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Wildlife conservation and animal welfare: two sides of the same coin?

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Abstract

*Human activities deprive wild animals of their life requisites by destroying or impoverishing their surroundings, causing suffering of individuals. Yet, the notion that animal welfare applies to wildlife has escaped many animal welfarists and conservationists. A well-accepted and applied ethical foundation for animal conservation that considers animal welfare is lacking. We address this by examining how worldviews of conservationists and animal welfarists are related. The clear conceptual link is that individuals within anthropogenically disturbed populations often endure suffering caused by humans. Accordingly, our objectives are to provide an overview of wildlife conservation, integrate ethical aspects of wildlife conservation and animal welfare, and encourage a 'wildlife welfare' ethic among conservationists. We describe the relationship between contemporary socioeconomic and environmental conditions and the impoverished status of North American wildlife. We then describe the ecological plight of large mammalian carnivores in North America. Finally, as a case study, we focus on the tenuous lives of grey wolves (*Canis lupus*) living in the midst of human-dominated landscapes. We conclude that the suffering wildlife endures because of humans is a collective responsibility that presents a moral imperative for animal welfarists and conservationists alike. Habitat destruction and impoverishment deprives species of life requisites, causing trauma, prolonged suffering, and eventually death. We suggest that a shared doctrine of animal welfare principles is needed, such as a modified version of the internationally recognised Five Freedoms. In essence, this would be an ethical affirmation for conservationists and animal welfarists.*

Keywords: *animal welfare, conservation biology, environmental ethics, large carnivores, stress, wolves*

Introduction

> "Ethics in our Western world has hitherto been largely limited to the relations of man to man. But that is a limited ethics. We need a boundless ethics which will include the animals also.… the time is coming when people will be amazed that the human race existed so long before it recognized that thoughtless injury to life is incompatible with real ethics. Ethics is in its unqualified form extended responsibility to everything that has life" (Albert Schweitzer 1924).

Human influences, inadvertent and intended, continue to threaten the survival of species and the maintenance of natural ecological and evolutionary processes worldwide (Parmesan 2006; Wilson 2006; Smith & Bernatchez 2008; Darimont *et al* 2009). Human population growth and technological development have resulted in dramatic reductions and alterations in quality and availability of wildlife habitat, over-use of a number of wildlife species, greater human dependence on domesticated animals, and changes in the functioning of most ecosystems. The average annual rate of loss for animal and plant populations and their habitats is now estimated to be 1% (Balmford *et al* 2003). Two-thirds of the world's terrestrial land area has been devoted directly to supporting human populations through agriculture, fisheries, urbanisation, or infrastructure (Millennium Ecosystem Assessment 2005). Moreover, the adverse influence of humans on the environment is intensifying, causing an unprecedented destruction of biodiversity, and raising vexing questions about the ethical foundation of contemporary society (Wilson 2006; United Nations Environment Programme 2007).

From an ecological perspective, civilisation is being purchased by the subversion of nature for the sole benefit of humans (Hardin 1968; Daly 1993; Daly & Townsend 1993; Czech *et al* 2000; Bandura 2007). The most widespread problem is that expanding human demands deprive native species of life-sustaining habitats, or at the very least diminish the effectiveness of these habitats to support these species (Czech 2000; The Wildlife Society 2007). The rate of environmental damage is now so fast that many indigenous wildlife populations are responding to their changing environment with difficulty (Stockwell *et al* 2003; Parmesan 2006; Hendry *et al* 2008). Without question, the unrelenting

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increase in human activity is driving the loss or modification of species and seriously impoverishing the lives of those that survive (Ceballos & Ehrlich 2002; Bradshaw *et al* 2005; Morrison *et al* 2007; Darimont *et al* 2009).

Most conservation scientists now agree that global ecological conditions are seriously impaired (Millennium Ecosystem Assessment 2005) primarily because the human enterprise has proceeded with inadequate scientific and moral guidance, characterised by a blatant disregard for non-human animals. In general, one set of ecological and ethical principles has applied to humans and another to the rest of nature. Consequently, most of the cost of human hegemony is being borne by other species. Although rarely considered, depriving animals of their life requisites by destroying or impoverishing their surroundings causes suffering of individuals through displacement, stress, starvation, and reduced security (Bekoff 2002; Goodall & Bekoff 2002; Bradshaw *et al* 2005). The same human activities driving the current extinction crisis are also causing suffering, fear, physical injury, psychological trauma, and disease in wild animals (Bradshaw *et al* 2005). These discomforts are well beyond and additive to what might occur naturally (ie non-anthropomorphic).

Accordingly, human-caused environmental degradation and the associated suffering of animals should be of concern for conservationists and animal welfarists alike — a common ground on which to coalesce. Overall, however, neither group has unequivocally recognised that human-caused suffering of wildlife is a welfare concern that deserves serious consideration (see Ehrenfeld 1991; Glenn 1991; Perry & Perry 2008). Perhaps, as Bandura (2007) suggests, unintentional and selective moral disengagement has allowed individuals and society to pursue practices harmful to wildlife without the restraint of self-censure. We do this by investing ecologically harmful practices with worthy purposes through social, national, and economic justifications. Accepting this discomforting possibility represents a challenge that few people, including conservation and animal welfare scientists, have been willing to confront.

These vexing ethical problems are further compounded because the public and decision-makers fail to recognise the difference between existence of a species and long-term persistence of ecological systems upon which the species depends, a relationship that also applies to humans. Simply, intact ecological systems are characterised not only by the species (components) that inhabit them but also by ecological functions and processes that link species with their environment (eg migration, predator-prey relationships). Although species may continue to exist long after natural ecological relationships have been altered or destroyed, most ecologists believe such impoverished systems are not sustainable and do not typify healthy environments (Millennium Ecosystem Assessment 2005; Wilson 2006).

Although the health and quality of all life is indisputably dependent on natural systems, North America's natural lands are continually lost and converted to human uses such as farming, urban development, resource extraction, and industry. Therefore, the dominant ethic upon which modern technological society is derived — progress conceived as the continuous development and expansion of the artificial environment necessarily at the expense of the natural environment — can be looked upon from the ecological and animal welfare perspectives as morally insensitive. Although several of the assumptions of this human-centric worldview have been questioned and criticised by philosophers, poets, religious spokespeople, and others from different philosophical backgrounds for the last 500 years, a shift to applied 'ecological consciousness' has been a slow process (Leopold 1949; Naess 1973; Devall & Sessions 1985; Naess 2002).

Nevertheless, the ongoing destruction of the natural environment has precipitated a global response which, among other goals, seeks to preserve wilderness and protect wildlife populations. Many proponents of this conservation movement are motivated by an ethical concern for the welfare of wildlife populations and individual animals (Bekoff 2002; Goodall & Bekoff 2002; Jickling & Paquet 2005; Vucetich & Nelson 2007; Brennan & Yeuk-Sze 2008). In part, their efforts are intended to alleviate the suffering of animals caused by humans. At present, however, we lack a well-accepted and applied ethical foundation for animal conservation that considers animal welfare (cf Devall & Sessions 1985; Birch 1993; Grey 1993; Jickling & Paquet 2005; Minteer & Collins 2005; Mathews *et al* 2010). We begin to address this here, with a focus on wildlife.

Humans and wildlife often converge on and compete for the same habitat because both require similar environmental conditions for survival (Morrison *et al* 2007). Accordingly, we have chosen North American wildlife as a model system on which to expand the notion and application of animal welfare. We view it as a fertile area for discussion because relatively little has been written about the relationship of animal conservation and animal welfare (Soulé 1985; Goodall & Bekoff 2002; Mathews *et al* 2010). This is disturbing because what has been written clearly indicates that most conservation scientists understand neither the relationship between ecological research and animal welfare nor how they ought to be related (Song & M'Gonigle 2001; Linklater 2003; Hutchins 2007).

Herein, drawing from our perspectives as advocates for wildlife conservation and animal welfare, we examine how these worldviews are closely related. We begin by briefly describing the relationship between contemporary socioeconomic and environmental conditions and the status of North American wildlife. Due to the profound influence large carnivores exert on the persistence of other species and the dynamics of ecosystems, as well as their iconic role as flagships for nature and conservation worldwide, we then describe the ecological plight of large North American carnivores. Finally, as a case study, we focus on the lives of grey wolves (*Canis lupus*) living in human-dominated landscapes. We believe wolves can help society come to terms with the ethical questions regarding conservation and

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animal welfare because efforts to coexist with wolves cause us to consider the comparative value of tangible and intangible aspects of our lives (Pimlott *et al* 1969; Haber 1996). Ironically, the species once regarded as a threat to our survival is turning out to be a test of how likely we are to achieve sustainability and coexistence with the elements that sustain us (Paquet & Carbyn 2003).

Objectives

For our purposes, 'animal welfare' consists of three elements: the basic health and functioning of animals, their affective states (eg pain, fear, suffering, etc), and their ability to live in a manner to which they are adapted (Fraser *et al* 1997). We also assume that any realistic praxis necessitates some killing, exploitation, and suppression (Naess 1973). In contrast, 'animal rights' focuses on deeper political or philosophical claims about the status of animals. Historically, animal welfare has applied primarily or exclusively to animals under human care, such as farm animals and pets, whether used for food, work, companionship, or research. In our view, the extension of this ethic to wild animals (ie those not under our care) is conspicuously missing. In part, this is because some environmental discomforts affecting wild animals are recognised as natural processes that are present even in pristine conditions (Fraser 2008). Therefore, our emphasis here is on welfare issues associated with humans and their activities.

As we outline below, finding commonalities and unifying concepts relevant to both conservationists and welfarists is straightforward, although not without difficulties. Principal among them is that animal conservationists and animal welfarists apply their concern for animals at different scales. Wildlife conservationists are primarily concerned with populations and habitats, whereas animal welfarists are principally concerned with individuals (Hutchins 2007). Only recently has the ecology of individuals been recognised as an important and fertile area for research programmes (for a review see Bolnick *et al* 2003). Bridging this disconnect requires careful consideration and education. Accordingly, our objectives are to: i) provide an overview of wildlife conservation for those interested in animal welfare; ii) integrate the two fields conceptually by showing that the integrity of habitats and the populations they contain are inextricably linked to the welfare of the individual animals that constitute those populations and occupy those habitats; and iii) encourage a 'wildlife welfare' ethic among conservationists.

A wildlife conservation primer for animal welfarists

Socio-economic problems

A number of conservation scientists, including ourselves, propose that a general lack of ecological knowledge is not the only limit on effective conservation (for a related perspective Erlich 1995; Vucetich & Nelson 2007). Rather, a combination of bad management, self-interest, and overpopulation is causing a degradation of the natural environment which, in turn, is causing the loss and impoverishment of species. Although overkill, habitat destruction, and exotic species are the proximate ecological causes of species endangerment (Diamond 1989), the ultimate problem is fundamentally sociological (Hardin 1968; Diamond 2005).

Over the last 200 years, the North American landscape has been modified by an economy that ignores the environment, or worse, views it as an obstacle to overcome. This attitude continues to prevail because only monetary benefits and costs associated with resource products are recognised in conventional marketplace transactions (Costanza 1991; Czech 2000). Whereas conservation and restoration efforts are directed at improving current and future conditions for animals (and especially wildlife), market interests usually discount future benefits and costs in favour of present consumption and sales. Since information about the future is limited, and shareholders require quick returns on investment, a premium is placed on the present (Czech *et al* 2000). Accordingly, short-term profits are usually favoured over the uncertain profits of the future (Paquet & Carbyn 2003; The Wildlife Society 2003).

Modern economic theory is an extreme reflection of this human-centric worldview. In essence, by placing humans above and outside the laws of nature it is a counterpoint and refutation of elementary ecological and physical principles. Claims to non-consumptive and sustainable economic growth do not conform to our fundamental understanding of trophic ecology (Czech 2000). Whilst ecology recognises the interconnectedness of all things living or not, economics is hierarchically focused and explicitly subsumes all lifeforms to the needs of humans. Neoclassical economists view economic growth as a benchmark of societal progress (Heilbroner 1992). Within this context, the decline of nature has been considered a measure of the success of an enterprising economy. Thus, given the irrefutable association between environmental destruction and the suffering of individual animals as we explain below, contemporary economics is in conflict with the goals of conservation and animal welfare. Ethical questions are most often matters of principle which need to be unmistakably distinguished from matters of price (Sagoff 2004).

Ecological problems

Globally, wildlife must contend with an ominous future on a planet where humanity's economic appetite consumes most resources (Smith & Bernatchez 2008). According to recent scientific reports, humans now appropriate over 40% of the net primary productivity (the green material) produced on earth each year (Vitousek *et al* 1986, 1997; Rojstaczer *et al* 2001). Humanity consumes 35% of the productivity of the oceanic shelf (Pauly & Christensen 1995), and uses 60% of freshwater run-off (Postel *et al* 1996). Between one-third and one-half of the land surface has been transformed by human action and this area continues to expand (Vitousek *et al* 1997). Morrison *et al* (2007) estimate "that less than 21% of the earth's terrestrial surface still contains all of the large (20 kg) mammals it once held, with the proportion varying between 68% in Australasia to only 1% in Indomalaya". Although the

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presence of large mammals offers no guarantee of the occurrence of other animals, their absence provides an ecological measurement of the human influence on biodiversity. Based on fundamental ecological principles (eg niche breadth and competitive exclusion), growth of the human economy (the synthesis of population size and per capita consumption) proceeds at the expense of nearly all wildlife. Therefore, economic growth is the limiting factor for sustainability of wildlife, and by extension the welfare of all animals (Czech 2000).

Anthropogenic influences have severely reduced the amount, availability, and effectiveness of habitat for indigenous wildlife (Kellert 1993; Jędrzejewska *et al* 2004; Lalbierte & Ripple 2004; Morrison *et al* 2007). The consequent loss to land conversion of locally adapted populations within species, and of genetic material within populations, is a human-caused change that reduces the resilience of species and ecosystems. Although the scale and nature of threats have changed over time, there is widespread concern within the scientific community that adverse anthropogenic effects could lead to permanent loss or modification of some and perhaps most large mammalian and other sensitive wildlife species (Ceballos & Ehrlich 2002; Cardillo *et al* 2006; Morrison *et al* 2007; Darimont *et al* 2009).

In North America, ecosystem health has declined precipitously ever since European settlement. Humans have profoundly influenced the way wildlife use the natural landscape (Laliberte & Ripple 2004). We are now documenting sudden leaps in aberrant ecosystem behaviour long predicted by ecologists. Consequently, populations of native species have crashed, disappeared, or as an adaptation to novel anthropogenic stresses, modified their behaviour to accommodate humans. At the same time, many exotic and invasive species have irrupted causing conflicts with native wildlife and humans. What were once alien cultural practices, such as intense landscape modification, massive impoundments of water, overgrazing, and fire suppression, have now become increasingly common. Concurrently, new infectious diseases, crown fires, and destructive infestations of invasive insects — once rare phenomena — have emerged as dominant disturbance regimes. The rates, scales, kinds, and combinations of changes occurring now are different from those at any other time in history (Covington 2000). Notably, we are changing the landscape more rapidly than we understand it or species are able to adapt.

Habitat alienation, destruction and fragmentation

Animal use of a particular area varies in relation to cues in the landscape that signal the availability of food, shelter, or other resources favoured by the particular species. This use often fluctuates seasonally and changes at different life-history stages. Individuals or groups of individuals are drawn to food and suitable physical structures, and avoid areas of lower quality. The term habitat, although often used loosely as an indication of environmental quality, refers to the combination of physical and biological features preferred by a particular species. Different habitat preferences reflect the evolution and adaptation of diverging species.

As noted, human population pressures and associated activities have physically supplanted large areas of natural habitat. Moreover, habitat alienation (the abandonment of habitats because of human presence) has converted extensive portions of habitat from optimal to unsuitable for wildlife. The effects are additive to those of habitat lost due to physical development. Alienation results from proximity of a habitat patch to sensory disturbances (eg noise), direct human intrusion (eg off-roading, snowmobiling, hiking), isolation from other habitats, and other less obvious disruptions (eg inadequate thermal or visual cover). The factors that influence alienation vary among species, the size of the habitat patch, configuration of the habitat patch, the matrix between patches, the nature of disturbance, frequency of the disturbance, and the level of individual habituation. Unlike losses resulting from removal of habitat, alienation can be temporary and does not permanently foreclose mitigative options.

The ongoing degradation of habitat via physical destruction, alienation, and occlusion of travel corridors is confining wildlife populations into small, insular fragments of often inhospitable land. This subdivision of habitat into many detached and isolated patches is referred to as habitat fragmentation. As a result of their natural insularity, mountainous and coastal archipelago environments exacerbate the problem. Many of these discontinuous habitat fragments are being rendered ecologically marginal or ineffective by small size, irregular shape, and isolation. Although the severity of disturbance varies with the scale of disruption and the species affected, small patches of habitat isolated in a landscape are likely to have an impoverished biota. This concern is based on convincing evidence that isolation and constriction of natural communities reduce biodiversity and the numbers of animals that occupy an area (Franklin 1980; Gilpin & Soulé 1986; Newmark 1987, 1995; Soulé 1987). Accordingly, the fragmentation of continuous, natural landscapes is one of the most important factors contributing to the loss of biological diversity (Wilcox & Murphy 1985).

Conservation biologists agree that most species are adversely affected by fragmentation of the natural landscape. Recent information shows that natural populations of some species persist as a set of linked subpopulations each of which is prone to instability. Such persisting 'metapopulations' are sensitive to the number of subpopulations and ease of movements among them. Thus, any reduction of habitat size or fragmentation of habitat runs the risk of disrupting the whole system, either by reducing the number of subpopulations below some critical level required for the combined metapopulation to persist, or by interfering with the dispersal required to link the locally unstable subpopulations. Consequently, there is an increased probability of random disturbance pushing many populations toward extinction (see *The extinction vortex* below). Overall, the implications are clear: anthropogenic fragmentation of landscapes modifies the composition of species, diversity of species, and density of populations.

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Corridors and landscape linkages

Habitats and landscapes can fragment when they become partially subdivided by inhospitable travel corridors, especially as the intervening landscape matrix becomes increasingly dominated by humans. The occlusion of travel routes that link critical habitats restricts essential daily, seasonal, and dispersal movements of wildlife. Wildlife displaced to suboptimal habitats and travel routes are exposed to higher risks of mortality, increased stress from sensory disturbances, and energetically less efficient foraging behaviour. In addition, ensured connectivity is important for wildlife exposed to a high risk of mortality from humans or vehicles when travelling across settled landscapes. Thus, maintaining connectivity between patches of quality wildlife habitat and providing a means for dispersal is critical for maintaining ecological integrity (Newmark 1987, 1995; Noss 1987; Noss *et al* 1997; Woodroffe & Ginsberg 1998; Ehrlich & Hanski 2004). In general, fragmented and isolated habitats and regional reserves will not maintain viable populations of all wildlife species in the long term. Therefore, habitats and regions must be linked (interconnected) to allow for ongoing genetic exchange and long-distance dispersal among separated populations.

The extinction vortex

Advances in conservation biology have mapped likely pathways to species extirpation (ie local or regional extinctions) and extinction (see Soulé 1985; Gilpin & Hanski 1991; Boyce 1992; Schonewald-Cox & Buechner 1992). In theory, systematic disturbances involving excessive loss of individuals or habitats lead to reductions in population size and/or distribution. Subdivision and loss of suitable habitat help push subpopulations into a size range where random events are likely to terminate them, increasing the probability of regional extinction (Gilpin & Soulé 1986). As losses mount and subpopulations become smaller, fewer, and more isolated, the population becomes increasingly susceptible to stochastic (ie random) genetic, demographic, environmental, and catastrophic factors. These different forces operate in synergistic and unanticipated fashion — in different ways for different species — to plunge a population into an 'extinction vortex' (Lacy 1993).

Status of North American large mammalian carnivores

Most mammalian carnivore populations in North America are adversely affected by anthropogenic influences, including habitat loss due to development, recreational facilities, oil and gas exploration, and logging, as well as injury and mortality due to highways, railways, depredation control, novel diseases, and hunting (Nowak *et al* 2005). Combined, these activities have generally degraded the environment for predators and their prey species. In effect, much of North America has become a 'wilderness ghetto' for large carnivores relegated to suboptimal living conditions (Hummel & Pettigrew 1992; Clark *et al* 1996). The suite of large carnivores observed today once occurred over a much greater extent of North America (Hummel & Pettigrew 1992). However, as human activities spread, carnivore distribution and abundance decreased dramatically (for a review of range contractions, see Laliberte & Ripple 2004). Loss of habitat and deliberate extermination of populations resulted in extirpation of large carnivores across the continent. The retreating line of large carnivores reflects a set of conditions in which human disturbances have exceeded the resiliency of these species and/or the habitats that support them (Weaver *et al* 1996).

But how did this happen? Large carnivores share an array of ecological and life-history traits that make them particularly sensitive to human influences and vulnerable to extinction (Weaver *et al* 1996). Typically, large carnivores occur at low population densities, range over large areas, and are reclusive. If small populations are vulnerable to extirpation, large carnivores are especially prone because their high trophic or feeding position constrains them to living at low population densities. Carnivore populations are also commonly exposed to strong external pressures because their biological requirements conflict with those of local people. Where large carnivores survive outside protected areas, intentional or accidental killing by humans frequently limit their numbers (Woodroffe & Ginsberg 1998; Carroll *et al* 2004).

Activities that fragment, dissect, and isolate habitat have undesirable effects on large carnivores. The scale of fragmentation relevant to these animals is most frequently caused by construction of roads, railways, agriculture, and logging. The amount of habitat disruption that can be tolerated is not known, but the negative effects appear stronger for grizzly bear (*Ursus arctos*), wolf, and cougar (*Puma concolor*) than wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), black bear (*U. americanus*), and coyote (*C. latrans*). Equally important, preservation of habitat quality requires maintenance of linkages, connectedness, and an interspersion over geographic areas large enough to benefit individuals and join individuals into populations (Carroll *et al* 2001, 2004). Riparian areas appear to be important elements in wolf, cougar, and grizzly bear home ranges and may be dispersal avenues. This is probably also true for other large carnivores. Therefore, protection of riparian corridors is an important management concern.

Historically, large-scale extermination and loss of habitat were the major threats to large carnivores. At present, however, the most significant and pernicious ecological threats to carnivore survival are related to loss, alienation, and alteration of habitat resulting from exploitation of natural resources, permanent facilities, and associated infrastructure (Paquet & Hackman 1995; Clark *et al* 1996). These activities and structures are contributing to the fragmentation of landscapes, occluding essential regional dispersal corridors, and creating linear impediments to inter- and intra-territorial movements. Barriers, such as highways and railways, are exacerbating the landscape-related problems because they are also direct and increasingly important causes of mortality (Beier 1993; Paquet *et al* 1996; Paquet & Carbyn 2003). Moreover, the permanence of these facilities has largely foreclosed future opportunities for restoration of impaired landscapes.

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The combined deleterious effects could lead to permanent loss of some and possibly all large carnivore populations in most of North America. Loss of a keystone carnivore species, such as the grizzly bear or wolf, can affect interspecific associations by disrupting mutualistic relationships or food webs (Terborgh *et al* 1999; Hebblewhite *et al* 2005). This, in turn, may cause secondary extinctions or unanticipated ripple effects in populations of other species (Wilcox & Murphy 1985; Wilcove *et al* 1986; Hebblewhite *et al* 2005). For example, the loss of larger carnivores may precipitate the increase of smaller carnivores (mesopredators) that are more tolerant of humans but in turn cause the decline of smaller prey like songbirds (Crooks & Soulé 1999).

The grey wolf as a case study

The grey wolf originally occupied all habitats in North America north of about 20°N latitude. On the mainland, wolves were found everywhere except the southeastern United States, California west of the Sierra Nevada, and the tropical and subtropical parts of Mexico. The species also occurred on large continental islands, such as Newfoundland, Vancouver Island, the islands off the coast of southeast Alaska, and throughout the Arctic archipelago and Greenland, but was absent from Prince Edward Island, Anticosti, and the Queen Charlotte Islands. An increase in the human population in North America, a relentless expansion of agriculture, overhunting of ungulate prey by people, and intensive predator control aimed at the complete eradication of wolves initiated a general decline in the distribution and abundance of the species in the conterminous United States and adjoining parts of Canada (Paquet & Carbyn 2003).

Now wolves are confined primarily to the northern half the continent (ie Alaska and Canada). In the conterminous United States, small populations exist in the Great Lakes region and parts of the Pacific Northwest. A successful programme to reintroduce wolves from Canada to Yellowstone National Park and Idaho was carried out in 1995 and 1996, respectively. In the Southwest US and Mexico, the Mexican wolf (*C. l. baileyi*) is effectively extinct in the wild, although reintroductions were begun in Arizona in 1998. Since humans have disturbed or destroyed much of the North American landscape favoured by wolves (Paquet & Hackman 1995; Paquet & Carbyn 2003), the species is now found mostly in remote and undeveloped areas with sparse human populations (Paquet & Carbyn 2003).

Wolves in human-dominated landscapes

Wolves continue to suffer from exposure to high levels of human activity resulting in physical loss of habitat, degradation of habitat quality, disease (Mech & Goyal 1993; Carmichael 2005), and mortality on roads and the railway (Paquet *et al* 1996; Paquet & Carbyn 2003). Disturbances include resource extraction (eg gravel, forestry), hydroelectric development, road corridors, utility corridors, air pollution, water pollution, noise pollution, light pollution, and recreational development. The resultant habitat use by humans results in deaths of wolves, as well as usurpation, fragmentation, alienation of natural habitat, and loss of genetic diversity (Paquet & Carbyn 2003; Musiani & Paquet 2004; Leonard *et al* 2005). Consequently, much of the remaining wolf habitat now exists as widely scattered patches. Overall, transformation of the natural landscape and displacement of wolves by humans has resulted in altered ecosystems throughout North America, thereby affecting all of the species inhabiting them.

The specific conditions in which wolves are 'disturbed' (ie that their distribution, movements, survival, or fecundity are impaired) are believed to be highly variable. The extent and intensity of disturbance appear to vary with environmental and social context, and the individual animal (Paquet & Carbyn 2003). Although wolves are sensitive to human predation and harassment (Thiel 1985; Jensen *et al* 1986; Fuller 1989; Mech 1989; Fuller *et al* 1992; Thurber *et al* 1994; Mladenoff *et al* 1995, 1999), we have very limited empirical information on tolerance to indirect human disturbance (Heilhecker *et al* 2007). Previous studies suggest the main factor that limits wolves, where they are present and tolerated by humans, is adequate prey density (Fuller *et al* 1992). Although human activities have been shown to influence the distribution (Thiel 1985; Fuller *et al* 1992; Mladenoff *et al* 1995; Paquet *et al* 1996; Jędrzejewski *et al* 2004, 2005) and survival of wolves (Mech *et al* 1995; Mladenoff *et al* 1997, 1999), human-caused mortality is consistently cited as the major cause of extirpation (eg Fuller *et al* 1992; Mech & Goyal 1993).

Avoidance of humans by wolves is temporal (Boitani 1982) and spatial (Mladenoff *et al* 1997; Jędrzejewski *et al* 2004, 2005). The selection or avoidance of particular habitat types is directly related to human use levels and habitat potential (Paquet *et al* 1996; Hebblewhite *et al* 2005). Wolves use disturbed habitats less than expected, which suggests the presence of humans alters their behaviour at a cost to their fitness (Paquet *et al* 1996). Very low intensity disturbance does not have a significant influence on wolves, nor does it seriously affect the ecological relationships between wolves and their prey. At low to intermediate levels of human activity, wolves are dislocated from suboptimal habitats. Higher levels of activity result in partial displacement but not complete abandonment of preferred habitats. As disturbance increases, wolves avoid using some of the most favourable habitats.

This pattern of displacement suggests that the presence of humans repulses wolves, although a strong attraction to highly-preferred habitats increases a wolf's tolerance for disturbance (Paquet *et al* 1996). As conditions become less favourable, preferred habitats probably take on greater importance. For example, we know that wolves select reproductive areas near intense human activity when suitable denning areas are limited, or where innocuous human activity occurs (Chapman 1977). The presence of artificial food sources (eg carrion pits, garbage dumps) also attracts wolves and reduces avoidance of human activity (Chapman 1977; Paquet *et al* 1996).

The tension between attraction and repulsion is probably expressed differently by different individuals, packs, and populations (Paquet *et al* 1996; Paquet & Carbyn 2003;

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Heilhecker *et al* 2007). Attraction to an area is a complex sum of physiography, security from harassment, positive reinforcement (eg easily obtained food), population density, and available choice. Moreover, the response to a particular disturbance seems to depend on disturbance-history, a critical concept in understanding the behaviour of long-lived animals that learn through social transmission (Curatolo & Murphy 1986).

Several studies that used road densities as an index of human influence concluded that human activities associated with roads affect the survival and behaviour of wolves (Paquet & Carbyn 2003). Interpretation, however, was confounded because many human activities associated with roads result in the death of wolves. Thus, absence of wolves in an area may not be the result of behavioural avoidance *per se*. Data from Ontario, Wisconsin, Michigan, and Minnesota suggest that population persistence is usually assured at road densities below 0.58 and 0.70 km per km^2 (Thiel 1985; Jensen *et al* 1986; Mech *et al* 1988; Fuller 1989; Mech 1989; Fuller *et al* 1992, but see Merrill 2000 for exception). A study in Alaska concluded that wolves avoid heavily-used roads and areas inhabited by humans, despite low human-caused wolf mortality (Thurber *et al* 1994). Landscape level analysis in Wisconsin found mean road density was much lower in pack territories (0.23 km per km^2 in 80% use area) than in random non-pack areas (0.74) or the region overall (0.71). Few areas of use exceeded a road density of > 0.45 km per km^2 (Mladenoff *et al* 1995).

Recent reports suggest wolves in Minnesota tolerate higher levels of disturbance than previously thought possible. Wolves, for example, are now occupying ranges formerly assumed marginal because of prohibitive road densities and high human populations (Mech 1993, 1995). Legal protection and changing human attitudes are cited as the critical factors in the wolf's ability to use areas they abandoned decades ago. If wolves are not killed, they seem able to occupy areas of greater human activity than previously assumed (Fuller *et al* 1992; Mech 1993). Based on these observations, Mech (1995) comments that misconceptions about the wolf's inherent ability to tolerate human activity encourage unwarranted protectionism. Nonetheless, wolves in Minnesota continue to avoid populated areas, occurring primarily where road density and human population are low (Fuller *et al* 1992).

Several North American studies (Fuller *et al* 1992; Mladenoff *et al* 1995, 1999) have examined systematically and explicitly human population density and wolf distribution (cf Jędrzejewski *et al* 2004, 2005 for Europe). All were conducted at a landscape scale and assessed population-level responses of wolves to humans. In Wisconsin, human population density was much lower in pack territories than in non-pack areas. Wolf pack territories also had a higher proportion of public land, and lower proportions of agricultural land. Notably, no difference was detected in the densities of deer (primary prey) between pack territories and non-pack areas. Overall, wolves selected those areas that were most remote from human influence (Mladenoff *et al* 1995, 1999). Most wolves in Minnesota (88%) were in townships with < 0.70 km roads per km^2 and < 4 humans per km^2 or with < 0.50 km^2 and < 8 humans per km^2. High human or road densities likely precluded the presence of wolf packs in several localities within contiguous, occupied wolf range (Fuller *et al* 1992). In Italy, wolf absence was related to human density, road density, urban areas, cultivated areas, and cattle and pig density. However, because human density, road density, and urbanised areas were highly intercorrelated, no specific human effect was established (Corsi *et al* 1999). In all studies, the absence of wolves in human-dominated areas may have reflected high levels of human-caused mortality, displacement resulting from behavioural avoidance, or some combination of both.

In most parts of North America where wolves persist, human disturbance has already, or is now, displacing wolves from favourable habitat. Additional disturbances, additive to current background disruption, may surpass the level of habituation or innate behavioural plasticity that allows wolves to cope with human encroachment. Multiple small-scale disturbances resulting in displacement of wolves from habitats that provide limited nutritional or sanctuary requirements can have an influence disproportionate with the landscape area. This is particularly true in mountainous and island environments that have limited amounts of useful habitat (Darimont & Paquet 2002).

Given a choice, wolves prefer to avoid humans. However, extensive and growing convergence of human activity and wolf habitat has seriously compromised the availability and effectiveness of wolf habitat worldwide, reducing the distribution of wolves to a fraction of their original geographic range. Accordingly, disruptions resulting from human influence combined with unrelenting and lethal antipathy have created an impoverished environment that may not sustain surviving wolf populations into the future. Fuller *et al* (2002) summarise all the various means by which humans purposely cause harm and (typically, but not always) death to wolves. These include but are not limited to aerial hunting, deadfall traps, large fishhooks, guns, poisoning, snares, and traps. If wolves do persist, we wonder what diminished quality of life must be endured to survive in a human-dominated landscape.

Discussion

Conservation biology and animal welfare science are conspicuous and distinctive among scientific disciplines for explicitly embracing ethics (Soulé 1985). Conservation biology is specifically founded on an appreciation for non-human life. The implicit moral premise is that protection of non-human life and ecological processes that depend on such life are good and right (Soulé 1985; Vucetich & Nelson 2007). This is an ethical claim and the principle that underlies and motivates the scientific discipline of conservation biology (Groom *et al* 2005). In striking contrast with other academic fields (eg medicine), however, the ethical dimensions of conservation science are infrequently discussed (Kellert 1993; Vucetich & Nelson 2007).

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We believe all animal scientists, including those interested in wildlife, should critically evaluate both the ethical implications of human activities that degrade the environment and the effects of conservation efforts to combat these destructions. Assuming that the goal of conservation is to maintain free-ranging and self-sustaining wildlife populations, then conservation efforts must focus on sustaining the natural environment while meeting human needs. Similarly, if the goal of animal welfare is to sustain a quality of life for all species, such that the activities of humans are not a cause of stress and suffering, then welfare efforts must focus on stopping humans from seriously encroaching upon other species. Since current circumstances demand that we conserve wildlife in human-dominated landscapes, achieving both of these goals is a considerable problem.

The problem is not easily resolved given that one of the major cornerstones of the modern social paradigm is an all-pervasive anthropocentricity compounded by competing and often conflicting social perspectives, inflexible legislative constraints, and shifting political agendas. Specifically, the pending social question is: what probability of species' persistence and environmental quality is acceptable to society and compatible with economic goals? The answer varies depending on which sector of the public is queried. To date, however, the prevailing human attitude has been to show little consideration for other species, as evidenced by the condition of the environment and number of species on the brink of extinction. Proponents of this established worldview implicitly accept or openly invoke the idea of 'human exceptionalism' as a justification for ignoring fundamental ecological principles and the plight of other species (cf Taylor 1981, 1986; Varner 1998).

Human exceptionalism refers to a belief that humans have special status in nature based on their unique capacities. This special status conveys special rights, such as the right to life, even at the expense and suffering of other non-human life. This form of anthropocentrism, or human-centeredness, has been posited by some environmental philosophers as the underlying if unstated reason why humanity dominates and sees the need to 'develop' most of the earth (Naess 1973; Kellert 1993; Brennan & Yeuk-Sze 2008). Anthropocentrism has been identified by these writers and others as a root cause of the ecological crisis, human overpopulation, and extinctions of many non-human species, and it is used to draw attention to a systematic bias in traditional Western attitudes to the non-human world (Naess 1973; Brennan & Yeuk-Sze 2008). Similarly, the animal liberation movement claims that it is the ability to feel pain, rather than humanhood, which bestows equal moral value. The unresolved philosophical question is whether we will remove humans from the pedestal of moral exceptionalism and extend the ancient principle of ethical consistency (Gensler 1996) to all species: ''treat others only as you would consent to be treated in the same situation''. Clearly, ethical consistency calls for a science that serves humans and other animals alike without making one suffer at the expense of the other (Bradshaw & Marino 2007).

Ultimately, the seriousness of human disturbance is a human judgement and, as such, some may even consider the destruction of the natural environment and wildlife to be desirable. In addition, government agencies and other decision-makers are confronted with the difficult problem of achieving often-conflicting ecological, social, and economic objectives within the constraints of legislation and the lobbying of special interests. Unmistakably, the impoverished condition of the environment provides strong evidence that most decisions represent disproportionally the interests of humans at the expense of wildlife. Since most decision-making is based on social/political rather than ecological periods, environmental concerns are often subsumed to commercial needs, and future options largely foreclosed by irreversible decisions. Further, politicians must appeal to a divided public and powerful commercial interests without jeopardising re-election.

Even in conservation science, the interests of individuals are, on occasion, traded off against perceived benefits that accrue to higher levels of organisation: populations, species, and ecosystems. Although many contemporary biologists and conservationists value both the welfare of individual animals and the well-being of populations, species, and ecosystems, the conservation of species and populations often trumps all other values, including the welfare of individuals (Soulé 1985). The contention is that animal welfare and conservation are largely incompatible, because what is good for conservation is not always in the best interest of individual animals and vice versa. In other words, the end justifies the means. Hutchins (2007), for example, asserts that "focusing too narrowly on the rights of individual animals may be taking us down a path that will ultimately prove detrimental to the conservation of species, populations, and ecosystems". Although seldom recognised or addressed, this trade-off is an ethical choice that subsumes the welfare of individual animals to a supposedly higher value of population viability. Nevertheless, sentience is commonly assumed an ethically important quality (Regan 1983; Singer 1990; Rawles 2004). As such, the belief that sentient individuals have value beyond their contribution to the viability of a population is widely held and not limited to animal-rights advocates (Kellert 1996; Manning 2003) as implied by many conservationists (Hutchins 2007).

Undoubtedly, independent consideration of the needs of individuals and populations can lead to very different decisions when converted into wildlife management or conservation policy. Animal protection advocates who promote the welfare of individual animals are often marginalised by environmental scientists because their perspectives are perceived as obstacles to conservation efforts. Rawles (2004), however, clearly demonstrates that forsaking sentient non-human organisms in the name of protecting biodiversity is not obviously justified. Although no precise definition of 'sentience' has universal acceptance among ethicists, there is little controversy that sentience and suffering are morally relevant qualities. Moreover, sentience may be usefully equated with the capacity to

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suffer (Singer 1990; Chandroo *et al* 2004a,b). Therefore, ignoring the cost to individuals, or asserting that concern for individuals is misplaced, runs the serious risk of transforming conservation research and management into what some environmental philosophers have referred to as 'environmental fascism' (see Nelson 1996). The essential point is that judging the ethical appropriateness of sacrificing sentient individuals in the name of conservation is very difficult precisely because populations and individuals are both valuable (Leopold 1949).

Estes (1998) eloquently and succinctly gets to the substance of the matter in his discussion of whether to rehabilitate oiled wildlife, specifically California sea otters (*Enhydra lutris*):

> "The differing views between those who value the welfare of individuals and those who value the welfare of populations should be a real concern to conservation biology because they are taking people with an ostensibly common goal in different directions. Can these views be reconciled for the common good of nature? I'm not sure, although I believe the populationists have it wrong in trying to convince the individualists to see the errors of their ways. The challenge is not so much for individualists to build a program that is compatible with conservation — to date they haven't had to — but for conservationists to somehow build a program that embraces the goals and values of individualists because the majority of our society has such a deep emotional attachment to the welfare of individual animals. As much as many populationists may be offended by this argument, it is surely an issue that must be dealt with if we are to build an effective conservation program".

Estes' admonition highlights an unresolved philosophical breach between wildlife 'populationists' and 'individualists'. We believe advocates of animal conservation and animal welfare have failed to coalesce on common ground because the history and practise of animal welfare stems from the use of domesticated animals by humanity, and the unique responsibility that such use dictates. Consequently, welfarists have focused attention largely on animals used for production of food and clothing, draught power, companionship, recreation, scientific research, and education. Similarly, conservation has largely focused on managing the utilitarian relationship of wild animals and humans (eg hunting, trapping). Even though the founders of the North American conservation movement emphasised our moral association with individual wild animals (Meffe & Carroll 1997; Brennan & Yeuk-Sze 2008), the biological importance of populations now trumps the fate of individuals (Soulé 1985; Hutchins 2007). In general, the notion that animal welfare actually applies to wildlife has escaped most welfarists and conservationists.

Yet, our overwhelming use and abuse of the planet's resources means that humanity does use wildlife, regardless of whether the use is for food, sport hunting, or destruction of habitat. As such, the human-caused suffering that wildlife endures is our responsibility, and presents an additional moral imperative for welfarists and conservationists to consider carefully. Habitat destruction, for example, deprives species of essential life requisites, likely causing pain, prolonged suffering, and eventually death.

Discussions of how to incorporate ethical considerations into animal conservation are on the rise (for example, see Goodall & Bekoff 2002; Jickling & Paquet 2005; Vucetich & Nelson 2007; Mathews *et al* 2010). In recent years, welfarists have raised concerns about wild animals that suffer because of human-induced harm caused by trapping, hunting, and landscape transformation. The Universities Federation for Animal Welfare (UFAW) recently announced 'wild animal welfare' awards for 2008 that included recognition of innovations to alleviate or prevent human-induced harm to animals in the wild. In turn, many conservationists have embraced these concerns, particularly those influenced by the writings of Aldo Leopold (1949) and America's early environmental philosophers (Meffe & Carroll 1997; Vucetich & Nelson 2007). However, the ethical dimensions of conservation as they relate to animal welfare have not been codified (cf Goodall & Bekoff 2002) in a manner endorsed by conservation practitioners (Hutchins 2007, see however *Guidelines for Wildlife Research* 2008). The resulting lack of awareness is an impediment to the implementation of comprehensive welfare policies for wild animals.

Recommendations

We believe our goal as conservationists is to accommodate human activity and occupancy while protecting native diversity (individuals, species, populations, ecosystems) and the ecological functions and processes that maintain that diversity. Therefore, our primary objective is to develop measures that avoid and ameliorate the negative effects of human activities on the natural environment. Accordingly, we think thoughtful practices and careful planning can help mitigate the human influence on species and ecosystems. For example, we can work to reduce the rate at which we alter natural environments. Ecosystems and the species they support may cope more effectively with the changes we impose, if those changes are slow. Our footprint might then be stabilised at a point where enough space and resources remain to sustain most of the other species, for their sake and our own. Another approach is to determine which human behaviours enable coexistence. Accordingly, human disturbances that mimic or simulate natural disturbances are less likely to threaten ecological integrity than disturbances radically different from the natural regime. From an evolutionary perspective, species and biological systems are robust and fragile to different perturbations, being particularly robust to perturbations that are common to their niche or environment.

An elementary principle of animal conservation has always been the retention, protection, and restoration of key habitats. Recently, this has been expanded to include the securing of safe travel opportunities between critical habitats and provision for latitudinal or elevational movements in response to seasonal and long-term climate change. Thus, conservation efforts should now focus on maintaining and restoring ecosystems, as well as reconnecting habitat fragments in landscapes cumulatively influ-

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enced by roads, human land uses, and high human population density. This approach benefits individual wild animals by improving and preserving their environment.

We also believe a shared doctrine of animal welfare principles is needed, such as a modified version of the internationally recognised Five Freedoms of Animal Welfare (see below). Working from a premise of universal consideration, and minding the ethical basis of knowledge claims, enables richer conceptions of environmental ethics and creates new possibilities for animal welfare and managing for wildlife (Jickling & Paquet 2005). In essence, this would be an ethical affirmation for conservationists and welfarists. Welfare ethics need to be rooted in the life and mind of involved people to be successful in the long run. The clear conceptual link to conservation is that individuals within anthropogenically disturbed populations often endure suffering caused by humans, which is beyond the suffering that occurs naturally. Thus, the Five Freedoms might be adapted as follows to specifically reflect the suffering borne by wildlife for which humans are responsible:

• Freedom from thirst, hunger, and malnutrition caused by humans;

• Freedom from discomfort due to environmental disruption caused by humans;

• Freedom from fear and distress caused by humans;

• Freedom from pain, injury, and disease caused by humans;

• Freedom to express normal behaviour for the species.

In addition, the international research community has encouraged for many years the development of guidelines to improve harmonisation of the care and use of animals in research. Most of these guidelines are directed towards animal experiments in the laboratory. However, increased efforts are now being made to produce and disseminate guidelines for the care and use of animals in wildlife research (Guidelines for Wildlife Research 2008). In Norway, the participants at an international meeting (Harmonisation of the Care and Use of Animals in Field Research 2008) recently issued a consensus statement summarising their view of the current state of knowledge, including recommendations for implementing the 3Rs of Russell and Burch (1959): Replacement, Reduction and Refinement.

Finally, we list below several principles of conservation biology which apply to preserving, restoring, and improving the natural environment (Meffe & Carroll 1997). Some of these principles are established generalisations, some are testable hypotheses, and others are practical guides that we assessed as important for the maintenance of ecosystem health, ecological integrity, and the welfare of individual animals. Although not cast specifically in terms of animal welfare, adherence to these principles will help protect and enhance the lives of wild animals. In short, these can be 'scaled down' and are useful in preventing the suffering of individual animals:

• Animal conservation must be concerned with multiple levels of biological organisations and with many different spatial and temporal scales;

• Species well distributed across their native range are less susceptible to extinction than species confined to small portions of their range;

• Large blocks of habitat containing large populations of a target species are superior to small blocks containing small populations;

• The welfare of individuals, the integrity of populations, and the preservation of species depends on the maintenance of ecological processes;

• Dispersal and population exchanges can help counteract the isolating effects of habitat fragmentation;

• Reducing adverse human effects on the environment demands the slowing and reversing of human population growth and using resources efficiently;

• Animal conservation and welfare advocates must emphasise a vision of nature that emphasises the ethical, aesthetic, and spiritual motives for conservation as opposed to one in which countable, measurable, and monetary aspects dominate.

Animal welfare implications and conclusion

The adverse environmental consequences of unrestrained human population growth and industrial development are not something we face in the future. They are with us now. In North America, human alteration of the natural environment is substantial and growing. The loss of species and suffering of individuals parallel an increase in human activity. In many areas, prevailing conditions will not sustain wildlife or the ecosystems upon which they depend. Most of these changes are ongoing and accelerating, though many were entrained long before we recognised their importance.

Although ecological literacy and awareness have improved in recent years, we have yet to heed the persistent warnings of the conservation biologists. As a society, we still lack a fundamental understanding of the functions and processes that underpin natural systems, which is a prerequisite for appreciating the issues and links to our actions. Moreover, no established approach or field within professional or practical ethics is devoted to identifying and reasoning through the complex ethical and philosophical dilemma of sustaining diverse populations of wild species without sacrificing individual animals (Minteer & Collins 2005). Accordingly, there is a conspicuous absence of scholarship regarding the ethical relationship of conservation and the welfare of individual animals (Vucetich & Nelson 2007). Is it even possible to design economically viable societies that protect the welfare of animals and are ecologically sustainable?

We believe the primary cause of environmental destruction is deeply rooted in anthropocentrism, whereby natural laws are easily disregarded because there are no imminent adverse consequences for people. From an ecological perspective, human dominance of nature manifests as an extreme case of competitive exclusion, where wild animals have no voice and human priorities always prevail. Although there is an undeniable association between human-caused ecological degradation and the distress of wildlife, the suffering of wild animals is largely an unin-

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tended and ignored outcome of anthropocentrism. That is, most people do not intend for animals to suffer at the expense of humans, but are unwilling to make the changes necessary to prevent degradation of the environment. Recognising these troublesome consequences of the human enterprise requires a re-examination and possible reformation of what is often considered the self-evident truth of human exceptionalism. Rather than using exceptionalism as a license to exploit the environment for our benefit at the expense of other species, we should assume the responsibility to protect all life from human-caused suffering (cf Passmore 1974; Birch 1993; Goodall & Bekoff 2002).

In a manner similar to those who invoke human exceptionalism to justify their behaviour, conservation scientists sometimes rationalise suffering of individual animals as being necessary to achieve more important ecological goals of population or species preservation, or even their own research goals (Darimont *et al* 2008). In other words, the means (sacrificing individual animals) is used to justify the end (for the good of a population or species). From an ethical perspective, this is usually an unacceptable and indefensible justification.

Obviously, human-caused suffering of animals is a contentious subject with religious and moral overtones that many would prefer to ignore. Nevertheless, despite different conceptual underpinnings, advocates of animal conservation and animal welfare need to work toward a consistent and coherent ethical framework, with a willingness to recognise that no single value always or automatically trumps all other values (Vucetich & Nelson 2007). Individual animals, including humans, have value. Conservation has value. How we reconcile these values equitably is the ethical conundrum for all of us (Vucetich & Nelson 2007).

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