et al. (1994b) recommended that harvesting of male white-tails be regulated to conserve interpopulation gene flow due to the male-biased dispersal pattern exhibited by white-tailed deer.

Unique Genetic Stocks

Besides monitoring individual and population genetic variation, molecular genetic techniques are useful for

identification of unique genetic stocks or conservation units (Vogler and DeSalle 1994), which has management implications for large mammals. For example, white-tailed deer populations in the southeastern U.S. are a mixture of native stocks and those influenced by trapping and transplanting programs in the 1930s–1960s (Ellsworth et al. 1994a,b; Leberg et al. 1994; Leberg and Ellsworth 1999). If protection of native genetic stocks is desirable, further translocations into areas containing these stocks should be discouraged. Likewise, populations of pronghorn antelope in western Texas have been influenced by translocations, complicating the interpretation of conservation units (Lee et al. 1989, 1994). Bison herds with mtDNA from domestic cattle could threaten genetically pure bison herds (Polziehn et al. 1995, Ward et al. 1999). Besides affecting the genetic integrity of a population, hybrid individuals may complicate the legal status of threatened or endangered species (O'Brien and Mayr 1991, Rhymer and Simberloff 1996).

SOCIAL ISSUES

Ownership of Wildlife Resources

Public Trust Doctrine

“The guiding philosophy of our North American system of wildlife management is that endemic wildlife belong not to the individual, but to the people of the state and responsibility for managing that wildlife is entrusted to the governmental regulatory agency. This contrasts with the European system of wildlife management where wildlife is the property of the owner of the land on which the wildlife reside” (Stinson et al. 1999:8).

The concept that the government holds certain natural resources, including wildlife, in trust for the benefit of all people is known as the public trust doctrine. “The doctrine’s roots extend back to Roman law, which held that by natural law, mankind held the common right to the use of resources such as air, wildlife, running water, and the oceans and their shores. In Common Law England the doctrine was transformed, so that ownership and disposition of rights to use these resources, particularly the beds of navigable waters, vested in the sovereign, and at least since the Magna Carta, these rights have been held in trust for the benefit of the people” (Meyers 1989:728).

Historically, the public trust doctrine has been found to apply most easily to water resources and their accompanying fauna, which in turn has led to the general recognition of the trust principle with respect to wildlife (Horner 2000). Meyers (1989) argued that, of all natural resources, wildlife is perhaps the most similar to water with regard to the difficulty of possession, and that there is a sound historical basis for extension of the doctrine to wildlife.

Meyers (1989) “was one of the first commentators to vigorously embrace the specific application of the public trust doctrine to wildlife management. He accurately noted that while there is little doubt that from the historical standpoint the public trust doctrine is applicable to wildlife, currently few, if any, states actively use the doctrine to protect wildlife or wildlife habitat. Most cases that have addressed the public trust in wildlife have focused on whether a state had the power to enact laws regulating the resource, and what might be the limits of such authority” (Horner 2000:27).

The application of the public trust doctrine to wildlife is deeply rooted in the history, beliefs, and court opinions of the United States, as has been well documented by Meyers (1989), Bean and Rowland (1997), Horner (2000) and others. In the 1842 case of *Martin v. Waddell*, “Chief Justice Roger Taney ruled that when the colonists became independent from England, property (including wildlife) formerly claimed by the king belonged to the state. This decision laid the groundwork for the doctrine of state ownership of wildlife” (Bean and Rowland 1997, as cited in Stinson et al. 1999:8).

In the 1896 landmark case, *Geer v. Connecticut*, the U.S. Supreme Court stated: “Whilst the fundamental principles upon which the common property in game rests have undergone no change, the development of free institutions has led to the recognition of the fact that the power or control lodged in the State, resulting from the common ownership, is to be exercised, like all other powers of government, as a trust for the benefit of all people, and not as a prerogative for the advantage of the government, as distinct from the people, or for the benefit of private individuals as distinguished from the public” (Horner 2000:40).

Horner (2000:40) concluded that the Supreme Court’s decision in *Geer v. Connecticut* also “placed meaningful restraint on the ability of the government to privatize this resource” (wildlife), that “in the century that has passed since *Geer*, the courts have not backed off from the recognition of this trust relationship,” and that “we have within the common law ample authority that the states, and the federal government where applicable, hold wildlife in trust for the benefit of all persons.” Although the courts have consistently supported states’ authority to enact laws regulating the wildlife resource, Horner points out they “have rarely addressed what obligations might co-exist with such authority.”

In her comprehensive review of the application of the public trust doctrine to wildlife, Horner concluded:

- 1) “At the turn of the millennium, it can no longer be debated seriously that wildlife is held in trust for the public by the states. There is no need to ‘extend’ the doctrine to this ‘resource.’ The trust is there to be enforced” (2000:29).
- 2) “Not only is there ample rationale for the application of the doctrine to wildlife management, the states have had an unequivocal duty to manage wildlife in trust for all people since at least the Nineteenth Century” (2000:29–30).
- 3) “Because wild animals in their natural state are subject to neither private ownership nor actual state ownership, but ‘belong’ to everyone, claims of private property ‘takings’ as a result of wildlife regulation in the public trust fall flat” (2000:30).
- 4) “While the public trust doctrine has been universally accepted as a viable part of our legal heritage in the late Twentieth Century, it is anything but a working tool in the practices of public interest and conservation advocates across the nation” (2000:24). “The unfortunate fact is that most agency employees, or their governing boards or commissions, have never even heard of the public trust doctrine, much less understand it as any part of their mandate.” However, “administrative officials cannot be expected to utilize and apply responsibly a legal principle that they do not know exists, and which appears nowhere in their agency mandate” (2000:42).
- 5) “The first step to making the implementation of trust principles a reality in the every day management of wildlife is the adoption of a recognizable statutory or constitutional directive” (2000:42).

Achievements of North American Conservation

The North American model of wildlife conservation has been described as the world’s “most successful, economically productive, and most imitated system of wildlife conservation” (Geist 1988:17). Although he did not use the phrase, “public trust doctrine,” Geist (1988:16) recognized the public trust concept when he stated that “the North American system of wildlife management is unique in that, with few exceptions, it makes the public both de jure and de facto owner of the wildlife resources.” Geist (1988:16) also identified three primary policies basic to the success of wildlife conservation in North America: 1) the absence of market in the meat, parts, and products of game animals, shore- and songbirds; 2) the allocation of the material benefits of wildlife by law, not by the market place, birthright, land ownership, or social position; and 3) the prohibition on frivolous killing of wildlife.

Stinson (1999:9) summarized the remarkable North American conservation achievements reported by Geist (1988) as follows:

- 1) Restoration of decimated wildlife populations that remain wild and live in sustainable association with human culture.
- 2) Development of a large service and manufacturing industry centered around wildlife-related recreation.
- 3) A system of wildlife management based on state-employed wildlife managers responsible to elected representatives.
- 4) Development of conservation societies to fund and restore wildlife habitat and management activities.
- 5) Self-imposed taxation on behalf of wildlife (Pittman-Robertson, Dingell-Johnson, and Fish and Wildlife Conservation Acts of 1980).
- 6) Protection of extensive areas of wildlife habitat by state, Federal, and private conservation initiatives.
- 7) International treaties to conserve migratory birds and mammals.
- 8) Preservation of large predators as part of our North American wildlife heritage.
- 9) Development of a relatively inexpensive and efficient system of wildlife protection that allowed wildlife to recover and thrive.

Trends in Ownership of Wildlife Resources

“Private property rights or ownership of wildlife is an extremely contentious issue in the United States” (Teer 1998:67). Although the public trust doctrine dictates that wildlife is held in trust by the government for the benefit for the public, a basic tenet of United States property law is that landowners control access to their property and, thus, the public’s access to wildlife resources on private lands.

Geist (1988) warned that attempts to switch wildlife from public to private control threaten to replace North America’s highly successful system of wildlife conservation with one that, historically, has promoted neither the welfare of wildlife nor that of the public. Thomas (1997) reported that various interest groups have repeatedly attempted privatization of public lands in the United States. Although legal devolution of ownership of public lands from the State to the private sector has generally failed, transfer of ownership of wildlife on private lands has been more successful (Teer 1998).

“Wildlife conservation on private lands is evolving from regulatory to participatory management, from State to private control, from protectionism to sustainable use, and from free uses to all persons and societies to outright commercialization. These trends have had an impact on ownership of wildlife and its uses” (Teer 1998:67).

While some states, such as Wyoming, have aggressively protected the public’s interests by banning privately owned game farms, other states have moved in the opposite direction. Teer (1998:67) reported that Texas “leads the nation in devolution of wildlife to the private sector.” In contrast with former systems in which partnerships between users and owners were the norm, in Texas “wildlife is now being considered a commodity for sale and or exclusive use by the private property owner.” “Wildlife is ‘claimed’ through such devices as high fences to contain large mammals,” and landowners can “obtain permit(s) to capture deer from wild stocks, pen and breed them much the same as domestic livestock, and return them to the wild...” (Teer 1998:67). The reduction of a public resource to private ownership is a fundamental issue underlying the discussion of confinement of wild ungulates behind high fences for private or commercial purposes (Stinson et al. 1999). Geist (1992:558) argued that legalization of game ranching, of which the confinement of wild ungulates is a prerequisite, is in conflict with the underlying principles of the North American system of wildlife conservation. According to Geist, game ranching “transfers affected wildlife into the private domain,” “is an abdication of public responsibility for wildlife,” and “aims to create legal markets in venison and wildlife parts.”

“Allowing private possession and sale of native wildlife in this manner requires a profound change in the guiding philosophy of North American wildlife management” (Stinson et al. 1999:9).

Hunting Ethics

Sportsmanship

One common theme concerned with hunting promotes a theory that modern man could not have evolved without the high protein meat diet provided by killing other animals. In a second common theme, it is argued that hunting is simply an immoral demonstration of mankind’s baser instincts. The process of discussing and finding answers in this debate leads invariably to demonstration that ethical behavior is an essential component of hunting as we know it. Historically, the conversion from hunter-gatherer to an agricultural mode of existence has seen wildlife become the property of government, usually the king or the emperor. Hunting was reserved for royalty. “America is one of the very few countries on earth where the citizens, not landowners or the government, own the wildlife” (Smith 1993:108). This fact, unique in itself, has taken many species of American wildlife through a period of market hunting to near extinction, to the passage of game and fish protection laws, and to a wildlife abundance that is again unique in all the world. An interesting observation on this phenomenon not often recognized is “that laws alone were insufficient to stop the

'excesses of democracy' imposed on wildlife by mass participation in wildlife harvest. What arose to restrain these excesses was a philosophy called 'sportsmanship'" (Muth and Jamison 2000:843).

Defining sportsmanship and describing a satisfactory hunter ethic for modern conditions has not been an easy task or one that is likely to be concluded in our lifetime. Among the most widely published essays on this subject are those by the Spanish philosopher Jose Ortega y Gasset. He observes (1942:88) that hunting, "like every human activity, has an ethic which distinguishes virtues from vices." Aldo Leopold (1933:391) wrote, "Hunting for sport is an improvement over hunting for food in that there has been added to the test of skill an ethical code, which the hunter formulates for himself, and must live up to without the moral support of bystanders." More recently, Jim Posewitz (1994:16) has defined the ethical hunter as a "person who knows and respects the animals hunted, follows the law, and behaves in a way that will satisfy what society expects of him or her as a hunter."

That these discussions must continue and be expanded is perhaps demonstrated best by the success of a series of meetings that were started when Governor Stan Stephens and the state of Montana sponsored the first Governor's Symposium on North America's Hunting Heritage in 1992. The success of this initial symposium led to a series: a Second Annual Governor's Symposium on North America's Hunting Heritage in Pierre, South Dakota (1993); a Third Annual Governor's Symposium in Little Rock, Arkansas (1994); a fourth Symposium (1995) in Green Bay, Wisconsin; and a fifth Symposium (1998) in Hershey, Pennsylvania. In 2000, A Symposium on North America's Hunting Heritage was held in Ottawa, Ontario, and, in 2003, the sixth United States Governor's Symposium will be held in Austin, Texas.

Decker et al. (1993:23) clarified value and meaning: "The term 'heritage' tells us hunting is more than simply a particular form of outdoor recreation. You don't hear people, even the most avid participants, talking about our skiing heritage, hiking heritage, camping heritage, boating heritage, birdwatching heritage, or any other 'heritage' related to outdoor recreation." In truth and in fact, the reason hunting heritage is separated from all other outdoor endeavors is that hunting requires and imposes ethical standards on the participants. At every one of these meetings, professional wildlife biologists, outfitters, guides, wildlife managers, farmers, and ranchers explored the motivations and satisfactions of hunting and the methods needed to preserve the North American hunting heritage. Ethics, and the maintenance of ethics in hunting have been common themes through all the symposia.

Fritzell (1995:53) explained that ethics were important because, "to my mind, hunting will be tolerated by the American public only if it is perceived as having positive values that counterbalance the apparent negative ones." And what are acceptable values? Duda (1998:44) reported, "In general, hunting for food, hunting to manage game populations, and hunting for animal population control are very acceptable to Americans while hunting strictly for recreation or hunting for a trophy are much less acceptable." The degree to which some hunting is judged less acceptable is very often a consideration of fairness. This consideration has led to the development of the "fair chase" concept.

Fair Chase

Although native Americans had a hunting credo in which fairness was a major consideration (Nelson 1992), the origin of the term "fair chase" is generally credited to Theodore Roosevelt and the founders of the Boone and Crockett Club in 1887. The Boone and Crockett Club initially encouraged sportsmanlike methods of hunting, which by 1893 had developed into a "Credo of Fair Chase." Any trophy submitted to the Boone and Crockett Club's record book after 1963 had to be accompanied by an affidavit that the trophy was taken in Fair Chase (Ferguson 1964:22). Ferguson noted, however, "The Boone and Crockett Club realizes full well that sportsmanship cannot be legislated. The hunter who has a few days, intense desire for a trophy, and no scruples will not be detained by a rule in the book—nor even by a state law." However, as Nelson (1992:27) points out, "it would be a mistake to deny the existence of conservation ethics simply because we discover isolated cases where these ethics have been breached."

Posewitz (1994) provided a modern overview of hunter ethics with emphasis on the following points: 1) The ethical hunter knows and respects the animals hunted, follows the law, and behaves in a socially acceptable manner; 2) Fair chase is fundamental to ethical hunting because it addresses a balance that allows hunters to occasionally succeed, while animals generally avoid being taken; 3) Fair chase is important to hunting because the general public will not tolerate hunting under any other circumstance; and 4) Failure of high ethical standards and fair chase risks doing what is right for wildlife, risks the opportunity to hunt, and risks the self respect of the hunter.

"Canned" Hunts

Jose Ortega y Gasset (1942:49–50) explained, "It is not essential to the hunt that it be successful. On the contrary, if the hunter's efforts were always and inevitably successful it would not be the effort we call hunting, it would be something else." That "something else" is the "canned" hunt, in which the client pays the game rancher to kill a

specific type of animal under conditions where the probability of failure is reduced. As described by Lanka (1993:41), in some cases, “a ‘hunter’ picks and pays for a specific animal before the ‘hunt’ begins. In others, wildlife is baited to specific locations with feed or enclosed inside a small pasture before the ‘hunt’ begins. Many hunters and non-hunters alike find these types of practices unethical. Situations such as these could be used by anti-hunters in their attempts to ban all hunting.” Causey (1992:54) is even more direct in questioning this practice: “Can shooting an actually or functionally captive animal enhance one’s understanding of natural processes? Does...shoot[ing] exotic animals located for you by a guide honor your cultural heritage?”

Proponents of the game-farm industry and these practices tend to describe commercial game production “[as] divided into four categories: game farming, game ranching, game herding, and game cropping...” (Renecker 1993:20), and to imply a clear separation among categories. “Game ranching is the harvesting by hunting for a fee of wild animals.... Game farming, on the other hand, is the raising of domesticated deer or elk for the wholesale or retail meat market...” (Brown 1993:120). Geist (1988:18), however, explains that game ranching “differs from ‘Game Farming,’ a legal designation in Canada that denotes the raising of animals for viewing or live sale. Game ranching denotes the raising of big game to be killed for sale, or by paid hunting.”

According to Renecker (1993:23), “Game ranching is an extensive type of enterprise that occurs on private or communal...properties... of at least 25 km² (6,178 acres) ... [from which] surplus animals [are] sold as breeding stock or slaughtered for meat. Owners could also exploit hunting opportunities on the ranch.” Game farming, on the other hand, “occurs on private, deeded land that is again fenced to define ownership.... This strategy takes full advantage of all economic opportunities. For wapiti farming, this includes velvet antler sales, meat sales, and sale of breeding stock.” Neither of these authors mentioned Seidel’s (1993:109) estimate that the “acreage involved in an average ‘farm’ (50 acres) would not in most cases create a barrier to migration.” Neither, obviously, would it provide much opportunity for a “wild” animal to escape harvest or a “hunter” to demonstrate any particular skill.

Leopold (1933:394) penned the relatively timeless observation that, “The recreational value of a head of game is inverse to the artificiality of its origin, and hence in a broad way to the intensiveness of the system of game management which produced it.” Brown (1993), on the other hand, presented arguments in favor of hunting on elk ranches. Several of his points are presented here with contrasting views:

1) “Private ownership of elk or at least commercial gain from elk hunting can provide the impetus for habitat acquisition and improvement. Landowners are faced with a variety of options of using their land for farming, cattle ranching, mining, timber harvest or commercial development. Successful competition for hunting and non-consumptive enjoyment of elk will allow this alternate use to increase elk numbers and habitat” (Brown 1993:122).

In contrast, Geist (1985:597) described, “The notion of wildlife as a crop to be harvested by the public, with the emphasis on festive, wholesome enjoyment, is an American idea. It’s a tradition rooted in history, an ideal to be cherished. There is danger in allowing wildlife to become a symbol of the rich, making hunting a frivolous pastime of the wealthy....” Lenzini (1992:47) concurs in writing, “Like politics, full-scale privatization of wildlife can strike at common use, smack of special privilege, and eventually put a public resource beyond the reach of the public.”

2) “Elk ranching can help improve the public perception of hunting as a sport. Fee hunting is usually carefully monitored, and can propagate the notion among the non-hunting public that hunting is an ethical and safe sport, non-detrimental to the propagation of the species. Such evidence is necessary if the public is to continue to support the sport of hunting, and the costs associated with hunter education, law enforcement, game management and research” (Brown 1993:122).

In contrast, Posewitz (1994:58) stated “The concept of fair chase is important to hunting. The general public will not tolerate hunting under any other circumstance.” Fritzell (1995:53) stated, “The motivation, attitudes and behavior of hunters will ultimately influence social acceptability of the practice.” The slogan, “Real Hunters Don’t Shoot Pets,” used during debate over the Game Farm Reform Initiative in Montana in 2000, suggests segments of the public do not have a positive perception of fee hunting when it involves a “canned” hunt situation.

3) “Elk ranching can help maintain the hunting legacy in this country. Aldo Leopold, considered the father of wildlife management in this country, listed the tools of the wildlife manager as the ax, the cow, the plow, fire, and the gun. If we are to continue to use hunting as a tool of wildlife management, then we must propagate hunters. In our fast-paced society, few people have the time to scout out hunting territory and learn the biology and behavior of their prey. Public hunting areas are often overcrowded, and hunting experiences can be unpleasant and unproductive, especially for youth. Fee hunting can allow for a pleasant, ethical, safe and productive hunting experience, thus helping to ensure

that young hunters continue future participation in the sport” (Brown 1993:122).

Other wildlife professionals have a different perspective on fee hunting at an elk ranch. Peyton (2000:775) asked, “What lessons are learned by the young hunter placed in a blind to opportunistically harvest a game animal?” The Montana Chapter of The Wildlife Society (2000) believes that hunting on game farms reduces the concept of fair chase, is morally indefensible, and is degrading to both the shooter and the animal. Posewitz (1994:97) wrote, “The ethics of pursuing a trophy animal are closely tied to why we seek such an animal. If you hunt these animals because they represent the survivors of many hunts, and you respect that achievement, then you have selected a high personal standard. If, on the other hand, you pursue a trophy to establish that you, as an individual hunter, are superior to other hunters, then you have done it to enhance your personal status, and that crosses the ethical line.” Geist (1989:176) observed that, “paid hunting must discriminate against the young or newly married or anyone with a modest income.”

In his summary, Brown (1993:123) expressed concern over unlimited expansion of fee hunting; “If we become a society wherein only the wealthy can afford to hunt, then we incur the wrath of the disenfranchised hunters, and the general public will quickly lose interest in financial support of our hunting legacy. In that event, all of us...will be the losers, as will our precious elk herds.”

Public Perception of Hunting

The right to hunt for meat has extensive public support, but opposition to hunting is considerable and a growing concern among hunters and wildlife managers (Kellert and Smith 2000:51). Organizations, such as the Humane Society of the United States and People for the Ethical Treatment of Animals, have media programs condemning sport hunting (Muth and Jamison 2000:845). While the field of environmental philosophy addresses the ethical and moral justifications for hunting, the anti-hunting movement continues to emphasize animal welfare and rights issues (Kellert and Smith 2000:51). In an increasingly urban society that lacks an appreciation of hunting as a recreational pastime or wildlife management tool, wildlife managers should be prepared to address the ethical concerns of anti-hunters and the general public (Kellert and Smith 2000:51). Sadly, “the American public has good reason to hold a dim view of the body collective known as hunters” (Kerasote 1993:50).

Posewitz (1993) called for an ethical agenda to improve hunting management, hunting practices, and hunting’s

image. Aasheim (1994) agreed that image is a common problem for the North American hunter. Possible courses of action intended to change that image may be difficult. Holsman (2000:808) suggested that “hunters often hold attitudes and engage in behaviors that are not supportive of broad-based, ecological objectives.” Changing such attitudes and behaviors could be valuable because “an exhibition of stewardship among the hunting community may earn the respect of the non-hunting public” (Peyton 2000:777). Public perceptions within a democracy are critical because the majority perception could determine the future legality of hunting (Hayden 1992).

Commercialization and Domestication of Wild Ungulates

One of the recurring philosophical and legal questions concerning ungulates behind fences involves “wildness” versus domesticity. This is not simply a question of semantics because the definition often carries substantial legal and management implications. Free-ranging native wild ungulates are public property, and management and regulatory responsibility usually reside with a state wildlife agency. As domestic livestock, ungulates become a private responsibility, and the regulatory responsibility often resides with a department of agriculture.

According to the Fact Sheet of The North American Elk Breeders Association (Rich 1993:8), “Alternative livestock by common, academic and legal definition are agricultural resources that should be managed by the departments of agriculture or jointly with the departments of wildlife (natural resources).” In support of this definition, Rich (1993:8) cites 2 other publications: “a species is domestic if both reproduction and the habitat critical for reproduction are under human management. It is therefore semi-wild or semi-domesticated, if only one of the elements is met and wild if neither is met...” (Prescott-Allen and Prescott-Allen 1986), and “domestic animals are husbanded rather than hunted, produced rather than procured” (Hudson 1989).

Kahn (1993) contrasted the vast differences between “domestic” and “wild” ungulates, stating that the domestication process takes thousands of generations to facilitate the changes in behavior, conformation, color, and temperament necessary to distinguish domestic animals from wild animals. Most of the elk in captive situations in Colorado came from the Yellowstone area during the past 50–75 years. Croonquist (1993) and Dratch (1993) stated that captivity does not make elk into domesticated animals.

Lanka (1993:36) quotes Van Gelder (1979), who defines domestic animals as “populations that, through direct selection by man, have certain inherent morphological, physiological, or behavioral characteristics by which they

differ from their ancestral stocks.” Lanka (1993:38) also notes that, “Judge William A. Taylor of the Eighth Judicial District, State of Wyoming, ...ruled that confining wildlife in an agricultural setting does not by itself make them domestic.”

A major impetus for expansion of the game farm industry in North America has been to diversify production on agricultural land when income is already restricted by acreage limitations on some crops and by relatively low prices for traditional domestic livestock. Despite the substantial initial investment for fencing, some landowners are attracted to the range of commercial products apparently produced by “alternative livestock” ungulates held behind fences.

There are 4 primary products in the game-farm industry: velvet, meat, breeding stock, and shooter bulls. Typically, the benefits of raising ungulates for venison are presented to the prospective investor as summarized by Brown (1993:121): 1) There is an economic market niche in this country for venison production, 2) Venison itself is a healthy product, 3) Very often, deer and elk are more efficient users of land than are more traditional livestock, and 4) Deer farming allows farmers and ranchers to diversify.

The general experience of many western game ranchers is that the venison market niche is very limited and mostly filled by imports from New Zealand. Brown (1993:122) continues with the observation that “my personal feeling about deer and elk farming is that the public will accept the production of venison from exotic animals much more readily than they will native species.”

Lacking a strong market for venison, Rich (1993:2) admits that “Most elk farms today supply the velvet antler market, generally for export.” As described by Renecker (1993), most of the world’s velvet antler production comes from maral (*Cervus elaphus maral* and *C. elaphus sibiricus*), elk, red deer, sika deer (*C. nippon*), and reindeer (*Rangifer tarandus*).

Korea was once the major importer of North American velvet, but both Korea and Japan have prohibited imports following the CWD outbreaks in Saskatchewan and Colorado. North American producers are further isolated by marketing methods mostly controlled by Pacific Rim buyers. Some recent exception to this pattern has been the FDA approval of velvet pills produced in Oklahoma under the brand name *Nature’s Force Velvet Capsules*, and in Minnesota as *Natural Velvet Capsules*. In both cases, as near as it is possible to determine in the advertising, the product has been approved for a single game farm rather than an industry cooperative or some more efficient operation.

Even as the venison and velvet markets have proved to be somewhat illusory, an already declining market for breeding stock has been impacted by a United States Department of Agriculture declaration of CWD as an animal health emergency (United States Department of Agriculture 2001a). Interstate, and even intrastate, movement of animals has been severely restricted or banned by some state regulations. Prior to this ruling, interstate shipment was significant in the development of the captive cervid industry in the northern United States. For example, a total of 936 deer and elk were shipped out of Michigan between 1997 and 1999 (Coon et al. 2002). Shipments of deer and elk into Michigan originated from Missouri, Wisconsin, Ohio, Minnesota, and Canada (Coon et al. 2002). If sale of live animals is limited, for many game farmers, the only remaining potential income source is selling the opportunity for shooting the enclosed animals.

Ecological Stewardship

Wildlife managers recently have begun to discuss the ethics of wildlife management as practiced in the modern world. A recent issue of *Wildlife Society Bulletin* carried a series of introspective papers examining and questioning relationships among hunters, trappers, and wildlife managers.

Leopold (1933) saw game management as an integrating profession in which all facets of ecological systems received consideration and yet, as the twentieth century came to a close, arguments were presented that the wildlife profession concentrated too much on consumptive use and control of populations (Wagner 1989). Organ and Fritzell (2000:785–786) agreed that, “hunting is typically marketed as an effective way to control wildlife populations and an important source of revenue for conservation programs. This marketing approach has a subliminal emphasis on killing and an overt emphasis on generating funds that are inconsistent with the historical development of sport hunting.” Geist (1991) emphasized that wildlife should be killed only for cause, a concept that prohibits waste and encourages subsistence.

“In many states, game management programs are being challenged by concepts like ‘ecosystem management,’ ‘biodiversity,’ and ‘conservation biology’” (Peyton 2000:774). The reason for this challenge is that, “In the enthusiasm to produce a wildlife surplus and then to harvest it, a critical ingredient often missing is the relationship of the hunter with the hunted and the ecosystem involved. That relationship...is essential to fostering an effective and well-informed sense of ecological stewardship among the hunting community. Farmers and hunters who are focused on maximizing production of cattle or deer and who do not understand or do not care how their product depends on and impacts the ecosystem will make poor stewards of the land

and its natural attributes” (Peyton 2000:777). “It is time to examine our own professional efforts in wildlife management to determine whether we are encouraging stewardship or simply promoting a form of agriculture among hunters...” (Peyton 2000:778).

The public perception of wildlife management, in some respects, parallels that of the professionals, but with far less introspection. Although wildlife biologists may understand Leopold’s (1949) statement that conservation is a state of harmony between men and land, Peyton (2000) questioned how well the statement is understood and accepted by our consumptive wildlife user partners. Lenzi (1992:47) observed that a “startling number of citizens have lost all real connection to the land,” and as a result, “it is regrettable that wildlife management is being politicized. Leopold set out in the 1920s to establish wildlife management as a professional discipline, some say a science, possessing a structure of its own. Today the principles of that discipline are succumbing to the belief that nothing matters beyond politically desirable results.”

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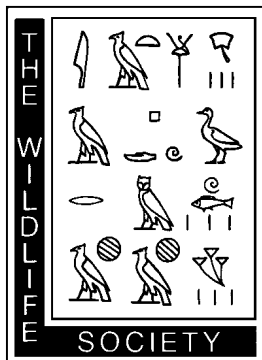
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