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Mammal Conservation: Old Problems, New Perspectives, Transdisciplinarity, and the Coming of Age of Conservation Geopolitics

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Abstract

I review the shocking current status of terrestrial mammals and then describe an approach to solving it, embracing a continuum of spatial and intellectual scales, from groundedness to geopolitics. Starting with an illustrative arena, the interface between agriculture and wildlife, I then outline the litany of threats to mammals and some successful approaches to their conservation, and document some broad-scale patterns regarding ecosystems, the mammalian communities within, and some implications for conservation. Observing that the battle for mammalian conservation is being badly lost, I dedicate the third part of this article to a combination of top-down and bottom-up, interdisciplinary studies, aspiring to a holistic approach that sets conservation in the wider sphere of the human enterprise and that I term transdisciplinary conservation.
INTRODUCTION

Over the short span of human history, major innovations such as livestock domestication, the development of agriculture, the Industrial Revolution, and advances in medicine have increased the human population dramatically, resulting in fundamental ecological effects. Although the world’s 7.6 billion people represent a mere 0.01% of the total biomass of all living things (Table 1), since

Table 1  Summary of estimated total biomass for abundant taxonomic groups

| Taxon                              | Mass (GtC) | Uncertainty (-fold) |
|------------------------------------|------------|---------------------|
| Plants                             | 450        | 1.2                 |
| Bacteria                           | 70         | 10                  |
| Fungi                              | 12         | 3                   |
| Archaea                            | 7          | 13                  |
| Protists                           | 4          | 4                   |
| Animals                            | 2          | 5                   |
| Arthropods, terrestrial            | 0.2        |                     |
| Arthropods, marine                 | 1          |                     |
| Chordates, fish                    | 0.7        |                     |
| Chordates, livestock               | 0.1        |                     |
| Chordates, humans                  | 0.06       |                     |
| Chordates, wild mammals            | 0.007      |                     |
| Chordates, wild birds              | 0.002      |                     |
| Annelids                           | 0.2        |                     |
| Molluscs                           | 0.2        |                     |
| Cnidarians                         | 0.1        |                     |
| Nematodes                          | 0.02       |                     |
| Viruses                            | 0.2        | 20                  |
| Total                              | 550        | 1.7                 |
the start of civilization humankind has caused the loss of 80% of all wild mammals and half of plants by biomass (1), with livestock kept by humans currently estimated at an annual production of 70 billion animals (http://www.fao.org/statistics/en/). Of all the mammalian biomass on Earth today, 60% is livestock, 36% is human, while wild mammals comprise only 4% (1). The mammal conservationist might pause to consider that approximately 300,000 wolves, *Canis lupus*, survive globally alongside almost one billion of their descendant domestic dogs. In the United Kingdom, approximately 6 million domestic cats—albeit only a few genes adrift from their wildcat progenitor, *Felis silvestris lybica* (2)—are contributing to the genetic dilution of their close cousin, the Scottish wildcat, *F. s. silvestris*, of which somewhere between none and 350 remain (3). With regard to cows, although wild ones such as banteng and anoa are precariously few (the progenitor aurochs are gone, European and American bison more than decimated), when ecologist Mike Norton-Griffiths (4) famously asked “How many wildebeest do we want?” (to this day a knockout question) a sobering perspective is that the answer for cows would appear to be one and a half billion (for wildebeest about one and a half million remain). Such is the impact of humanity on the balance of Nature and, as this article makes clear, the “How many do we want?” question cannot be dodged for any wild mammals, and especially the big ones (5).

But exactly what is a mammal? A full answer is given in my essay (6); however, in short, mammals can formally be described as animals that nurse their infants with milk and have backbones, bodies insulated by hair, and a unique jaw articulation. This drably diagnostic description fails to convey their astonishing diversity. The smallest mammal, Kitti’s hog-nosed bat, weighs 1.5 g; the largest mammal, the blue whale, weighs 100 million times as much; the naked mole rat gives birth to litters of up to 28; the orangutan gives birth to only one; the naked mole rat never leaves one burrow, whereas the wolf may travel through 1,000 km²; the elephant may live 70 years, whereas the male brown antechinus never sees a second season and dies before the birth of the first and only litter he fathers. Mammals’ versatility has allowed them to colonize all of the major habitats of the globe except the frozen poles, and they are found on all continents except Antarctica, with greatest richness and phylogenetic diversity in the Andes, the Afromontane regions of Africa, and Southeast Asia (7). There are nearly 6,000 species of mammals among which ancient relationships permit subdivisions into approximately 1,250 genera, 156 families, 28 orders, and 2 subclasses (8; see also http://tolweb.org) (Figure 1). Even within these taxonomic compartments, there is a bewildering variation in the size, shape, and life histories of mammals. Indeed, it is especially characteristic of mammals that even individuals of the same species behave differently depending on their circumstances.

One might expect an article on mammal conservation to recite a dirge of losses, but between 1992 and 2008 Schipper et al. (7) reported an increase of 19% in numbers of mammalian species; however, beware the illusion: Although some were new to science in a classical sense, of the 349 newly described, most were the result of splitting on the basis of new taxonomic work, and 512 were subspecies elevated to specific status (10, 11).

Despite these gains, the path ahead for mammals is dismal. This review first details the current status of terrestrial mammals, which is shocking, and then describes an approach to solving it—embracing a continuum of spatial and intellectual scales, from groundedness to geopolitics, perhaps from earthiness to erudition. This journey begins with a brief sortie into one, illustrative arena, the interface between wildlife and agriculture. Second, and although briefly rehearsing the familiar litany of threats and some successful approaches to their conservation, I document some broad-scale patterns regarding ecosystems, the mammalian communities that are among their working parts, and some implications for conservation. Then, noting that although many battles are being won by ingenious, innovative science and dedicated effort, the metaphorical war is being lost—badly. Is there any possibility of reversing this? In the spirit of hopefulness, the third part of
This article discusses, briefly but importantly, a combination of top-down and bottom-up, interdisciplinary studies, aspiring to a holistic approach that sets conservation in the wider sphere of the human enterprise and which I term transdisciplinary conservation, which embraces everything from groundedness to geopolitics (12).

CURRENT CONSERVATION STATUS OF TERRESTRIAL MAMMALS

More than one-fifth (22%) of all mammals are currently considered to be threatened. Additionally, insofar as those species classified as Data Deficient turn out to be threatened, the tally might…
Transdisciplinary conservation: rather than combining insights generated by separate academic disciplines (interdisciplinarity), transdisciplinarity works across disciplinary boundaries to generate holistic forms of knowledge.
Figure 2

(a) Percentage of order listed as threatened. (b) Total number of species within the order (upper, lighter bars) and number of species threatened (lower, darker bars). Data per the IUCN Red List, version 2017–1 (see https://www.iucnredlist.org/).
in extinction risk research). Approximately one-quarter (26.4%, 78 species) of carnivore species are threatened, whilst 61% of 31 “large carnivores” (>15 kg) (23) and 60% of the 74 largest terrestrial herbivores (>100 kg) are threatened (24).

Across the Western Hemisphere, on average, 9.2% of mammals at a given location will likely be unable to keep pace with climate change. In some places, up to 39% of mammals may be unable to track shifts in suitable climates. Eighty-seven percent of mammalian species are expected to experience reductions in range size, and 20% of these range reductions will likely be due to limited dispersal abilities as opposed to reductions in the area of suitable climate (25). Autecological studies (for example of beavers; 26, 27) illustrate the demographic mechanisms underlying these changes.

The situation has worsened over recent years: Analysis of changes in the Red List Index (RLI) between 1996 and 2008 revealed a decline in index values at a rate of 0.07% per year for mammals (slower than amphibians—0.14% per year—but faster than birds—0.02% per year; Figure 3), equating to (a net of) 156 species each moving one Red List category closer to extinction over the period (28) and, as Hoffmann et al. (13) put it, “one small step up the Red List hierarchy is one giant leap towards extinction” (p. 2602). During this period, 171 species were documented to have deteriorated, 160 by one category step, 8 by two category steps, and 3 by three category steps—the latter were the Tasmanian devil, Woodlark cuscus (from Papua New Guinea), and woylie (from Australia) (13).

Figure 3
Red List Indices (RLI) for reef-forming corals, birds, mammals, and amphibians. Coral species are moving toward increased extinction risk most rapidly, whereas amphibians are, on average, the most threatened group. An RLI value of 1.0 equates to all species qualifying as Least Concern (i.e., not expected to become extinct in the near future). An RLI value of 0 equates to all species having gone extinct. A constant RLI value over time indicates that the overall extinction risk for the group is constant. If the rate of biodiversity loss were reducing, the RLI would show an upward trend. Adapted from figure 1, Summary Statistics, IUCN Red List, version 2017–1 (see https://www.iucnredlist.org/).
Mammal species at greatest risk of extinction tend to be those that require large home ranges, live at low population densities, are weaned at a late age, have small geographic ranges, occur where human densities are high, have slow life histories, and do not disperse well (25, 29–31).

Hoffmann et al.’s (13) analysis showed that not only are larger-bodied mammals more threatened than other mammals, but collectively they have also undergone the steepest deterioration in the RLI: For those >100 kg, RLI deteriorated by 3.5% between 1996 and 2008, compared with 2.0–2.2% for mammals between 1 and 100 kg, and 0.4% for those <1 kg (13). However, Davidson et al. (31) suggest that it is not absolute body size that matters; rather, what matters is how large a species is relative to other species that share similar ecological traits. Lifestyle also plays a role: Fossorial species have consistently lower risk, volant species have higher risk, and thus small species can be at equal risk to large species, depending on their ecologies (31). This is illustrated by two examples: A large species (>5.5 kg) with a small geographic range (<1.5 million km$^2$) has negligible risk if it has a fast reproductive rate for its body size; fossorial species between 304 g and 5.5 kg, with small geographical ranges (<28,000 km$^2$), have a 9% risk of extinction, whereas for arboreal, terrestrial, or volant species of similar body and range size, extinction risk is 68%. It is the interaction between traits, rather than any one trait per se, that creates a pathway to extinction.

Habitat loss is listed by the IUCN as a major threat to >2,000 (threatened and nonthreatened) mammal species, whereas utilization and persecution together are listed as major threats for approximately 1,200 (IUCN Red List, version 2016–3; see http://www.iucnredlist.org). Hunting affects large mammals disproportionately: 90% in Asia, 80% in Africa, and 64% in the Neotropics, compared with 28, 15, and 11% of small mammals (7; see also 32), and, for species whose fate is worsening, although hunting was the primary driver of deterioration for fewer species than agriculture and logging (62 mammal species versus 78) between 1996 and 2008, it tends to drive a higher proportion of changes to the highest threatened categories. (For example, 40% of deteriorating species listed as Critically Endangered were impacted by hunting versus 11% impacted by agriculture; 13.) Small, narrowly distributed species are affected by habitat loss but are not exploited (32). Other threats include invasive species, fire and human disturbance, accidental mortality, pollution, natural disasters, and newly introduced disease (http://www.iucnredlist.org) and climate change (25)—and, in general, more vulnerable species tend to be affected by a greater number of threats (32). Jono & Pavoine (33) suggest that it is threat diversity rather than threat type that determines extinction risk.

Considering that we now refer to the survivors of past anthropogenic extinctions (e.g., 34), most threatened mammals occur in sub-Saharan Africa (120 in Madagascar alone), South and Southeast Asia, Mexico, and South America (table 5, IUCN Red List, version 2017–1; see https://www.iucnredlist.org/). Concentrations of threatened species occur in the tropical Andes, Cameroonian Highlands, Albertine Rift, and Western Ghats in India, regions with high species richness, high endemism, and high human pressure, with the highest numbers and the highest loss rates in Southeast Asia, where habitat loss due to commercial logging, and conversion of land to rice paddies, coffee, oil palm and other crops, has been intense (13). Among primates, for example, 79% of species in South and Southeast Asia are threatened with extinction (7). Rodrigues et al. (35) found that >50% of the global deterioration in the conservation status of birds, mammals, and amphibians is concentrated in <1% of the surface area of the globe, 39 of 1,098 ecoregions (4%), and 8 of 195 countries (4%)—Australia, China, Colombia, Ecuador, Indonesia, Malaysia, Mexico, and the United States.

So much for generalizations: Important as they are as a backdrop, any conservation practitioner will wryly note that what underpins both the problems and the solutions to most conservation issues are specific to the circumstances of a particular time and place, superimposed on the detailed
Conservation geopolitics: the linkages between conservation outcomes and the political, social, and economic arrangements within and (resulting from) relationships between countries

Understanding often lurks in the detailed behavior of individual animals (12), or the particular attitudes of people (e.g., 37), and solutions require alignment of diverse factors (38), in ways that are invariably holistic, whether for broad categories (such as large mammals; 5) or fine-tuned to particular taxa such as canids (39) or felids (40) or musteloids (41). After highlighting reviews of earthy, local examples, I turn to one illustration of human wildlife conflict at the interface of wildlife and agriculture, before providing some broad patterns of mammalian community function, all setting the stage for an introduction to conservation geopolitics.

Writing from the United Kingdom, the interface between wildlife and agriculture is clearly a tumultuous source of conservation problems ranging from consumption and spoiling of crops, depredation on stock, transmission of epizootic disease (42, 43)—with an ample garnish of perennial controversies such as the merits of hunting (44) or of nonlethal control (45). It should come as no surprise that these problems are, albeit in microcosm and only sometimes with less extreme outcomes, directly paralleled around the world: A fox kills your chicken; a lion or leopard kills your cow [similarly garnished with debate on the merits of hunting (46) or of nonlethal control (47)]. Whether the problem is cheetahs killing goats (48) or elephants trampling crops (49), it is likely to lead to retributive killing: Of the 13 species of otter, at least 8 are threatened by persecution due to their perceived impact on fisheries (50). Mitigations may be traditional, inventive, or varied, but they almost all prove extremely hard to test (51). Some solutions are required at the scale of the individual farm, some at the farming system, and some, such as some financial instruments, at the global scale (52, 53). All are deployed alongside increasingly high densities of people (e.g., 54, 55), and in a context of global urbanization and agricultural expansion. [Between 1995 and 2007, agricultural land in developing countries increased by 400 million ha, and demand is predicted to increase by up to 50% in 2050 (56).] In 2014, there were approximately 3.9 billion ruminant livestock on Earth, which is 400 times more than the approximately 8.5 million of the 51 (out of 71) wild megaherbivore species for which population data were available (57).

As an illustrative case study of agricultural conflict, between 2008 and 2013, Kuiper et al. (58) recorded 1,527 incidents (2,039 animals killed, 306 injured) over three study sites in northwestern Zimbabwe, caused predominantly by lions and spotted hyenas (leopards were responsible for <10% of attacks, with a handful by cheetahs, caracal, and black-backed jackal), and involving mostly cattle and donkeys (and some goats). Predators generally attacked livestock similar in size to their preferred wild prey, and most attacks occurred when livestock were roaming outside protective enclosures (83% of attacks outside versus 17% inside) at night (80% versus 20% during the day). Overall, 64% of attacks were at night outside a boma. Average annual financial losses were US$49,412, $28,510, $1,347, and $79 due to lions, hyenas, leopards, and cheetahs, respectively. Ironically, livestock fitted with bells suffered a disproportionate number of attacks (58). The practice of herding cattle during the growing (wet) season away from crop fields (usually adjacent to villages) to avoid crop damage, and thus further from home enclosures and closer to Protected Area boundaries, increased vulnerability of cattle to lion predation during the growing season (58).

COMMUNITIES AND INTERSPECIFIC INTERACTIONS

Ecological communities are assembled according to natural rules that underpin the diversity of species and their roles. For example, there are strong associations between predator and prey richness at global and regional scales, even when covariation with climate, productivity, and human influence is accounted for (60). Similarly, interspecific competition within guilds is an important force in community structure, and it is particularly apparent among carnivores (61). Macdonald and colleagues (62, pp. 10–11, for canids; 63, pp. 12–13, for felids; and 41, chapters 1 and 6, for the...
superfamily Musteloidea) provide three different types of carnivore examples of fierce and often fatal intraguild hostility, with fundamental implications for conservation resulting from mesopredator release or suppression (64–66). The principles of ecosystem assembly and function take the spotlight off single species and onto communities when it comes to conservation (67). Conservation is about many things, but salient among them are unintended consequences and consumer choices. These choices can be about what particular constituencies want the countryside, or various approximations to wilderness, to be, and in some parts of the world the options are analogous to, or directly about, farming (42, 43). As an arbiter of these choices a purist yardstick of “natural” is increasingly close to meaningless, even when the focus is on processes rather than components (40).

**Predators and Prey**

Awkwardly, endangered predators eat endangered prey, a memorable example being when endangered dhole or Asiatic wild dog (Cuon alpinus)—sole survivor of its genus, lost from >75% of its former range, and down to one or two thousand individuals (68)—were deemed responsible for the decline in endangered banteng (Bos javanicus) (69).

A recurrent debate at the intersection of predator-prey relations and conservation concerns the protection of prey from predators (e.g., 70). Take the case of killing wolves with the intention of providing more ungulates for ungulate hunters to hunt; a complication is that not only do the hunters get satisfaction from killing the deer, but they, or others, also get satisfaction from killing the wolves, so there can be a potential ulterior motive. Macdonald et al. (70) list the logical conditions that must be satisfied to justify predator control, and in the case of killing wolves purportedly to increase the satisfaction of deer hunters, the following is necessary:

Wolves have to be having a significant limiting effect on the ungulate population. This is sometimes, but not always, the case, and hard to assess (71) and discerning the answer can take years (e.g., 72).

One would have to reduce wolf abundance enough through hunting to result in a significant increase in ungulate abundance. Hunting wolves strongly risks impairing wolves’ ecological function - which is an important motivation for wolves’ conservation in the first place. That function of course is to limit ungulates. In some cases, reducing wolves to the point of significantly increasing ungulate abundance may require reducing wolf abundances to the point of being in violation of conservation laws (e.g., Endangered Species Act in US, Habitat Directives in EU).

This is, yet again, where conservation revolves around consumer choice. (An extreme example for wolves includes their possible return to Scotland; 73.) In this case of deer hunters, the purpose of killing the wolves is to give hunters the satisfaction of killing deer (and killing wolves too). Other constituencies could take satisfaction in other outcomes; foresters and agriculturalists might prefer fewer deer, but the web becomes more tangled as to whether society deems wolves or deer hunters more appropriate to limit deer numbers and, indeed, which more effective (71, 72, 74).

Sometimes the intervention is stimulated not by the desires of hunters but of conservationists. Take the case of the American mink (Neovison vison), an invasive species in the United Kingdom and Continental Europe where, respectively, they are killed by conservationists in the attempt to protect prey in the form of water voles (Arvicola amphibius) (75, 76) or subordinate victims of intraguild hostility, in the form of European mink (Mustela lutreola) (77). The killing of American mink to conserve water voles provides, by the way, an unusual opportunity to see the progression of a conservation story from the discovery of a problem to its solution, and an answer to the difficult question of when we will know enough to act (78). Conservationists can also shift predator-prey
Intraguild Hostility

Also awkwardly, bigger carnivores bully, sometimes fatally, other carnivores, some of which are endangered. This occurs whether they are small (for example European mink harassed by American mink; 77), medium (swift or kit foxes killed by coyotes; 80), or large (leopards displaced by lions; 81) in size. In an early study of intraguild processes, Hersteinsson & Macdonald (82) deduced that behavioral, ecological, and climatic factors all interacted to determine the distributions of red and arctic foxes. A clear example of both behavioral and demographic effects comes from du Preez et al.’s studies of leopards and lions in the Bubye Valley Conservancy in Zimbabwe (B. du Preez, A.J. Loveridge & D.W. Macdonald, submitted manuscript). There, at approximately 19 lions per 100 km$^2$, lion density is among the highest in Africa, and an elegant natural experiment was provided by the existence of, and then removal of, a fence that initially offered leopards a lion-free refuge, which was then lost. To reduce risk from lions, leopards move to denser habitat types (where they can hide) when lions are nearby: du Preez et al. satellite tracked leopards that meandered through diverse habitats on the lion-free side of the fence, but when they jumped the fence into lion country (which lions were insufficiently agile to do into the leopard refuge), they hugged the river beds, skulking in dense vegetation. Indeed, satellite tracking 9 female and 12 male lions and 7 female and 8 male leopards, du Preez et al. discovered that leopards were more likely to move from grassland to scrub, and quickly to vacate the vicinity, when lions were around. Satellite tracking studies of lions, cheetahs, wild dogs, and spotted hyenas in Botswana’s Okavango Delta revealed similar behavioral responses to intraguild hostility. Prevailing wisdom had been that cheetahs and wild dogs were diurnal/crepuscular to avoid nocturnal lions and hyenas, but Cuzzi et al. (83) found that approximately one-quarter of the activity budget of cheetahs and wild dogs was at night, rising to approximately 40% when the moon was full, with the consequence that 43.8% of cheetah activity and 51.3% of wild dog activity was during the main activity periods of lions and hyenas. It seems likely, then, that the activity patterns of these subordinate species are primarily constrained by light availability for hunting small, high-speed prey over long distances rather than by the activities of larger dominant species. (32.5% of cheetah feeding behavior occurred at night; 84.) What, then, of intraguild hostility, especially when it emerges that, for example, cheetahs and lions were occupying habitats in very similar proportions? Broekhuis et al. (85) found that the answer was segregation at a much finer scale: When cheetahs sense lions in the vicinity they, much like leopards, quickly decamp: On average, they maintained a distance of 5 km from the nearest collared lion, and a similar but less pronounced aversion to hyenas.

The consequences of such power imbalances affect predator communities. In the case of leopards, camera traps revealed that while protected by the fence, and thus when lions were excluded, three-quarters of leopard cubs were recruited, whereas afterward none were. As for cheetahs, it has been conventional wisdom that lions are inimical to cheetah conservation, not just because they take their prey (kleptoparasitism of 12.9% of their prey), but also because they—as do spotted hyenas—kill cheetah cubs (causing 73% of cheetah cub mortality in the Serengeti National Park). Mills & Mills (86) have challenged this view, or at least its applicability in the Kalahari, and Swanson et al. (87) found that higher lion numbers were not associated with lower cheetah numbers, but were associated with fewer wild dogs. They also noted that although Serengeti...
lion numbers nearly trebled between 1966 and 1998 (the hyena population also increased from the 1960s to 1977, remaining stable thereafter), during this time numbers of wild dogs, but not cheetah, declined.

The Collision of Deaths: Predation and Guilds

Of course, the topics of predator-prey and intraguild relationships intersect dynamically, and not only through mortality but also fear; and people, as top predators, are players in the game (88). For example, Rasmussen & Macdonald (89) noted that wild dogs harassed by people were less active in the day than where they were untroubled by people, an adjustment that had the happy outcome of reducing the likelihood of them encountering people by 64% but increasing their potential for encounters with lions and hyenas by 37% and 70%, respectively. This dilemma—“trapped between an anthropogenic rock and a kleptoparasitic hard place”—would doubtless play out differently under different circumstances, and in this case the wild dogs’ evaluation of the odds may have been affected by the relative rarity of lions in the human-dominated landscape.

From Individual Behavior to Landscape Ecology

Individual mammals are adapted to their environment through their behavior, and behavior, in turn, often holds the key to their conservation (12). But populations, and their dynamics, are the emergent property of individual behavior and life histories, and are often the unit on which conservation interventions focus. There is a growing and important field of landscape ecology that translates the behavior of individuals into that of populations across entire geographic ranges (90). Valeix et al. (91) studied the movement patterns of individual lions, underpinning the extrapolations of Elliot et al. (92) who modeled dispersing lions in terms of landscape resistance, a progression culminating in an analysis of core areas and corridors for most of Zimbabwe and Botswana (93). Comparable studies of Sunda clouded leopards, Neofelis diardi, built on forest loss projections (94) for Borneo used expert opinion and camera-trapping (95) to anticipate the species’ conservation status, which Kastza et al. then challenged with national development plans for road and rail networks (K. Kaszta, S.A. Cushman, A.J. Hearn, D. Burnham, E.A. Macdonald & D.W. Macdonald, submitted manuscript). Macdonald et al. (96) expanded the habitat use models for Sunda clouded leopards to encompass their entire Malaysian and Indonesian ranges, highlighting conservation priority areas.

Species Richness: Past, Present, and Future

In a mesh of feedback loops, the species richness and abundance of predators result from a bottom-up effect, and circles back through top-down effects on prey. Starting at the bottom, and especially considering large mammals, predator species richness is strongly linked to prey species richness: Large predators depend on relevantly sized prey. This has huge conservation implications. Wolf & Ripple (97) list 494 species preyed upon by hefty (>15 kg) carnivores, and conclude that 25% of these prey are threatened. In particular, clouded leopard, Sunda clouded leopard, tiger, dhole, and Ethiopian wolf all have at least 40% of their prey classified as threatened, with even more declining due to agriculture, deforestation, and bushmeat hunting.

Being obligate carnivores, felids are a particularly revealing family. In a compendious analysis of felid diets (creating a new diet dataset, FelidDiet) Sandom et al. (98) documented 2,564 primary prey species of extant felids, of which 21.5% are threatened, with a further 13.2% declining. For 7 of the 32 species of felid, more than one-third of their primary prey species are threatened. (For
8 felid species, >50% of their primary prey are threatened or declining.) Indeed, the mean proportion of threatened primary prey is much higher for large felids than smaller species, at 55.9% versus 26.5%, respectively. The Sunda clouded leopard is perhaps in the direst situation, with 66% of its primary prey species threatened across the board. All of the North African cheetah’s primary prey are threatened or declining, as are up to 88.9% of the tiger’s primary prey in any given region. Indo-Malaya has the highest proportion (34.2%) of threatened large felid primary prey, rising to 58.3% if declining prey are included.

The threat to each felid species posed by defaunation depends on the availability of other suitable prey, and the competition for it. Sandom et al. (98) calculated a metric of resistance to defaunation using the number of primary prey species in a cell, the number of felids competing for each prey species, and the proportion of prey that are locally declining or threatened. Of big cats, snow leopards and tigers emerge as least resistant to defaunation, but the Iberian lynx fared worse, with zero resistance, with just one, declining, prey species. Modeling the relationship between prey richness and felid presence suggests large felids are at risk of defaunation across 24.7% of their range. Loss of prey poses a real threat to large felid survival across much of the globe.

Mindful that during the Late Quaternary humans likely contributed to the extinction of ≥166 large mammals and the continental extirpation of 11 more (99, 100), Sandom et al. (101) wondered what the modern felid fauna might have been in the absence of anthropogenic defaunation. Unsurprisingly, considering the proven relationship between felid presence and prey diversity, they found that 9 of the 10 extant large felids would have been more widely distributed today had it not been for man-made defaunation of their prey. Indeed, under this “natural” scenario, 86% of cells would have recorded an additional felid species nowadays, and 10% of cells would have supported four to five more. The greatest differences between how things are and how they might have been are in the Nearctic and Paleartic, where up to five fewer big cats are present today than might have been. Today, the Nearctic only hosts the puma; under the modeled “natural” scenario, five (sometimes six) hypothetical felids inhabit much of the region. Similarly, 95% of the Neotropics are missing at least one felid. Three species could have populated 88% of the Afrotropics; today all three persist across only 20% of the region. Many an aphorism highlights the importance of studying history to understanding the future, which is exactly what Sandom et al. (101) had in mind with this counterfactual analysis, which reveals that across the Afrotropics, Indo-Malaya, West and Central Neotropics, loss of prey likely puts one to five large-bodied felids at risk in any cell. In short, loss of prey explains a lot about the present distribution of felids, and ominously suggests what lies ahead; it also emphasizes the importance of conserving prey species to ensure that carnivore conservation does not become a castle built on sand. Painter et al. (102) emphasize the ecological roles of larger mammalian herbivores, including modifying abiotic processes involving nutrient cycles, soil properties, fire regimes, and primary production, roles that cannot be taken by smaller herbivores (but see 103 for an account of the impala when considering the definition of large herbivores).

The interaction between predators and prey is two way, with both directions having major conservation implications. In addition to the bottom-up effect of predator communities being shaped by their food, there are also top-down effects where predator species richness affects prey species richness, and where prey populations are shaped by those eating them.

The loss of large predators can transform landscapes (through their influence on herbivore abundance, directly as a result of reduced predation or indirectly through reduced intraguild competition—i.e., mesopredator release), with the result that vegetation can be reduced or increased depending on the number of trophic levels in the system—structuring ecosystems along multiple food-web pathways.
Nonlethal (fear) effects of large carnivores can be even greater (88, 104), including those of people (105). Trophic cascades in perturbed systems are difficult to untangle (106) but have been documented for 7 of the 31 largest (terrestrial or semiaquatic) mammalian carnivores (23). An obvious example is the absence of wolves in parts of North America and Europe leading to a sixfold increase in cervid densities and consequential shifts in plant communities, or, paradigmatically, predation by sea otters limiting herbivorous sea urchins and enhancing kelp forests (107).

**Umbrellas and Efficiencies**

Funds are crippledly inadequate for conservation, so prioritization and efficiency are crucial. With this in mind, Macdonald et al. (108) undertook a comprehensive analysis of Conservation Action Plans (CAPs) for felids to demonstrate that threats to wild cats are often similar and occur in the same place. But what about benefits shared among major taxa? Felids and primates, for example, also face many of the same threats—primarily, habitat loss, hunting, conflict, and trade in body parts or live animals (which affects 88%, 60%, 36%, and 32% of threatened felids, respectively; and 96%, 69%, 12%, and 40% of threatened primates). According to CAPs, habitat loss and hunting were the most serious issues for taxa, but fewer primates than felids were judged to be affected by conflict with humans. Both also have global distributions that overlap widely: Burnham et al. (109) report that jaguars, for example, co-occur with up to 15 primate species and 8 other felid species in a single grid cell, and tigers with 10 primate species and 8 other felid species, whereas widespread felid guilds could act as potential umbrellas for up to 18 primate species. Furthermore, the distribution of primates and felids threatened by habitat loss and hunting is very similar, but different from that of conflict and trade. For example, trade is a greater concern for both felids and primates in Asia than it is in the Neotropics or in Africa. In India, both felids and primates are threatened by habitat loss, but not hunting. Conflict with humans tends to be associated with crop raiding (for primates) or perceived threats to livestock or human safety (for felids) and as such tends to occur in areas that are not those facing habitat loss, hunting, or poaching pressure (all of which typically occur around forests); conflict was more frequently cited by the CAPs as a threat in Africa and the Neotropics (especially for felids).

So, there are shared distributions and commonality of problems, but what about shared solutions? Some, such as captive-breeding and reintroduction, may be specific; others, such as regulating and policing hunting and trade, as well as protecting habitats, can have shared benefits. For example, if loss of habitat for clouded leopards were prevented, there are a multitude of both primates and other felids also threatened by habitat loss in Southeast Asia that would potentially benefit from this conservation action. The payoffs of this multitaxon approach could be considerable: Macdonald et al. (108) calculated that conserving 15% of felid range where felids and primates threatened with habitat loss occur, would also conserve 70% of primates facing this threat, whilst tackling hunting in 15% of the area occupied by felids threatened by hunting would also benefit 65% of primates threatened by hunting.

**Illegal Wildlife Trade and Private Possession**

Between April 2015 and March 2016, 4,354 Japanese badgers and raccoon dogs were killed by farmers in response to alleged damage to crops and residential property across the Japanese island of Kyushu, allegations that coincided with a new trend in exotic bushmeat dishes in chic Tokyo restaurants to include such species (110). However, such utilitarian reasons for exploitation pale in comparison to the illegal wildlife trade (IWT) in mammal species across Asia. China is the world’s biggest consumer of ivory, and in 2012, 35,000 elephants were slaughtered to support...
this industry, despite counterstrategies such as the promotion of alternative synthetic ivory (111) and reformation of legislation on ivory ownership in China (112). Perhaps surprisingly, too, it is not poverty that drives the IWT in Asia, but affluence, with exotic animals and derived products imbuing social status (113). And, although flagship issues such as ivory steal the limelight, other Evolutionarily Distinct and Globally Endangered—EDGE—species, such as pangolins (*Manis javanica* and *M. pentadactyla*), are also cruelly and excessively exploited in the Chinese IWT (21).

Notebooks apprehended in 2009 from one trafficking syndicate revealed 22,000 pangolins killed in just 21 months in the Bornean state of Sabah and destined for the Chinese market. With such extensive trade, rescue, rehabilitation, and rerelease efforts are near futile. Of 326 pangolins placed in the Yunnan Wildlife Sanctuary since 2008, only 76 Malayan pangolins and 22 Chinese pangolins survived; a further 20 Chinese pangolins were released into the wild (21). With euthanasia of confiscated animals not permitted in China, these rescue centers are often overcrowded and perpetuate further poor welfare standards (114).

**WHAT NEXT? EMERGING QUESTIONS FOR TRANSDISCIPLINARY CONSERVATION**

It is clear that in recent decades the practitioner’s “medical kit” for conservation has advanced hugely, and is now replete with ingenious sticking plasters and analgesics, with a local effectiveness that would have previously been unimaginable. However, to push the analogy, tireless practitioners apply their medical kit in the absence of an effective “health service.” In short, treating the malaises of conservation requires thinking much bigger. Therefore, I think the moment has arrived for a new sort of conservation for mammals, and indeed biodiversity in general. It is hard to define this new conservation but, as Justice Stewart remarked famously of obscenity, I know it when I see it. It is not merely interdisciplinarity, if by that one means taking the methods and insights of one discipline and adopting them in another. It does embrace the spectrum of scales at which conservation operates from groundedness to geopolitics, and does so in a way that is surely interdisciplinary at each step on that continuum but, more than that, it demands a holistic integration of the whole. [Macdonald & Chapron (115) describe a step on this journey.] I call this holism transdisciplinarity (116), acknowledging the unity of all knowledge beyond disciplines [being nonetheless aware that the seemingly innocent notion of unity of knowledge has proven provocative (117, p. 225)]. Thus I defer to Lewis Carroll’s egg, Humpty Dumpty, who sagely remarked that “when I use a word it means exactly what I wish it to mean, neither more nor less” and in that spirit I coin the umbrella term transdisciplinary conservation to integrate with organismic and environmental sciences the assemblage of higher level (i.e., beyond biology) insights offered to conservation by economics, political science, law, sociology, international relations, development, ethics and disciplines with less quantitative epistemologies such as anthropology, environmental history, human geography and the like. These disciplines together inform choices, and effect behavior change, at scales from individuals to empires. Transdisciplinary conservation is most vibrant at the interface between top-down and bottom-up modes of decision making. This holism feels new from the perspective of a field biologist, and it is revealing that from the perspective of a geographer or social scientists it feels so “old hat” that it even predates the entry of biologists into the discussion.1 Certainly, a scalar view has been in the ether for some time (remember the 1960s exhortation to act local think global) and already has spawned inventive dimensions to conservation beyond (and inseparable from) organismic biology—or natural history as it was.

1Putting aside the theological perspective, the nub of the issue was clear in George Perkins Marsh’s (118, p. 1) summation that “man has too long forgotten that earth was given to him for usufruct alone, not for consumption, still less for profligate waste.”
once more attractively known. For example, conservation politics (119), conservation marketing (120) and conservation ethics (121, 122) are important ingredients. To these, and considering the importance of geography in all its many forms for international politics, I add a new element of transdisciplinary conservation, namely conservation geopolitics (see below).

The transdisciplinary philosophy, with its emphasis on explaining things from all angles, and from both top-down and bottom-up perspectives, resonates pleasingly with the four dimensions to how and why questions posed by my early mentor, Niko Tinbergen (123): adaptation, causation, ontogeny and phylogeny (these questions themselves being an evolution of Aristotle’s “four causes”). The horizontal and vertical integration of these four questions provide the holistic explanation (i.e., the causes) of why an animal behaves the way it does, and animal behavior remains the foundation of the moving parts of conservation. Hence it is fitting that this Tinberian transdisciplinarity should permeate the desire to understand not just the behavior of the animals whose well-being conservation seeks to foster, but also the well-being of people, societies, economies, and nations that are all factors to be considered in transdisciplinary conservation. Such transdisciplinarity extends through Wilson’s (124) understanding of consilience, framed explicitly to benefit conservation thinking (and to resonate with the spirit of this quest for holism it is not really necessary to follow Wilson all the way to Physics as the common denominator of all natural processes).

This new voice for conservation is not the shrill treble of a peripheral sector striving to be heard, but a bass thunder that resounds throughout the web of global, societal and personal choices that will shape the future of the human enterprise. It has that importance, from individual to empire, because wildlife, more grandly called biodiversity, is a crucial working part of the environment on which humanity depends and which, in addition, fuels an aesthetic purpose which might sometimes converge with spirituality. For now, I present transdisciplinary conservation as the formidably potent intersection of top-down (nations) and bottom-up (citizens) approaches (Figure 4). From both trajectories, and based on earthily evidence-based research, the goal is behavior change.

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**Figure 4**
Top-down and bottom-up approaches to conservation.
**Bottom-Up Thinking in Conservation**

Conservation marketing is fundamental to bottom-up conservation and strives to channel revenue and political will to conservation initiatives, and away from damaging enterprises. This channeling necessitates knowing what various publics value, and how they behave, before using that information either to advance conservation or, as necessary, to encourage them to think and act differently.

That encouragement is likely to be more persuasive if it goes with the flow of evolution (our own and the mammals we seek to conserve)—an idea Macdonald et al. (125) call Natural Governance, which develops the principles of mammalian ecology and mammalian cooperation in the service of conservation.

Conservation marketing and ambassadors: charismatics meet umbrellas. Macdonald et al. (126) mapped, for all 4,320 terrestrial mammals, an umbrella score based on the range overlap of each with other threatened mammals, and Macdonald et al. (127) assessed the relative charisma of 100 different mammals (representing 25 orders and 69 families) and the factors that may drive it. Macdonald et al. (126) then predicted the charisma scores of all 4,320 mammals and then combined this with their umbrella score to identify “ambassadors”—charismatic mammals whose distribution overlaps more than average numbers of other species.

Twenty-seven species were “top ambassadors” (with efficiency and appeal scores >1 standard deviation above the mean) and, of these, 18 were carnivores, highlighting potential benefits of carnivore conservation campaigns for other co-occurring mammals that are unlikely to generate similar levels of attention and funding. Potent ambassadors included the puma and the leopard, both of them with soaring charisma scores. Ambassador species did not have to be of high conservation priority themselves; only 22% of ambassadors were listed as threatened by the IUCN Red List. The authors also identified “Celebrity” species—species with high appeal but limited efficiency due to their restricted ranges and low overlap, e.g., Indian, Sumatran, and Javan rhino and the Iberian lynx.

**Behavioral dissonance, animal attractions, and inappropriate pets.** Moorhouse et al. (128) highlighted that many wildlife tourist attractions (WTAs) that do not have benefits for wildlife still receive millions of visitors per annum. A general solution may lie in identifying opportunities for guiding tourists’ choices, with the aim of creating a “green market” that drives revenue to beneficial venues (e.g., 129). Currently, there is no mechanism regulating standards, but Moorhouse et al. (130) found that respondents to an experimental survey were less likely to visit types of WTA likely to have detrimental standards if first primed to consider the ethical outputs of the WTAs, and their own role in determining the impacts of WTAs. Moorhouse et al. (130) also investigated the messages that might alter the preferences of a self-selecting sample of consumers potentially interested in purchasing exotic pets such as kinkajous and squirrel monkeys, discovering that “selfish motivations,” transmission of zoonotic disease, or illegal ownership reduced by 39% the probability of purchase, whereas information on likely impacts on animal welfare or conservation had no significant effect.

**Where conservation meets social justice.** Community-based natural resource management is intended to give poor local communities affected by supplying conservation a stake in conservation outcomes. People who feel unfairly treated are likely to undermine conservation outcomes, suggesting that local communities are more likely to buy into conservation if deliberative stakeholder participation enables them to influence decisions that affect their lives. Vucetich et al. (131) propose basic principles for introducing social justice to the resolution of human-wildlife conflict.
Top-Down Thinking in Conservation

Central to this approach is the relatively new concept of conservation geopolitics.

Conservation geopolitics. Conservation geopolitics may be characterized as the linkages between conservation outcomes and the political, social, and economic arrangements within and (resulting) relationships between countries.

Geopolitical perspective: taxon-scale priorities and efficiencies. Dickman et al. (132) argued that in allocating priorities for felid conservation it was essential to appreciate not only each country’s ranking on the endangerment of its species, but also its capacity to offer a return to conservation on the investment, consequently devising a national conservation likelihood (NCL) score. The component indices covered the countries’ governance and stability, economics and welfare, human pressure on natural habitats, and support for engagement with international conservation policy. NCL scores plotted against NCP (Figure 5) reveal, for felids, that 28 high priority countries had above median NCL scores, and these supported all but one of the 36 felid species...
but covered on average only 44% (range 2.8–100%) of those 35 species’ ranges. Indeed, nearly two-thirds (61%) of countries had below average NCL scores, flagging the challenges of delivering conservation outcomes for felids there. In the low likelihood/high priority countries, containing 32 species of felids, the principal problem was poor governance in 62.5% of them and poverty in 25%. Circumstances can differ between taxa, so repeating this exercise for musteloids revealed that most, and most of the highest priority species, occur in high likelihood countries (133).

Geopolitical perspective: species scale. An influential species in Dickman et al.’s analysis of felid priorities and practicalities was the lion, a species that has shockingly been lost from more than 80% of its historical geographic range, and now as few as 23,000 to 39,000 remain. Lindsey et al. (134) found that 134 lion management/conservation experts, across 21 of the 25 lion range countries, consider the key threat to lion populations in protected areas to be poaching/snaring for bushmeat (26.7% of respondents), human-wildlife conflict (25.5%), and encroachment by livestock (11.4%). Drilling further into the status of lion populations, Dickman et al. (A. Dickman, D.W. Macdonald & colleagues, manuscript in preparation) identified two important dimensions to fragility: ecological and sociopolitical (Figure 6)—the former including such relevant ecological conditions as geographical area, extent of edge, population isolation, etc., and the latter, governance, economics, and national policy. According to the sociopolitical fragility scores, Botswana is least fragile, followed by Namibia, and Sudan and the Democratic Republic of Congo were most fragile, both suffering from poor governance and conservation policy. Two states hold more than half the world's lions [Botswana (~12.7%) and Tanzania (~40%)], whereas another

![Figure 6](image-url)

Figure 6
Characterizing each country’s lion population by sociopolitical and ecological fragility.
11 together support <1%. Dickman et al.’s geopolitical analysis culminates in the indictment of conservation that protected areas alone could support >83,000 lions.

Among the constellation of higher level elements to conservation geopolitics is the law, both national and international. Trouwborst et al. (135) summarizes how law influences conservation of wild mammals. For example, although five international wildlife treaties might apply across lions’ range, range states have signed different combinations of them. Hodgetts et al. (136) combine multiple concordant assessments of lion populations to highlight nine categories of threat—human-lion conflict, bushmeat poaching, human encroachment, trophy hunting, trade in lion bones, unpredictable environmental events, socioeconomic factors, policy failures, and governance/institutional weakness—and then assess how the treaties address these different categories of threat.

Who pays? Lindsey et al. (137) created a Megafauna Conservation Index (Figure 7) of 152 nations from around the globe, creating a benchmarking system based on (a) the proportion of the country occupied by each mammalian megafauna species that survives in the country (countries scoring higher with a higher proportion of species covering), (b) the proportion of megafauna species range that is protected (higher proportions score higher), (c) and the amount of money spent on conservation relative to GDP. According to this index, poorer countries tended to take a more active approach to biodiversity protection than did richer nations.

Good et al. (138) invoked a cultural conscience—for example, estimating that 85% of the 34 million eggs consumed in Britain daily bear the British Lion Quality Seal, and if each lion stamp were to earn the species one-tenth of a penny, that would be £10.5 million a year for lion conservation.
**Ethics.** Vucetich & Macdonald (139) point out that if something is valued only for its utility, there is a risk its utility will not justify its costs. Thus, Nature’s utility is an important, but grossly insufficient motivation for conservation. Vucetich et al. (131) argue that both the humans and wildlife deserve fair treatment, proposing this candidate principle: “Humans should not infringe on the well-being of others (including other humans, large carnivores, or other parts of nature with intrinsic value) any more than is necessary for a healthy, meaningful life. When the ability to live a healthy, meaningful life genuinely seems to infringe on the well-being of some intrinsically valuable element of nature (such as large carnivores), then the just solution will less often be found in depriving large carnivores and more often be found in rectifying an unjust inequality among humans” (p. 23). This principle also focuses attention on a few ultimate causes of species loss and conflict: gross inequalities in wealth distribution within and among nations, gross inequalities in the costs associated with conservation, the crippling and pervasive influence of plutocracy, and the impact of human population growth. Of course, different constituencies can hold starkly opposing opinions about wildlife, but as Dickman et al. (140) argue that any action that has a negative conservation impact does not acquire more validity by being rooted in tradition or culture, as compared with any other motive. The acknowledgment of an ethical element to conservation was highlighted by the death of Cecil the lion, which may have triggered a global opinion change towards conservation (46). Indeed, the case of Cecil, and trophy hunting in general, highlights the emerging urgency for ethical consideration of mammalian conservation [a proposition underlying Macdonald & Baker’s review of welfare science in mammalian conservation (D.M. Macdonald & S.E. Baker, submitted manuscript)], and in the specific case of lion hunting highlighted by Macdonald et al. (141) and elaborated in a formal ethical analysis by Vucetich et al. (121).

**SUMMARY POINTS**

1. More than one-fifth (22%) of all mammals are currently considered to be threatened—if most species currently classified as Data Deficient turn out to be threatened, this tally may rise to 36%.

2. The situation has worsened over recent years: Analysis of changes in the Red List Index 1996–2008 shows a decline in index values of 0.07% per year for mammals, equating to 156 species each moving one Red List category closer to extinction over that period.

3. Transdisciplinary conservation aims to integrate with organismic and environmental sciences the assemblage of higher level (i.e., beyond biology) insights offered to conservation by economics, political science, law, sociology, international relations, development, ethics, and disciplines such as anthropology, environmental history, human geography, etc.

4. Transdisciplinarity should permeate the desire to understand not just the behavior of the mammals whose well-being conservation seeks to foster, but also the well-being of people, societies, economies, and nations.

5. Transdisciplinary conservation is intended to be the formidably potent intersection of top-down (nations) and bottom-up (citizens) approaches. From both trajectories, and based on earthily evidence-based research, the goal is behavior change at scales from individuals to empires.

6. Examples of this approach touched on here include identifying “ambassador” mammals, investigating what motivates purchasers of exotic mammalian pets, implementing
community-based natural resource management, appreciating not only a country's ranking on the endangerment of its mammals but also its capacity to deliver meaningful conservation (national conservation likelihood), assessing ecological and sociopolitical fragility pertaining to threatened mammalian species, the role of international wildlife treaties, promoting a cultural conscience among consumers, acknowledging that while Nature's utility is important it is a grossly insufficient motivation for conservation, accepting that traditions and cultures do not validate actions with negative impacts on conservation, and addressing the crippling role of human population growth on mammalian conservation worldwide.

FUTURE ISSUES

1. Are charismatic mammals whose distributions overlap more than average numbers of other species ("ambassadors") a key to engaging a wider public in conservation efforts?
2. How best can the consumer be dissuaded from purchasing exotic mammalian pets?
3. What are the best mechanisms to ensure poor local communities affected by supporting conservation of mammalian megafauna have a stake in the conservation outcome?
4. Poor governance blunts conservation efforts for mammals, especially large mammals—what can and should the conservation movement do to both minimize the effects of poor governance on conservation projects and effect improvements in governance itself?
5. How can the legal protection of endangered mammalian species be made less repetitive and complicated and therefore more effective?
6. Acknowledging that poorer countries tend to contribute more than richer countries to biodiversity protection, especially mammalian megafauna, how can the governments of the rich nations of the world be persuaded to play their part? step up to the mark more?
7. What is the best way to financially access and develop the cultural conscience of those in the richer nations?
8. How best can the ethical argument that both humans and wildlife, with a focus on mammals, deserve fair treatment be argued and promulgated?
9. The liberal agenda that “tradition” or “culture” can excuse what are patently unethical impacts on mammals, either individually or at the population level, needs to be forcibly argued against; how best can this be achieved?
10. The conservation movement, considering mammals, must face head-on the fundamental and pervasive cause of the biodiversity crisis—the growth of human population and consumption. How can it—and surely it must if not doomed to become an irrelevant sideshow—influence these factors at individual, regional, governmental, and ethical levels?

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Contents

II. Earth’s Life Support Systems

The State and Future of Antarctic Environments in a Global Context
Steven L. Chown and Cassandra M. Brooks .......................................................... 1

Island Biodiversity in the Anthropocene
James C. Russell and Christoph Kueffer ............................................................. 31

Mammal Conservation: Old Problems, New Perspectives, Transdisciplinarity, and the Coming of Age of Conservation Geopolitics
David W. Macdonald ......................................................................................... 61

The State of the World’s Mangrove Forests: Past, Present, and Future
Daniel A. Friess, Kerrylee Rogers, Catherine E. Lovelock, Ken W. Krauss, Stuart E. Hamilton, Shing Yip Lee, Richard Lucas, Jurgenne Primavera, Anusca Rajkaran, and Subua Shi ......................................................... 89

III. Human Use of the Environment and Resources

Food Loss and Waste: Measurement, Drivers, and Solutions
Edward S. Spang, Laura C. Moreno, Sara A. Pace, Yigal Achmon, Irwin Donis-Gonzalez, Wendi A. Gosliner, Madison P. Jablonski-Sheffield, Md Abdul Momin, Tom E. Quested, Kiara S. Winans, and Thomas P. Tomich .......................................................... 117

Sustainable Living: Bridging the North-South Divide in Lifestyles and Consumption Debates
Bronwyn Hayward and Joyashree Roy ................................................................. 157

Status, Institutions, and Prospects for Global Capture Fisheries
Christopher Castello and Daniel Ovando ............................................................ 177

Illegal Wildlife Trade: Scale, Processes, and Governance
Michael ’t Sas-Rolfes, Daniel W.S. Challender, Amy Hinsley, Diogo Verissimo, and E.J. Milner-Gulland ................................................................. 201

Ecotourism for Conservation?
Amanda L. Stronza, Carter A. Hunt, and Lee A. Fitzgerald ................................... 229
Land-Management Options for Greenhouse Gas Removal and Their Impacts on Ecosystem Services and the Sustainable Development Goals

Pete Smith, Justin Adams, David J. Beerling, Tim Beringer, Katherine V. Calvin, Sabine Fuss, Bronson Griscom, Nikolas Hagemann, Claudia Kammann, Florian Kraasner, Jan C. Minx, Alexander Popp, Phil Renforth, Jose Luis Vicente Vicente, and Saskia Keesstra

Sanitation for Low-Income Regions: A Cross-Disciplinary Review

Christopher Hyun, Zachary Burt, Yoshika Crider, Kara L. Nelson, C.S. Sharada Prasad, Swati D.G. Rayasam, William Tarpeh, and Isha Ray

IV. Management and Governance of Resources and Environment

Co-Producing Sustainability: Reordering the Governance of Science, Policy, and Practice

Carina Wyborn, Amber Datta, Jasper Montana, Melanie Ryan, Peat Leith, Brian Chaffin, Clark Miller, and Lorrae van Kerkhoff

Social Synergies, Tradeoffs, and Equity in Marine Conservation Impacts

David A. Gill, Samantha H. Cheng, Louise Glew, Ernest Aigner, Nathan J. Bennett, and Michael B. Mascia

Toward REDD+ Implementation

Danae Maniatis, Joel Scriven, Inge Jonckheere, Jennifer Laughlin, and Kimberly Todd

Solar Geoengineering: Social Science, Legal, Ethical, and Economic Frameworks

Jane A. Flegal, Anna-Maria Hubert, David R. Morrow, and Juan B. Moreno-Cruz

V. Methods and Indicators

Is Natural Capital Really Substitutable?

François Cohen, Cameron J. Hepburn, and Alexander Teytelboym

Indexes

Cumulative Index of Contributing Authors, Volumes 35–44

Cumulative Index of Article Titles, Volumes 35–44

Errata

An online log of corrections to Annual Review of Environment and Resources articles may be found at http://www.annualreviews.org/errata/environ