



Conservation of the world's mammals: status, protected areas, community efforts, and hunting

R. TERRY BOWYER,* MARK S. BOYCE,[•] JACOB R. GOHEEN, AND JANET L. RACHLOW

Institute of Arctic Biology, Box 757000, University of Alaska Fairbanks, Fairbanks, AK 99775, USA (RTB)

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2R3, Canada (MSB)

Department of Zoology and Physiology, University of Wyoming, 1000 East University Avenue, Laramie, WY 82071, USA (JRG)

Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, MS 1136, Moscow, ID 83844, USA (JLR)

* Correspondent: bowyterr@isu.edu

Mammals are imperiled worldwide. Threats to terrestrial species are primarily from habitat loss or modification, and in some instances from commercial, illegal, or unregulated hunting. Terrestrial species are negatively affected throughout the tropics from deforestation. Threats to marine mammals are related to harvest, strikes in shipping lanes, pollution, and depleted levels of food resources. Hazards to marine species are pronounced in the North Atlantic Ocean, North Pacific Ocean, and oceans and seas flanking southeastern Asia. Protected areas designed to conserve mammals often are too small, too few, poorly delimited or isolated, and too unreliably supported. The new conservation science proposes that human livelihoods be considered alongside traditional preservationist perspectives. For conservation outside of protected areas to succeed, the protection of wild mammals and their habitats should result in benefit to local people, especially in rural or poor communities. Concerns about declining populations of large mammals in North America during the late 19th and early 20th centuries resulted in the institution of regulations that contributed to the recovery of many populations. Today, in North America and Europe, wild populations are thriving and legal hunting is allowed for a number of mammals, something that is less common in many developing countries, where illegal killing remains a threat to conservation. Nevertheless, populations of large mammals are resilient to regulated hunting because of density-dependent processes that result in increased reproduction, survival, and growth rates. Unfortunately, hunting is unregulated for cultural and economic reasons over much of the Earth. We are beginning to see effects of climate change and invasive species on risk of extinction for many species. The future of mammals, however, is entwined ultimately with the size, growth, and resource demands of the human population.

Los mamíferos están en riesgo en todo el mundo. Las principales amenazas a las especies terrestres son la pérdida y modificación del hábitat, y en algunos casos la cacería comercial, ilegal o no regulada. Las especies terrestres son negativamente afectadas a lo largo de los trópicos por la deforestación. Las amenazas a los mamíferos marinos están relacionadas con la extracción ilegal, colisiones con embarcaciones, contaminación y agotamiento de recursos alimentarios. Los peligros para las especies marinas están más acentuados en el Atlántico Norte, el Pacífico Norte y los mares y océanos que rodean el sureste asiático. Las áreas protegidas diseñadas para proteger mamíferos frecuentemente son muy pequeñas, escasas, pobremente delimitadas o aisladas, además de contar con un mantenimiento incierto. La nueva ciencia de la conservación propone que las necesidades humanas sean consideradas en conjunto con las perspectivas preservacionistas tradicionales. Para que la conservación fuera de las áreas protegidas sea exitosa, la protección de los mamíferos silvestres y sus hábitats debería redundar en beneficios para los habitantes locales, especialmente en comunidades rurales o con altos niveles de pobreza. La preocupación por las poblaciones en declive de grandes mamíferos en Norteamérica durante finales del siglo XIX y principios del XX, resultaron en la implementación de regulaciones que contribuyeron a la recuperación de muchas poblaciones. En la actualidad, las poblaciones silvestres de Norteamérica y Europa son saludables, y la cacería legal es permitida para varias especies de mamíferos, algo que es menos común en muchos países en desarrollo, donde la cacería ilegal continúa siendo una amenaza para la conservación. Sin embargo, las poblaciones

de grandes mamíferos son resilientes a la cacería regulada debido a procesos denso-dependientes que resultan en incrementos en las tasas de reproducción, supervivencia y crecimiento poblacional. Desafortunadamente, la cacería no está regulada por razones culturales y económicas en la mayor parte del mundo. Estamos comenzando a ver los efectos del cambio climático y de las especies invasoras sobre el riesgo de extinción de muchas especies. El futuro de los mamíferos, sin embargo, está finalmente ligado al tamaño, crecimiento y demanda de recursos de las poblaciones humanas.

Key words: conservation, density dependence, extinction, habitat, harvest, human-occupied landscapes, hunting, protected areas, reserves, threat levels

Mammals capture our attention and engender curiosity, thereby enhancing their intrinsic value. This likely occurs because humans are mammals and because of our close and long-term association with canids, felids, and other domestic mammals as companions or livestock (Clutton-Brock 1999; Diamond 2002), and our traditional reliance on wild mammals for food and sport (Hull 1964). This affiliation between humans and mammals creates opportunities for education about populations, ecological communities, ecosystems, global climate, and conservation of all species. Thus, mammals are the most likely group to motivate investment of resources for conservation. Nonetheless, mammals are in jeopardy worldwide.

We review the conservation of mammals, and do so by examining threats to orders of mammals, differentiating among factors threatening terrestrial and aquatic species. We also examine strengths and weaknesses of protected areas, and how to achieve conservation objectives in human-occupied landscapes. We further explore the role of hunting in the conservation of mammals, differentiating between legal, regulated harvests, and illegal killing. Our goal is to provide an informed perspective on the threats to mammals and discuss feasible approaches to their worldwide conservation.

STATUS AND THREATS

Mammalian extinctions.—Mammals are imperiled worldwide. Of 5,487 species recognized by the IUCN Red List, 76 (1.4%) have been declared extinct since 1500, with little chance that any still exist (IUCN 2017). Extinctions are spread across the 27 orders of mammals, and most occur in orders that are species-rich: Primates (2 extinctions), Carnivora (5), Chiroptera (5), Cetartiodactyla (7), Diprotodontia (7), Eulipotyphla (7), and Rodentia (36). Slightly over one-half (55.6%) of the 27 mammalian orders are not known to have experienced extinctions since 1500 (IUCN 2017). Rates of recent mammalian extinctions, however, far exceed past levels, necessitating increased efforts to conserve threatened mammals (Ceballos and Ehrlich 2002; Isaac et al. 2007; Pimm et al. 2014). Moreover, > 70% of endangered mammals are characterized by declining populations, which bodes poorly for their continued existence (Ceballos et al. 2017). Also, extinctions alone fail to describe the full extent of the threat faced by mammals.

Categories of threatened mammals.—Combining Red List (IUCN 2017) categories of Extinct (EX), Extinct in the Wild

(EW), Critically Endangered (CR), Endangered (EN), and Vulnerable (VU), 1,219 species of mammals (22.2%) are ranked as Threatened or Extinct. These categories are based on the quantitative IUCN system for classifying threatened species (Mace et al. 2008). The median percent of Threatened or Extinct species for the 27 orders is 19.0%; only six comparatively small orders (i.e., Dermoptera, Hyracoidea, Microbiotheria, Monotremata, Notoryctemorphia, Tubulidentata) have no species in that combined category. Those numbers, although disturbing, likely underestimate the true threat to mammals because an additional 323 (5.9%) species are categorized as Near Threatened (NT), with a median for the 27 orders of 0.6%. Chiroptera (23.8%) and Rodentia (31.9%) have the largest percentage of NT species. Moreover, many NT species exhibit downward trends in their population sizes (Schipper et al. 2008; Ceballos et al. 2017). Slightly more than one-half of mammalian species (56.7%) are considered to be of Least Concern (LC), with a median of 54.7% across orders. An additional 836 (15.2%) species of unknown status are listed as Data Deficient (DD), with a median of 13.6% across the 27 orders. Orders with relatively large numbers of Data Deficient species are Primates (56), Cetartiodactyla (62), Eulipotyphla (77), Chiroptera (204), and Rodentia (369). Data Deficient species of terrestrial mammals are concentrated in tropical forests, and Data Deficient marine species are clustered in the Antarctic Convergence (Schipper et al. 2008). In addition to identifying a need for further research on the status of Data Deficient species, this category holds import for determining how Threat Levels are assessed for mammals.

Threat Levels for orders of mammals.—The IUCN Red List currently recognizes 5,411 species of extant mammals (IUCN 2017). The Threat Level (sensu Schipper et al. 2008) for those mammals can be assessed and bracketed by evaluating whether Data Deficient species would be categorized as threatened or not threatened. Therefore, Threat Level = $[(VU + EN + CR + EW) / (Total - DD)] \times 100$, where acronyms represent the number of species within those IUCN Red List categories. The lower bound for the Threat Level = $[(VU + EN + CR + EW) / Total] \times 100$; the upper bound for the Threat Level = $[(VU + EN + CR + EW + DD) / Total] \times 100$. The median Threat Level across 27 orders of mammals is 23.0%, with a median for the lower bound of 18.8%, and a median for the upper bound of 33.8%. Davidson et al. (2017) reported that 36% of Data Deficient

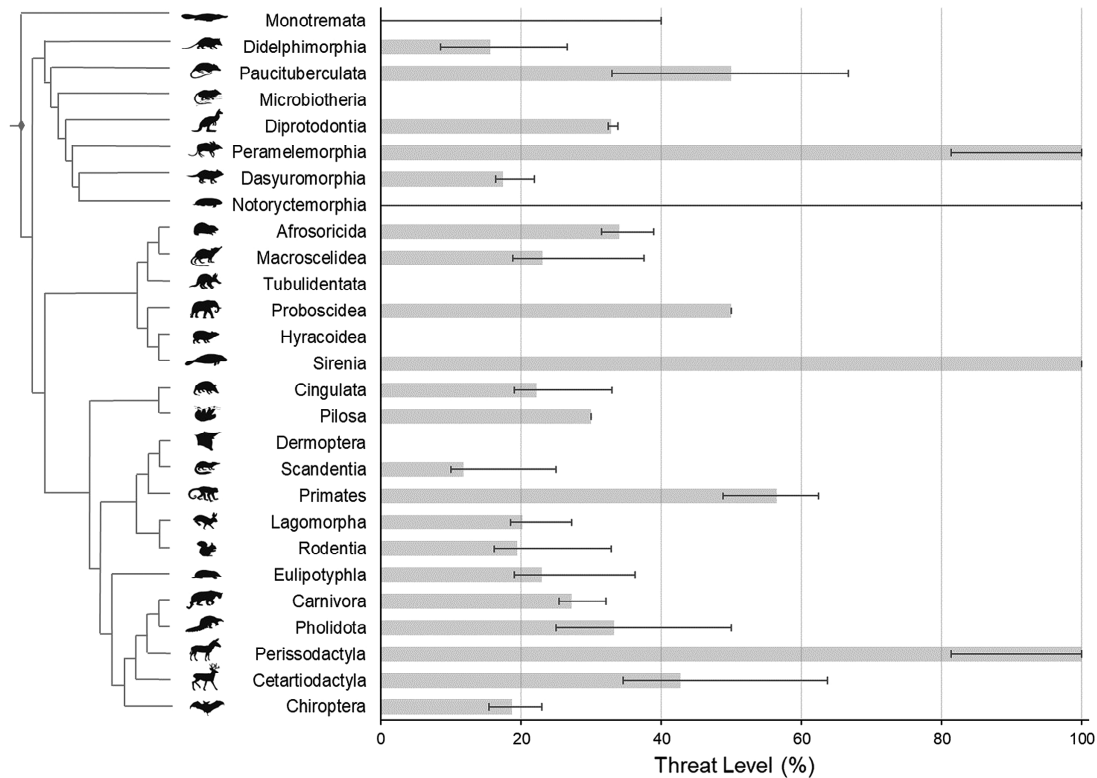


Fig. 1.—Threat Levels for 27 orders of mammals. Error bars indicate lower and upper bounds for Threat Levels. Threat Level = $[(VU + EN + CR + EW) / (Total - DD)] \times 100$. The lower bound for the Threat Level = $[(VU + EN + CR + EW) / Total] \times 100$; the upper bound for the Threat Level = $[(VU + EN + CR + EW + DD) / Total] \times 100$ (Schipper et al. 2008). This analysis is based on the IUCN system for classifying threatened species (Mace et al. 2008): VU = number of Vulnerable species; EN = number of Endangered species; CR = number of Critically Endangered species; EW = number of species Extinct in the Wild; DD = number of species that are Data Deficient. Data from IUCN (2017). J. Kenagy and J. Bradley provided access to the phylogeny for inclusion in this figure.

species of mammals have extrinsic and intrinsic factors associated with a high risk of extinction in other species. Threat Levels are extremely variable (Fig. 1), and large differences exist in causes of potential risk of extinction among mammalian orders (Davidson et al. 2009, 2017). Orders containing large-bodied species (e.g., Cetartiodactyla, Primates, Perissodactyla, Proboscidea, Sirenia, and Carnivora) have comparatively high Threat Levels (Fig. 1). In addition to taxonomic order and body size, other intrinsic characteristics such as small geographic range, inhabiting islands as opposed to the mainland, and having a slow speed of life history (e.g., low adult mortality, iteroparity, small litter size, high maternal investment in young, long generation times, low intrinsic rates of increase) are associated with high risks of extinction (Davidson et al. 2017).

Geographic patterns of species richness.—Land mammals exhibit a peak in species richness centered on the equator (Grenyer et al. 2006; Schipper et al. 2008; Ceballos et al. 2017). Species richness is especially pronounced in the Andes Mountains of South America, and in the mountains of Africa and the southern Arabian Peninsula (Afrotropical forests). High species richness also occurs in Asia, particularly in southwestern China, Malaysia, and Borneo (Heaney 1986; Schipper et al. 2008).

Marine mammals have zones of high species richness clustered around 40° North or 40° South latitude. The prominent exception is in the North Atlantic Ocean, resulting from past exploitation by humans (Schipper et al. 2008; Davidson et al. 2012). Notable areas of high species richness for marine mammals include tropical and temperate coastal benches, as well as offshore portions of the Tasman and Caribbean Seas, and the Southern Indian Ocean (Grenyer et al. 2006; Schipper et al. 2008; Pompa et al. 2011). Areas with threatened species of terrestrial and marine mammals are characterized by high species richness, high endemism, and high human pressure (Schipper et al. 2008; Ceballos et al. 2017).

Geographic patterns and types of threats.—Threatened land mammals are concentrated in southern and southeastern Asia, tropical portions of the Andes Mountains in South America, the highlands of Cameroon, the Albertine Rift in Africa, and the Western Ghats in India (Schipper et al. 2008; Ceballos et al. 2017). For marine mammals, threatened species occur in the North Atlantic Ocean, North Pacific Ocean, and oceans and seas proximate to southeastern Asia (Davidson et al. 2012). Species of mammals with small geographic ranges are especially threatened in southeastern Asia, whereas species with large geographic ranges are threatened in Africa, and portions of Asia and the Arctic (Davidson et al. 2017). Fundamental

differences exist for mammals inhabiting the Northern and Southern Hemispheres. Endemics of the southern-temperate zone have smaller geographic range sizes and are at a greater risk of extinction than are their counterparts from the Northern Hemisphere (Lamoreux and Lacher 2010). Moreover, southern-temperate endemics are less likely to occur within protected areas than are those from the Northern Hemisphere (Lamoreux and Lacher 2010).

Habitat loss and degradation (40% of affected species), and overharvesting (17%) pose the greatest threats to mammals worldwide (Schipper et al. 2008). Those threats are usually driven by human population density and climate change, which pose increasingly greater threats to the future of mammals (Davidson et al. 2017). Threats to land mammals, however, differ markedly from those for marine species. Terrestrial species are negatively affected throughout the tropics from deforestation, especially in the Americas, Asia, and Africa (Schipper et al. 2008). Negative effects of illegal killing on land mammals are most pronounced in Asia, but also in portions of Africa and South America. Overharvesting may result from poaching for food, the bushmeat trade, and use of animals for medicinal and other purposes, as well as from accidental capture in snares set for other species (Schipper et al. 2008; Harrison et al. 2016). Overharvesting disproportionately affects larger mammals (Cetartiodactyla, Primates, Perissodactyla, Proboscidea, and Carnivora) compared with smaller ones, possibly because large mammals have slower life histories and larger home ranges compared with small mammals—characteristics that can increase vulnerability to harvest (Cardillo et al. 2005; Schipper et al. 2008). Nonetheless, legal and regulated sport hunting, as practiced in much of North America and Europe, seldom threatens and may offer conservation benefits to land mammals (Organ et al. 2010).

Disease is a threat to extinction for comparatively few (2%) species of mammals (Schipper et al. 2008). Nevertheless, some diseases can have catastrophic effects on particular species. For example, a transmissible facial cancer in Tasmanian devils (*Sarcophilus harrisii*) devastated populations of this marsupial, yet because of their rapid evolutionary response, hope exists that they may not become extinct (Epstein et al. 2016). White-nose syndrome, caused by a pathogenic fungus (*Pseudogymnoascus*), has killed millions of bats (Chiroptera) since its emergence in eastern North America in 2006 (Frick et al. 2016). Nonetheless, a possibility exists for limiting the spread of this disease because the fungus is extremely sensitive to ultraviolet light, which might be applied to hibernating bats with a few seconds of exposure from a portable light source (Palmer et al. 2018). Chronic wasting disease, which is caused by a prion, is uniformly fatal in cervids, and presents enormous management difficulties in coping with the spread of this infectious disease (Saunders et al. 2012; Potapov et al. 2016). How emerging infectious diseases might interact with other threats to mammals, such as habitat loss and climate change, is uncertain. For instance, recent mass die-offs of the endangered saiga antelope (*Saiga tatarica*), associated with a common bacterium

(*Pasteurella multocida*) under conditions of warmer temperatures and higher humidity, indicate that threats from diseases are likely to increase in unanticipated ways in the future (Kock et al. 2018).

In addition to threats posed by disease-causing microorganisms, invasive animal and plant species threaten mammals worldwide. Based on IUCN data from 2014, alien species were listed as a causal threat for 70% ($n = 30$) of 43 extinctions (Bellard et al. 2016). Furthermore, during recent decades, increased globalization has accelerated rates of movement and introduction of alien species. Moreover, trade and transport of goods and people globally have created new pathways for biological invasions and new challenges for stemming the loss of biodiversity resulting from the spread of alien species (Hume 2009).

Invasive species can threaten mammal populations in diverse and interacting ways. First, invasive predators often are effective in killing naive prey, and this is especially prevalent for insular populations. A recent review identified 189 mammals representing 45 families that have been negatively affected by invasive predators, with the greatest numbers occurring in Australia and Central America (Doherty et al. 2016). At least 28 of Australia's endemic mammals have become extinct since European settlement, and extinctions continue to occur at a rate of one to two per decade, primarily as a result of predation by invasive alien predators (Woinarski et al. 2015). Generalist predators such as feral cats (*Felis catus*), canids, and rodents are among the most challenging for island mammals. Feral cats have been reported to threaten ≥ 27 mammalian species on ≥ 120 islands (Medina et al. 2011). Efforts to remove invasive predators from islands have met with success and offer hope for restoration of island fauna (Jones et al. 2016). Recent summaries indicate that efforts to eradicate invasive species have achieved $> 85\%$ success rates (Genovesi 2011). Nonetheless, growing recognition of the complexity of multispecies interactions also cautions that unintended consequences can occur following removal or reduction of invasive species (Lurgi et al. 2018).

Second, invasive species can compete with native ones directly for key resources and indirectly through the spread of parasites (Dunn et al. 2012) and facilitation of predation (i.e., apparent competition). Introduction of feral pigs (*Sus scrofa*) to the California Channel Islands provided abundant food for golden eagles (*Aquila chrysaetos*) that colonized the islands and subsequently preyed heavily on the native Channel Island foxes (*Urocyon littoralis*)—Roemer et al. 2002). Such novel biological interactions can reduce fitness of native mammals, resulting in population declines that lead to extirpations.

Third, plant invasions can alter community composition with numerous potential consequences for mammals and the ecosystems they inhabit (Vilà et al. 2011). Such effects include reduction in availability or quality of forage for herbivores, changes in hydrological cycles (Huxman et al. 2005), and alteration of historic fire regimes (Brooks et al. 2004). Invasion

of exotic annual plants, including cheatgrass (*Bromus tectorum*), in the western United States has increased frequency and severity of fires (Balch et al. 2013), killing sagebrush (*Artemisia* spp.) shrubs and precipitating loss of shrub-steppe habitats that support sagebrush-dependent mammals such as pygmy rabbits (*Brachylagus idahoensis*) and sagebrush voles (*Lemmyscus curtatus*). The uncertainty associated with effects of invasive species under changing climate regimes is an emerging threat to mammals. We address the issue of climate change later, but emphasize here that shifts in climate have the potential to alter consequences of species invasions in ways that have yet to be imagined. We view this as an important area for research to support future conservation of mammals.

For marine mammals, the principal threats are from accidental mortality (affecting 78% of species), including fisheries bycatch and vessel strikes, and pollution (60% of species). Pollution involves chemicals, marine debris, noise, and climate change (Schipper et al. 2008). Harvesting of marine mammals remains a concern (52% of species) largely because of commercialization, notwithstanding improvements via international agreements (Davidson et al. 2012; Bowen and Lidgard 2013; McCaughy et al. 2015).

Comparisons of terrestrial and aquatic taxa within Cetartiodactyla.—A positive relationship exists between threat of extinction and body size (Purvis et al. 2000; Cardillo et al. 2005). Evaluating threats to large mammals of the Cetartiodactyla may offer insights into patterns that species in other orders may face.

For the 10 families of terrestrial species within Cetartiodactyla, a median of 55.5% of the species in those families are Threatened or Extinct. All species in three small families (Giraffidae, Hippopotamidae, Moschidae) are in that category. Threatened or Extinct species compose 37.3% of the species-rich Bovidae (142 species) and 49.0% of the Cervidae (54 species). Comparatively few species (16) from those two large families are Data Deficient, which is a small percentage (6.7%) of their extant species. Nevertheless, Threat Levels for terrestrial families of Cetartiodactyla (Table 1) are high compared with other mammalian orders (Fig. 1). A median Threat Level of 58.3%, with large lower (53.5%) and upper (61.8%) bounds are a clear cause for concern.

For the 11 families of aquatic species (some are not marine) within Cetartiodactyla, no species, with the possible exception of the baiji (*Lipotes vexillifer*), was thought to be extinct (Turvey et al. 2007). The IUCN (2017) lists that species as Critically Endangered with an unknown population trend. A median of 33.3% of aquatic species in Cetartiodactyla were categorized as Threatened (Table 2). This value likely is biased low because of the large number (45) of Data Deficient species, which constituted 51.7% of aquatic species. Threat Levels to aquatic species within Cetartiodactyla (Table 2) are high compared with other orders (Fig. 1), with a median of 50.0% (the lower bound for Threat Levels was 33.3% and the upper bound 75%). The upper bound for Threat Levels for aquatic families exceeded that for terrestrial families

Table 1.—Threat levels with upper and lower bounds for families of terrestrial mammals in the order Cetartiodactyla. Threat Level = $[(VU + EN + CR + EW) / (Total - DD)] \times 100$. The lower bound for the Threat Level = $[(VU + EN + CR + EW) / Total] \times 100$; the upper bound for the Threat Level = $[(VU + EN + CR + EW + DD) / Total] \times 100$. VU = number of Vulnerable species; EN = number of Endangered species; CR = number of Critically Endangered species; EW = number of species Extinct in the Wild; DD = number of species that are Data Deficient. Data from IUCN (2017).

Family	Extant species (n)	Threat level (%)	Lower bound (%)	Upper bound (%)
Antilocapridae	1	0.0	0.0	0.0
Bovidae	142	36.0	35.0	37.9
Camelidae	3	33.0	33.0	33.0
Cervidae	54	57.8	48.1	64.8
Giraffidae	2	100.0	100.0	100.0
Hippopotamidae	2	100.0	100.0	100.0
Moschidae	7	100.0	100.0	100.0
Suidae	17	58.8	58.8	58.8
Tayassuidae	3	66.7	66.7	66.7
Tragulidae	10	14.2	0.0	40.0

Table 2.—Threat levels with upper and lower bounds for aquatic families in the order Cetartiodactyla. Threat Level = $[(VU + EN + CR + EW) / (Total - DD)] \times 100$. The lower bound for the Threat Level = $[(VU + EN + CR + EW) / Total] \times 100$; the upper bound for the Threat Level = $[(VU + EN + CR + EW + DD) / Total] \times 100$. VU = Vulnerable; EN = Endangered; CR = Critically Endangered; EW = Extinct in the Wild; DD = Data Deficient. Data from IUCN (2017).

Family	Extant species (n)	Threat level (%)	Lower bound (%)	Upper bound (%)
Balaenidae	4	50.0	50.0	50.0
Balaenopteridae	8	60.0	37.5	75.0
Ziphiidae	21	0.0	0.0	90.5
Delphinidae	36	15.8	8.3	55.6
Monodontidae	2	0.0	0.0	0.0
Eschrichtiidae	1	0.0	0.0	0.0
Iniidae	3	100.0	66.7	100.0
Neobalaenidae	1	0.0	0.0	100.0
Physeteridae	3	100.0	33.3	100.0
Phocoenidae	7	60.0	42.9	71.4
Platanistidae	1	100.0	100.0	100.0

within Cetartiodactyla, largely because of the numerous Data Deficient aquatic species.

The primary factors threatening terrestrial Cetartiodactyla are similar across families based on the top three threats listed by the IUCN (2017) for each family (as determined by the number of species experiencing those threats). The category of “biological resource use” resulting principally from hunting and trapping was a primary threat for all 10 families. Nonetheless, many of those threats pertained to historical use of species, or illegal killing; no such reports listed legal and regulated sport harvest of mammals as a threat. Likewise, all 10 families included the IUCN category of “agriculture and aquaculture” as a threat, mostly a result of livestock farming or ranching. One-half of the families listed “residential and commercial development” as a threat, 20% included “human intrusions and development,”

10% listed “natural system modifications,” and 10% identified “invasive and other problematic species and diseases.” All of those categories except hunting and disease can be considered to be a consequence of habitat loss or modification.

The 11 families of aquatic species within Cetartiodactyla also face common threats. Foremost among those primary threats is “biological resource use” (90.9%), denoted mostly as harvest, fisheries bycatch, or harvesting of other aquatic resources. The only family that did not list “biological resource use” as a threat is the monotypic Neobaliniidae, for which no threats were listed because the pygmy right whale (*Caperea marginata*) was categorized as Data Deficient. “Pollution” also is a common threat (63.6%) in aquatic families; followed by “climate change and severe weather” (45.5%); “transportation and service corridors” (27.3%), which involve principally risks of collisions in shipping lanes; and “invasive and other problematic species and diseases” (18.2%).

Understanding patterns of extinction.—Mammals face dire threats throughout their distribution; the continued existence of many species, especially large-bodied, vagile taxa, is in question. Our results, however, are extremely conservative and do not fully address threats to mammalian species. The IUCN Red List considers only species-level taxa in categorizing the status of mammals, and consequently does not reflect threats to subspecies or local populations (Butchart and Dunn 2003; Ceballos et al. 2017). For instance, the pronghorn (*Antilocapra americana*) is listed as a species of Least Concern, yet the Sonoran pronghorn (*A. a. sonoriensis*) is Endangered (Hosack et al. 2002). Bighorn sheep (*Ovis canadensis*) also is a species of Least Concern, but the Sierra Nevada subspecies (*O. c. sierrae*) is Endangered (Schroeder et al. 2010). The white-tailed deer (*Odocoileus virginianus*) has a wide distribution in the Americas and is a species of Least Concern, yet the Florida Key deer (*O. v. clavium*) is Endangered (Haversohn et al. 2004).

Another problematic component of the IUCN database relates to the number of extant mammalian species. For instance, the Mammal Diversity Database (<https://mammaldiversity.org>) currently recognizes 6,399 species of extant mammals, with 96 species recently extinct (Burgin et al. 2018). Moreover, a long-term average of 25 new species has been described each year (Burgin et al. 2018). Undescribed species probably have experienced some extinctions, which would result in further underestimating extinction rate. Moreover, analyses based on IUCN (2017) data have 912 fewer mammalian species than recognized by the Mammal Diversity Database. The IUCN statistics clearly document past threats to mammals but may not track current ones, especially for rapidly occurring changes in the status of some mammalian species. Indeed, population status for many species is poorly documented in developing countries of the world, and nonexistent for the 912 mammal species that do not occur on the IUCN list (Burgin et al. 2018).

Further, the IUCN Red List has been criticized as unscientific and in need of additional or revised metrics for classifying threatened species (Mace and Lande 1991; Nowak 2009; Joppa et al. 2016). Nevertheless, some of those criticisms are based on misconceptions concerning the manner in which species

are classified into categories (Collen et al. 2016). Despite some shortcomings, we believe the IUCN Red List provides a benchmark against which the changing status of mammal species may be judged. The emphasis on extinction of species, regardless of the database used, has resulted in underestimating threats to mammals (Ceballos et al. 2017).

Some mammals have experienced massive contractions in their geographic ranges during historic times (Laliberte and Ripple 2004), and many species of Least Concern are declining, which may result in local extinctions (Craigie et al. 2010; Ceballos et al. 2017). Large mammals, in particular, have the potential to greatly influence ecosystems that they inhabit (McNaughton 1979; Stewart et al. 2006), but we must find ways to implement conservation measures that will benefit a diversity of mammalian taxa (Ford et al. 2017). Ultimately, the fate of mammals is intertwined with the size, growth, and resource demands of the human population (Vitousek et al. 1997; Czech et al. 2000; Gaston 2005; McKee et al. 2013).

Loss of habitat and habitat fragmentation (Wilcox and Murphy 1985) are quintessential factors threatening most mammals, especially terrestrial taxa. Habitat restoration holds the potential to reduce rates of extinction in fragmented woodlands (Newmark et al. 2017). Although there has been rapid progress in developing protected areas, those sites do not necessarily protect biodiversity (Andelman and Willig 2003; Pimm et al. 2014; Bleich 2016).

EFFICACY OF PROTECTED AREAS

Human livelihoods versus protection.—Curbing extinction and preserving populations are two major goals of mammal conservation. Historically, protected areas (national parks, reserves, and other legal designations intended to limit human activities with the overarching goal of conserving nature) have been a hub for conservation efforts. Recently, however, conservationists have come to realize that protected areas often are too small (Woodroffe and Ginsberg 1998; Bleich 1999, 2005; Gonzalez-Maya et al. 2015), too few (Gaston et al. 2008; Newmark 2008; Durant et al. 2017), poorly delimited or isolated (Bleich 2014, 2016), or too unreliably supported (Andelman and Willig 2003; Caro and Scholte 2007; Craigie et al. 2010) to meet many long-term (centuries to millennia) conservation prospects. Consequently, some conservationists are transitioning to a model in which the improvement of human livelihoods is considered (or even prioritized) alongside traditional preservationist views.

This outcome has been dubbed the “new conservation science” (Kareiva and Marvier 2012), and it is reminiscent of the creation of Integrated Conservation and Development Projects (ICDPs). In the mid-1980s, and largely in response to failures perceived with traditional conservation efforts in protected areas (i.e., “fences and fines” approaches), the World Wide Fund for Nature introduced 19 ICDPs in an attempt to meet socioeconomic priorities of rural communities and conservation goals simultaneously (Hughes and Flintan 2001). These ICDPs were established across Africa and South America, normally

in conjunction with national parks and typically funded by western governments and nongovernment organizations, with the goal of benefiting local communities through tourism dollars and job creation (Hughes and Flintan 2001). The validity of the ICDP model for conservation rests on at least two assumptions. First, local peoples are hostile toward formally protected areas, and their livelihoods pose a direct threat to biodiversity (Hughes and Flintan 2001). Second, ICDPs offer complementary or alternative livelihoods to locals that are sustainable, will increase living standards, and will reduce threats posed to biodiversity (Newmark and Hough 2000). These assumptions are rarely tested and are sometimes wrong. Moreover, a possible (but not universal—Salerno et al. 2014) unintended consequence of ICDP establishment is the increased immigration of people toward the outskirts of protected areas (Barrett and Arcese 1995; Scholte 2003; Guerbois et al. 2013).

Generally, shifts from traditional conservation to emphasis on human livelihoods are controversial (e.g., Kareiva and Marvier 2012; Doak et al. 2014, 2015; Vucetich et al. 2015), and are exemplified by two quotations: “Nature preserves...are not places to be saved to be used at a later stage when an ever-growing human population claims more land because of lack of economic development” (Prins 1992); and “Why should all that land be set aside for tourists when it can be used for farming? These white people care more about one dead elephant than they do for a hundred black children” (Obama 1995, quoting his sister). At the heart lies debate over the validity of two frequent claims (Young 2006): conservation and improved human livelihoods are compatible; and economic interests, particularly those of rural communities, must be satisfied for conservation to be successful (i.e., “wildlife must pay its way”). Appealing though they may be, evidence for the two claims is equivocal in that valid examples refuting or supporting each are readily available. Each is true for some conservation efforts, in some areas, some of the time.

With these considerations in mind, we review the costs and benefits of protected areas and multi-use, human-occupied landscapes, with particular attention to if and how each has shaped conservation outcomes for mammals. We then consider two examples in which on-the-ground conservation efforts are relying on a combination of formally protected areas and landscapes inhabited by local communities to bolster populations of two related, rare antelopes (Bovidae). Although these examples are broadly applicable, we focus attention on eastern and southern Africa, which house iconic protected areas (Kruger National Park, Serengeti National Park, Maasai Mara National Reserve, Mara Conservancy, and other nearby conservancies), and are occupied by people and their livestock over 75–85% of the landscape, and thus lack formal protection (Chape et al. 2005; Newmark 2008).

Costs, benefits, and logistics of protected areas for conserving wild mammals.—We follow Dudley (2008) in defining a protected area as a “clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.” By this definition, the

world’s first protected area (the Main Ridge Forest Reserve in Tobago) was created in 1776 via British parliamentary ordinance to collect rainfall for agriculture elsewhere on the island (UNESCO 2011). Since this time, more than 202,000 protected areas have been established across nearly 15% of the Earth’s terrestrial surface (U.N. Environment Conservation Monitoring Centre 2017). Many successes in mammal conservation have arisen precisely because of the establishment of, or targeted efforts within, formally protected areas, which also can serve as critical reference points for restoration (Arcese and Sinclair 1997; Berger 2008). For the 24 species of wild mammals for which populations have been bolstered by conservation efforts in recent decades, one-half have benefitted demonstrably from conservation in protected areas (Hoffmann et al. 2010, 2011). In an extreme example, conservation within a protected area (the Serengeti National Park–Maasai Mara National Reserve complex) almost certainly prevented the conservation status of common wildebeest (*Connochaetes taurinus*) from deteriorating from Least Concern to Critically Endangered (Hoffmann et al. 2015).

Alternative views exist regarding the utility of protected areas as ecological baselines. For example, Sarmiento and Berger (2017) demonstrate that increased rates of human visitation to Glacier National Park have caused mountain goats (*Oreamnos americanus*) to relax antipredator behaviors, thereby potentially reshaping predator–prey interactions. More generally, protected areas (even those designated as “wilderness”) often are too small, too isolated, or both to buffer wide-ranging ungulates and carnivores from human influence outside their borders (Woodroffe and Ginsberg 1998; Bleich 2016). Therefore, there is some risk that our view of “pristine” is illusory, and our perception of ecological baselines subjective.

Conservation within protected areas requires a combination of reduction (or exclusion) of people and the creation of economic benefits from wildlife to people around protected areas. With regard to the former, Hilborn et al. (2006) demonstrated that enhanced antipoaching efforts in Serengeti National Park were sufficiently strong to increase numbers of buffalo (*Syncerus caffer*), African elephant (*Loxodonta africana*), and black rhinoceros (*Diceros bicornis*). Examples of effective enforcement within protected areas are rare, despite their critical importance for conservation. Some have suggested that increased funding for antipoaching patrols, rather than increased sentences for captured poachers, is a more economically efficient means of deterring poaching (Dobson and Lynes 2007). Because poaching reduces the effective size of protected areas, and because protected areas display classic species–area relationships (Fig. 2), economic inputs toward enforcement should result in less disparity between the true size of a protected area and its effective size (Leader-Williams and Milner-Gulland 1993; Dobson and Lynes 2007).

Fencing of protected areas has been a particularly contentious subject in recent years, although this debate is rooted in discussions from the mid-1980s. The controversy (Creel et al. 2013; Packer et al. 2013a, 2013b) is related to how best to minimize retaliatory killing of large carnivores (particularly African

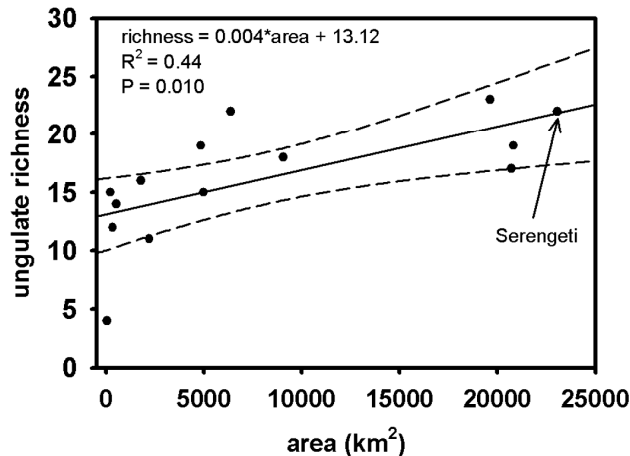


Fig. 2.—Species richness of large (> 10 kg) ungulates displays a classic species–area relationship (power function) for protected areas in East Africa, implying extinction risk is a function of size of protected areas (Brashares et al. 2001). Protected areas comprise savanna woodland or grassland habitats in eastern and southern Africa, and include Amboseli National Park, Bontebuck National Park, Etosha National Park, Kora National Reserve, Kruger National Park, Lake Manyara National Park, Lake Nakuru National Park, Moremi Game Reserve, Nechisar National Park, Queen Elizabeth National Park, Serengeti National Park, South Luanga National Park, Tsavo National Park (East and West combined), and West Caprivi Game Reserve. Data from the IUCN World Database on Protected Areas (<https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-areas>).

lions, *Panthera leo*) following livestock depredation, as well as effects of habitat loss and degradation from livestock and farming, and depletion of native prey because of their use as bushmeat and competition with livestock. On one hand, population persistence of African lions is projected to be highest within well-funded and fenced protected areas (where African lions are limited primarily by density dependence), and lowest within poorly funded, unfenced protected areas associated with high population densities of people (Packer et al. 2013a). Conversely, critics have argued that African lion densities are artificially high within fenced protected areas, and these are too expensive to install and maintain in most locales (Creel et al. 2013). One point of agreement is that African lion conservation requires a larger, sustained financial base to be successful over the long term.

Still, protected areas are not a panacea, and often fall short as a stopgap to prevent population declines, local extirpations, or even extinction. This happens for a number of reasons, foremost among them illegal hunting within protected areas that exist in name only, but that lack adequate enforcement (so-called “paper parks”—Gates 1999). Although they occur largely in protected areas, West African chimpanzees (*Pan troglodytes verus*) are on the brink of extinction in several countries; the same is true for addax (*Addax nasomaculatus*) and dama gazelle (*Nanger dama*), despite occurring in the largest protected area on the continent (the 100,000 km² Termit Massif Reserve in Niger). In 2000, Miss Waldron’s red colobus monkey (*Piliocolobus waldronae*) was declared extinct in a network of national parks in

Ghana and Ivory Coast (Oates et al. 2000; but see the following section). Additionally, extinction risk is amplified in small reserves in West Africa via demographic stochasticity (Brashares et al. 2001) and in the Horn of Africa because of compromised ability of several antelopes with small geographic ranges to track suitable habitats as drying and warming intensifies (Payne and Bro-Jørgensen 2016).

Because protected areas generally are viewed as safeguards in which pristine and fragile nature is physically separated from human activities, protected areas risk being perceived as incompatible with human livelihoods. This observation is particularly applicable to developing countries, where more affluent nations are responsible for the bulk of conservation funding (Hickey and Pimm 2011; Miller et al. 2013). Such division between the nations that fund conservation and nations that bear the costs of conservation can result in mistrust of government agencies and other organizations dedicated to conservation in protected areas. By virtue of their proximity to protected areas, local peoples are asked to tolerate direct (e.g., livestock depredation, crop loss) or indirect (e.g., restrictions on development, competition from game species) economic losses to wild mammals (Waylen et al. 2010; Bruskotter et al. 2017). Perceptions aside, local peoples derive at least some benefits from protected areas, as evidenced by growing human populations on the outskirts of national parks and reserves in Africa and Latin America (Wittemyer et al. 2008), and increasing human pressures within a substantial fraction of protected areas (Jones et al. 2018).

Costs, benefits, and logistics of human-occupied landscapes for conserving wild mammals.—We consider conservation in human-occupied landscapes (areas with conservation needs that also include people) as synonymous with community-based conservation, in which local involvement in areas lacking formal protection is aimed at enhancing conservation and maintaining or improving living standards (Berkes 2004). Conservation in human-occupied landscapes may complement conservation in formally protected areas, or it may be the only option through which conservation can occur (Western et al. 2015). The latter is particularly the case in developing nations, where governments lack the authority or resources to advance conservation. In such instances, the explicit consideration of human livelihoods may be crucial for curbing extinction and bolstering population sizes of rare or declining mammals.

Conservation failure is the norm in human-occupied landscapes, but it is by no means a foregone conclusion. For conservation outside of formally protected areas to succeed, the protection of wild mammals and their habitats should result in some benefit to local people. Examples include direct payments from ecotourism (Sindinga 1995) and trophy hunting (Lindsey et al. 2006), ecosystem services in the form of enhanced forage quality (Odadi et al. 2011), and reduced risk of tick-borne diseases (Allan et al. 2017). These benefits arise from the diversification of land uses, which increasingly are being implemented to buffer against unpredictable climates and livestock markets (Reid et al. 2014). These benefits also should be tied directly to decisions made by local residents, who should oversee conservation efforts (Goodwin and Roe 2001).

COMMUNITY EFFORTS IN HUMAN-OCCUPIED LANDSCAPES

As with protected areas, examples of conservation success in human-occupied landscapes are many. Black-footed ferret (*Mustela nigripes*) restoration is occurring on privately owned rangelands in Wyoming because of a recent clause of the Endangered Species Act, affording regulatory relief for land-owners in the form of relaxed prohibitions on take (USFWS 2014). Similar to ferrets, other species of mammals thought to be extinct, have been rediscovered in human-occupied landscapes, including the Philippine naked-backed fruit bat (*Dobsonia chapmani*) on Cebu and Negros Islands (rediscovered in 2000—Paguntalan et al. 2004), and the Miss Waldron's red colobus monkey in the Ehy Forest of Ivory Coast (rediscovered in 2002—McGraw 2005). Engaging local people in participatory forest management has been very effective in reducing forest loss around Chitwan National Park, Nepal (Stapp et al. 2016).

Human–wildlife conflict frequently constrains opportunities for conservation in human-occupied landscapes, particularly in the absence of strong local investment in conservation or transparent benefits to individuals from conservation. This occurs because common resources, such as rangelands, forests, and water, are susceptible to overexploitation via the Tragedy of the Commons (Hardin 1968). Self-governance of common resources can benefit wildlife, if major decisions are made locally by communities (Fennell 2011). Ostrom (1990) articulated eight principles that are necessary to prevent a commons tragedy from arising, four of which are particularly germane when considering conservation efforts in human-occupied landscapes:

- 1) Clearly defined common resources, and effective exclusion of unentitled parties;
- 2) Collective choice, such that users of common resources can participate in decision-making (or elected officials serve as proxies in decision-making);
- 3) Sanctions for those who violate community rules in appropriating common resources; and
- 4) Recognition of leaders by higher-level authorities of the community.

The success of conservation in human-occupied landscapes hinges strongly on those principles. Ultimately, their implementation requires strong leadership through heads, elders, or other respected individuals in the community, who have strong public support (e.g., Kothari et al. 2013; Hazzah et al. 2014). Local conservation requires local knowledge, which is necessary but insufficient for conservation in human-occupied landscapes. Local conservation also requires local leaders.

In the following section, we detail two cases in which current conservation efforts rely on a combination of protected areas and human-occupied landscapes to bolster population sizes of two species of imperiled antelope. Both lean heavily on strong local knowledge and local leadership. At first glance, these examples seem similar: the antelope species are close relatives,

occur in Kenya, and share the landscape with people and their livestock. But each example highlights a truism: while conservation is a global problem, the solutions are typically local, and require sustained input over the long term (Pringle 2017). Inevitably, such long-term dedication necessitates a focus on place: intimate knowledge of system-specific details of the protected areas or human-occupied landscapes in which conservation challenges occur and can be fixed.

Case study 1: livestock production as a tool to lessen apparent competition for hartebeest.—The aim of this project is to reverse declines of hartebeest (*Alcelaphus buselaphus*) inhabiting the 10,000 km² Laikipia Plateau of central Kenya over one or more decades. Since the mid-1980s, hartebeest and several other populations of wild ungulates in Laikipia have declined, due to the increasing tolerance of ranchers toward large carnivores, particularly African lions. The rate and timing of these declines is the same, indicating one or more common underlying mechanisms. Georgiadis et al. (2007a) tested seven nonexclusive hypotheses (including poaching, parasitism, interspecific competition, intraspecific competition, habitat conversion, displacement by humans, and exceptional rainfall patterns) for those declines, rejecting all but predation. Further, the authors suggested that many species of wild ungulates in Laikipia, the hartebeest in particular, were suppressed via apparent competition with plains zebra (*Equus burchelli*), a wild ungulate that has not exhibited the same steep declines characteristic of others in Laikipia, and that is the most common prey of African lions (Georgiadis et al. 2007b; Frank 2011).

At Ol Pejeta Conservancy in Laikipia, Ng'weno et al. (2017) reported support for the hypothesis that African lions had suppressed population growth of hartebeest. Additionally, hartebeest were preferred by African lions over 10 wild ungulate species with which they co-occurred, and exhibited an African lion-mediated Allee effect (Ng'weno 2017). Risk of mortality to hartebeest from African lion predation increased in association with plains zebra and dense vegetation (Ng'weno et al. 2017). These observations support the idea that an increasing African lion population in Laikipia has been subsidized by plains zebra and caused hartebeest to decline to < 10% of their historical abundance.

Finding lethal control of African lions improper and extirpation of hartebeest populations undesirable, Ng'weno (2017) implemented a solution to bolster numbers of hartebeest that did not require lethal control of African lions. Within Laikipia, ranchers corral livestock nightly in temporary, circular corrals (“bomas”) to reduce predation (Ogada et al. 2003). Bomas are occupied between 1 and 6 months, after which they are abandoned and livestock are moved in a rotational scheme. Over 1 year, bomas transition into nutrient-rich grazing lawns, as dung and urine break-down and enrich the soil (Veblen 2012; Porensky and Veblen 2015). Those grazing lawns are attractive to plains zebra, but are virtually ignored by hartebeest. Consequently, Ng'weno (2017) used bomas to create grazing lawns away from hartebeest territories, thereby manipulating the distribution of primary prey (zebra) on the landscape and providing a spatial refuge from African lion predation for

hartebeest. This approach more than doubled survival rates of hartebeest, although it is too early to know whether this effect is sufficiently strong to reverse population declines of hartebeest.

Case study 2: engaging Somali communities to conserve hirola antelope.—This project involves hirola (*Beatragus hunteri*), a close relative of hartebeest that is classified as Critically Endangered by the IUCN, with a global population size of < 500 individuals (King et al. 2011). Hirola have never been common, and are restricted to grassland habitats east of the Tana River on the Kenya–Somalia border; such small-ranged species are particularly susceptible to demographic stochasticity, and thus present major conservation challenges (Caughley 1994). In the mid-1980s, geographic range collapse (and the associated global population crash) occurred in response to a rinderpest (*Morbillivirus*) outbreak (IUCN 2008), such that hirola are now restricted to an approximate 1,200 km² swath of land on the Kenya–Somalia border. Nonetheless, eradication of rinderpest from the Horn of Africa in the early 2000s did not prompt hirola recovery (Ali et al. 2017). At approximately the same time that hirola populations plummeted, financial backing for the only protected area in the region, Arawale National Reserve, dwindled because of remoteness of the area, lack of a viable tourism industry, and lack of local involvement.

Motivated by increasing calls for in situ conservation and local involvement, the Ishaqbini Hirola Conservancy was established in eastern Kenya in 2005 by Terra Nuova (an Italian nongovernmental organization) and has been overseen since by the Northern Rangelands Trust (a Kenyan nongovernment organization supported largely by USAID, The Nature Conservancy, and other international donors). This marked a major shift in attempts to conserve hirola, as local Somali communities were engaged, and indeed were the driving force behind those efforts. In 2012, a predator-proof sanctuary was constructed within Ishaqbini to serve as a source for future reintroductions of hirola throughout their historical range, the first of which is slated for 2018. Interestingly, populations of hirola have grown within Ishaqbini at the same time that they remained stable or declined slightly within a protected area to which they were introduced in the mid-1990s (Tsavo East National Park—Probert et al. 2014; Ali et al. 2018).

Despite its successes, Ishaqbini is small (72 km²) and therefore insufficient for the long-term persistence of hirola. At approximately the same time as the sanctuary was being created, a coordinated, parallel effort (the Hirola Conservation Programme; HCP) was established. The HCP's mission is to “regazette” Arawale National Reserve and restore hirola populations throughout their 7,600 km² historical range, which would result in the downlisting of hirola from Critically Endangered to Endangered. In the aftermath of rinderpest eradication, hirola populations have been suppressed by a combination rangeland deterioration via tree encroachment and predation by African lions, cheetahs (*Acinonyx jubatus*), and African wild dogs (*Lycaon pictus*), each of which is an IUCN red-listed species (Ali et al. 2017, 2018).

Because predator control is arguably undesirable and logistically impossible, efforts have centered on identifying strategies to revert *Acacia*-dominated woodlands to the open grasslands that characterized the historical range of hirola. Local communities support restoration strategies that have been successful elsewhere, including manual clearing of trees and reseedling of grasses over large areas (Ali 2016). Although it is too early to know whether range-restoration efforts have been successful, signs are encouraging because several of Ostrom's (1990) criteria for combating the Tragedy of the Commons are being met: well-defined community boundaries exist within the hirola's range, rules are being created for the provision of restored grasslands to individuals, and participatory decision-making is being overseen by a small number of elders who have broad community support (Ali 2016). Mammal conservationists await results with cautious optimism.

The cases of hartebeest conservation in Laikipia and hirola conservation in eastern Kenya represent place-based, system-specific conservation efforts. Those efforts would not be possible without elements of conservation in protected areas and human-occupied landscapes in tandem, and neither would be possible without strong local leadership. Such is the norm for mammal conservation throughout the globe. Although several contributions over the past decade have been key in identifying common challenges associated with protected areas (e.g., Woodroffe and Ginsberg 1998; Tranquilli et al. 2014; Venter et al. 2017) and human-occupied landscapes (e.g., Walpole and Thouless 2005; Chapron et al. 2014), workable solutions often are difficult to apply generally. In the previous examples, each conservation solution arose because of particularities inherent to the study system. In the first, secondary prey of African lions (hartebeest) are not attracted to grazing lawns to the same degree as are primary prey of African lions (zebra), thereby offering potential for physical separation and spatial refugia. In the second, Somali pastoralists typically do not hunt wild ungulates, and ascribe to hirola a near-mythical status (because hirola are associated with high-quality, abundant grasses Kimitei et al. 2015). Such is the nuance of successful conservation efforts, for which we expect both protected areas and human-occupied landscapes to play key roles in the 21st century and beyond.

HUNTING

Patterns of use and exploitation.—Humans have been hunting other mammals throughout our species' existence (Bunn and Gurtov 2014). The primary motivation for hunting always has been for food, and this remains among the most common justifications for hunting, whether it be for bushmeat by aboriginal peoples in tropical areas of Asia (Harrison et al. 2016), Africa (Fa et al. 1995), Australia (Finch et al. 2014), or South America (Hames and Vickers 1982), or for highly regulated hunting in North America and Europe (Responsive Management 2013). Culling is another term for hunting, but culling is most often used when removals are motivated to reduce population size to

lessen conflicts with agriculture or to control predators (Quirós-Fernández et al. 2017).

When tied to economic incentives and commercial markets, however, hunting has led to excessive harvests and declines in wild mammal populations (Geist 1988; Harrison et al. 2016). In some instances, this has been the consequence of market hunting, for example, in the bushmeat trade in Asia (Scheffers et al. 2012; Harrison et al. 2016) and Africa (Fa et al. 1995) or early exploitation of elk (*Cervus elaphus*) in North America (Geist 1988). During the 18th and 19th centuries, beavers (*Castor canadensis* and *C. fiber*) and otters (*Endydra lutris*, *Lontra canadensis*, and *Lutra lutra*) were extirpated from most of North America and Europe because of a lack of regulations and high economic demand for fur (Ray 1974; Estes 2016).

In North America, deliberate exploitation was used to eliminate bison (*Bison bison*) from the Great Plains during warfare by the United States government against aboriginal people who depended on bison for food (Allen 1954). Likewise, European bison (*B. bonasus*), deer (*C. elaphus* and *Capreolus capreolus*), and beavers (*C. fiber*) were severely overharvested across vast regions of Europe. Large carnivores have been especially persecuted, including wolves (*Canis lupus*), large cats (*P. leo* and *Puma concolor*), and bears (*Ursus* spp.) that were killed to prevent livestock depredation (Ripple et al. 2014).

Declining populations and restorations.—Concerns about declining wildlife populations in the late 19th century prompted Theodore Roosevelt and an elite group of hunters and nature enthusiasts to form the Boone and Crockett Club to initiate major conservation initiatives (Organ et al. 2010; Krausman and Bleich 2013). Regulations limiting hunting, with restricted seasons and quotas, were implemented in many areas early in the early 20th century, and reintroduction programs were conducted to restore depleted or extirpated populations of a number of species, including bighorn sheep (Bleich et al. 2018), elk, beavers, and otters (Geist 1995). More recently, large carnivores have returned to parts of their former range even though they are still persecuted in many areas (Ripple et al. 2014). Generally, however, these conservation measures were highly effective for a number of mammal species, and today, in North America and Europe, wild mammal populations are thriving to the extent that legal hunting is allowed for a number of species (Organ et al. 2010). Indeed, hunters in North America have contributed billions of dollars toward conservation and wildlife management (Southwick and Allen 2010).

Patterns of management.—In developing countries, management of hunting varies substantially because of societal views and economics. Artiodactyls threatened with extinction, for example, occur most often in poor countries with unregulated hunting (Price and Gittleman 2007). Hunting of wildlife is banned in several countries, notably China and India, although illegal hunting (i.e., poaching) is known to be a concern in most places to various degrees and has been exceedingly challenging for the black rhinoceros, white rhinoceros (*Ceratotherium simum*), three species of Asian rhinoceros (*Rhinoceros sondaicus*, *R. unicornis*, *Dicerorhinus sumatrensis*), and African elephant. In some countries, including Namibia and South Africa,

trophy hunting generates substantial revenues for local communities and for conservation, and justifies maintaining and restoring native vegetation with benefits for biodiversity protection (Lindsey et al. 2007).

The legal killing of a telemetered male African lion near Hwange National Park in Zimbabwe prompted huge public media discussions about the ethics of trophy hunting (Di Minin et al. 2016; Macdonald et al. 2016). Although still controversial, a report by the IUCN (2016) details circumstances when trophy hunting can be an effective tool for conservation and offers guidelines. The IUCN report details many examples including the local-community management of trophy hunting to support conservation of the Suleiman markhor (*Capra falconeri*) and the Afgan urial (*Ovis orientalis*) in Pakistan (Woodford et al. 2004) and Tajikistan.

Sustainability of harvest.—In most places where hunting is legal, it is regulated to ensure that harvests are sustainable, but sustainable harvests may not ensure hunting in some instances (Fig. 3). Hunting is sustainable, in part, because of density-dependent survival or reproduction (Boyce et al. 1999; Kokko 2001; Bowyer et al. 2014). Hunting reduces population density, resulting in increased food availability per capita, with consequent enhanced nutrition increasing survival or fecundity, thereby compensating for animals removed by harvest (Owen-Smith 2006). These density-dependent responses to exploitation include increased survival, especially of juveniles (Eberhardt 2002; Bonenfant et al. 2009), and increased growth rates (Schmidt et al. 2007; Gamelon et al. 2017; Monteith et al. 2018). Also, life-history responses influencing reproduction can include larger litter sizes and reproductive output (Bowman et al. 1999; Hanson et al. 2009; Gamelon et al. 2017), higher pregnancy rates (Stewart et al. 2005), and earlier age at first reproduction (Boyce 1981). Density dependence facilitates



Fig. 3.—Grizzly bear (*Ursus arctos*) in central British Columbia, Canada. Trophy hunting for grizzly bears in British Columbia was closed in 2017 because of public opposition to hunting even though research indicated that the hunt was sustainable. Photograph by Mark Boyce.

resilience to harvest removals and promotes persistence of hunted populations of large mammals.

The hydra effect.—Although hunter harvest or culling typically reduces population size, density-dependent responses in seasonal environments can interact with hunter harvest in a way that can actually increase annual survival (Boyce et al. 1999) and total population size (Jonzén and Lundberg 1999; Abrams 2009). Such overcompensation responses to hunting removals (where harvests result in increased survival or increased population size) have been termed the “hydra effect” (Abrams and Matsuda 2005). A variety of mechanisms can cause the hydra effect in multispecies systems (Cortez and Abrams 2016). Likewise, culling of predators resulting in trophic-level interactions can create counterintuitive results (Mitchell et al. 2015; Costa et al. 2017). For example, in a tri-trophic system on Little Barrier Island, New Zealand, culling of feral cats (*F. catus*) resulted in increased abundance of Pacific rats (*Rattus exulans*) that caused Cook’s petrel (*Pterodroma cookii*) populations to decline (Rayner et al. 2007). In a similar example, harbor seals (*Phoca vitulina*) were culled to enhance the fishery, but seal removals allowed Pacific hake (*Meluccius productus*) populations to increase, which subsequently caused a decrease in the abundance of Pacific herring (*Clupea pallasii*) (Bowen and Lidgard 2013). Finally, removal of dingos (*Canis lupus dingo*) in Australia has resulted in population increases by red fox (*Vulpes vulpes*) with resulting predation that caused a reduction in native marsupials (Letnic and Koch 2010).

Behavioral outcomes from hunting.—Hunting also can have complex consequences for social structure and behavior of individuals in harvested populations. In African lions and brown bears (*Ursus arctos*), removal of an adult male by hunting can result in sexually selected infanticide (Packer and Pusey 1983; Swenson et al. 1997; Whitman et al. 2004). After a mature male has been removed by hunting, subordinate males will move into the area vacated by the removal, and will kill young to bring females into estrus so that they can breed with the females in their new home range (Packer et al. 2011).

Other behavioral consequences of hunting, such as disruption of social structure in African elephant populations (Shannon et al. 2013) and elimination of individuals with “bold personalities” in elk (Ciuti et al. 2012), have been documented. Vigilance behavior of black-tailed prairie dogs (*Cynomys lewdicianus*) is disturbed by hunting, which results in reduced body condition and fitness (Pauli and Buskirk 2007). Exposure to hunting can influence learning whereby older animals adopt behaviors to reduce the chances that they will be killed by hunters (Thurfjell et al. 2017). In this example, young North American elk were more vulnerable to hunter harvest, resulting in high turnover among younger individuals in the population. Nonetheless, because elk learn to avoid hunters (Lone et al. 2015), by the time that elk are 9–10 years old, it is highly unlikely that they will be killed by a hunter. This outcome is important because older individuals know migration routes, seasonal foraging areas, and calving sites, and retaining older individuals in the population can potentially enhance population resilience (Thurfjell et al. 2017).

Effects of selective harvests.—Clearly, hunting can be selective, if certain individuals are more vulnerable to harvest than others (Festa-Bianchet 2017). Yet, hunters usually are not highly selective, often taking the first opportunity to kill a legal animal (Heffelfinger 2018) and uncertainty remains about the possibility that selective hunter harvests can have detrimental effects (Mysterud 2011). An evolutionary response requires intense selection on highly heritable traits for an extended period (Coulson et al. 2018; Festa-Bianchet and Mysterud 2018). Clearly, hunting can alter the demography of a population, thereby increasing population turnover, changing sex and age ratios, or both (Milner et al. 2007; Monteith et al. 2013, 2018; Hewitt et al. 2014). Moreover, a small amount of immigration from an unhunted area can be sufficient to swamp the effect of size-selection by hunting (Tenhumberg et al. 2004). In landscapes with private land ownership, variation in hunter access can be sufficient to ensure that effects of hunting are overwhelmed by spatial patterns on the landscape, because nearby areas exist with fewer hunters and more ungulates (McCullough 1996).

Conservation.—Unregulated or illegal hunting of wild mammals by humans continues to be a threat to the conservation of some mammals, especially in tropical regions with diverse mammal faunas (Van Vliet et al. 2015). Yet, in North America, Europe, and parts of Africa, hunting has been the basis for effective programs to ensure conservation of essential habitats and to restore wild populations (Organ et al. 2010). Resilience of populations to hunting driven by density dependence has proven to be a powerful stabilizing force that ensures sustainable harvests if hunting is managed. Unfortunately, unregulated or illegal hunting continues for cultural or economic reasons over much of the Earth. Finding ways to overcome such cultural and economic barriers to conservation remains among those obstacles preventing continued loss of mammalian diversity.

CRITICAL AREAS FOR FUTURE RESEARCH

Climate change.—A rapidly changing climate with accelerating risks of extinction for mammals as well as other taxonomic groups (Urban 2015) augurs poorly for the continued existence of many species. Life-history traits that make mammalian species vulnerable to extinction also make them more susceptible to a changing climate (Davidson et al. 2017). Moreover, geographical areas associated with risk of extinction for mammals may be modified under a rapidly changing climate as a result of altered landscapes or from the decoupling of phenology and life-history events (Davidson et al. 2017). Indeed, threats from climate change are prevalent for both marine and terrestrial mammals (Simmonds and Isaac 2007; Mallory and Boyce 2018).

Large-scale climatic variability has negatively influenced growth, development, fecundity, and demographic trends in northern ungulates (Post and Stenseth 1999). In addition, increases in rain or snow events may promote icing and adversely affect cold-adapted mammals at high latitudes (Berger et al. 2018). Changes in snow conditions influencing

subnivalian spaces may adversely affect small mammals that rely on those seasonal refugia (Pauli et al. 2013).

A warming climate can affect species composition and quality of forage plants available to large herbivores (Lenart et al. 2002). This holds demographic consequences for some of those mammals (Burthe et al. 2011), although not all large herbivores respond immediately to such changes (Bowyer et al. 1998). Shifts in forage phenology also may influence diets and behaviors for large omnivores, with unknown consequences for the community and ecosystem (Deacy et al. 2017). Recruitment in moose (*Alces alces*) near the southern extent of their range was negatively affected by warm temperatures (Monteith et al. 2015). In addition, climate change has affected long-term population growth of pronghorn populations (Gedir et al. 2015). A free-ranging population of Soay sheep (*Ovis aries*) experienced reduced twinning and size of neonates, as well as delayed sexual maturation during warmer winters (Forchhammer et al. 2001). Large mammals, as well as those with nocturnal activity patterns, were more likely to respond as expected to climate change than were other species with regard to local extirpations, decreased abundance, range contractions and shifts, and morphological and genetic changes (McCain and King 2014). Only 52% of all mammalian species studied by McCain and King (2014) responded as expected to climate change. In addition, climate change may require a rethinking of how public lands are managed for native ungulates to lessen effects of competition with domestic and feral herbivores (Beschita et al. 2013). Linkages between climate change and population demography of mammals, including latitudinal and elevational shifts, require additional study (Moritz et al. 2008; Meserve et al. 2011; Baltensperger et al. 2017). Future research should evolve from descriptions of shifting patterns to investigations of consequences resulting from a changing climate. Species respond to thermal landscapes in complex ways that require information about considerably more than ambient temperatures (Bowyer and Kie 2009; Long et al. 2014). For instance, northward range shifts in the distribution of snowshoe hares (*Lepus americanus*) were related to decreasing persistence of snow cover, which created a color mismatch, and ostensibly lead to increased mortality of white hares on a brown landscape (Saultaire et al. 2016; Zimova et al. 2016). Similarly, Atmeh et al. (2018) reported that a white morph of weasels (*Mustela nivalis*) was declining compared with their brown counterparts because of a shortening of days with snow cover, likely from increased predation. Much remains to be discovered about how and when a changing climate will affect mammals. For many species, factors that threaten them cannot be eliminated entirely, and those species will need to be managed to ensure their persistence. Such species are “conservation reliant” (Goble et al. 2012), and long-term conservation of many if not most wild mammals will require more intensive efforts.

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LITERATURE CITED

- ABRAMS, P. A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. *Ecology Letters* 12:462–474.
- ABRAMS, P. A., AND H. MATSUDA. 2005. The effects of adaptive changes in prey on the dynamics of an exploited predator population. *Canadian Journal of Fisheries and Aquatic Sciences* 62:785–766.
- ALI, A. H. 2016. Range collapse, demography, and conservation of the critically endangered hirola antelope in Kenya. Ph.D. dissertation, University of Wyoming, Laramie.
- ALI, A. H., ET AL. 2017. Resource selection and landscape change reveal mechanisms suppressing population recovery for the world’s most endangered antelope. *Journal of Applied Ecology* 54:1720–1729.
- ALI, A. H., ET AL. 2018. Demographic drivers of a refugee species: large-scale experiments guide strategies for reintroduction of hirola. *Ecological Applications* 28:275–283.
- ALLAN, B., ET AL. 2017. Can integrating wildlife and livestock enhance ecosystem services in central Kenya? *Frontiers in Ecology and the Environment* 15:328–335.
- ALLEN, D. L. 1954. Our wildlife legacy. Funk & Wagnalls Company, Inc., New York.
- ANDELMAN, S. J., AND M. R. WILLIG. 2003. Present patterns and future prospects for biodiversity in the Western Hemisphere. *Ecology Letters* 6:818–824.
- ARCESE, P., AND A. R. E. SINCLAIR. 1997. The role of protected areas as ecological baselines. *Journal of Wildlife Management* 61:587–602.
- ATMEH, K., A. ANDRUSKIENICZ, AND K. ZUB. 2018. Climate change is affecting mortality of weasels due to camouflage mismatch. *Scientific Reports* 8:7648.
- BALCH, J. K., B. A. BRADLEY, C. M. D’ANTONIO, AND J. GÓMEZ-DANS. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19:173–183.
- BALTENSPERGER, A. P., J. M. MORTON, AND F. HUETTMAN. 2017. Expansion of American marten (*Martes americana*) distribution in response to climate and landscape change on the Kenai Peninsula, Alaska. *Journal of Mammalogy* 98:703–714.
- BARRETT, C. B., AND P. ARCESE. 1995. Are integrated conservation-development projects (ICDPs) sustainable? *World Development* 23:1073–1084.
- BELLARD, C., P. CASSEY, AND T. M. BLACKBURN. 2016. Alien species as a driver of recent extinctions. *Biology Letters* 12: 20150623.
- BERGER, J. 2008. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. *Oryx* 42:139–142.
- BERGER, J., C. HARTWAY, A. GRUZDEV, AND M. JOHNSON. 2018. Climate degradation and extreme icing events constrain life in cold-adapted mammals. *Scientific Reports* 8:1156.
- BERKES, F. 2004. Rethinking community-based conservation. *Conservation Biology* 18:621–630.

- BESCHITA, R. L., ET AL. 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. *Environmental Management* 51:474–491.
- BLEICH, V. C. 1999. Wildlife conservation and wilderness management: uncommon objectives and conflicting philosophies. *North American Wild Sheep Conference Proceedings* 2:195–205.
- BLEICH, V. C. 2005. Politics, promises, and illogical legislation confound wildlife conservation. *Wildlife Society Bulletin* 33:66–73.
- BLEICH, V. C. 2014. Thoughts on the Wilderness Act. *The Wildlife Professional* 8:7.
- BLEICH, V. C. 2016. Wildlife conservation and wilderness: wishful thinking? *Natural Areas Journal* 36:202–206.
- BLEICH, V. C., G. A. SARGEANT, AND B. P. WIEDMANN. 2018. Ecotypic variation in population dynamics of reintroduced bighorn sheep: implications for management. *Journal of Wildlife Management* 82:8–18.
- BONENFANT, C., ET AL. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in Ecological Research* 41:313–357.
- BOWEN, W. D., AND D. LIDGARD. 2013. Marine mammal culling programs: review of effects on predator and prey populations. *Mammal Review* 43:207–220.
- BOWMAN, J. L., B. T. BOND, B. D. LEOPOLD, M. J. CHAMBERLAIN, AND J. M. ROSS. 1999. Effect of harvest on previously unexploited populations of fox and gray squirrels. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 53:282–295.
- BOWYER, R. T., V. C. BLEICH, K. M. STEWART, J. C. WHITING, AND K. L. MONTEITH. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. *California Fish and Game* 100:550–572.
- BOWYER, R. T., AND J. G. KIE. 2009. Thermal landscapes and resource selection by black-tailed deer: implications for large herbivores. *California Fish and Game* 95:128–139.
- BOWYER, R. T., V. VAN BALLEMBERGHE, AND J. G. KIE. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *Journal of Mammalogy* 79:1332–1344.
- BOYCE, M. S. 1981. Beaver life history responses to exploitation. *Journal of Applied Ecology* 18:749–753.
- BOYCE, M. S., A. R. E. SINCLAIR, AND G. C. WHITE. 1999. Seasonal compensation of predation and harvesting. *Oikos* 87:419–426.
- BRASHARES, J. S., P. ARCESE, AND M. K. SAM. 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London, B. Biological Sciences* 268:2473–2478.
- BROOKS, M. L., ET AL. 2004. Effects of invasive alien plants on fire regimes. *AIBS Bulletin* 54:677–688.
- BRUSKOTTER, J. T., ET AL. 2017. Modernization, risk, and conservation of the world's largest carnivores. *Bioscience* 67:646–655.
- BUNN, H. T., AND A. N. GURTOV. 2014. Prey mortality profiles indicate that early Pleistocene *Homo* at Olduvai was an ambush predator. *Quaternary International* 322–323:44–53.
- BURGIN, C. J., J. P. COLELLA, P. L. KAHN, AND N. S. UPHAM. 2018. How many species of mammals are there? *Journal of Mammalogy* 99:1–14.
- BURTHE, S., A. BUTLER, K. R. SEARLE, S. J. HALL, S. J. THACKERAY, AND S. WANLESS. 2011. Demographic consequences of increased winter births in a large seasonally breeding mammal (*Bos taurus*) in response to climate change. *The Journal of Animal Ecology* 80:1134–1144.
- BUTCHART, S., AND E. DUNN. 2003. Using the IUCN Red List criteria to assess species with declining populations. *Conservation Biology* 17:1200–1202.
- CARDILLO, M., ET AL. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- CARO, T., AND P. SCHOLTE. 2007. When protection falters. *African Journal of Ecology* 45:233–235.
- CAUGHLEY, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- CEBALLOS, G., AND P. R. EHRLICH. 2002. Mammal population losses and the extinction crisis. *Science* 296:904–907.
- CEBALLOS, G., P. R. EHRLICH, AND R. DIRZO. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America* 114:E6089–E6096.
- CHAFE, S., J. HARRISON, M. SPALDING, AND I. LYSSENKO. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 360:443–455.
- CHAPRON, G., ET AL. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346:1517–1519.
- CIUTI, S., T. B. MUHLY, D. G. PATON, A. D. MCDEVITT, M. MUSIANI, AND M. S. BOYCE. 2012. Human selection of elk behavioural traits in a landscape of fear. *PLoS One* 7:e50611.
- CLUTTON-BROCK, J. 1999. *The natural history of domesticated mammals*. Cambridge University Press, Cambridge, United Kingdom.
- COLLEN, B., ET AL. 2016. Clarifying misconceptions of extinction risk with the IUCN Red List. *Biology Letters* 12:20150843.
- CORTEZ, M. H., AND P. A. ABRAMS. 2016. Hydra effects in stable communities and their implications for system dynamics. *Ecology* 97:1135–1145.
- COSTA, M. I., P. V. ESTEVES, L. D. FARIA, AND L. DOS ANJOS. 2017. Prey dynamics under generalist predator culling in stage structured models. *Mathematical Biosciences* 285:68–74.
- COULSON, T., S. SCHINDLER, L. TRAILL, AND B. E. KENDALL. 2018. Predicting the evolutionary consequences of trophy hunting on a quantitative trait. *Journal of Wildlife Management* 82:46–56.
- CRAIGIE, I. D., ET AL. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation* 143:2221–2228.
- CREEL, S., ET AL. 2013. Conserving large populations of lions - the argument for fences has holes. *Ecology Letters* 16:1413, e1–1413, e3.
- CZECH, B., P. R. KRAUSMAN, AND P. K. DEVERS. 2000. Economic associations among causes of species endangerment in the United States. *BioScience* 50:593–601.
- DAVIDSON, A. D., M. J. HAMILTON, A. G. BOYER, J. H. BROWN, AND G. CEBALLOS. 2009. Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences of the United States of America* 106:10702–10705.
- DAVIDSON, A. D., ET AL. 2012. Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences of the United States of America* 109:3395–3400.
- DAVIDSON, A. D., ET AL. 2017. Geography of current and future global mammal extinction risk. *PLoS One* 12:e0186934.
- DEACY, W. W., ET AL. 2017. Phenological synchronization disrupts trophic interactions between Kodiak brown bears and salmon. *Proceedings of the National Academy of Sciences of the United States of America* 114:10432–10437.

- DIAMOND, J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418:700–707.
- DI MININ, E., N. LEADER-WILLIAMS, AND C. J. A. BRADSHAW. 2016. Banning trophy hunting will exacerbate biodiversity loss. *Trends in Ecology & Evolution* 31:99–102.
- DOAK, D. F., V. J. BAKKER, B. E. GOLDSTEIN, AND B. HALE. 2014. Moving forward with effective goals and methods for conservation: a reply to Marvier and Kareiva. *Trends in Ecology & Evolution* 29:132–133.
- DOAK, D. F., V. J. BAKKER, B. E. GOLDSTEIN, AND B. HALE. 2015. What is the future of conservation? *Trends in Ecology & Evolution* 29:77–81.
- DOBSON, A., AND L. LYNES. 2007. How does poaching affect the size of national parks? *Trends in Ecology and Evolution* 4:177–180.
- DOHERTY, T. S., A. S. GLEN, D. G. NIMMO, E. G. RITCHIE, AND C. R. DICKMAN. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences USA* 113:11261–11265.
- DUDLEY, N. (ED.) 2008. Guidelines for applying protected areas management categories. IUCN, Gland Switzerland.
- DUNN, A. M., ET AL. 2012. Indirect effects of parasites in invasions. *Functional Ecology* 26:1262–1274.
- DURANT, S. M., ET AL. 2017. The global decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of the National Academy of Sciences of the United States of America* 114:528–533.
- EBERHARDT, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854.
- EPSTEIN, B., ET AL. 2016. Rapid evolutionary response to a transmissible cancer in Tasmanian devils. *Nature Communications* 7:12684.
- ESTES, J. A. 2016. Serendipity: an ecologist's quest to understand nature. University of California Press, Berkeley.
- FA, J. E., J. JUSTE, J. PEREZ DEL VAL, AND J. CASTROVIEJO. 1995. Impact of market hunting on mammal species in Equatorial Guinea. *Conservation Biology* 9:1107–1115.
- FENNELL, L. A. 2011. Ostrom's Law: property rights in the commons. *International Journal of the Commons* 5:9–27.
- FESTA-BIANCHET, M. 2017. When does selective hunting select, how can we tell, and what should we do about it? *Mammal Review* 47:76–81.
- FESTA-BIANCHET, M., AND A. MYSTERUD. 2018. Hunting and evolution: theory, evidence, and unknowns. *Journal of Mammalogy* 99:1281–1292.
- FINCH, N., P. MURRAY, J. HOY, AND G. BAXTER. 2014. Expenditure and motivation of Australian recreational hunters. *Wildlife Research* 41:76–83.
- FORCHHAMMER, M. C., T. H. CLUTTON-BROCK, J. LINDSTRÖM, AND S. D. ALBON. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* 70:721–729.
- FORD, A. T., S. J. COOKE, J. R. GOHEEN, AND T. P. YOUNG. 2017. Conserving megafauna or sacrificing biodiversity? *BioScience* 67:193–196.
- FRANK, L. G. 2011. Living with lions: lessons from Laikipia. Pp. 73–83 in *Conserving wildlife in African landscapes: Kenya's Ewaso ecosystem* (N. J. Georgiadis, ed.). Smithsonian Institution Press, Washington, D.C.
- FRICK, W. F., S. J. PUECHMAILLE, AND C. K. R. WILLIS. 2016. White-nose syndrome in bats. Pp. 245–262 in *Bats in the Anthropocene: conservation of bats in a changing world* (C. Voight and T. Kingston, eds.). Springer, New York.
- GAMELON, M., ET AL. 2017. Reproductive allocation in pulsed-resource environments: a comparative study in two populations of wild boar. *Oecologia* 183:1065–1076.
- GASTON, K. J. 2005. Biodiversity and extinction: species and people. *Progress in Physical Geography* 29:239–247.
- GASTON, K. J., S. F. JACKSON, L. CANTÚ-SALAZAR, AND G. CRUZ-PIÑÓN. 2008. The ecological performance of protected areas. *Annual Review of Ecology and Systematics* 39:93–223.
- GATES, J. F. 1999. Myth and reality in the rainforest, how conservation strategies are failing in West Africa. University of California Press, Berkeley.
- GEDIR, J. V., J. W. CAIN III, G. HARRIS, AND T. T. TURNBALL. 2015. Effects of climate change on long-term population growth of pronghorn in an arid environment. *Ecosphere* 6:art189.
- GEIST, V. 1988. How markets for wildlife meat and parts, and the sale of hunting privileges, jeopardize wildlife conservation. *Conservation Biology* 2:15–26.
- GEIST, V. 1995. North American policies of wildlife conservation. Pp. 75–129 in *Wildlife conservation policy* (V. Geist and I. McT. Cowan, eds.). Detselig Enterprises, Limited, Calgary, Alberta, Canada.
- GENOVESI, P. 2011. Are we turning the tide? Eradications in times of crisis: how the global community is responding to biological invasions. Pp. 5–8 in *Island invasives: eradication and management* (C. R. Veitch, M. N. Clout, and D. R. Towns, eds.). IUCN, Gland, Switzerland.
- GEORGIADIS, N. J., F. IHWAGI, J. G. N. OLWERO, AND S. S. ROMANACH. 2007a. Savanna herbivore dynamics in a livestock-dominated landscape: ecological, conservation, and management implications of predator restoration. *Biological Conservation* 137:473–483.
- GEORGIADIS, N. J., G. OJWANG, J. G. N. OLWERO, AND S. S. ROMANACH. 2007b. Savanna herbivore dynamics in a livestock-dominated landscape: dependence on land use, rainfall, density, and time. *Biological Conservation* 137:461–472.
- GOBLE, D. D., J. A. WIENS, J. M. SCOTT, T. D. MALE, AND J. A. HALL. 2012. Conservation-reliant species. *BioScience* 62:869–873.
- GONZALEZ-MAYA, J. F., L. R. VÍQUEZ-R, J. L. BELANT, AND G. CEBALLOS. 2015. Effectiveness of protected areas for representing species and populations of terrestrial mammals in Costa Rica. *PLoS One* 10:e0124480.
- GOODWIN, H., AND D. ROE. 2001. Tourism, livelihoods, and protected areas: opportunities for fair-trade tourism in and around national parks. *International Journal of Tourism Research* 3:377–391.
- GRENYER, R., ET AL. 2006. Global distribution and conservation of rare and threatened vertebrates. *Nature* 444:93–96.
- GUERBOIS, C., A. B. DUFOUR, G. MTARE, AND H. FRITZ. 2013. Insights for integrated conservation from attitudes of people toward protected areas near Hwange National Park, Zimbabwe. *Conservation Biology* 27:844–855.
- HAMES, R. B., AND W. T. VICKERS. 1982. Optimal foraging theory as a model to explain variability in Amazonian hunting. *American Ethnologist* 9:358–378.
- HANSON, L. B., M. S. MITCHELL, J. B. GRAND, D. B. JOLLEY, B. D. SPARKLIN, AND S. S. DITCHKOFF. 2009. Effect of experimental manipulation on survival and recruitment of feral pigs. *Wildlife Research* 36:185–191.
- HARDIN, G. 1968. The tragedy of the commons. *Science* 162:1243–1248.
- HARRISON, R. D., ET AL. 2016. Impacts of hunting on tropical forests in Southeast Asia. *Conservation Biology* 30:972–981.

- HAVERSOHN, P. M., L. L. LOPEZ, N. J. SILVY, AND P. A. FRANK. 2004. Source-sink dynamics of Florida Key deer on Big Pine Key, Florida. *Journal of Wildlife Management* 68:909–915.
- HAZZAH, L., ET AL. 2014. Efficacy of two lion conservation programs in Maasailand, Kenya. *Conservation Biology* 28:851–860.
- HEANEY, L. R. 1986. Biography of the mammals of Southeast Asia: estimates of rates of colonization, extinctions, and speciation. *Biological Journal of the Linnean Society* 28:127–165.
- HEFFELFINGER, J. 2018. Inefficiency of evolutionarily relevant selection in ungulate trophy hunting. *Journal of Wildlife Management* 82:57–66.
- HEWITT, D. G., M. W. HELICKSON, J. S. LEWIS, D. B. WESTER, AND F. C. BRYANT. 2014. Age-related patterns of antler development in free-ranging white-tailed deer. *Journal of Wildlife Management* 78:976–984.
- HICKEY, V., AND S. L. PIMM. 2011. How the World Bank funds protected areas. *Conservation Letters* 4:269–277.
- HILBORN, R., ET AL. 2006. Effective enforcement in a conservation area. *Science* 314:1266.
- HOFFMANN, M., ET AL. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330:1503–1509.
- HOFFMANN, M., ET AL. 2011. The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 366:2598–2610.
- HOFFMANN, M., J. W. DUCKWORTH, K. HOLMES, D. P. MALLON, A. S. RODRIGUES, AND S. N. STUART. 2015. The difference conservation makes to extinction risk of the world's ungulates. *Conservation Biology* 29:1303–1313.
- HOSACK, D. A., P. S. MILLER, J. J. HEVERT, AND R. C. LACY. 2002. A population viability analysis for the endangered sonoran pronghorn, *Antilocapra americana sonoriensis*. *Mammalia* 66:207–220.
- HUGHES, R., AND F. FLINTAN. 2001. Integrating conservation and development experience: a review and bibliography of the ICDP Literature. International Institute for Environment and Development, London, United Kingdom.
- HULL, D. B. 1964. Hounds and hunting in ancient Greece. University of Chicago Press, Chicago, Illinois.
- HUME, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46:10–18.
- HUXMAN, T. E., ET AL. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86:308–319.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN). 2016. Informing decisions on trophy hunting. IUCN, Morges, Switzerland. www.iucn.org/downloads/iucn_informingdecision-sontrophyhuntingv1.pdf.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN). 2017. The IUCN red list of threatened species. Version 2017-1. <https://www.iucnredlist.org/>. Accessed August 2017.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN) SPECIES SURVIVAL COMMISSION. 2008. *Beatragus hunteri*. The IUCN red list of threatened species. Version 2014.2. www.iucnredlist.org. Accessed July 2018.
- ISAAC, N. J., S. T. TURVEY, B. COLLEN, C. WATERMAN, AND J. E. BAILLIE. 2007. Mammals on the edge: conservation priorities based on threat and phylogeny. *PLoS one* 2:e296.
- JONES, H. P., ET AL. 2016. Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences of the United States of America* 113:4033–4038.
- JONES, K. R., ET AL. 2018. One-third of global protected land is under intense human pressure. *Science* 360:788–791.
- JONZÉN, N., AND P. LUNDBERG. 1999. Temporally structured density dependence and population management. *Annales Zoologici Fennici* 36:39–44.
- JOPPA, L. N., ET AL. 2016. Impact of alternate metrics of estimates of extinction risk. *Conservation Biology* 30:362–370.
- KAREIVA, P., AND M. MARVIER. 2012. What is conservation science? *Bioscience* 62:962–969.
- KIMTEI, K. K., J. KIMANZI, AND S. A. ANDANJE. 2015. Habitat suitability modelling for hirola (*Beatragus hunteri*) in Tsavo East National Park, Kenya. *African Journal of Ecology* 53:550–559.
- KING, J., ET AL. 2011. Aerial survey of hirola (*Beatragus hunteri*) and other large mammals in southeastern Kenya. Technical Report to the Kenya Wildlife Service files.
- KOCK, R. A., ET AL. 2018. Saigas on the brink: multidisciplinary analysis of the factors influencing mass mortality events. *Science Advances* 4:eao2314.
- KOKKO, H. 2001. Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildlife Biology* 7:141–150.
- KOTHARI, A., P. CAMILL, AND J. BROWN. 2013. Conservation as if people also mattered: policy and practice of community-based conservation. *Conservation and Society* 11:1–15.
- KRAUSMAN, P. R., AND V. C. BLEICH. 2013. Conservation and management of ungulates in North America. *International Journal of Environmental Studies* 70:372–382.
- LALIBERTE, A. S., AND W. J. RIPPLE. 2004. Range contractions of North American carnivores and ungulates. *BioScience* 54:123–138.
- LAMOREUX, J. F., AND T. E. LACHER, JR. 2010. Mammalian endemism, range size and conservation status in the southern temperate zone. *Diversity and Distributions* 16:922–931.
- LEADER-WILLIAMS, N., AND E. J. MILNER-GULLAND. 1993. Policies and enforcement of wildlife laws: the balance between detection and penalties in Luangwa Valley, Zambia. *Conservation Biology* 7:611–617.
- LENART, E. A., R. T. BOWYER, J. VER HOEF, AND R. W. RUESS. 2002. Climate change and caribou: effects of summer weather on forage. *Canadian Journal of Zoology* 80:664–678.
- LETNIC, M., AND F. KOCH. 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* 35:167–175.
- LINDSEY, P. A., R. ALEXANDER, L. G. FRANK, A. MATHIESON, AND S. S. ROMANACH. 2006. Potential of trophy hunting to create incentives for wildlife conservation in African where alternative wildlife-based land uses may not be viable. *Animal Conservation* 9:283–291.
- LINDSEY, P. A., P. A. ROULET, AND S. S. ROMANACH. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* 134:455–469.
- LONE, K., L. E. LOE, E. L. MEISINGSET, I. STAMNES, AND A. MYSTERUD. 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour* 102:127–138.
- LONG, R. A., R. T. BOWYER, W. P. PORTER, P. MATHEWSON, K. L. MONTEITH, AND J. G. KIE. 2014. Behavior and nutritional condition buffer a larger-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs* 84:513–532.
- LURGI, M., E. G. RITCHIE, AND D. A. FORDHAM. 2018. Eradicating abundant invasive prey could cause unexpected and varied

- biodiversity outcomes: the importance of multispecies interactions. *Journal of Applied Ecology* 55:2396–2407.
- MACDONALD, D. W., P. J. JOHNSON, A. J. LOVERIDGE, D. BURNHAM, AND A. J. DICKMAN. 2016. Conservation or the moral high ground: siding with Bentham or Kant. *Conservation Letters* 9:307–308.
- MACE, J. M., AND R. LANDE. 1991. Assessing extinction threats—toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148–157.
- MACE, G. M., ET AL. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology* 22:1424–1442.
- MALLORY, C. D., AND M. S. BOYCE. 2018. Observed and predicted effects of climate change on arctic caribou and reindeer. *Environmental Reviews* 26:13–25.
- MCCAIN, C. M., AND S. R. KING. 2014. Body size and activity times mediate mammalian responses to climate change. *Global Change Biology* 20:1760–1769.
- MCCAUGHLEY, D. C., M. L. PINSKY, S. R. PALUMVI, J. A. ESTES, F. A. JOYCE, AND R. R. WARNER. 2015. Marine defaunation: animal loss in the global ocean. *Science* 347:236–247.
- MCCULLOUGH, D. R. 1996. Spatially structured populations and harvest theory. *Journal of Wildlife Management* 60:1–9.
- MCGRAW, W. S. 2005. Update on the search for Miss Waldron's red colobus monkey. *International Journal of Primatology* 26:605–619.
- McKEE, J., E. CHAMBERS, AND J. GUSEMAN. 2013. Human population density and growth validated as extinction threats to mammal and bird species. *Human Ecology* 41:773–778.
- MCAUGHTON, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *American Naturalist* 113:691–703.
- MEDINA, F. M., ET AL. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology* 17:3503–3510.
- MESERVE, P. L., D. A. KELT, M. A. PREVITALI, W. B. MILSTED, AND J. R. GUTIERREZ. 2011. Global climate change and small mammal populations in north-central Chile. *Journal of Mammalogy* 92:1223–1235.
- MILLER, D. C., A. AGRAWAL, AND J. T. ROBERTS. 2013. Biodiversity, governance, and the allocation of international aid for conservation. *Conservation Letters* 6:12–20.
- MILNER, J. M., E. B. NILSEN, AND H. P. ANDREASSEN. 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology* 21:36–47.
- MITCHELL, C. D., R. CHANEY, K. AHO, J. G. KIE, AND R. T. BOWYER. 2015. Population density of Dall's sheep: effects of predator harvest? *Mammal Research* 60:21–28.
- MONTEITH, K. L., R. W. KLAVER, K. R. HERSEY, A. A. HOLLAND, T. P. THOMAS, AND M. J. KAUFFMAN. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia* 178:1137–1148.
- MONTEITH, K. L., R. A. LONG, V. C. BLEICH, J. R. HEFFELFINGER, P. R. KRAUSMAN, AND R. T. BOWYER. 2013. Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. *Wildlife Monographs* 183:1–26.
- MONTEITH, K., R. A. LONG, T. R. STEPHENSON, V. C. BLEICH, R. T. BOWYER, AND T. N. LASHARR. 2018. Horn size and nutrition in mountain sheep: can ewe handle the truth? *Journal of Wildlife Management* 82:67–84.
- MORITZ, C., J. L. PATTON, C. J. CONROY, J. L. PARRA, G. C. WHITE, AND S. R. BEISSINGER. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322:261–264.
- MYSTERUD, A. 2011. Selective harvesting of large mammals: how often does it result in directional selection? *Journal of Applied Ecology* 48:827–834.
- NEWMARK, W. D. 2008. Isolation of African protected areas. *Frontiers in Ecology and the Environment* 6:321–328.
- NEWMARK, W. D., AND J. L. HOUGH. 2000. Conserving wildlife in Africa: integrated conservation and development projects and beyond. *BioScience* 50:585–592.
- NEWMARK, W. D., C. N. JENKINS, S. L. PIMM, P. B. MCNEALLY, AND J. M. HALLEY. 2017. Targeted habitat restoration can reduce extinction rates in fragmented forests. *Proceedings of the National Academy of Sciences of the United States of America* 114:9635–9640.
- NG'WENO, C. C. 2017. Predator-prey interactions and apparent competition following the restoration of lions to a human-occupied savanna. Ph.D. dissertation, University of Wyoming, Laramie.
- NG'WENO, C. C., N. J. MAIYO, A. H. ALI, A. K. KIBUNGEL, AND J. R. GOHEEN. 2017. Lions influence the decline and habitat shift of hartebeest in a semiarid savanna. *Journal of Mammalogy* 98:1078–1087.
- NOWAK, R. 2009. Conservation's Red List is unscientific and often wrong. *New Scientist* 201:8–9.
- OATES, J. F., M. ABEDI-LARTEY, W. S. MCGRAW, T. T. STRUHSACKER, AND G. H. WHITESIDES. 2000. Extinction of a West African red colobus monkey. *Conservation Biology* 14:1526–1532.
- OBAMA, B. 1995. *Dreams from my father*. Times Books, New York.
- ODADI, W. O., M. K. KARACHI, S. A. ABDULRAZAK, AND T. P. YOUNG. 2011. African wild ungulates compete with or facilitate cattle depending on season. *Science* 333:1753–1755.
- OGADA, M. O., R. WOODROFFE, N. O. OGUGE, AND L. G. FRANK. 2003. Limiting depredation by African carnivores: the role of live-stock husbandry. *Conservation Biology* 17:1521–1530.
- ORGAN, J. F., S. P. MAHONEY, AND V. GEIST. 2010. Born in the hands of hunters: the North American model of wildlife conservation. *The Wildlife Professional* 4:22–27.
- OSTROM, E. 1990. *Governing the commons: the evolution of institutions for collective action*. Cambridge University Press, Cambridge, United Kingdom.
- OWEN-SMITH, N. 2006. Demographic determination of the shape of density dependence for three African ungulate populations. *Ecological Monographs* 76:93–109.
- PACKER, C., H. BRINK, B. M. KISSUI, H. MALITI, H. KUSHNIR, AND T. CARO. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology* 25:142–153.
- PACKER, C., AND A. E. PUSEY. 1983. Adaptations of female lions to infanticide by incoming males. *American Naturalist* 121:716–728.
- PACKER, C., ET AL. 2013a. Conserving large carnivores: dollars and fence. *Ecology Letters* 16:635–641.
- PACKER, C., ET AL. 2013b. The case for fencing remains intact. *Ecology Letters* 16:1414, e4.
- PAGUNTALAN, L. M., M. G. PEDREGOSA, AND M. J. GADIANA. 2004. The Philippine bare-backed fruit bat *Dobsonia chapmani*: rediscovery and conservation status on Cebu Island. *Silliman Journal* 45:113–122.
- PALMER, J. M., K. P. DREES, J. T. FOSTER, AND D. L. LINDNER. 2018. Extreme sensitivity to ultraviolet light in the fungal pathogen causing white-nose syndrome of bats. *Nature Communications* 9:35.
- PAULI, J. N., AND S. W. BUSKIRK. 2007. Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed

- prairie dog *Cynomys ludovicianus*. *Journal of Applied Ecology* 44:1219–1230.
- PAULI, J. N., B. ZUCKERBERG, J. P. WHITEMAN, AND W. PORTER. 2013. The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment* 11:260–267.
- PAYNE, B. L., AND J. BRO-JØRGENSEN. 2016. Disproportionate climate-induced range loss forecast for the most threatened African antelopes. *Current Biology* 26:1200–1205.
- PIMM, S. L., ET AL. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344:1246752.
- POMPA, S., P. R. EHRLICH, AND G. CEBALLOS. 2011. Global distribution and conservation of marine mammals. *Proceedings of the National Academy of Sciences of the United States of America* 108:13600–13605.
- PORENSKY, L. M., AND K. E. VEBLEN. 2015. Generation of ecosystem hotspots using short-term corrals in an African savanna. *Rangeland Ecology and Management* 68:131–141.
- POST, E., AND N. C. STENSETH. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80:1322–1339.
- POTAPOV, A., E. MERRILL, M. PYBUS, AND M. A. LEWIS. 2016. Chronic wasting disease: transmission mechanisms and the possibility of harvest management. *PLoS One* 11:e0151039.
- PRICE, S. A., AND J. L. GITTLEMAN. 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proceedings of the Royal Society of London, B. Biological Sciences* 274:1845–1851.
- PRINGLE, R. M. 2017. Upgrading protected areas to conserve wild biodiversity. *Nature* 546:91–99.
- PRINS, H. H. T. 1992. The pastoral road to extinction: competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation* 19:117–123.
- PROBERT, J., B. EVANS, S. ANDANJE, R. KOCK, AND R. AMIN. 2014. Population and habitat assessment of the critically endangered hirola *Beatragus hunteri* in Tsavo East National Park, Kenya. *Oryx* 49:514–520.
- PURVIS, A., J. L. GITTLEMAN, G. COWLISHAW, AND J. M. MACE. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London, B. Biological Sciences* 267:1947–1952.
- QUIRÓS-FERNÁNDEZ, F., J. MARCOS, P. ACEVEDO, AND C. GORTÁZAR. 2017. Hunters serving the ecosystem: the contribution of recreational hunting to wild boar population control. *European Journal of Wildlife Research* 63:57.
- RAY, A. J. 1974. *Indians in the fur trade*. University of Toronto Press, Toronto, Ontario, Canada.
- RAYNER, M. J., M. E. HAUBER, M. J. IMBER, R. K. STAMP, AND M. N. CLOUT. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences of the United States of America* 104:20862–20865.
- REID, R. S., M. E. FERNÁNDEZ-GIMÉNEZ, AND K. A. GALVIN. 2014. Dynamics and resilience of rangelands and pastoral peoples around the globe. *Annual Review of Environment and Resources* 39:217–242.
- RESPONSIVE MANAGEMENT. 2013. *Nationwide survey of hunters regarding participation in and motivations for hunting*. Harrisonburg, Virginia.
- RIPPLE, W. J., ET AL. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- ROEMER, G. W., C. J. DONLAN, AND F. COURCHAMP. 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences of the United States of America* 99:791–796.
- SALERNO, J. D., M. BORGERHOFF MULDER, AND S. C. KEFAUVER. 2014. Human migration, protected areas, and conservation outreach in Tanzania. *Conservation Biology* 28:841–850.
- SARMENTO, W. M., AND J. BERGER. 2017. Human visitation limits the utility of protected areas as ecological baselines. *Biological Conservation* 212:316–326.
- SAUNDERS, S. E., S. L. BARTELT-HUNT, AND J. C. BARTZ. 2012. Occurrence, transmission, and zoonotic potential of chronic wasting disease. *Emerging Infectious Diseases* 18:369–376.
- SCHEFFERS, B. R., R. T. CORLETT, A. DIESMOS, AND W. F. LAURANCE. 2012. Local demand drives a bushmeat industry in a Philippine forest preserve. *Tropical Conservation Science* 5:133–141.
- SCHIPPER, J., ET AL. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225–230.
- SCHMIDT, J. I., J. M. VER HOEF, AND R. T. BOWYER. 2007. Antler size of Alaskan moose *Alces alces gigas*: effects of population density, hunter harvest and use of guides. *Wildlife Biology* 13:53–65.
- SCHOLTE, P. 2003. Immigration: a potential time bomb under the integration of conservation and development. *Ambio* 32:58–64.
- SCHROEDER, C. A., R. T. BOWYER, V. C. BLEICH, AND T. R. STEPHENSON. 2010. Sexual segregation in Sierra Nevada big-horn sheep (*Ovis canadensis sierrae*): ramifications for conservation. *Arctic, Antarctic, and Alpine Research* 42:476–489.
- SHANNON, G., ET AL. 2013. Effects of social disruption in elephants persist decades after culling. *Frontiers in Zoology* 10:62.
- SIMMONDS, M. P., AND S. J. ISAAC. 2007. The impacts of climate change on marine mammals: early signs of significant problems. *Oryx* 41:19–26.
- SINDINGA, I. 1995. Wildlife-based tourism in Kenya. *Journal of Tourism Studies* 6:45–55.
- SOUTHWICK, R., AND T. ALLEN. 2010. Expenditures, economic impacts and conservation contributions of hunters in the United States. Pp. 308–313 in *World symposium: ecologic and economic benefits of hunting*. World Forum on the Future of Sport Shooting Activities, Windhoek, Namibia.
- STAPP, J. R., R. J. LILIEHOLM, J. LEAHY, AND S. UPADHAYA. 2016. Linking attitudes, policy, and forest cover change in buffer zone communities of Chitwan National Park, Nepal. *Environmental Management* 57:1292–1303.
- STEWART, K. M., R. T. BOWYER, B. L. DICK, B. K. JOHNSON, AND J. G. KIE. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* 143:85–93.
- STEWART, K. M., R. T. BOWYER, R. W. RUESS, B. L. DICK, AND J. G. KIE. 2006. Herbivore optimization by North American elk: consequences for theory and management. *Wildlife Monographs* 167:1–24.
- SULTAIRE, S. M., J. N. PAULI, K. J. MARTIN, M. W. MEYER, M. NOTARO, AND B. ZUCKENBERG. 2016. Climate change surpasses land-use change in the contracting range boundary of a winter adapted mammal. *Proceedings of the Royal Society of London, B. Biological Sciences* 283:20160020.
- SWENSON, J. E., F. SANDEGREN, A. SÖDERBERG, A. BJÄRVALL, R. FRANZEN, AND P. WABAKKEN. 1997. Infanticide caused by hunting of male bears. *Nature* 386:450–451.
- TENHUMBERG, B., E. J. TYRE, A. R. POPLÉ, AND H. P. POSSINGHAM. 2004. Do harvest refuges buffer kangaroos against evolutionary responses to selective harvesting? *Ecology* 85:2003–2017.

- THURFJELL, H., S. CIUTI, AND M. S. BOYCE. 2017. Learning from the mistakes of others: how female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PLoS One* 12:e0178082.
- TRANQUILLI, S., ET AL. 2014. Protected areas in tropical Africa: assessing threats and conservation activities. *PLoS One* 9:e114154.
- TURVEY, S. T., ET AL. 2007. First human-caused extinction of a cetacean species? *Biology Letters* 3:537–540.
- U.N. EDUCATIONAL, SCIENTIFIC, AND CULTURAL ORGANIZATION (UNESCO). Tobago Main Ridge Forest Reserve. 2011. <https://whc.unesco.org/en/tentativelists/5646/>. Accessed 22 May 2018.
- U.N. ENVIRONMENT WORLD CONSERVATION MONITORING CENTRE, INTERNATIONAL UNION FOR CONSERVATION OF NATURE, WORLD DATABASE ON PROTECTED AREAS. 2017. www.protectedplanet.net. Accessed May 2018.
- U.S. FISH AND WILDLIFE SERVICE (USFWS). 2014. Black-footed ferret 10(j) rule. USFWS Mountain Prairie Press Release, Lakewood, Colorado.
- URBAN, M. C. 2015. Climate change. Accelerating extinction risk from climate change. *Science* 348:571–573.
- VAN VLIET, N., J. FA, AND R. NASI. 2015. Managing hunting under uncertainty: from one-off ecological indicators to resilience approaches in assessing the sustainability of bushmeat hunting. *Ecology and Society* 20:7.
- VEBLER, K. E. 2012. Savanna glade hotspot: plant community development and synergy with large herbivores. *Journal of Arid Environments* 78:119–127.
- VENTER, O., ET AL. 2017. Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions. *Conservation Biology* 32:127–134.
- VILÀ, M., ET AL. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- VITOUSEK, P. M., H. A. MOONEY, J. LUBENCHO, AND J. M. MELILLO. 1997. Human domination of the Earth's ecosystems. *Science* 277:292–499.
- VUCETICH, J. A., J. T. BRUSKOTTER, AND M. P. NELSON. 2015. Evaluating whether nature's intrinsic value is an axiom or anathema to conservation. *Conservation Biology* 29:321–332.
- WALPOLE M. J., AND C. R. THOULESS. 2005. Increasing the value of wildlife through non-consumptive use? Deconstructing the myths of ecotourism and community-based tourism in the tropics. Pp. 122–139 in *People and wildlife, conflict or coexistence?* (R. Woodroffe, S. Thirgood, and A. Rabinowitz, eds.). Cambridge University Press, Cambridge, United Kingdom.
- WAYLEN, K. A., A. FISCHER, P. J. MCGOWAN, S. J. THIRGOOD, AND E. J. MILNER-GULLAND. 2010. Effect of local cultural context on the success of community-based conservation interventions. *Conservation Biology* 24:1119–1129.
- WESTERN, D., J. WAITHAKA, AND J. KAMANGA. 2015. Finding space for wildlife beyond national parks and reducing conflict through community-based conservation. *Parks* 21:51–62.
- WHITMAN, K., A. M. STARFIELD, H. S. QUADLING, AND C. PACKER. 2004. Sustainable trophy hunting of African lions. *Nature* 428:175–178.
- WILCOX, B. A., AND D. D. MURPHY. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879–887.
- WITTEMYER, G., P. ELSEN, W. T. BEAN, A. C. BURTON, AND J. S. BRASHARES. 2008. Accelerated human population growth at protected area edges. *Science* 321:123–126.
- WOINARSKI, J. C., A. A. BURBIDGE, AND P. L. HARRISON. 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America* 112:4531–4540.
- WOODFORD, M. H., M. R. FRISINA, AND G. A. AWUN. 2004. The Torghar Conservation Project: management of the livestock, Sulieman markhor (*Capra falconeri*) and Afghan urial (*Ovis orientalis*) in the Torghar Hills, Pakistan. *Game and Wildlife Science* 21:177–187.
- WOODROFFE, R., AND J. R. GINSBERG. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.
- YOUNG, T. P. 2006. Declining rural populations and the future of biodiversity: missing the forest for the trees? *Journal of International Wildlife Law and Policy* 9:319–334.
- ZIMOVA, M., L. S. MILLS, AND J. J. NOWAK. 2016. High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters* 19:299–307.

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