Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide

ADRIAN TREVES*‡ AND K. ULLAS KARANTH†

*Center for Applied Biodiversity Science, Conservation International, 6010 South Hill Drive, Madison, WI 53705, U.S.A.
†Wildlife Conservation Society, International Programs, 2300 Southern Boulevard, Bronx, NY 10460, U.S.A.

Abstract: *Carnivore conservation depends on the sociopolitical landscape as much as the biological landscape. Changing political attitudes and views of nature have shifted the goals of carnivore management from those based on fear and narrow economic interests to those based on a better understanding of ecosystem function and adaptive management. In parallel, aesthetic and scientific arguments against lethal control techniques are encouraging the development of nonlethal approaches to carnivore management. We anticipate greater success in modifying the manner and frequency with which the activities of humans and domestic animals intersect with those of carnivores. Success should permit carnivore populations to persist for decades despite human population growth and modification of habitat.*

Conflicto entre Humanos y Carnívoros y Perspectivas de la Gestión Mundial de Carnívoros

Resumen: *La conservación de carnívoros depende tanto del paisaje sociopolítico como del paisaje biológico. Cambios en las actitudes políticas y percepciones de la naturaleza han cambiado las metas de manejo de carnívoros de aquéllas basadas en el miedo y las intereses económicos estrechos a metas basadas en un mejor entendimiento del funcionamiento del ecosistema y en el manejo adaptativo. A su vez, los argumentos estéticos y científicos en contra de las técnicas de control letal están fomentando el desarrollo de planteamientos no letales en la gestión de carnívoros. Anticipamos un mayor éxito en la modificación del modo y la frecuencia en que las actividades de humanos y animales domésticos intersectan con las de carnívoros. El éxito debe permitir que las poblaciones de carnívoros persistan por décadas a pesar del crecimiento de la población humana y la modificación de hábitats.*

Introduction

The members of the mammalian order Carnivora number about 226 species, almost all of which are predators. As a group, carnivores exert a profound influence on biological communities via predation and interspecific competition. Carnivores often regulate or limit the numbers of their prey, thereby altering the structure and function of entire ecosystems (Schaller 1972; Estes et al. 1998; Berger et al. 2001; Terborgh et al. 2002). As a result, carnivore management is of central concern to conservation biologists. In this context, human-carnivore conflicts (carnivore-related threats to human life, economic security, or recreation) pose an urgent challenge worldwide because these conflicts often pit human communities against carnivores and against other humans who seek to preserve or restore wildlife populations (Torres et al. 1996; Bangs et al. 1998; Berg 1998; Karanth & Madhusudan 2002).

Human-carnivore conflict arises for several reasons. Carnivores' protein-rich diet and large home ranges draw them into recurrent competition with humans, who have somewhat similar needs. Indeed, many larger carnivore species are specialized for ungulate predation; therefore, some individuals readily kill domesticated ungulates when opportunities arise (Meriggi & Lovari 1996; Karanth

‡*Current address: Living Landscapes Program, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, U.S.A., email atreves@wcs.org*
Paper submitted February 3, 2003; revised manuscript accepted May 7, 2003.

et al. 1999; Polisar 2000). This is a worldwide problem, exemplified by wolves (*Canis lupus*) and bears (*Ursus* spp.) killing sheep in North America and Europe; pumas (*Puma concolor*) and jaguars (*Panthera onca*) taking cattle in South America; numerous carnivore genera preying on cattle and goats in Africa; and tigers (*P. tigris*) and leopards (*P. pardus*) killing livestock in Asia (Jackson & Nowell 1996; Kaczensky 1999; Karanth & Madhusudan 2002). Under some conditions, individual carnivores attack humans, with tragic consequences for all (Brain 1981; McDougal 1987; Treves & Naughton-Treves 1999; Rajpurohit & Krausman 2000; Karanth & Madhusudan 2002). This competition over food and space is not restricted to big, fierce predators. Smaller carnivore species have long been involved in competition with humans over game species, crops, apiaries, fish stocks, and poultry (Gipson 1975; Jorgensen et al. 1978; Reynolds & Tappen 1996).

The frequency and economic cost of conflicts between humans and carnivores appears to be on the increase in many areas (Halfpenny et al. 1991; Mech 1998; Karanth 2002; Rajpurohit & Krausman 2000; Treves et al. 2002). Conflicts between humans and wildlife increase with the expansion and growth of human populations, farming frontiers, and housing (Thouless & Sakwa 1995; Torres et al. 1996; Woodroffe 2000; Naughton-Treves et al. 2003 [this issue]). Under a variety of demographic, economic, and social pressures, human alteration of carnivore habitat or exploitation of carnivores has led to escalated conflicts (Mladenoff et al. 1997; Liu et al. 2001; Naughton-Treves et al. 2003 [this issue]). Humans have also allowed the recovery of carnivores, which has promoted conflicts in some areas. For example, changing land-use practices exemplified by the regrowth of forests in many regions of the United States are providing room for potential recolonization by previously extirpated carnivores (Mladenoff et al. 1997). Also, successful recovery programs for extirpated carnivores have raised concerns about conflict (Bangs et al. 1998; Breitenmoser 1998). Conservationists must now resolve human-carnivore conflicts in a setting of rapid social and ecological changes across the landscape.

Opponents of carnivore recovery or population persistence remain active both politically and on the ground. For example, intentional killing of carnivores by humans is a major and rising threat to carnivore population viability (Rabinowitz 1986; Jhala & Giles 1991; Bangs et al. 1998; Woodroffe & Ginsburg 1998; Landa et al. 1999). At the same time, new social constituencies have emerged to promote carnivore preservation as a part of broader social mobilizations in support of nature protection or animal welfare (Harbo & Dean 1983; Torres et al. 1996; Berg 1998; Breitenmoser 1998; Forbes et al. 1998; Fox 2001). In this new sociopolitical context, past strategies of managing carnivores may need to be re-evaluated. Preventing and mitigating human-carnivore conflict must be based on an improved understanding of carnivore behavioral ecology and public acceptance of wildlife management, and it must draw upon accumulated empirical knowledge and local experiences. To suggest some directions for the future, we examined past management of carnivores in the light of modern research into human-carnivore conflicts.

Overview of Past Approaches

Governments have used three primary strategies to manage wild carnivores. The three strategies can be defined by population management goals—eradication, regulated harvest, or preservation—and reflect economic cost-benefit ratios and varying social perceptions of carnivore species. Eradication is designed to reduce the negative economic or ecological impacts of carnivores, as in the elimination of exotic species that harm native fauna or flora or the attempted extirpation of native carnivores perceived as valueless. Regulated harvest involves controlling the timing, location, method, or number of carnivores killed by hunters, sometimes in combination with low-intensity monitoring of carnivore populations. Preservation aims to protect carnivores with more careful monitoring of their numbers and methods to prevent them being objects of poaching or illicit killing. Preservation is generally used in protected areas or for carnivore populations considered endangered, rare, or valuable.

The three primary strategies are neither immutable nor mutually exclusive. Often, we can understand changes in carnivore management policy by examining the records of human-carnivore interactions and their change over time (Suminski 1982; Harbo & Dean 1983; Torres et al. 1996; Breitenmoser 1998). For example, eradication gave way to regulated harvest as the value of leopard skins and their rarity increased from 1920 to 1960 in Uganda (Treves & Naughton-Treves 1999). Conflicts with carnivores often underpin changes in management policy. For example, lynx (*Lynx lynx*) harvest quotas have been directly tied to livestock losses in Norway (Sunde et al. 1998). We reviewed past examples of eradication, regulated harvest, and preservation policies to elucidate their costs, benefits, and constraints, and the conditions under which each may best be applied.

Eradication

Governments pursue policies of carnivore eradication through bounties to private hunters or systematic, widespread elimination by trained agents (Boumez 1989; Linton 1998; Treves & Naughton-Treves 1999; Rangarajan 2001). Campaigns to eradicate populations of carnivores have now largely been terminated, except for some against exotic carnivores that threaten native fauna. The justification for eradication of carnivores is usually prevention of agricultural loss or protection of other species.

These policies have a mixed record of success (Evans 1983; Theberge & Gauthier 1985; Reynolds & Tappen 1996; Ratnaswamy et al. 1997). A full treatment of this subject is beyond the scope of this paper, but failures to stem the perceived negative impacts of carnivores, through eradication, sometimes reflect inadequate understanding of the individual predator's interactions with the prey or resource valued by humans. For example, carnivores may select weak, aged, or young individuals unlikely to reproduce successfully (Evans 1983; Karanth & Sunquist 1995; Palmqvist et al. 1996). Eradication also has several costs. The first is political: conservation groups oppose threats to wildlife populations, and animal welfare groups oppose harm to individual animals. Eradication campaigns can also be costly to taxpayers if bounties are paid or involve expensive methods such as aerial hunting (Wagner & Conover 1999). Other costs may be ecological if the decline of carnivore populations upsets ecosystem function or leads to dramatic changes in the populations of other taxa (Estes et al. 1998; Berger et al. 2001; Terborgh et al. 2002). For example, small to medium-sized carnivores often benefit from reductions in large carnivores—a phenomenon referred to as mesopredator release (Newby & Brown 1958; Reynolds & Tappen 1996; Crooks 2002).

Regulated Harvest

In many regions, carnivores are managed by hunting (Jorgensen et al. 1978; Harbo & Dean 1983; Stowell & Willging 1992; Okarna 1993; Landa et al. 1999; Andersone & Ozolins 2000). The carnivore population is monitored to ensure sustainable harvests, usually by indirect, inexpensive, regional techniques rather than by intensive, systematic monitoring. For example, the previous year's harvest may be used to set current bag limits (Sunde et al. 1998). In our view, a policy of regulated harvest must include scientific monitoring by methods sensitive enough to detect significant population declines. This will generally require enforceable limits on the number of carnivores killed. Sound harvest policies also address the timing, location, and method of hunting, and the distribution of benefits to all stakeholders. Unregulated killing of carnivores is not a management strategy by our typology.

The cost of regulated harvests tends to be low. Placing control in local hands can satisfy the proponents of private property rights and self-determination while possibly raising public tolerance for dangerous carnivores (Linnell et al. 2001; Du Toit 2002). For example, between 1992 and 2001, black bears (*Ursus americanus*) killed 429 livestock in the state of Wisconsin (U.S.A.), whereas wolves killed 164 livestock (Treves et al. 2002; Wisconsin Department of Natural Resources, unpublished data). Yet political opposition to wolves is persistent, and opposition to bear populations is invisible (Stowell & Willging 1992; Naughton-Treves et al. 2003 [this issue]). This variation may reflect the fact that bear hunting is permitted and licenses are tremendously oversubscribed, whereas wolves cannot currently be hunted legally. With hunter cooperation, regulated harvests can provide information on carnivore populations and interactions with humans (Jorgensen et al. 1978; Faraizl & Stiver 1996; Andersone & Ozolins 2000). Licensed hunting can also provide funding for protection or rural development (Stowell & Willging 1992; Du Toit 2002). For example, Stowell and Willging (1992) described how the increasing revenue from harvests led managers of black bear populations to enforce protection outside the hunting season, translocate problem bears rather than destroy them, and closely regulate permits to kill problem bears. By combining regulated harvest with preservation tactics, managers could optimize political, economic, and ecological priorities.

However, carnivore harvests face increasing political opposition in the United States and Europe (Berg 1998; Breitenmoser 1998). This majority is increasingly composed of rural residents, as well as urban and suburban ones (Forbes et al. 1998). Critics of carnivore hunting cite concerns about animal welfare, conservation, tourism, and scientific issues (Harbo & Dean 1983; Haber 1996; Manfredo et al. 1998; Harden 2002; Treves 2002). Such opposition can limit managers' flexibility (Mansfield 1991; Torres et al. 1996).

Harvests intended to reduce crop and livestock losses have had limited effectiveness (Treves et al. in press). Private hunters and government culling agents often do not selectively target the individuals that cause economic losses (Jackson & Nowell 1996; Sunde et al. 1998; Sacks et al. 1999). Many individual carnivores pose no threat to crops, domestic animals, or humans, despite having access to them for years (Jorgensen 1979; Suminski 1982; Tompa 1983; Wydeven et al. in press). Hunters can even increase the risk of conflict if they wound rather than kill carnivores (Rabinowitz 1986; Hoogesteijn et al. 1993; Linnell et al. 1999). In short, hunting is unlikely to reduce human-carnivore conflict and might even increase it.

Preservation

In recent years, many countries have implemented strict protections following dramatic carnivore population declines. For example, the large felids are totally protected by law both inside and outside protected areas in India, and the laws are enforced reasonably well (Karanth et al. 1999; Rangarajan 2001). Even problem carnivores that stray into human settlements and kill livestock (and sometimes even humans) are not automatically killed; many protected-area managers prefer translocation (Sanyal 1987; Chellam & Johnsingh 1993; Karanth & Madhusudan 2002).

We see two primary benefits of preservation. First, it has resulted in the recovery of several carnivore populations from the brink of extinction in the last century and holds out hope for many other populations in severe decline (Wydeven et al. 1995; Bangs et al. 1998; Breitenmoser 1998; Karanth et al. 1999). Without strictly protected sites, it is nearly impossible to conduct longitudinal studies of carnivores that are critical to scientific management and shaping positive public attitudes toward wildlife (Mech 1970; Schaller 1972; Caro & Durant 1995; Haber 1996; Karanth et al. 1999).

On the other hand, preservation requires heavy investments of personnel, time, and resources in interaction with the public because managers have to demarcate and patrol boundaries, interdict and prosecute poachers, engage community participation, or verify damage claims. The costs of managing human-carnivore conflicts within preservation policies can also be high because many nonlethal methods are complex and expensive to maintain (Thouless & Sakwa 1995; Linnell et al. 1997; Angst 2001; Karanth & Madhusudan 2002; Shivik et al. 2003 [this issue]). A political cost of preservation is the opposition mounted by livestock producers, hunters, and local communities (Naughton-Treves et al. 2003 [this issue]). Hunters tend to range into carnivore habitats with firearms, and farmers can place poisoned bait and other traps on their land (Newby & Brown 1958; Tompa 1983). Few wildlife agencies have the wherewithal to prevent such illicit killing and must depend on the goodwill of farmers and hunters. Incentive schemes and compensation often aim to generate goodwill among these constituencies (Hötte & Bereznuk 2001; Mishra et al. 2003 [this issue]; Montag 2003; Naughton-Treves et al. 2003 [this issue]). Hence, the role of farmers and hunters in carnivore management policy exceeds their numerical representation.

Future Directions

Carnivore management now stands at a crossroads in many regions of the world. In some areas, carnivore populations have recovered to the point that regulated harvest is being considered. In others, threats to carnivores are growing despite efforts at preservation. We believe that the tactics employed for the mitigation of human-carnivore conflict will determine the future course of carnivore management in both these situations. We suggest that solutions to human-carnivore conflict can be classified as those that modify behavior (that of humans, livestock, or carnivores) and those that prevent the activities of humans and carnivores from intersecting in space.

Modifying Behavior

The most drastic ways to modify carnivore behavior are to kill the individual, sterilize it, or relocate it to a new site. Some workers argue that these control operations can have a positive effect on conservation and management if they are highly selective (Sacks et al. 1999; Treves 2002; Treves et al. 2004), whereas others believe that lethal control is essential to balancing political and conservation goals even if methods are not highly selective (Mansfield 1991; Mech 1995). However, opposition to lethal control of carnivores has impeded its use in some areas because the control operations are accused of preferential catering to livestock producers and hunters (Harbo & Dean 1983; Torres et al. 1996; Fox 2001). In addition to public opposition, there is reason for scientific skepticism about some forms of lethal control. For example, a survey of systematic studies of lethal control (Treves et al. 2004) suggests that 11–71% of the carnivores killed to prevent conflict showed no evidence of having been involved in recent conflicts (Gipson 1975; Horstman & Gunson 1982; Sacks et al. 1999). In the United States from 1996 to 2001, federal agents killed 13.7 million animals to control agricultural damages (U.S. Department of Agriculture Wildlife Services 2003). If error rates resemble those cited above, 1.5–9.7 million animals were killed without cause. Studies also show that conflicts recur in the same locations even after removal of a few individuals (Evans 1983; Hoare 2001; Karanth & Madhusudan 2002; Treves et al. 2004).

If lethal control can be applied selectively to reduce future conflicts or remove only the problem carnivores, it may be a useful component within both preservation and regulated harvest strategies. For instance, elimination of repeat offenders may facilitate public approval of protection for the remainder. Moreover, the surviving carnivores that avoid humans and their domesticates may gain a relative advantage and pass on their learned or genetic avoidance to future generations (Jorgensen et al. 1978; Treves 2002). Otherwise, lethal control is simply an expedient approach to satisfying stakeholders for a brief period at best (Hoare 2001). Selective removal of problem carnivores will require further advances in such areas as toxic defenses (Burns et al. 1996; Mason et al. 2001) or forensic techniques (Treves & Woodroffe in press).

From a conservation perspective, nonlethal removal may often be tantamount to killing when translocated animals die. In Wisconsin, for example, translocated adult and yearling wolves had significantly higher mortality than other radiocollared adults or yearlings (Wisconsin Department of Natural Resources, unpublished data). Translocation of bears, wolves, and some smaller carnivores has been reviewed by others (Jorgensen et al. 1978; Stander 1990; Linnell et al. 1997), so we summarize their findings here. Translocation can work if the individual is transported sufficiently far that it cannot return home and is placed in suitable habitat with territorial vacancies. Translocation of carnivores into protected areas or habitat already occupied by conspecifics can lead to social disruptions such as infanticide and intraspecific aggression that may result in many more carnivore deaths than would simply killing the problem animal

(K.U.K., unpublished data). If individual carnivores are extremely valuable—as the last individuals in a population or as trophy animals for sport hunters—translocation may be a cost-effective alternative to lethal removal (Stowell & Willging 1992). Public acceptance of translocation varies markedly, so its effective use may also depend on public education efforts and community participation (Manfredo et al. 1998; Naughton-Treves et al. 2003 [this issue]). Otherwise, the effort, expense, and high rates of mortality associated with translocation render it unsuitable for most situations.

Other forms of modifying carnivore behavior include nonlethal deterrence. Aversive stimuli are meant to trigger negative gustatory, olfactory, visual, or tactile sensations in carnivores to repel them from a resource that is important to humans. Chemicals that cause aversive responses when ingested have limited utility because they do not inhibit predatory behavior per se, their effect may be temporary, and they often have unpredictable, unintended effects on nontarget species (Ratnaswamy et al. 1997; Mason et al. 2001). Sound and light stimuli used to repel wildlife have a long history. Most research in this area has been conducted on canids and ursids (Jorgensen et al. 1978; Linhart et al. 1984; Smith et al. 2000; Bangs & Shivik 2001). Shivik et al. (2003 [this issue]) note the great potential of these devices if stimuli vary unpredictably and if the devices are triggered by the behavior immediately preceding conflict with humans. Electrical or mechanical sensory aversion has been advocated in some cases (Sanyal 1987; Musiani et al. 2003 [this issue]). A consensus is emerging that multiple nonlethal defenses must be deployed simultaneously, must be designed and installed with a particular species in mind, and must be modified periodically to avoid habituation by target species. In many cases, highly technical interventions are not practical within the socioeconomic constraints of developing countries or rural communities.

Interventions that modify human or livestock behavior include changes in husbandry and guarding practices. Decades of study indicate that animal and crop husbandry practices affect vulnerability to carnivores. Risk increases where more livestock are present, when sick or pregnant animals roam far from humans or buildings, when carcasses are left exposed, when humans are distant or absent, and when herds roam near cover (Mech et al. 2000; Stahl & Vandel 2001; Ogada et al. 2003 [this issue]; Treves et al. 2003 [this issue]). Reducing human-carnivore conflict at farms will require changes in the behavior of producers. Such changes are resisted typically for reasons of economy or inertia. Research is underway to determine whether incentive schemes and outreach campaigns can promote the needed behavioral changes (Fox 2001; Mishra et al. 2003 [this issue]).

When carnivores threaten humans themselves, education campaigns may help reduce risks (Sanyal 1987; Beier 1991; Rajpurohit & Krausman 2000). A systematic study of the effectiveness of education campaigns is badly overdue.

Changing husbandry practices to include the use of guard animals begins by modifying human behavior, although its mode of action is ultimately to affect carnivore behavior (Coppinger et al. 1988; Green & Woodruff 1989; Andelt 2001). Domestic dogs and some breeds of livestock, such as donkeys (*Equus asinus*) and llamas (*Lama glama*), may counterattack some carnivores or act in such a way as to interrupt predatory behavior. Preliminary conclusions can be drawn. Donkeys and llamas can repel coyotes (*Canis latrans*) or smaller canids, but there is no evidence that they guard against other carnivores (Wagner & Conover 1999; Meadows & Knowlton 2000). Guard dogs can also repel coyotes but less often wolves; likewise, they are effective against black bears but less so against the larger grizzly bears (*Ursus arctos*) (Green & Woodruff 1989; Bangs & Shivik 2001). Studies of the efficacy of guard animals against felids have not been published to our knowledge, but cheetahs (*Acinonyx jubatus*) appear to be deterred by guard dogs in Namibia (L. Marker, unpublished data).

Avoiding the Intersection of Human and Carnivore Activities

Barriers such as fences, trenches, and walls have been used for millennia. When made from local materials and using traditional technologies, barriers are generally inexpensive to maintain and sustainable under local socioeconomic constraints (Jackson & Wangehuk 2001; Ogada et al. 2003 [this issue]). Some barriers may be undermined by the very people they are meant to protect if resources on the other side are needed (Karanth & Madhusudan 2002). Electrified barriers are both expensive in capital and time (Shelton 1984; Angst 2001) and produce undesirable ecological side effects when they isolate wildlife populations or are dismantled and used as wire snares (Thouless & Sakwa 1995; L. Osborne, unpublished data). Limitations exist to even the most intensive barrier maintenance efforts. Carnivores that have become dedicated predators on livestock or humans have not been impeded by most barriers for long (Corbett 1954; Turnbull-Kemp 1967; Brain 1981). Given time, some individuals learn to penetrate any barrier (Thompson 1978; Shelton 1984; Thouless & Sakwa 1995). In sum, barriers are an important part of protecting humans and their resources, but they must be coupled with other approaches that address transgressions by either humans or carnivores.

Where human settlements are expanding within the last remaining habitats of highly endangered carnivores, enforced zoning schemes may need to be considered. Protected areas that prohibit certain human activities are a form of zoning. The debate over the effectiveness of parks and their political challenges is beyond the scope of this paper, but the use of zoning specifically to mitigate human-carnivore conflicts has begun to receive more attention (Breitenmoser 1998; J. Linnell unpublished data). Because human-wildlife conflicts of all sorts are concentrated at the edges of protected areas (Woodroffe & Ginsburg 1998; Naughton-Treves et al. 2000), zoning may simply relocate conflicts without preventing them. More work is needed to understand zoning and its effectiveness in limiting the intersection of human and carnivore activities.

Voluntary resettlement is an extreme form of zoning. It has been employed for over 30 years in India to move human settlements out of lion (*Panthera leo*) and tiger habitat, leading to a substantial reduction in conflict and recovery of carnivore populations at many sites (Karanth et al. 1999; Karanth 2002; Karanth & Madhusudan 2002). To be successful in the long run, these relocation schemes should be truly voluntary, with participants gaining a net benefit such as improved access to jobs or essential services. The schemes should also be driven by incentive rather than coercion and must entail a fair, transparent participatory process. When conflicts with wildlife result in human casualties, or catastrophic loss of home and income, human communities may wish to relocate their settlements (Karanth 2002; Karanth & Madhusudan 2002). Resettlement schemes may face political opposition from groups seeking to protect local land claims or culture. These concerns must also be addressed adequately. For many large carnivores in densely populated regions, however, such as in southern Asia, resettlement may increasingly be the only conservation option for some time (Karanth 2002).

Conclusions

Carnivore management is as much a political challenge as a scientific one. Public opposition can block translocations, reintroductions, and the natural recovery of carnivores to former habitats. Successful conservation of carnivores depends on tolerant sociopolitical landscapes and favorable ecological conditions because humans have caused most of the carnivore mortality worldwide and most of the recent extirpations of carnivore populations. The human dimensions of carnivore conservation can trap carnivore managers between powerful interest groups and inflexible legislation. As a result, carnivore managers must now invest in intense and prolonged public outreach and engage social scientists to study public approval for management tactics. This investment will earn dividends if interested members of the public assist in necessary management tasks, such as monitoring and education. Thus, public involvement in carnivore policy can have a salutary effect but may also have a negative outcome. Negative outcomes are common in carnivore policy discussions when interest groups polarize debate and litigation leads to formal and inflexible rules. This outcome undermines the principles of adaptive management so important to conserving wildlife in human-dominated ecosystems.

We believe that future carnivore managers will increasingly employ a mix of strategies involving nonlethal modification of carnivore behavior, a change in human behavior, prevention of conflicts through spatial separation, and use of lethal controls only where absolutely essential. These solutions must be situation-specific and driven by scientific data (both biological and social), not by fears and prejudices against carnivores. We recommend that attention be directed to understanding and reducing human causes of carnivore mortality because this may result in the speedier recovery of many populations. In addition, information on the locations and participants in human-carnivore conflict may aid in the prediction, prevention, and mitigation of future conflicts (Treves et al. 2004). The job of conservation biologists is to inform the public and policy-makers about locally feasible options based on careful research. Close coordination with managers will be essential.

Literature Cited

Andelt, W. F. 2001. Effectiveness of livestock guarding animals for reducing predation on livestock. Endangered Species Update **18:**182–185.

Andersone, Z., and J. Ozolins. 2000. First results of public involvement in wolf research in Latvia. Folia Therologica Estonica **5:**7–14.

Angst, C. 2001. Electric fencing of fallow deer enclosures in Switzerland–a predator-proof method. Carnivore Damage Prevention News **3:**8–9.

Bangs, E., and J. Shivik. 2001. Managing wolf conflict with livestock in the northwestern United States. Carnivore Damage Prevention News **3:**2–5.

Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack, and C. C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho and Wyoming. Wildlife Society Bulletin **26:**785–793.

Beier, P. 1991. Cougar attacks on humans in the United States and Canada. Wildlife Society Bulletin **19:**403–412.

Berg, K. A. 1998. The future of the wolf in Minnesota: control, sport or protection? Pages 40–44 in N. Fascione, editor. Proceedings of the restoring the wolf conference. Defenders of Wildlife, Washington, D.C.

Berger, J., B. Stacey-Peter, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian Neotropical migrants. Ecological Applications **11:**947–960.

Boumez, J. B. 1989. Coyote control in Alberta. Great Plains Wildlife Damage Control Workshop **9:**40–43.

Brain, C. 1981. The hunters or the hunted? An introduction to African cave taphonomy. University of Chicago Press, Chicago.

Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. Biological Conservation **83:**279–289.

Burns, R. J., D. E. Zemlicka, and P. J. Savarie. 1996. Effectiveness of large livestock protection collars against depredating coyotes. Wildlife Society Bulletin **24:**123–127.

Caro, T. M., and S. M. Durant. 1995. The importance of behavioral ecology for conservation biology: examples from Serengeti carnivores. Pages 451–472 in A. R. E. Sinclair and P. Arcese, editors. Serengeti II. University of Chicago, Chicago.

Chellam, R., and A. J. T. Johnsingh. 1993. Management of Asiatic lions in the Gir Forest, India. Symposium of the Zoological Society of London **65:**409–424.

Coppinger, R., L. Coppinger, G. Langeloh, L. Gettler, and J. Lorenz.

1988. A decade of use of livestock guarding dogs. Proceedings of the Vertebrate Pest Conference **13:**209–214.

Corbett, J. 1954. The man-eating leopard of Rudrapayang. Oxford University Press, London.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology **16:**488–502.

Du Toit, J. T. 2002. Wildlife harvesting guidelines for community-based wildlife management: a southern African perspective. Biodiversity and Conservation **11:**1403–1416.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282:**473–476.

Evans, W. 1983. The cougar in New Mexico: biology, status, depredation of livestock and management recommendations. New Mexico Department of Game and Fish, Santa Fe.

Faraizl, S. D., and S. J. Stiver. 1996. A profile of depredating mountain lions. Proceedings of the Vertebrate Pest Conference **17:**88–90.

Forbes, S. E., W. R. Forbes, R. E. Wilson, and R. M. Reinhold. 1998. Spatial distribution of wolf support. Pages 94–99 in N. Fascione, editor. Proceedings of the restoring the wolf conference. Defenders of Wildlife, Washington, D.C.

Fox, C. H. 2001. Taxpayers say "no" to killing predators. Animal Issues **32:**1–2.

Gipson, P. S. 1975. Efficiency of trapping in capturing offending coyotes. Wildlife Management **39:**45–47.

Green, J. S., and R. A. Woodruff. 1989. Livestock-guarding dogs reduce depredation by bears. Pages 49–53 in L. R. Quaife, editor. Bear-people conflicts–Proceedings of a symposium on management strategies. Northwest Territories Department of Renewable Resources, Edmonton, Alberta, Canada.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology **10:**1068–1081.

Halfpenny, J. C., M. R. Sanders, and K. A. McGrath. 1991. Human-lion interactions in Boulder County, Colorado: past, present and future. Pages 10–16 in C. E. Braun, editor. Mountain lion-human interaction symposium and workshop. Colorado Division of Wildlife, Denver.

Harbo, S. J., and F. C. Dean. 1983. Historical and current perspectives on wolf management in Alaska. Pages 51–64 in L. N. Carbyn, editor. Wolves in Canada and Alaska: their status, biology and management. Canadian Wildlife Service, Edmonton.

Harden, B. 2002. In fight over turf in Montana valley, it's man vs. grizzly. New York Times, 14 May:A1.

Hoare, R. 2001. A decision support system for managing human-elephant conflict situations in Africa. African Elephant Specialist Group, Species Survival Commission, World Conservation Union, Nairobi.

Hoogesteijn, R. H., A. H. Hoogesteijm, and E. Mondolfi. 1993. Jaguar predation and conservation: cattle mortality caused by felines on three ranches in the Venezuelan llanos. Symposium of the Zoological Society of London **65:**391–407.

Horstman, L. P., and J. R. Gunson. 1982. Black bear predation on livestock in Alberta. Wildlife Society Bulletin **10:**34–39.

Hötte, M., and S. Bereznuk. 2001. Compensation for livestock kills by tigers and leopards in Russia. Carnivore Damage Prevention News **3:**6–7.

Jackson, P., and K. Nowell. 1996. Problems and possible solutions in management of felid predators. Journal of Wildlife Research **1:**304–314.

Jackson, R., and R. Wangehuk. 2001. Linking snow leopard conservation and people-wildlife conflict resolution: grassroots measures to protect the endangered snow leopard from herder retribution. Endangered Species Update **18:**138–141.

Jhala, Y. V., and R. H. Giles. 1991. The status and conservation of the wolf in Gujarat and Rajasthan, India. Conservation Biology **5:**476–483.

Jorgensen, C. J. 1979. Bear-sheep interactions, Targhee National Forest. International Conference on Bear Research and Management **5:**191–200.

Jorgensen, C. J., R. H. Conley, R. J. Hamilton, and O. T. Sanders. 1978. Management of black bear depredation problems. Proceedings of the Eastern Workshop on Black Bear Management and Research **4:**297–321.

Kaczensky, P. 1999. Large carnivore depredation on livestock in Europe. Ursus **11:**59–72.

Karanth, K. U. 2002. Nagarahole: limits and opportunities in wildlife conservation. Pages 189–202 in J. Terborgh, C. P. van Schaik, M. Rao, and L. C. Davenport, editors. Making parks work: identifying key factors to implementing parks in the tropics. Island Press, Covelo, California.

Karanth, K. U., and M. D. Madhusudan. 2002. Mitigating human-wildlife conflicts in southern Asia. Pages 250–264 in J. Terborgh, C. P. Van Schaik, M. Rao, and L. C. Davenport, editors. Making parks work: identifying key factors to implementing parks in the tropics. Island Press, Covelo, California.

Karanth, K. U., and M. E. Sunquist. 1995. Prey selection by tiger, leopard and dhole in tropical forests. Journal of Animal Ecology **64:**439–450.

Karanth, K. U., M. E. Sunquist, and K. M. Chinnappa. 1999. Long-term monitoring of tigers: lessons from Nagarahole. Pages 114–122 in J. Seidensticker, S. Christie, and P. Jackson, editors. Riding the tiger: tiger conservation in human-dominated landscapes. Cambridge University Press, Cambridge, United Kingdom.

Landa, A., K. Gudvangen, J. E. Swenson, and E. Røskaft. 1999. Factors associated with wolverine (*Gulo gulo*) predation on domestic sheep. Journal of Applied Ecology **36:**963–973.

Linhart, S. B., R. T. Sterner, G. J. Dasch, and J. W. Theade. 1984. Efficacy of light and sound stimuli for reducing coyote predation upon pastured sheep. Protection Ecology **6:**75–84.

Linnell, J. D. C., R. Aanes, J. E. Swenson, J. Odden, and M. E. Smith. 1997. Translocation of carnivores as a method for managing problem animals: a review. Biodiversity and Conservation **6:**1245–1257.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: do "problem individuals" really exist? Wildlife Society Bulletin **27:**698–705.

Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favorable. Animal Conservation **4:**345–349.

Linton, D. 1998. Wolves and humans on the Olympic Peninsula: a brief history of interspecific relations. Pages 6–13 in N. Fascione, editor. Proceedings of the restoring the wolf conference. Defenders of Wildlife, Washington, D.C.

Liu, J., M. Linderman, Z. Ouyang, L. An, J. Yang, and H. Zhang. 2001. Ecological degradation in protected areas: the case of Woolong Nature Reserve for giant pandas. Science **292:**98–101.

Manfredo, M. J., H. C. Zinn, L. Sikorowski, and J. Jones. 1998. Public acceptance of mountain lion management: a case study of Denver, Colorado, and nearby foothill areas. Wildlife Society Bulletin **26:**964–970.

Mansfield, T. M. 1991. Mountain lion damage to property in California. Pages 75–78 in C. E. Braun, editor. Mountain lion-human interaction symposium and workshop. Colorado Division of Wildlife, Denver.

Mason, J. R., J. A. Shivik, and M. W. Fall. 2001. Chemical repellents and other aversive strategies in predation management. Endangered Species Update **18:**175–181.

McDougal, C. 1987. The man-eating tiger in geographical and historical perspective. Pages 435–448 in R. L. Tilson and U. S. Seal, editors. Tigers of the world. Noyes, Park City, New Jersey.

Meadows, L. E., and F. F. Knowlton. 2000. Efficacy of guard llamas to reduce canine predation on domestic sheep. Wildlife Society Bulletin **28:**614–622.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology **9**:270–278.

Mech, L. D. 1998. Estimated costs of maintaining a recovered wolf population in agricultural regions of Minnesota. Wildlife Society Bulletin **26**:817–822.

Mech, L. D., E. K. Harper, T. J. Meier, and W. J. Paul. 2000. Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. Wildlife Society Bulletin **28**:623–629.

Meriggi, A., and S. Lovari. 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? Journal of Applied Ecology **33**:1561–1571.

Mishra, C., M. D. Madhusudan, P. Allen, and T. McCarthy. 2003. The role of incentive programs in conserving the snow leopard. Conservation Biology **17**:1512–1520.

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems. BioScience **47**:21–31.

Montag, J. 2003. Compensation and predator conservation: limitations of compensation. Carnivore Damage Prevention News **6**:2–6.

Musiani, M., C. Mamo, L. Boitani, C. Callaghan, C. C. Gates, L. Mattei, E. Visalberghi, S. Breck, and G. Volpi. 2003. Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. Conservation Biology **17**:1538–1547.

Naughton-Treves, L., R. A. Rose, and A. Treves. 2000. Social and spatial dimensions of human-elephant conflict in Africa: a literature review and two case studies from Uganda and Cameroon. World Conservation Union, Gland, Switzerland.

Naughton-Treves, L., R. Grossberg, and A. Treves. 2003. Paying for tolerance: rural citizens' attitudes toward wolf depredation and compensation. Conservation Biology **17**:1500–1511.

Naughton-Treves, L., J. L. Mena, A. Treves, N. Alvarez, and V. C. Radeloff. Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. Conservation Biology **17**:1106–1117.

Newby, F., and R. Brown. 1958. A new approach to predator management in Montana. Montana Wildlife **8**:22–27.

Ogada, M. O., R. Woodroffe, N. O. Oguge, and L. G. Frank. 2003. Limiting depredation by African carnivores: the role of livestock husbandry. Conservation Biology **17**:1521–1530.

Okarna, H. 1993. Status and management of the wolf in Poland. Biological Conservation **66**:153–158.

Palmqvist, P., B. Martinez-Navarro, and A. Arribas. 1996. Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. Paleobiology **22**:514–534.

Polisar, J. 2000. Jaguars, pumas, their prey base, and cattle ranching: ecological perspectives of a management issue. Ph.D. thesis. Department of Wildlife Ecology and Conservation, University of Florida, Gainesville.

Rabinowitz, A. R. 1986. Jaguar predation on domestic livestock in Belize. Wildlife Society Bulletin **14**:170–174.

Rajpurohit, R. S., and P. R. Krausman. 2000. Human-sloth-bear conflicts in Madhya Pradesh, India. Wildlife Society Bulletin **28**:393–399.

Rangarajan, M. 2001. India's wildlife history. Permanent Black, New Delhi.

Ratnaswamy, M. J., R. J. Warren, M. T. Kramer, and M. D. Adam. 1997. Comparisons of lethal and nonlethal techniques to reduce raccoon depredation of sea turtle nests. Journal of Wildlife Management **61**:368–376.

Reynolds, J. C., and S. C. Tappen. 1996. Control of mammalian predators in game management and conservation. Mammal Review **26**:103–127.

Sacks, B. N., K. M. Blejwas, and M. M. Jaeger. 1999. Relative vulnerability of coyotes to removal methods on a northern California ranch. Journal of Wildlife Management **63**:939–949.

Sanyal, P. 1987. Managing the man-eaters in the Sundarbans Tiger Reserve of India: a case study. Pages 427–434 in R. L. Tilson and U. S. Seal, editors. Tigers of the world. Noyes, Park City, New Jersey.

Schaller, G. B. 1972. The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago.

Shelton, M. 1984. The use of conventional and electric fencing to reduce coyote predation on sheep and goats. Texas Agricultural Experiment Station, College Station.

Shivik, J. A., A. Treves, and P. Callahan. 2003. Nonlethal techniques for managing predation: primary and secondary repellents. Conservation Biology **17**:1531–1537.

Smith, M. E., J. D. C. Linnell, J. Odden, and J. E. Swenson. 2000. Review of methods to reduce livestock depredation. II. Aversive conditioning, deterrents and repellents. Acta Agriculturae Scandinavica Section A Animal Science **50**:304–315.

Stahl, P., and J. M. Vandel. 2001. Factors influencing lynx depredation on sheep in France: problem individuals and habitat. Carnivore Damage Prevention News **4**:6–8.

Stander, P. E. 1990. A suggested management strategy for stock-raiding lions in Namibia. South African Journal of Wildlife Research **20**:37–43.

Stowell, L. R., and R. C. Willging. 1992. Bear damage to agriculture in Wisconsin. Proceedings of the Eastern Wildlife Damage Control Conference **5**:96–104.

Suminski, H. R. 1982. Mountain lion predation on domestic livestock in Nevada. Vertebrate Pest Conference **10**:62–66.

Sunde, P., K. Overskaug, and T. Kvam. 1998. Culling of lynxes *Lynx lynx* related to livestock predation in a heterogeneous landscape. Wildlife Biology **4**:169–175.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabudin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2002. Ecological meltdown in predator-free forest fragments. Science **294**:1923.

Theberge, J. B., and D. A. Gauthier. 1985. Models of wolf-ungulate relationships: when is wolf control justified? Wildlife Society Bulletin **13**:449–458.

Thompson, B. C. 1978. Fence-crossing behavior exhibited by coyotes. Wildlife Society Bulletin **6**:14–17.

Thouless, C. R., and J. Sakwa. 1995. Shocking elephants: fences and crop raiders in Laikipia District, Kenya. Biological Conservation **72**:99–107.

Tompa, F. S. 1983. Problem wolf management in British Columbia: conflict and program evaluation. Pages 112–119 in L. N. Carbyn, editor. Wolves in Canada and Alaska: their status, biology and management. Canadian Wildlife Service, Edmonton.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin **24**:457–460.

Treves, A. 2002. Wolf justice: managing human-carnivore conflict in the 21st century. Wolf Print **13**:6–9.

Treves, A., and L. Naughton-Treves. 1999. Risk and opportunity for humans coexisting with large carnivores. Journal of Human Evolution **36**:275–282.

Treves, A., R. R. Jurewicz, L. Naughton-Treves, R. A. Rose, R. C. Willging, and A. P. Wydeven. 2002. Wolf depredation on domestic animals: control and compensation in Wisconsin, 1976–2000. Wildlife Society Bulletin **30**:231–241.

Treves, A., L. Naughton-Treves, E. L. Harper, D. J. Mladenoff, R. A. Rose, T. A. Sickley, and A. P. Wydeven. 2004. Predicting human-carnivore conflict: a spatial model based on 25 years of wolf predation on livestock. Conservation Biology **18**:(in press).

Treves, A., R. Woodroffe, and S. Thirgood. 2004. Evaluation of lethal control for the reduction of human-wildlife conflict. In press in R. Woodroffe, S. Thirgood, and A. Rabinowitz, editors. People and wildlife: conflict or coexistence? Cambridge University Press, Cambridge, United Kingdom.

Turnbull-Kemp, P. 1967. The leopard. Howard Timmins, Cape Town.

U.S. Department of Agriculture (USDA) Wildlife Services 2003. Annual tables. USDA Wildlife Services, Washington, D.C. Available from http://www.aphis.usda.gov/ws/tables (accessed 6 February 2003).

Wagner, K. K., and M. R. Conover. 1999. Effect of preventive coyote hunting on sheep losses to coyote predation. Journal of Wildlife Management **63:**600–612.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation **3:**165–173.

Woodroffe, R., and J. R. Ginsburg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280:**2126–2128.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring a recovering gray wolf population in Wisconsin, 1979–1995. Pages 147–156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.

Wydeven, A. P., A. Treves, B. Brost, and J. Wiedenhoeft. 2004. Characteristics of wolf packs depredating on domestic animals in Wisconsin, USA. In press in N. Fascione, A. Delach, and M. Smith, editors. Predators and people: from conflict to conservation. Island Press, Washington, D.C.