

Biological, Conservation, and Ethical Implications of Exploiting and Controlling Wolves

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Abstract: *The widespread claim that wolf populations can withstand 25–50% or greater annual reductions without major biological consequences is based primarily on the observation that populations often maintain their size from year to year as harvest or control continues or recover within a few years afterward. This emphasis on numerical status overlooks the likelihood of major, lingering impacts on the size, number, stability, and persistence of family-group social units, on reproductive, hunting, and territorial behavior, on the role of learning and related traditions, on within- and between-group patterns of genetic variation, and on overall mortality rates. The tendency of biologists and agencies in northern North America to promote wolf harvests that are four to eight times greater than ungulate harvests, in accord with the wolf versus ungulate difference in reproductive rates but contradictory to a broad array of differences in social organization and related behavior, is reason enough to question the logic of this prevailing management view. True sustained-yield management requires more emphasis on qualitative biological features to determine the extent to which wolves and other species with evolutionary histories as predators rather than as prey should be harvested. Most recent government-sponsored wolf control programs and proposals, including sterilization, relocation, and “redirected” killing, have been based on questionable claims about ungulate or livestock problems and have not adequately considered potential biological costs (especially to the target wolf populations), benefits, or management alternatives. The high sentience of wolves justifies overlapping biological-ethical concerns about such programs and especially about the heavy, indiscriminate, deceptively reported public hunting and trapping of wolves that is currently permitted throughout most of Alaska (U.S.A.)—including in national parks—and elsewhere.*

Implicaciones Biológicas, Conservacionistas y Éticas de la Explotación y Control de Lobos

Resumen: *La afirmación de que las poblaciones de lobos pueden soportar reducciones de 25–50% o más sin consecuencias biológicas mayores se basa principalmente en la observación de que las poblaciones bajo explotación o control a menudo mantienen su tamaño año a año o se recuperan pocos años después. El énfasis en el estatus numérico pasa por alto la posibilidad de impactos mayores sobre el tamaño, el número y la estabilidad de unidades sociales; sobre la conducta reproductiva, de cacería y territorial; sobre el papel del aprendizaje y tradiciones relacionadas; sobre los patrones de variación genética inter e intra grupales y sobre las tasas de mortalidad en general. La tendencia de biólogos y agencias en el norte de Norte América de promover sacrificios de lobos 4–8 veces más altos que de ungulados, de acuerdo con las diferencias de tasa reproductivas pero en contradicción con la alta gama de diferencias en organización social y conducta relacionada, es motivo suficiente para cuestionar la lógica de ésta visión prevaleciente de manejo. El verdadero manejo sustentable requiere de mayor énfasis en características biológicas para determinar el grado en que el lobo y otras especies, con historias evolutivas como depredadores y no presas, deben ser cosechados. Los programas y propuestas gubernamentales más recientes para el control del lobo, incluyendo esterilización, relocalización y muerte “redirigida” se han basado en afirmaciones cuestionables acerca de problemas con ungulados o ganado y no han considerado adecuadamente los potenciales costos biológicos (especialmente para las poblaciones de lobos), ni los beneficios o alternativas de manejo. La gran sensibilidad de los lobos justifica el traslape de preocupaciones biológico-éticas acerca de tales programas especialmente acerca de la*

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intensa, indiscriminada y engañosamente reportada cacería y trampeo de lobos que actualmente se permite en casi todo Alaska (EUA), incluyendo parques nacionales y otras regiones.

Introduction

Wildlife scientists and managers are fond of calling Aldo Leopold (1949) the father of wildlife management. However, many professionals overlook or ignore one of his central messages, as embodied in one of his most famous quotations: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." I suggest Leopold saw a distinction between true sustained-yield management, in which wildlife systems are harvested only selectively in a way that tries to ensure their underlying structural and functional integrity, and what I would refer to as "farming" of these systems.

Two basic tenets of the prevailing farming approach are that (1) virtually all major wildlife populations/species can and should be harvested, and (2) many of them can be harvested to their full reproductive potential (to the limit of net annual increments for ungulates and certain others) on a more or less continuing basis.

In this paper, I examine one application of this thinking with regard to the management of wolves (*Canis lupus*). I question the prevailing way impacts of harvesting (hunting/trapping) and control reductions are evaluated and suggest that much more emphasis should be given to the qualitative features of wolf biology. I then propose a general framework for determining the relative extent to which wolves and other species should be harvested, based on their evolutionary histories and sociality, and for adapting harvest policies to other natural patterns and processes. I end with some thoughts about the direction of wolf conservation and the ethics of wolf killing.

Biological Impacts and Wolf Social Organization

Wolf biologists and wildlife agencies regularly assume northern wolf populations can be harvested at ongoing annual rates of up to 25–50% or can withstand shorter-term control programs of up to 80–90% without significant biological impact (Elliot 1982; Keith 1983; Peterson et al. 1984; Ballard et al. 1987, 1991; Alaska Department of Fish and Game 1989, 1991a, 1991b, 1992a, 1992b, 1992c, 1995c; Mech 1970, 1991, 1994; Gasaway et al. 1992; Boertje et al. 1995; J. Morehead letter 10 January 1992 to D. Kelleyhouse, National Park Service files, Anchorage).

"Biological impact" is typically defined solely in terms of numerical status: The impact is considered negligible if the wolf population either maintains or soon recovers

to about the same size. Much the same standard is applied under the Endangered Species Act in judging whether or not wolves and other species are biologically threatened or endangered. Little more than the number of animals is considered, and sometimes not even this standard is maintained (Tear et al. 1993).

Recommended harvest levels for wolves are commonly four to eight times higher than for most ungulate and other populations simply because wolves have a higher reproductive capability. An application of this thinking, with regard to the alleged relative biological costs of wolf control versus bear control, is illustrated in a recent wolf control proposal from Alaska (Alaska Department of Fish and Game 1995a: 2, 1995b: 8):

... unlike wolves, bears have very low reproductive rates, making them vulnerable to overharvest and much slower to recover. Thus, we should reduce bear predation only if decreasing predation by wolves does not increase calf survival.

In Alaska (U.S.A.), wolves can be hunted and trapped for almost 9 months a year—10 August–30 April in most areas, including within most of the national park areas and national wildlife refuges (Alaska Board of Game 1995; Federal Subsistence Board 1995; Haber 1992, 1995a). Wolf pelts are considered almost worthless until late fall or winter, and few if any hunters eat wolf meat; nevertheless both the sport and "subsistence" wolf hunting seasons begin on 10 August to coincide with the opening of the caribou and sheep hunting seasons to maximize the potential kill of wolves via incidental encounters. Annual hunting limits generally range from 5 to 15 wolves per hunter. Some areas, including about half of the Arctic National Wildlife Refuge, have no hunting limit. The trapping season extends from 15 October or 1 November through March or April. There is no limit to the number of wolves that may be taken with a trapping license, which allows many methods of killing (actual trapping is not required except in park areas), including with the use of semi-automatic assault rifles, airplanes, and snowmachines. Saturation snaring is a common trapping method: wire snares are set virtually in walls, by the dozens per site, at numerous brushy, baited sites along well-used travel routes.

There are no restrictions, including in most of the national park areas, against killing adult wolves with dependent young or the young themselves. At these latitudes wolf pups are usually completely dependent on the care provided by adults through at least late September or early October (the end of the homesite period), and typically for at least several months after that (Haber

1977). Young are not allowed to hunt or travel regularly with the adults until the end of the homesite period. Thus, when adults are killed—especially from a small family group or a pair with a relatively large litter—the result can be much the same as if the pups were killed directly.

More than 1600 wolves, equal to nearly all of the wolves in Minnesota, were killed in Alaska during the 1993–1994 reporting period. The annual kill typically ranges from at least 800 to 1200 and averages about 1000 (Alaska Department of Fish and Game 1995c). The statewide population of wolves has been variously estimated by the Alaska Department of Fish and Game at 5000–10,000 since 1992 (Peterson 1995; Alaska Department of Fish and Game 1995c) but I estimate that it is 15–40% lower based on my aerial surveys in several of the Alaska Department of Fish and Game's highest priority counting areas (Game Management Units 13, 20A, 20B, 20C, 20D, 20E; Haber 1993b, 1994, 1995b, Haber letter 26 October 1995 to S. Martin, Denali National Park files, Haber letters 23 January and 28 February 1996 to F. Rue, Alaska Dept. of Fish and Game files; and unpublished data). Included in my counts were large regions where it has been possible since 1993 for the Alaska Department of Fish and Game or a cooperating agency and me to monitor most of the same resident wolf groups via aerial radio tracking (in 20D, 20E, and the southern half of 20C).

To understand the impact of heavy, ongoing public killing and shorter-term government control on wolf populations and why, in general, this makes little biological sense, requires an understanding of wolf social organization. Social behavior is strongly influenced by inheritance (Plomin 1990; Bouchard et al. 1990; Kelner and Benditt 1994) and is therefore very much within the realm of biology.

I have spent more than 11,000 hours observing wolves during 30 years of field research in Alaska. This research (e.g., Haber 1977, 1992, 1993b, 1994, 1995b) includes 14 established groups of wolves observed via ground and aerial observation in Denali National Park since 1966. I have observed 11 of these groups with aerial and ground radio tracking. I have observed 37 groups, 31 of these via aerial radio tracking, in other regions extending eastward from Denali to the Yukon border since 1993. I have also undertaken wolf research and reviewed wolf management programs in northern British Columbia and the Yukon Territory (Haber 1979, 1988, 1993a).

All the groups I have studied intensively (with the exception of one or two non-reproducing pairs) were, or soon became, family groups, in most cases extended families. Murie (1944), Peterson (1977), Allen (1979), Packard (1980), Harrington and Mech (1982), and Messier (1985) similarly concluded that the groups they studied were primarily families, especially extended families. These families were characterized by year-round integration between the sexes and among adult age classes, be-

havior that is unusual even for social mammals. Communal nonparental and parental provisioning of the young in multiple as well as single litters at the same and different homesites is common. There are complex divisions of labor and other sophisticated forms of cooperation, including extraordinary cooperation during hunting, with elaborate spatial coordination between individuals sometimes located (in visual contact) miles apart from each other (Haber 1977). Between well-established groups there is extreme hostility, and intense inbreeding appears to be routine under natural conditions, resulting in healthy, sometimes exceptionally large litters of young with high survival rates (Haber 1977; Peterson 1977; Allen 1979).

For long intervals, when my primary Denali study groups did not suffer any significant hunting/trapping losses, there was impressive social stability and continuity. For example, in one group (Toklat/East Fork) the same female maintained her position as alpha-female for 13–14 years, until she died naturally at about 18 years old. Murie (1944 and personal communication) observed similar indications of social stability and continuity in this group from 1939 to 1966. Our intensive ground and aerial observations of identifiable individuals indicate that this same family lineage has persisted for at least 56 years, and Murie (personal communication) felt it probably extended to at least 8–10 years earlier.

The adjacent Savage family (Haber 1977, 1987, 1992) was well established when I began observing it intensively in 1966. It persisted with relatively little social change until the winter of 1982/1983, when (based on strong circumstantial evidence) it was eliminated by hunting/trapping. The Headquarters family colonized this territorial vacancy in 1984. It persisted until May 1995, when the last wolf, the alpha-female, was snared. Hunting and trapping began taking a major toll on this group in the winter of 1993/1994 (Haber letter 30 May 1995 to Barbec/Martin, Denali National Park files). The Headquarters alpha-female had maintained her alpha status for at least 6–7 years, and remained mated to the same (alpha) male until he was killed during National Park Service helicopter darting activities in November 1993. A new ("Sanctuary") family—two adults and two of three pups they produced in May 1995—has now colonized this area.

Likewise, the Cottonwood family group of Yukon-Charley Rivers National Preserve has maintained a late winter size of 12–14 wolves (6–7 new pups annually), stable social relations among high ranking, radio collared and other identifiable individuals, the same large territory and natal sites, and the same basic pattern of coat colors since at least 1992, when this group was first radio-collared (Haber 1994, 1995b, unreported 1995–1996 data).

Unlike most other eusocial species, wolves feature one of the hallmarks of advanced vertebrate societies: prolonged dependency of the young, for up to 25–30%

of their normal lifespan (Haber 1977). This is longer than in human societies. Together with their sophisticated learning abilities, prolonged dependency provides the basis for major social as well as genetic transfer of information between generations. [Eusocial species feature groups or colonies in which at least two generations live together, reproduction is restricted to a few individuals, and nonbreeders cooperate to care for the offspring of breeders (Sherman et al. 1991, 1992)]. In short, wolves, along with only a few other species, display a rare form of sociality that represents a pinnacle of vertebrate social development.

It is difficult to dissect the impacts of wolf exploitation because detailed comparative information on behavior from both exploited and protected wolf populations is scarce. Nevertheless, some of the known or likely effects of removing 15–20% or more of a population annually are summarized as follows (see also Appendix 1). Comparisons are restricted primarily to similar systems in Alaska and northwestern Canada in which moose are available as prey, to minimize the influence of other variables (e.g., major differences in prey types can greatly influence the degree of sociality [Bowen 1981]):

- (1) Average late-winter group sizes decrease and the number of resident singles and groups combined in the population increases or remains relatively high even at reduced area-wide population densities (i.e., more population fragmentation) at least until the highest harvest or control intensities are reached.
- (2) Mating is less selective. There are more litters per population (more alpha pairs created) and higher mid- to late-winter pup ratios, followed by a sharp decrease at the highest harvest or control intensities in part because of pair bonding difficulties.
- (3) Moose kill rates are more variable, sometimes increasing as a function of group size over a much higher (two to three times) range of group sizes, and becoming more erratic at the smallest sizes (e.g., wolf pairs sometimes kill as often as groups of six or seven).
- (4) Territories and homesite patterns of use are more variable, with replacement by substantially different territorial mosaics at the highest harvest or control intensities.
- (5) There is a more direct relationship between territory size and resident wolf group size (versus territory size and prey availability), sometimes with an inverse relationship during initial colonization of large vacancies.
- (6) Overall annual, natural mortality rates (excluding the wolves killed via harvest or control) increase.

The first two impacts are not surprising; heavy indiscriminate harvest or control of a highly social species

could hardly be expected not to reduce and fragment its sociality and eventually produce less selectivity in other important aspects of behavior, as Peterson et al. (1984) also concluded. Similarly, it is difficult to imagine that such killing would not add greatly to the natural variations in territory boundaries and overall territorial mosaics and that it would not simplify homesite traditions within these territories.

Greater variability in moose kill rates and territory size–group size relationships is probably also explained in large measure by social changes and by the increased availability of temporary vacancies within territorial mosaics, which allows for more expansion of both surviving and new territories. Under natural conditions at group sizes of seven to nine or more in Denali National Park (Haber 1977), the highest-ranking family members were generally the most assertive and appeared to eat the most or at least showed the least variation in consumption from one moose kill to the next, even though the entire group typically crowded around each kill together. Other family members usually followed when the high-ranking wolves began a new hunt. There was relatively little variation in the refractory period of the high-ranking wolves. Therefore, successive hunts began after relatively constant intervals for each prey type, and kill rates remained fairly constant regardless of variations in (large) group sizes at the same prey densities.

Under conditions of moderate to heavy exploitation, with frequent replacement of key individuals, it would be difficult for wolves to maintain stable, well-defined dominance relationships such as I observed in well-established Denali family groups. There would likely be more overall variation in most relationships, dominance and otherwise. Territorial behavior and hunting would be determined more by interactions of various wolves than by the behavior of the same core of high-ranking group members. Competition would be less restrained, and when group size continued to increase there would probably be less of a difference in consumption rates among adults, lower average per-adult rates of consumption per moose kill, and shorter refractory periods leading to more time spent hunting, a continuing increase in kill rates, and probably more of a tendency for the group to try to expand its territory.

Additional kill rate differences reported for exploited populations might involve more subtle social or other types of distortions. Hayes et al. (1991) suggested that the sharp increase in kill rates they observed for groups reduced to pairs following heavy control was due to two factors: (1) The unusually large territories that colonizing pairs were able to occupy initially provided them with an increased selection of potentially vulnerable moose. (2) Higher per-kill losses to scavengers, especially ravens, prompted them to spend more time hunting. Heavy broadcast harvest or control implies a greater likelihood that pairs can settle into an area and hunt siz-

able territories with less risk of attack from nearby, much larger, established groups.

Other likely impacts of harvest and control include disruption of learning, increased population-wide mixing, and different within- and between-group genetic patterns, all of which would be difficult to identify with the sketchy comparative information available. However, these impacts might be among the most important. Disruption in the flow of learning from generation to generation would result in fewer, simpler learned behavioral traditions and in general a diminished role of these behaviors (Haber 1977, 1979, unpublished data) that help adapt individual family groups to the specific resources and other unique features of each area.

Wolves commonly live 7–10 years or more in well-established family groups subjected to little or no hunting and trapping in Denali National Park. As indicated, one alpha-female lived to about 18 years old. In contrast, few wolves live more than 5–7 years in exploited populations (Stephenson & Sexton 1974; Hayes et al. 1991). Hayes et al. for example, found that 77% of all adults were only 2–4 years old, only 9% were ≥ 5 years old, and only 3% were ≥ 7 years old. With such a high rate of turnover and young age structure, there is much less opportunity for wolves in these populations to accrue and transfer information from one generation to the next via the prolonged dependency period and complex learning sequences important to wolves under natural conditions (Haber 1977).

Fewer large, well-established family groups implies less intergroup hostility and more population-wide mixing and thus, almost certainly, some fundamental changes in genetic patterns. Under natural conditions, at least where moose are important prey for mainland wolf populations, the available behavioral evidence points to more overall genetic variation between groups and less within groups than some researchers have suggested is present based on blood and tissue samples taken primarily from exploited populations (Brewster and Fritts 1992) or from populations, including Denali, where underlying genetic patterns may not have fully recovered from earlier years and decades of exploitation in certain areas (Lehman et al. 1992; Meier et al. 1995). Observations in Denali (Murie 1944; Haber 1977) of eusocial behavior—intense inbreeding without obvious problems, extreme intergroup hostility, low rates of alien acceptance, and histories of distinct coat color differences for well established groups during long intervals of minimal human disruption—strongly suggest that normally the wolves of these groups share a high proportion of their genes, that there are major between-group genetic differences, and that kin selection plays an important role in the development of adaptive traits in such populations. These observations are consistent with Meier et al.'s (1995) observation from this population that between-group genetic relatedness was lowest among "longer-established" groups.

Even under natural conditions there is significant disruption of family groups, new group formation, and much dispersal usually ending in mortality (Haber 1977; Mech 1977). However, the natural area-wide pattern is likely to be one of larger, well-established, genetically distinct family groups in prime prey areas with smaller, less-stable groups in surrounding or nearby marginal areas, rather than of almost exclusively stable or unstable groups, as Meier et al. (1995) have portrayed the choices. Evidence for this kind of mixed mosaic of established and satellite or other unstable groups, in which many of the latter colonize nearby areas by "budding" from the former and continue to reassociate with them periodically at least for the short term, can be seen in both Meier et al.'s (1995) and my (Haber 1977; unpublished) data for Denali and for the upper Tanana-Fortymile-Yukon-Charley region of Alaska (Haber 1994, 1995*b*, unpublished).

The problem comes in separating out the effects of recent exploitation from the effects of natural instability and turnover, such as could be anticipated for newly formed groups in marginal prey areas (e.g., Wonder Lake family of Denali; Haber 1977). With heavy exploitation, especially ongoing harvest, there is bound to be much less opportunity for well-established groups to persist in relative isolation from each other. It is this distinction that sets the stage for most of the other behavioral and genetic changes I discuss here.

Sometimes it is claimed that heavy killing leads to the renewal of wolf populations, with the implication that this constitutes positive biological change. Such claims are questionable enough when applied to short-term control programs, but they are almost meaningless when applied to the heavy, much more widespread ongoing forms of exploitation via public hunting and trapping that predominate in the north, especially in Alaska. For example, of the more than 1600 wolves killed in Alaska during the August 1993–April 1994 reporting period, only 98 were killed via government control. It is important to understand how frequent the "renewals" and how short-lived the intervening "recoveries" of wolf populations subject to heavy, ongoing exploitation are likely to be. In Alaska it is only from the 30 April closing of one hunting/trapping season to the 10 August opening of the next that most populations are protected. Biologists and managers who dismiss concerns about the impacts of heavy killing on the qualitative aspects of wolf biology have not addressed this critical difference between formal control and ongoing exploitation, with regard to the duration and extent of these impacts.

Note the indications (Appendix 1) of lingering higher overall natural mortality rates for wolves that survive harvest and control, when compared to populations where there has been little or no recent harvest or control. This would appear to be a predictable result of the increased fragmentation, higher turnover, and greater

overall social disruption that accompanies heavy killing. This by itself provides a warning that the biological importance of a sophisticated, natural social structure is being greatly underrated. It may represent a simple quantitative indication of the impact of human killing on a range of qualitative features of wolf biology.

Sterilization and other forms of fertility control, "redirected killing," and relocation of juveniles are emerging as new approaches to wolf control in Alaska and the Yukon Territory. Control advocates are again arguing that there will be little more than temporary numerical reductions without significant biological costs. A current wolf sterilization-trapping-relocation proposal for the Fortymile region of Alaska (Alaska Department of Fish and Game 1995a; 1995b) is illustrative. At least 13 family groups of wolves (Alaska Department of Fish and Game 1995b: 8,13) would be reduced to alpha pairs if possible, via trapping, snaring, and relocation. The alpha pairs would be spared to maintain existing territories in order to prevent other wolves from moving into the region. Then, up to 30 males and/or 15 females would be sterilized. Potential biological impacts are described as follows:

Sterilization is a minor surgical procedure causing limited trauma. Current research indicates there is no change in wolf behavior. . . . Within 10 years, the wolf population should be back to current levels and should continue to increase. . . . Local trappers could assist this plan by shifting their efforts to wolves whose territories encompass the [caribou] calving and summer range, where little or no trapping currently occurs. The area-wide [wolf] harvest in the Fortymile is not expected to increase since trappers will be shifting their efforts [from peripheral areas], not increasing them. . . . Dispersal of young wolves is common and relocations would mimic this behavior. (Alaska Department of Fish and Game 1995a: 1,4; 1995b: 7, 8).

Given the unusual family-based social structure of wolves, it is simplistic to imply that reducing these complex societies to sterile pairs will not have significant behavioral or other biological consequences. The 5- to 10-year distortion in age structures and disruption in the flow of genetic and cultural information alone imply a likelihood of important changes.

The claim that there would be no increased trapping impacts because trappers would shift their efforts from the wolves they are already exploiting in peripheral areas to lightly or untrapped wolves again illustrates the assumption that little more than area-wide numbers are important biologically. Similarly, relocation of juvenile wolves might mimic natural dispersal to some extent, including in its most common outcome for the dispersers, mortality. However, many juveniles of this and nearby regions do not disperse. They remain in their family groups through adulthood and ultimately contribute in important ways (Haber 1977, 1994, 1995b, unreported 1995-1996 data). It is unavoidable that significant numbers of these juveniles, especially pups of the year (short

yearlings), would be relocated, which implies both individual and group impacts.

An Evolutionary Perspective

Wolf social behavior is remarkably adaptable, but the adaptations are primarily for cooperative hunting, not defense against sustained, heavy predation. It does not follow that wolves will be able to survive heavy exploitation and control just because they have held their own numerically against heavy killing for the past 40-50 years in places like Alaska. A few decades of heavy killing amount to the blink of an eye compared with the far longer period of evolutionary time over which wolves have evolved in response to the opposite pressures. Modern wolves have been present for at least 1-2 million years (Mech 1970) and for at least 500,000 years in Alaska.

The relationship between total population size (i.e., numerical status) and the integrity of component social systems appears to be subtle and nonlinear, just as we are now finding to be the case for many natural relationships. For example, a social breakdown can lead in the short term to more successful matings in the population and thus relatively stable or even higher total numbers (Appendix 1). Nevertheless, it is foolish to ignore the possibility that after some further lag, and lags are common in nature, there will finally come a dramatic collapse in total numbers. Serious problems with social organization and other important qualitative biological features must ultimately translate into a major, long-term decline in numbers, but the linkages are likely too indirect to rely on the numerical signal for a warning before the underlying qualitative problems become impossible to reverse.

In population viability simulations based on information from the Isle Royale wolf population, including social structure, Vucetich and Peterson (1995, personal communication) found that mean time to extinction was independent of population size for all populations above a threshold of only eight wolves. The number of social units was of much greater importance than total numbers in predicting the population's viability.

It is questionable as to whether a normally ultra-social species "survives" if its social organization is continually shredded by heavy exploitation. Heavy, ongoing exploitation implies a high potential for eventually reducing these complex societies to much simpler, more primitive forms, particularly when it is so likely to scramble their unusual genetic and cultural information transfer processes. Nonlethal forms of control, such as sterilization and relocation, could easily end up producing the same or similar results.

Natural selection leading to further speciation or the maintenance of a particular adaptive state probably operates on only a tiny portion of a species' genome in

most cases. This means many of the important natural forces of selection that distinguish one species from another are inherently small and subtle. For the wolf natural forces are likely to be swamped by the artificial, random forces associated with heavy annual killing, forces to which this species has not had time to adapt.

Those who try to defend heavy, ongoing killing and even some more limited forms of control, including sterilization, seem to view natural forms of wolf social organization as lacking intrinsic value. But, as with the basic organizational state of any well-established species, the sophisticated, highly developed sociality of wolves is the product of past selection forces and thus represents the level of organization most environmentally fit for this species.

A related biological view could help guide our exploitation of wild vertebrates in general and could sharpen the thinking that underlies the U.S. Endangered Species Act and similar legislation. This view emphasizes the differences among species in their adaptations for exploiting versus being exploited. Eusocial cooperative hunters, such as wolves and African wild dogs, represent one extreme, for which there is no biological rationale for harvesting and no way to undertake most control programs without major biological costs. Herbivores such as the ungulates represent virtually the opposite extreme. For ungulates, the interactions among individuals and generations are simple enough so that the survivors can quickly reorganize and carry on in about the same way when many others are removed.

Species of this kind are well adapted to exploitation within carefully defined limits (Haber 1977, 1980; Haber & Walters 1980; Walters et al. 1981), having persisted as prey throughout their long evolutionary histories. There are familiar scenes from the East African plains and elsewhere of hoofed grazers either ignoring kills by predators in their midst or resuming feeding activity within minutes.

Between the cooperative hunter and ungulate/herbivore prey extremes there is a "gradient of sociality" that might suggest differences in the way we exploit other species as well. This approach and more emphasis on protecting the integrity of underlying natural system, population, and group patterns and processes in general (Haber 1992: 15–24) when harvesting is biologically justified (e.g., for ungulates) represents the kind of selectivity that true sustained-yield management implies. This merely acknowledges that there are some key differences among species and that harvestable populations are components of dynamic systems rather than separate crops.

Implications for Conservation and Management

Although, in my view, there is no biological rationale for routine harvesting of wolf populations, short-term, re-

medial wolf control programs for ungulate population management may be warranted biologically in exceptional cases, for example, when natural patterns and processes have been seriously disrupted in unnatural ways at much larger scales and wolf predation is preventing recovery. A determination as to what "natural," "unnatural" and other such criteria mean in these situations will always be difficult and will require some subjectivity but in general should be possible. I predict that only rarely will such biological justification for control be found, even for major ungulate declines.

Haber (1977) and Haber & Walters (1980) provide an example of a set of circumstances where wolf control for ungulate management purposes was warranted. Overharvesting had triggered a premature major decline in the Western Arctic caribou herd—the primary center of abundance in the then depressed Alaska-Yukon caribou population—and wolf predation appeared to be a critical variable preventing a timely recovery. This was not merely a major decline of caribou in the western Arctic, which by itself would not necessarily be a matter of concern. It was a decline that created what appeared to be a premature, unnatural condition of low synchrony in the Alaska-Yukon system of caribou herds as a whole, quite unlike the present condition of high system-wide abundance and asynchrony.

Biologists, agencies, legislators, and others have subsequently proposed wolf control programs in response to much less obvious ungulate problems, where there are no problems, or where there is little prospect of resolving such problems with wolf control (especially with regard to caribou). There has been minimal consideration of the potential biological costs, especially for the target wolf populations. Most of the recent ungulate-related Alaska and northwestern Canada wolf control proposals and programs have been frivolous from these and other standpoints (Haber 1987, 1988, 1992, 1993a). My initial review of several new (October 1995) Alaska wolf control proposals, including Alaska Department of Fish and Game (1995a, 1995b), indicates the same for them (Haber letter 28 September 1995 to S. Todd, Alaska Department of Fish and Game files, Fairbanks).

Ungulate-related wolf (and bear) control proposals should be evaluated on a case-by-case basis and subjected to rigorous scientific review. Decision-makers and the public should be provided with more information on the potential biological (and other) costs, benefits, and alternatives for each proposal. There should be an a priori assumption that control is not warranted. This would help to ensure a more scientifically defensible approach, as demonstrated in hypothesis testing. The emphasis would shift from trying to find support for proposals to "falsifying" them. Proponents—agency and otherwise—should not oversee the review process.

Thus, I disagree with Mech's (1995) view that some form of wolf control will generally be necessary. Mech

fails to allow that there is disagreement as to what is necessary. His view as to the inevitability of control seems to reflect his belief that wolves do not socially limit their own population. On the contrary, social limitation appears to be of major importance under natural conditions. This is indicated by the relative stability in size of established, vigorously reproducing family groups even during periods of minimal hunting and trapping losses and ample prey (Murie 1944; Haber 1977, 1992, 1994, 1995*b*; Peterson 1977; Allen 1979) and by related annual variations in patterns of temporary group splitting and the dispersal or mortality of juveniles (Haber 1977). Although wolf social organization probably represents an adaptation for self regulation, human exploitation probably selects against self-regulating traits.

Mech dismisses opposition to ungulate-related wolf control as "politically" motivated and the result of misinformation by "animal-rights groups," despite negative evaluations by other professionals that focus exclusively on the biology of recent control proposals, to which he has not responded. He similarly dismisses opposition to wolf control for livestock depredation, without noting that in at least some major cases protest about this kind of control arises because it appears to be much less selective than is necessary and the law requires (Friends of Animals Inc. v. Babbitt et al., U.S. District Court, District of Connecticut, 7/10/95). In Minnesota (U.S.A.) for example, a suspected wolf kill of a livestock animal now often prompts federal officials to try to kill all or most of the wolves that subsequently visit the original carcass or supplemental baits a half mile or more from the original site for up to 30 days afterward, even though wolves scavenge dead ungulates (Haber 1977) and only one wolf may have been involved in the livestock kill.

Mech (1995) suggests that there is less protest about the much heavier kill of wolves in Alaska via public hunting and trapping than by government control because there is more political advantage to be gained in stirring up opposition to the government. He ignores the fact that leading opponents have long attempted to call attention to the public kill as being of at least as much biological impact as government control (Haber 1985, 1993*b*, 1993*c*, 1995*a*; Haber versus Mech debate: "Biological Impacts on Wolves of Exploitation and Control," at First Annual Conference of The Wildlife Society, 9/24/94). He seems unaware of the deceptive way in which the public kill is reported (Haber 1985, 1993*b*, 1995*a*). For example, most of this kill is reported as due to trapping. But as noted earlier, state and federal regulations define trapping to include direct hunting with firearms in most areas (semi-automatic weapons are commonly used for wolves, legally), without requiring any actual trapping, to permit the virtually direct use of airplanes and snowmachines, and to allow saturation snaring.

Mech (1995) recommends that control programs should be carried out by public hunting and trapping in-

stead of government agencies, in the interest of promoting more widespread recovery of wolves to areas of former range. He argues that agencies have become increasingly reluctant to promote recovery because of the controversy they fear in later trying to control the same wolves.

Mech's argument again assumes that control is generally necessary, which I believe more rigorous review would reveal not to be the case. I suggest that wolf advocates would be much more willing to accept control if it were proposed only when actually needed and carried out much more selectively. For ungulate-related wolf control, a more rigorous process would do much to prevent unrealistic user expectations about potential returns (Haber 1992: 43-44). In this sense, I agree with Mech (1995) that there are serious misconceptions, except that I attribute a large share of these to a failure by management agencies to provide adequate professional guidance for users.

Mech (1995: 272-273) portrays wolves as "inherently adaptable," such that, "In Spain wolves live like coyotes in wheat and sunflower fields" and (in Italy, Spain, and Portugal) obtain much of their food by scavenging garbage and livestock remains in and near rural villages. I agree that wolves are highly adaptable and that there are varying degrees of sociality, depending, for example, on the type of prey animals hunted (e.g., moose generally require more cooperation to kill than caribou; Haber 1977). And I agree that scavenging of dead ungulates is an important supplemental foraging activity for wolves. Nevertheless, Mech (1995) seems willing to accept almost any behavioral variation as "inherent." Should Mech's garbage-eating, largely solitary, sunflower-field canids really be regarded as wolves? Or are they the product of a lengthy, subtle process of "unwolving" via human persecution and habitat/prey displacement? Far from supporting his position, the examples he provides of "adaptability" may instead serve as a warning about the pitfalls of watching for numerical signals of endangerment while ignoring virtually all else about a creature's biology.

More detailed comparisons between exploited and unexploited wolf populations are needed. There is little problem in obtaining information about currently or recently exploited populations, where most of the research effort lies. However, opportunities to do research in areas that have remained free of harvest and control for a long period are rare. Even in such world-renowned wolf research areas as Algonquin Provincial Park, Ontario, and Denali National Park, Alaska, established resident family groups of wolves are still exploited to some extent via legal hunting and trapping, inside park boundaries as well as outside (J. Theberge, personal communication; Haber 1995*a*; Federal Subsistence Board 1995; Alaska Board of Game 1995).

For Denali the responsible agency biologists and managers continue to defend current policies that allow non-

selective 8- to 9-month annual harvests of up to 10 wolves per hunter and no-limit trapping, and to actively oppose creation of a protective buffer on state lands along critical boundary areas, with arguments about the health of total numbers ("numbers generally range between 100 and 130") and their view that "not many" wolves are likely to be taken (National Park Service 1995; S. Martin, testimony to Alaska Board of Game, March 1996). This is despite aerial radio-tracking surveys by the National Park Service and me that consistently yielded total counts of only 55–77 wolves in 9–11 family groups from November 1995 through April 1996, and despite the complete hunting/trapping loss of the Headquarters family group as of May 1995, the trapping loss of the alpha-male and at least three other wolves from the Toklat family group in November 1992, the likely hunting/trapping loss of the heavily viewed, intensively studied Savage family group (Haber 1977, 1987) in winter 1982/1983, and other such hunting/trapping losses through recent years. Nor are wolf hunters and trappers even required to report their kills until well after the fact—hunters not until 30 days afterward, trappers not until 30 May. In contrast, the 2000–3000 caribou of the Denali herd are off limits to all hunting. There are about 2000 moose in Denali, with a harvest limit of one bull per hunter, a season of only 60 days, a ban against hunting in the most accessible areas, and no hunting of white-phased or albinos (Federal Substance Board 1995; Alaska Board of Game 1995).

Ethical Considerations

High intelligence, expressiveness, and unusual emotional depth enable wolves to maintain sophisticated social bonds, to work together as highly skilled cooperative hunters (Haber 1977). This same extraordinary sentience that is so integral to their basic biology also provides an ethical reason for not allowing them to be harvested and for considering remedial short-term control only in the rarest of circumstances, when there are solid, irrefutable biological and cost-benefit arguments and no other reasonable alternatives. To treat them otherwise is wrong. Such higher standing is now generally accorded to other creatures of obvious high sentience, including whales, dolphins, gorillas, and chimpanzees, and it is time to extend it fully to wolves.

I have described some of the details of the heavy, indiscriminate killing of wolves that is still permitted in Alaska. Consider an additional problem for the wolves of Denali National Park: Although the Denali wolves still hunt and seem to behave socially and individually as they did when I first began studying them in 1966, over recent years they have become strongly habituated to people because of numerous close, friendly contacts with park visitors each summer. Based on my 10,000+

hours of wolf observations in Denali since 1966, I am convinced that most of this habituation involves a form of trust by the wolves. For the most part, they seem now to view people in a friendly, sometimes playful way. I have yet to see or hear of any obvious aggressive behavior.

As of 10 August each year whenever the same wolves step across the park boundary or enter the 1980 park additions they become legal quarry for hunters and as of 1 November they become legal quarry for trappers. We allow them to trust us inside the park and then look the other way when they become easier hunter-trapper fodder because of this diminished wariness. This was the predicament of the Headquarters family and of the alpha-male and others of the Toklat family who were shot, snared, and trapped recently. I knew these wolves well. They had almost no fear of people. They were an easy mark for the few hunters and trappers who were allowed to kill them.

In her 1958 classic, *Arctic Wild*, Lois Crisler wrote with great sensitivity about the wolves she knew during the early 1950s in northern Alaska. This is always one of the first publications I recommend to aspiring biologists and laypeople who are interested in wolves because it portrays them as the marvelously intelligent, expressive, emotional creatures they are. This was the account that first stirred my interest in wolves. Almost 40 years later I am obliged to also read the sterile National Park Service summaries (e.g., Adams & Stephenson 1986, 1988; Adams et al. 1989) of the 15–20% annual wolf harvests that are currently allowed within the same area—now Gates of the Arctic National Park—by native "subsistence" hunters with high-speed snowmachines.

I recognize that my strong opposition to the way wolves are managed in Alaska and elsewhere involves more than pure biology. I receive frequent criticism for this position from my peers. Nevertheless, Aldo Leopold did not hesitate to venture into such areas of overlap between biology and ethics, to distinguish between right and wrong in advocating improved management of natural systems. Other wildlife scientists who regard his ideals as a guiding light for the profession should not hesitate to do the same.

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Appendix 1

Known or likely impacts of heavy (15–20+% annual) exploitation and control on wolves.

Impact		Area	Source
1. Smaller late winter average group sizes; more population fragmentation.			
<i>Wolves/group</i>	<i>Groups/1000 km²</i>	<i>Wolves/1000 km²</i>	
No known heavy killing immediately before or during observation.			
7-14	0.77	5.4-10.8	Denali N.P., Alaska
6.2-10.9	0.82	4.0-11.2	Denali N.P., Alaska
4.7-8.7	1.0-1.1	4.1-8.1	Denali N.P., Alaska
5-8	0.85	4.2-6.8	Denali N.P., Alaska
No known heavy killing immediately before observation; heavy killing during observation.			
11.3 to 5.6 (annual exploitation: 7-18% to 25-31%) ^d	0.79 to 2.20	9.0 to 12.31	Kenai Pen., Alaska
8.6 to 3.6 to 5.5 (annual control rates: 38-39% to 66% to 23-29%) ^e	1.3 to 1.4 to 1.6	12.4 to 3.6 to 10.8	SW Yukon
12.0 to 4.5-7.0 to 7.6 (annual control rates: 61% to 85-86% to 0) ^f	0.83 to 1.03-1.15 to 1.92	10.0 to 5.19-7.12 to 14.62	Horseranch area, northern B.C.
Heavy killing during observation; known or likely heavy killing immediately before.			
2.9-4.7	0.75-1.52 ($\bar{X} = 1.14$)	2.6-7.1	Nelchina Basin, Alaska
5.1	1.50-3.07	15.67	GMU 20A, Alaska
2.0-3.5	1.10-1.61	2-5	Fortymile region, Alaska ^g
3.5-4.7	0.86	3-4	Fortymile/upper Tanana/Charley region, Alaska ^g
2.0-5.1	0.84-1.44	1.68-7.31	Minto area, Alaska
4.5-5.7	0.65-0.85	3.7-3.9	Gates of the Arctic N.P., Alaska
6.2 to 3.4-4.1 to 3.6 (annual control rates: 79% to 73-83% to 65%) ^b	2.53 to 3.65 to 3.11	15.73 to 12.50-15.02 to 11.13	Kechika area, northern B.C.
5.32 to 3.16-3.69 to 4.03 (annual control rates: 60% to 77 + 0% to 60%) ^f	7.38 to 3.5-6.0 to 4.52	39.30 to 12.93-18.95 to 18.25	Muskwa area, northern B.C.
Probably some heavy killing immediately before and/or during observation.			
7.7-8.4	1.85-2.01	15.44-15.60 ^j	Blue-Jennings area, northern B.C.
2. Mating less selective; more litters per population and generally higher mid-late winter pup ratios, except at highest exploitation intensities.			
No known heavy killing immediately before or during observation.			
Typically one litter per group; 0-15% of groups produced 2-4 litters annually (simultaneously). Fewer than 25-50% of adult females produce young. $\bar{X} = 37\%$ pups (18-60%).		Denali N.P., Alaska	Haber 1977 ^a ; Haber, NPS unpublished 1978-1995 ^c ; Mech et al. 1991 ^b ; Meier et al., 1995 ^b
No known heavy killing immediately before observation; heavy killing during observation.			
One litter per group (two in one group). 67% of adult females in estrus or previously pregnant. Percentage pups in population increased 26 to 54% as hunting and trapping increased 7-18% to 25-31%. ^d		Kenai Pen, Alaska	Peterson et al. 1984
No more than one litter per group. 82% of adult females (from before and during control samples combined) in estrus or previously pregnant. Percentage pups in population increased 36 to 45% (78%+ of groups reproduced annually) during two years of 38-39% control; percentage pups decreased to 16% the next year (39% of groups reproduced) following 66% control. ^e		SW Yukon	Hayes et al. 1991
Heavy killing during observation; known or likely heavy killing immediately before.			
89% of adult females in estrus or previously pregnant. $\bar{X} = 45\%$ pups in population (39-60%). Typically one litter per group; 7-10% of groups produced two litters annually. $\bar{X} = 57\%$ pups in population (42-74%). ^g		Interior Alaska Nelchina Basin, Alaska	Rausch 1967 Ballard et al. 1987
71% of adult females in estrus or previously pregnant. $\bar{X} = 30\%$ pups in population (25-33%). One litter per group. $\bar{X} = 32\%$ pups in population (31-33%).		GMU 20A, Alaska Fortymile/upper Tanana/Charley region, Alaska ^g	Gasaway et al. 1983 Haber 1994, 1995 ^b , unpublished 1995 data
Typically one litter per group. Approximately 41% pups in population.		Gates of the Arctic, N.P., Alaska	Adams & Stephenson 1988

Appendix 1

Continued.

	<i>Impact</i>	<i>Area</i>	<i>Source</i>
3.	More variable (moose) kill rates. No known heavy killing immediately before or during observation. Kill rates increased with increased group size over a range of 2 to 7-9 wolves, then leveled off through a group size of at least 19. ^a	Denali N.P., Alaska	Haber 1977
	No known heavy killing immediately before observation; heavy killing during observation. Kill rates of pairs often the same as for groups of 6-7 wolves. No significant correlation between kill rate and group size through a group size of at least 7 wolves, even when pairs are excluded. ^a	SW Yukon	Hayes et al. 1991
	Heavy killing during observation; known or likely heavy killing immediately before. Kill rates increased with increased group size over a range of 2-9 wolves, then apparently continued increasing more slowly through a group size of at least 20.	Nelchina Basin, Kenai Pen, Alaska	Ballard et al. 1987 (includes one data point from Peterson et al. 1984).
4.	More variable territories No known heavy killing immediately before or during observation. At least 3 of 15 territories in 1987-1988 were still occupied by the same groups in 1995, in approx. the same areas or (for one) in the core of the same area; 1-2 of these 3 territories/groups extend back to at least 1966-1974. Of the remaining 12 territories at least 6 were approx. the same in 1995 as in 1987-1988 but were apparently occupied by new groups; 2 of these turnovers were probably caused by hunting and trapping. The other 6 territories were not monitored adequately through 1995, although as of 1991-1992 at least one was occupied by the same group in approx. the same area, another was occupied by 2 neighboring groups via expansion of their territories (the previous group disappeared naturally), and a third was occupied by 3 smaller groups. A group occupying another, stable territory for 16+ years was eliminated in 1983, probably due to hunting/trapping. Most of this vacancy was occupied by another group for 11 years, until it was eliminated by hunting and trapping in 1993-1995. A new group began occupying essentially the same area in 1995.	Denali N.P., Alaska	Haber 1977 ^a ; Mech et al. 1991 ^b ; Meier et al., 1995 ^b ; Haber, NPS unpublished 1978-1995 ^c
	No known heavy killing immediately before observation; heavy killing during observation. 2 of the 3 territories covering most of the study area in 1976-1977 were occupied by the same groups in 1980-1981. One of the 3 territories was approx. the same size in 1980-1981, and another was centered in approx. the same location. There were 4 additional, occupied territories within the overall 1976-1977 area in 1980-1981. ^d	Kenai Pen, Alaska	Peterson et al. 1984
	None of 3 closely monitored "sample" territories was occupied by the same group in 1986-1987 as in 1982-1984. One of the 3 territories was of approx. the same size and location in 1986-1987. Within the overall wolf control area, "suspected" territory boundaries (>18-20 territories) suggested a substantially different mosaic in 1987-1988 versus 1982-1984. Control increased from 38-39% in 1982-1984 to 66% in 1984-1985, then decreased to 23-29% in 1986-1987. ^e	SW Yukon	Hayes et al. 1991
	Heavy killing during observation; known or likely heavy killing immediately before. 3-4 of 15 territories in 1975-1976 were occupied by the same groups in 1980-1982. 0-2 of these territories and 3-7 of the other 11-12 were of approx. the same size and location in 1980-1982. There were 2-4 additional, occupied territories within the overall 1975-1976 area in 1980-1982.	Nelchina Basin, Alaska	Ballard et al. 1987
5.	Less use of established dens. No known heavy killing immediately before observation; heavy killing during observation. 76% and 64% of known 1966-1982 and 1966-1993 within-summer homesite moves (following abandonment of the natal den; $n = 17,59$) by 2 family groups occupying approx. the same adjacent territories for 16+ and 50+ years, respectively, were to various established dens (versus rendezvous sites). 33% of known moves ($n = 12$) by wolves that colonized the "76%" territory in 1984, after the 16+ year residents were eliminated (probably by hunting/trapping) were to a den, in each case to the same established den. This group was eliminated by hunting/trapping in 1993-1995.	Denali N.P., Alaska	Haber 1977 ^a ; Haber, NPS, unpublished 1978-1995 ^c
6.	Territory size varies more directly with resident group size, sometimes with disproportionately much larger initial territories for colonizers. No known heavy killing immediately before or during observation. No significant relationship between territory size and group size over a range of at least 5-20 wolves/group. Territory size varied inversely with moose density.	Denali N.P., Alaska	Haber 1977 ^a ; Mech et al. 1991 ^b
	No known heavy killing immediately before observation; heavy killing during observation. Territory size varied significantly with group size (i.e., larger groups-larger territories) over a range of at least 5-20 wolves/group. Smaller, recolonizing groups, especially pairs, initially occupied disproportionately much larger territories (3-4 \times area/wolf) than were occupied by larger groups. ^d	Kenai Pen, Alaska	Peterson et al. 1984
	Smaller, recolonizing groups, especially 2-3 wolves, initially occupied disproportionately much larger territories (5 \times area/wolf) than were occupied by larger groups. ^e	SW Yukon	Hayes et al. 1991
	Heavy killing during observation; known or likely heavy killing immediately before. Territory size varied significantly with group size over a range of at least 2-15 wolves/group, and inversely with moose density.	Nelchina Basin, Alaska	Ballard et al. 1987

Appendix 1

Continued.

Impact	Area	Source
7. Higher overall natural mortality rates.		
No known heavy killing immediately before or during observation		
16-31% annual "losses"—i.e., natural mortality and dispersal combined; closely related to early winter group size for at least one established family group—this was the primary means by which the size of this group was limited.	Denali N.P., Alaska	Haber 1977 ^a
\bar{X} = 13% (7-18%) annual natural mortality.	Denali N.P., Alaska	Mech et al. 1991 ^b
\bar{X} = 20% annual natural mortality.	Denali N.P., Alaska	Meier et al., 1995 ^b
No known heavy killing immediately before observation; heavy killing during observation.		
\bar{X} = 25% annual natural mortality; increased from 14-21% to 25-38% as hunting and trapping increased from 7-18% to 25-31%. Population limited primarily by exploitation. ^d	Kenai Pen, Alaska	Peterson et al. 1984
\bar{X} = 60% annual natural mortality; increased from 32-36% to 79% as control increased from 38-39% to 66%; decreased to 49% the next year as control decreased to 29%, then increased to 78-84% for at least the next 2 years as control decreased to ~23%. ^e	SW Yukon	Hayes et al. 1991
Heavy killing during observation; known or likely heavy killing immediately before.		
\bar{X} = 29% annual natural mortality. Population limited primarily by exploitation and control.	Nelchina Basin, Alaska	Ballard et al. 1987

^a 1966-1992 for group sizes, groups/area, and wolf densities; 1966-1974 for reproductive info, kill rates, territory size versus group size, and mortality rates. Data for up to five established family groups primarily from periods when these groups suffered few if any hunting/trapping losses.

^b 1986-1992. Data for up to 16 groups, including some in areas of the park/preserve where there were moderate to heavy hunting and trapping losses over earlier years and decades and sporadic light to moderate losses during the period of observation.

^c 1978-1992 or 1993-1995. Data for up to 3 (1978-1992) or 11 (1993-1995) groups, including some in areas of the park/preserve where there were moderate to heavy hunting and trapping losses over earlier years and decades and sporadic light to moderate losses during the period of observation.

^d 1976-1982. Continuing heavy exploitation (hunting and trapping) applied to an initially lightly exploited population—i.e., exploitation increased from 7-18% to 25-31%. Data show changes in each variable during the period of observation.

^e Heavy government control applied to an initially lightly exploited population—i.e., control increased from 38-39% in 1982-1984 to 66% in 1984-1985 then decreased to 23-29% in 1986-1987. Data show changes in each variable during this period of observation. The first values shown for group sizes, groups/area, and wolf densities are from 1982-1983, just before the initial (38-39%) control was applied; the other two values shown for group sizes, groups/area, and wolf densities are from the subsequent heavy (66%) and then decreased (23-29%) control periods.

^f Heavy government control applied to an initially lightly exploited population—i.e., control increased from 61% in 1978 to 85-86% in 1979-1980. There was no further control after 1980. Data show changes in each variable from 1978 just before the initial (61%) control to 85-86% control in 1979-1980 to 1982 (2 years after control had ended).

^g Gasaway et al. 1992 data are for 1982-1989. Haber data are for 1993-1995 from Gasaway's area plus adjoining regions.

^h Heavy government control applied to a population probably subject to some illegal, nongovernment control. Government control was applied at rates of 79% in 1982, 73-83% in 1983-1984, and 65% in 1985. Data show changes in each variable from 1982 just before the initial (79%) control, to 73-83% control in 1983-1984, to 1985 just before the 65% control. Data for an additional year (1986) cannot be compared directly because the survey/control area was almost doubled.

ⁱ Heavy government control applied to a population probably subject to some illegal, nongovernment control. Government control increased from 60% in 1984 to 77% in 1985, then decreased to no control in 1986 and 60% in 1987. Data show changes in each variable from 1984 just before the initial (60%) control, to 77 + 0% control in 1985-1986, to 1987 just before the 60% control. No further data available.

^j 1985-1986. No government control but probably some illegal non-government control.

^k This pup ratio estimate was derived in part from ground trapping data. Ground trapping (with traps and snares versus airplane-assisted shooting/"trapping") is usually biased to catching pups, thus the actual pup ratio may be somewhat lower than shown here.

