The contribution of predators and scavengers to human well-being

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Abstract

Predators and scavengers are frequently persecuted for their negative effects on property, livestock, and human life. Research has shown that these species play important regulatory roles in intact ecosystems including regulating herbivore and mesopredator populations that in turn affect floral, soil, and hydrological systems. Yet predators and scavengers receive surprisingly little recognition for their benefits to humans in the landscapes they share. We review these benefits, highlighting the most recent studies that have documented their positive effects across a range of environments. Indeed, the benefits of predators and scavengers can be far reaching, affecting human health and well-being through disease mitigation, agricultural production, and waste-disposal services. As many predators and scavengers are in a state of rapid decline, we argue that researchers must work in concert with the media, managers, and policy makers to highlight benefits of these species and the need to ensure their long-term conservation. Furthermore, instead of only assessing the costs of predators and scavengers in economic terms, it is critical to recognize their beneficial contributions to human health and well-being. Given the ever-expanding human footprint, it is essential that we construct conservation solutions that allow a wide variety of species to persist in shared landscapes. Identifying, evaluating, and communicating the benefits provided by species that are often considered problem animals is an important step for establishing tolerance in these shared spaces.

Introduction

Coadaptation, the ability of humans and predators and scavengers to modify their behavior based on benefit trade-offs, is recognized as key for their coexistence in the 21st century[1,2]. However, coadaptation relies on human tolerance and the recognition of the wide range of benefits that predators and scavengers provide humanity[3,4]. It is well established in the ecological literature that predators play regulatory roles in intact ecosystems as they exert top-down pressures on prey communities, thereby reducing herbivory of plant species important to humans[5] and scavengers consume large amounts of carcasses and organic waste[6,7]. It is accepted that the disappearance of predators and scavengers from ecosystems can cause a suite of deleterious effects including the loss of plant species diversity, biomass, and productivity that in turn affect disease dynamics, carbon sequestration, and wildfire risk[8]. As a result, predators and scavengers are considered flagship and keystone species[9] and are sometimes treated as surrogates for the health of entire ecosystems[10].

Despite their ecological value, predators and scavengers often have a poor public reputation because of their real and perceived negative impacts on humans[11–13]. These negative impacts include livestock depredations[14], killing of pets[15], attacks on humans[13], and harboring of diseases and parasites[16]. The human culture of fear associated with predators hinders many local and regional species recovery efforts[17]. Populations of many predator and scavenger species are already declining[8,18] and are projected to continue to dramatically decline over the next 25 years in response to increasing human populations, political uncertainty, and climate change[8,19,20].

An understanding of the benefits of predators and scavengers on human well-being is important in strengthening conservation efforts in shared landscapes[2,21,22]. For example, Egyptian vultures (*Neophron percnopterus*), which are declining globally, thrive in the towns and villages of Socotra, Yemen where they are valued for their service of removing livestock and human waste[23] that would otherwise cause water contamination and are expensive to remove[7,24,25]. Similarly, the

Tigray region of northern Ethiopia harbours high populations of spotted hyenas (*Crocuta crocuta*) that are tolerated by human societies, as they consume cattle and donkey carcasses as well as human corpses in urban settlements, reducing disease risk[25]. Yet, these examples of human communities cohabitating and actively conserving scavengers and predators are few and far between.

Here, we highlight several key, yet often overlooked, benefits provided by native predators and scavengers in shared landscapes with humans (Figure 1). These potential benefits include disease regulation through host density reduction and competitive exclusion, increasing agricultural output through competition reduction and consumption of problem species that destroy crops, waste disposal services, and regulating populations of species that threaten humans. Although there are a growing number of examples of benefits provided by predators and scavengers, it is often unclear how widespread these benefits may be. While some benefits, such as carcass disposal, may be common and general, other benefits, such as protection from zoonotic disease, may be highly context-dependent effects that are localized in both space and time (Table 1). Management of predators and scavengers must also, therefore, be context-dependent and try to appropriately balance detrimental and beneficial effects. We focus primarily on economic and health aspects of human well-being, but we recognize that well-being can encompass other material, social, and subjective components of the human experience that are not covered in this paper[26].

Predators and scavengers regulate zoonotic diseases

Zoonoses, diseases that are maintained in animal populations but can be transmitted to humans, pose direct threats to human health as exemplified by recent outbreaks of the Zika virus[27], Ebola virus[28], and H5N1 avian influenza[29]. Accounting for over 60% of known human diseases[30], zoonotic disease outbreaks can decimate human societies and economies. For example, not only did the Ebola virus cause loss of life (>12,000 lives)[31], but it virtually halted all tourism to West Africa leading to dramatic economic suffering due to both local perception of disease risk and continent-wide economic concerns[32]. Because of these human health and economic impacts, control of zoonoses and their vectors is important and while they may be hosts themselves in some cases (e.g. carnivores sustaining rabies cycles in some African ecosystems[33]), predators and scavengers may play a role in disease regulation[34]. Indeed, some case studies have shown that they can control diseases by reducing host and vector densities[35], through local competitive exclusion[24], or directly through feeding on infected hosts[36] (see Figure 1).

Reduction of host species densities by predators can reduce the risk of disease transmission to humans by limiting the prevalence of disease in host populations when within-host transmission is density-dependent[37]. Predators can also reduce absolute host numbers, thereby limiting the opportunity of spillover to humans when within-host transmission is either density- or frequency-dependent[37]. For example, reduction in dog densities by leopards (*Panthera pardus*) greatly reduces the frequency of dog bites and hence human exposure to rabies near the Sanjay Gandhi National Park in Mumbai, India[38]. Similarly, generalist predators such as foxes may reduce Lyme disease risk in humans by controlling mice populations (*Peromyscus sp.*), the main reservoir for infected nymphal tick vectors (*Ixodes scapularis*)[39–41], and frog tadpoles may play a global role in reducing dengue fever by feeding on mosquito eggs[42] (see Figure 1 for global distribution of these species).

Predators and scavengers can also reduce disease risk in humans through competitive exclusion, the action of outcompeting disease hosts for resources or space. For example, vultures have been shown to outcompete stray dogs in finding and consuming carrion[24]. Markandya and colleagues (2008) linked the severe decline in vulture populations in India (92% loss from 1990-2000) to the widespread use of diclofenac and the striking increase in stray dog populations[24]. They suggest in the absence of vultures consuming carrion, stray dog populations will continue to rise, resulting in an increase in human dog bites and exposure to rabies. Furthermore, other facultative scavengers can replace vultures, including gulls, rats, and invasive foxes[43], all of which can pose risks to humans and can themselves be disease hosts.

Predators can indirectly increase agricultural output

Species that consume crops account for 10-20% of agricultural financial losses globally and current control measures are estimated to be only 40% effective on average[44]. Conventional pest-control methods, particularly chemical control, can be detrimental to human health[45] and costly. Biological control provides an alternative to unhealthy chemical control methods[46], and some case studies have shown that natural predators can reduce financial burden and crop loss by consuming problem species.

Airborne predators can play an important role in agricultural management[47], a reason why some bat and bird species are often considered the most economically important non-domesticated group of animals[48,49]. For example, field experiments show that some bat communities in the USA suppress pest larval densities of the detrimental corn earworm moth (*Helicoverpa zea*) and cucumber beetle (*Diabrotica undecimipunctata howardi*) by nearly 60% and significantly reduce associated pest fungal growth in large-scale corn productions[49]. Based on these experiments, the authors estimate that bat control of crop pests may save farmers more than US$1 billion globally per year, thereby providing a substantial service to farmer livelihoods[49]. Similarly, birds and bats in the tropical cacao plantations of Indonesia's central Sulawesi have been shown to save over 30% of crop output (~US$730 ha^{-1}) by hunting pest populations of Lepidoptera and Heteroptera species[50].

Large avian predators can also have marked impacts on problem species that cause agricultural damage (Figure 1). For example, the barn owl (*Tyto alba*) has a diet made up of ~99% agricultural pest species and reduces rodent density by over 33% in the alfalfa (*Medicago sativa*) fields of California, USA[51,52]. Similarly, barn owls reduce man-hours worked and baiting costs for rat (*Rattus sp.*) control in oil palm plantations of Malaysia[53]. Likewise, New Zealand falcons (*Falco novaeseelandiae*) have increased winery output in six New Zealand wineries by preying on four crop-raiding bird species[54].

Livestock depredation by carnivores can be costly for pastoralists[14], resulting in retaliatory killings of predators[3]. However, in pasture environments where livestock and wild herbivores are present, predators may increase livestock productivity by reducing competition with other herbivores[55]. For instance, the dingo (*Canis lupus dingo*) (Figure 3) has been shown to increase agricultural output by controlling populations of red kangaroo (*Macropus rufus*), Australia's largest native herbivore and a major competitor with livestock on commercial grazing land[56]. Cattle farmers often kill dingoes due to their reputation for killing valuable livestock but dingoes are estimated to increase pasture biomass by 53 kg ha^{-1} and improve profit margins by US$0.83 ha^{-1}[56].

The value of other predatory species as pest regulators requires further investigation. For example, pest insects form over 50% of the diet of a suite of frog species in the Nepalese rice plantations of Chitwan[57] and in southeast China, frog species depredate rice leaf rollers (*Cnaphalocrocis medinalis*), a problematic species that causes blight. By consuming leaf rollers, frogs increase the number of seedlings and stem width of rice plants[58] that may ultimately increase health and crop size for rice farmers. Similarly, skunks (*Miphitis spp.*) in North America have been shown to reduce pests in family gardens, potentially reducing the need for pest management[59].

Predators and scavengers provide benefits in urbanizing environments

Negative human-wildlife interactions are a longstanding and growing problem[17] that is often exacerbated in areas with high human density and an abrupt ‘wilderness’ interface[21]. Many species are attracted to the high calorie food items, shelter, and breeding resources common to urban areas, and they may form permanent populations in shared areas irrespective of wilderness proximity[60]. For instance, bobcat and puma densities in Colorado, USA, are the same across semi-urban areas and wildland habitats provided that prey densities are similar[61]. As a result, predators and scavengers will utilize urban areas, and some case studies have shown that they may provide benefits to humans above and beyond the disease benefits discussed above, including waste regulation and reduction of species abundances that cause direct human injury and death[7,38,62].

Scavengers provide organic waste regulatory services by feeding on carcasses or decaying food matter (Figure 1). For example, golden jackals (*Canis aureus*) reduce >3,700 tons of domestic animal waste in Serbia per year, including road-killed animals and waste dumps[7]. One estimate indicates that jackals remove >13,000 tons of organic waste across urban landscapes in Europe amounting to >US$0.5 million in saved waste-control[7] that would otherwise cause groundwater contamination and other health risks[24]. Vultures can also provide long-term carcass removal services for the livestock industry, leading to savings in man-hours and reduced disease risk in valuable herds[6]. This service has been observed in many developing regions, particularly in Africa and Asia where waste-disposal infrastructure is lacking[23,24,63].

Large terrestrial predators can provide services in urban landscapes by reducing abundances of species that cause human death and injury (Figure 1). For example, leopards reduce the density of stray dogs in Mumbai, India, thereby reducing bites and injury accrued on residents and save the municipality nearly 10% of their annual dog management budget[38]. Stray dogs are responsible for thousands of bites on Mumbai's citizens annually that result in hundreds of work days lost and subsequent financial burden[64]. As stray dog populations currently exceed well over 1 billion globally and are expected to continue to grow as the human population increases[65], large wild predators in these urban landscapes should be considered a valuable asset in reducing the ongoing and potential damage accrued from urban stray dogs on human health and well-being.

Predators can also reduce the abundance of species that are responsible for costly wildlife-vehicle collisions (Figure 1). Where large carnivores have declined or been extirpated, herbivore populations have often increased[66]. This trophic response not only impacts ecological structure, but can directly influence human well-being. Gilbert et al. (2016) found that the potential recolonization of cougars over a 30-year period in the eastern United States would reduce deer populations and thereby curtail deer-vehicle collisions by 22%[62]. They estimated that this reduction in collisions would result in 155 less human deaths, 21,400 less human injuries, and US$2.13 billion saved in costs. This study illustrates how the ecological effects of large predators can potentially save human lives and decrease government spending.

Predator and scavenger conservation in the 21st century

Only 12.5 percent of the earth's terrestrial surface is protected for conservation[67], and as the human population grows, and our global footprint expands, 'shared' landscapes will prevail across Earth's terrestrial surface[20,68]. Currently, predators and scavengers receive relatively high attention in protected landscapes[69], but receive relatively little conservation attention in shared landscapes[20,70] considering large portions of many species ranges occur in these areas[20]. For example, leopards have disappeared across 78% of their historic range[18], African lions (*Panthera leo*) are predicted to continue to decline by half outside of protected areas[71], and 17 out of the 22 vulture species are declining due to human activities[43]. Shared landscapes must be managed to achieve effective conservation for all species and improving our understanding of the services provided by predators and scavengers may facilitate their conservation[72].

One obstacle to effective conservation of predators and scavengers in shared landscapes is bias in media, government, and public perception. Skewed viewpoints can sensationalize the negative effects of predators and scavengers[12,73] that can have long-lasting repercussions on human perception, behavior, and policy[73,74]. For example, much of the media framed leopards as the perpetrators when attacks occurred in the city of Mumbai, India[12], and the main local newspaper in Bangladesh pointed to the tiger (*Panthera tigris*) as being the cause of conflict with a 2x higher frequency when compared to the international “The Guardian” newspaper[75]. In Florida, USA, instead of taking a neutral stance, local newspapers asserted risks that Florida panthers (*Puma concolor coryi*) might harm people and domestic animals[76]. Likewise, most media coverage in the USA and Australia emphasized the risks sharks pose to people despite the threatened status of many shark species[77]. An emphasis on wildlife-related risks from the media can lead to risk-averse policy such as when the Western Australia Government deployed drum lines to catch and kill sharks thought to be a threat to the public[73]. These “signals” the public receives from governments can influence human behavior directed toward wildlife. For example, Chapron and Treves (2016) suggest that the repeated policy signal to allow state culling of wolves in Wisconsin and Michigan, USA, may have sent a negative message about the value of wolves or acceptability of poaching to the public[78]. The authors contend that these policy signals contributed to poaching of wolves and slowed their population growth[78].

Another issue is the asymmetry between stakeholders that incur the costs from wildlife, such as the local communities living near them[79], and those that benefit from wildlife, such as specific industries (e.g. tourism) or society as a whole. For example, the international community values orangutans for their conservation and intrinsic value in Indonesia, yet local people incur the cost of crop raiding and personal injuries from orangutan attacks[80]. Consequently, local people kill orangutans to reduce those costs[80,81]. Likewise, although ecotourism companies benefit from predator-viewing activities in Bhutan's Jigme Singye Wangchuk National Park, low income agropastoralists suffer from depredated livestock by tigers and leopards. These losses amount to more than two-thirds of average annual household income[82].

Initiatives that have directly provided local stakeholders with benefits from large predators and scavengers have achieved substantial and sustained reductions in conflict. Two seminal examples include profit-sharing and compensation schemes in Kenya's Kuku group ranch and Mbirikani ranch, which provide local stakeholders with a proportion of tourist industry revenue. This has led to reductions in the incidence of lion deaths resulting from poisoning[71,83]. Such schemes may help balance the economic benefits between private stakeholders and the local public who accrue most of the costs of predators and scavengers. Similar incentive schemes have been used successfully by conservation NGO's and governments to promote changes in human behavior, such as reducing carnivore killings[84]. However, the success of these schemes can be jeopardised if they lack sufficient logistic and financial support, they do not award adequate compensation to offset losses, or if compensation is awarded inequitably[85]. Such schemes may also have limited effectiveness in reducing killings motivated by cultural, political or historical reasons[86]. Hence, profit-sharing and compensation schemes must be implemented in conjunction with broader management programs that attempt to identify and address the wide range of factors that contribute to killing of wildlife, and that encourage the participation of all stakeholders in an inclusive decision-making process that recognizes multiple systems of knowledge and values[87].

In addition to improving equity in various forms associated with predators and scavengers, there is also an urgent need to promote human tolerance to these species through education about benefits[88–91]. Dedicating outreach teams to communicate the benefits of endemic predators and scavengers to local communities could be an effective conservation strategy. Demonstrations of the effectiveness of education programs include: an improvement in the belief in potential for co-existence with alligators (*Alligator mississippiensis*) following education[88], greater tolerance of black bears (*Ursus americanus*) following education of benefits provided by bears[92], and greater tolerance of bats among Costa Rican men following education regarding ecosystem service provision[91]. Although more research is required to understand how long the benefits of education programs may last and how best to deliver them to people from a variety of cultural, educational and religious backgrounds, education can be an effective tool for conservation of predators and scavengers in shared landscapes.

In addition to the benefits predators and scavengers provide to the public as a whole, they may also benefit a wide range of business, agricultural, and tourism interests. Much can be done to bolster the services of predators and scavengers in these sectors through local government and individual action. For example, Italian city councils are encouraging residents to purchase bat nesting boxes in response to increasing mosquitos that cause chikungunya fever[93], although it is unclear the extent of impact that bats have on disease-carrying mosquitoes in this region.

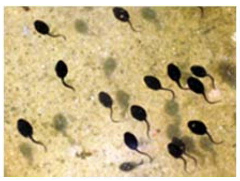
Similarly, the city of Dubai in the United Arab Emirates invests in consultancies that work with peregrine falcons to reduce feral pigeon populations that cause severe damage to infrastructure[94]. Ecotourism revenue can be substantial, though it is often difficult to estimate how much particular species contribute to overall economic value[95]. The presence of jaguars (*Panthera onca*) in Brazil, for example, may contribute greatly to Pantanal ecolodges. One study estimates that the large felids bring nearly US$7 million in annual land-use revenue, which is 52 times higher than other industries in the region[96].

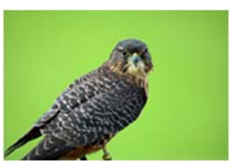
Predators may also benefit vehicle drivers by reducing insurance premiums in areas where predators have been effective in reducing the abundance of large prey like deer, which can be a leading source of vehicle collision damage[62]. Similarly, obligate scavengers have been shown to save ca. $50 million in insurance payments by farmers and national administrations in Spain by supplanting transportation of livestock carcasses to processing facilities[97]. Scavengers may also provide savings by reducing costs associated with meat contamination[98]. More work is needed to document the financial benefits of predators and scavengers to different sectors of society.

Managing the trade-offs between the costs and benefits of accommodating predators and scavengers in shared landscapes is a difficult and unresolved problem due to the complexity of human and ecological systems (Table 1). Risk-averse management may tend to place undue importance on eliminating the detrimental impacts of predators and scavengers over maintaining the benefits, particularly if the impacts include direct hazard to human life. In some cases, however, this may be a short-sighted and poorly justified perspective that could lead to a net increase in risk to humans if these animals also provide benefits that reduce exposure of risk to humans. Important unanswered questions include: how do the benefits from predators and scavengers change as the density of those species varies over time[99]? How does the composition of the predator guild alter human perception of the costs associated with those predators[100]? Integrating the natural and social sciences can help answer these questions by evaluating the full range of both costs and benefits. Doing so will enable conservationists to determine if and when there is a net-benefit in shared landscapes and develop strategies to encourage net benefits[81]. Moreover, as the extent of shared landscapes increases globally, it is imperative that we identify new approaches to management that allow wildlife and humans to coexist. Failing to do so is likely to result in the extinction of many species.

Human societies depend greatly on the living components of the natural world[101], and these natural services are being altered by human dominance of landscapes[102] and climate change[103]. While, predators and scavengers currently face great threats in shared landscapes[43,104], they can coexist in areas where local communities accept and tolerate these species[3,23,88]. Traditional conservation approaches such as safeguarding land may not lead to comprehensive protection of species in human-dominated areas[20], leading to a requirement for alternative approaches for saving species in these shared landscapes. An important alternative is using services that predators and scavengers provide for human well-being to enhance protection[72]. By adopting an approach that communicates and educates these benefits to communities that live with predators and scavengers while accounting for cultural values and equitable conservation decision-making, we may be able to stem the decline of these persecuted guilds and make progress toward more expansive protection and increased instances of a net-gain in shared landscapes.

Figure 1. IUCN global distribution of some species that are known to provide important services to humans over some portion of their range. Panel a) shows the ranges of some species known to contribution to agricultural production; Panel b) shows the ranges of some species that may reduce disease risk; Panel c) shows the ranges of some animals known to reduce species that cause human injury and death; Lastly, panel d) shows the ranges of some species known to remove dangerous organic waste.

Benefit	Predator/scavenger species & location of case study	Key finding(s)	Potential limitations of case study	Additional research needed to further demonstrate human well-being benefits
Regulating zoonoses	Leopard (*Panthera pardus*)[38] Mumbai, India 	Leopards consume nearly 1,500 feral dogs per year, reducing injury rates and potentially saving approximately 90 human lives.	Human benefit inferred from leopards consuming feral dogs that bite and infect humans, yet lacks direct measure of benefit, or controls for comparisons in similar dog-infested areas without leopards. Small spatial scale.	Conduct similar analyses in locations without leopard presence. Estimate prevalence of dog rabies rates in Mumbai and analysis of trade-offs between dog and leopard attacks on humans. Are these results in line with similar systems globally?
Regulating zoonoses	Red fox (*Vulpes vulpes*)[39] USA 	The decline of red foxes is spatially correlated with Lyme disease outbreaks.	Potential benefit inferred from correlation (cause and effect not established).	Better mechanistic understanding of system required to evaluate effect of multiple predators on prey (host) populations, and explicitly link this to host-pathogen dynamics.
Regulating zoonoses	Amphibian larvae (*Polypedates cruicger, Bufo melanostictus, Ramanella obscura, Euphlyctyis cyanophlyctis*)[42] Sri Lanka; Lab experiment 	Amphibian larvae feed aggressively on dengue mosquito (*Aedes aegypti*) eggs.	Lab-based experiment that does not account for alternative food availability that can dilute predatory effects. No direct quantification of human well-being. For example, lack of analyses on cost savings associated with vector control or reduced infection rates in humans as a result of amphibian predation of mosquito eggs.	Conduct field studies on amphibian larvae gut content across a variety of geographic areas subject to mosquito-borne diseases. Investigate whether predation of larvae by amphibians results in lower densities of adult mosquitos. Quantify how many human lives amphibian communities could affect.
Regulating zoonoses	Old world vultures (*Gyps spp.*)[24] India	Vulture declines are linked to increased feral dogs that cause	Potential benefit inferred from correlation (cause and effect not established).	Must identify other potential factors implicated in vulture declines and rule them out. Compare with vulture

		rabies.		population trends in areas in which feral dogs have not increased.
Increasing agricultural output	Barn owl (*Tyto alba*)[52,51] California, USA 	Barn owls consume >99% crop pests and reduce rodent density by over 33% in alfalfa fields.	No demonstration of increased crop yield. No calculation of cost savings from pest species consumption.	A controlled replicated experiment may be feasible to demonstrate a causal link between barn owls and increased crop yield. Calculate cost savings through work-hours, chemical control, and trap costs saved from pest predation by owls.
Increasing agricultural output	New Zealand falcon (*Falco novaeseelandiae*)[54] New Zealand 	New Zealand falcons reduce the presence of four crop-raiding bird species, increasing profit margins in wineries from US$234-326/ha.	Geographically- limited case study.	Replication in other areas and other systems required to better establish generality. Include calculations on work-hours saved by having falcons present on wineries.
Increasing agricultural output	Dingo (*Canis lupus dingo*)[56] New South Wales, Australia 	Dingoes increase gross profit margins by reducing the density of kangaroos, which compete with cattle.	Geographically-limited case study based on a metamodel.	Fieldwork needed to show that forage availability is proportional to kangaroo density. Must account for both forage quantity and quality effects. Include calculations on work-hours saved. Conduct exclusion experiments. Are the results similar to the metamodel?
Increasing agricultural output	Thirteen frog species (*Bufonidae, Microhylidaae, Ranidae,*	Frogs increase the number of rice seedlings and stem width	No calculation of increased crop yield or cost savings from pest species consumption.	Demonstrate crop yield increases when frogs are present, ideally using field experiments. Calculate cost

	Rhacopphoridae)[57] Chitwan, Nepal 	of rice plants by consuming leaf rollers (*Cnaphalocrocis medinalis*)		savings through work-hours, chemical control, and trap costs saved from pest predation by frogs.
Waste removal	Egyptian vulture (*Neophron percnopterus*)[23] Socotra, Yemen 	Vultures dispose of >22% of organic waste.	Clearer link to human well-being needed, such as disease implications and cost savings of waste scavenging. Small spatial scale.	Test water sources near waste dumps with and without vulture access. Additionally, assess costs of waste removal. Quantify how organic waste has negative impacts on humans.
Waste removal	Spotted hyena (*Crocuta crocuta*)[25] Tigray, Ethiopia 	Nearly 90% of studied hyenas were located at waste dumps.	Human benefit inferred from hyena abundance at waste dumps. Clearer link to human well-being needed, such as estimation of waste removal, disease implications, and cost savings. Small spatial scale.	Conduct diet analysis similar to Gangoso and colleagues[23], but take additional steps to address costs of waste removal and/or human disease implications.
Reducing species abundance that cause human injury/death	North American cougar (*Puma concolor*)[62] Eastern USA 	Potential recolonization of cougars over 30 years would curtail deer-vehicle collisions by 22%, saving 155 human lives, 21,400 injuries, and US$2.13 billion.	Human benefit based on a projected recolonization scenario for the eastern USA.	Account for the costs of cougar recolonization, such as increased incidences of livestock predation. Do the benefits on human well-being outweigh the costs?

Table 1. Featured case studies of predators and scavengers contributing to human well-being, their potential limitations, and suggestions for furthering the case human benefit.

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Contributions

C.J.O, J.E.M.W., and A.R.B. conceived the idea for the Review. C.J.O. wrote most of the manuscript and located case studies. H.L.B., E.M.M, and N.H.C. assisted with conceptual framing and style. All authors contributed with editing and writing.

Competing interests

The authors declare no competing financial interests.

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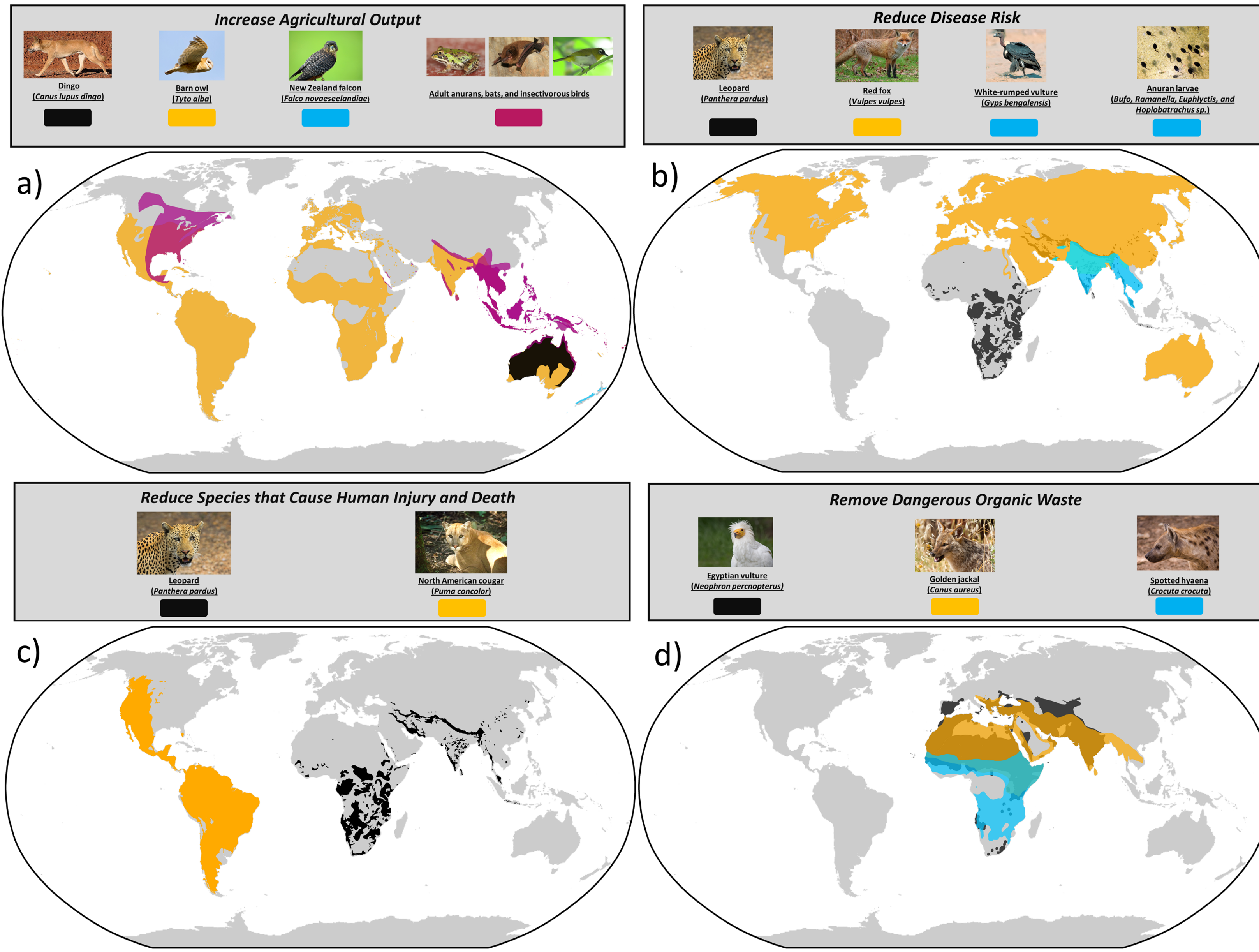
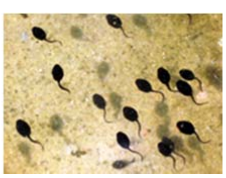
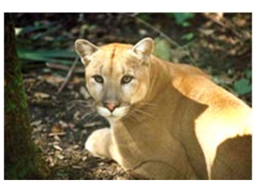

Increase Agricultural Output
Dingo
(Canus lupus dingo)
Barn owl
(Tyto alba)
New Zealand falcon
(Falco novaeseelandiae)
Adult anurans, bats, and insectivorous birds
a)
Reduce Disease Risk
Leopard
(Panthera pardus)
Red fox
(Vulpes vulpes)
White-rumped vulture
(Gyps bengalensis)
Anuran larvae
(Bufo, Ramanella, Euphlyctis, and Hoplobatrachus sp.)
b)
Reduce Species that Cause Human Injury and Death
Leopard
(Panthera pardus)
North American cougar
(Puma concolor)
c)
Remove Dangerous Organic Waste
Egyptian vulture
(Neophron percnopterus)
Golden jackal
(Canus aureus)
Spotted hyaena
(Crocuta crocuta)
d)

Benefit	Predator/scavenger species & location of case study	Key finding(s)	Potential limitations of case study	Additional research needed to further demonstrate human well-being benefits
Regulating zoonoses	Leopard (*Panthera pardus*)[1] Mumbai, India 	Leopards consume nearly 1,500 feral dogs per year, reducing injury rates and potentially saving approximately 90 human lives.	Human benefit inferred from leopards consuming feral dogs that bite and infect humans, yet lacks direct measure of benefit, or controls for comparisons in similar dog-infested areas without leopards. Small spatial scale.	Conduct similar analyses in locations without leopard presence. Estimate prevalence of dog rabies rates in Mumbai and analysis of trade-offs between dog and leopard attacks on humans. Are these results in line with similar systems globally?
Regulating zoonoses	Red fox (*Vulpes vulpes*)[2] USA 	The decline of red foxes is spatially correlated with Lyme disease outbreaks.	Potential benefit inferred from correlation (cause and effect not established).	Better mechanistic understanding of system required to evaluate effect of multiple predators on prey (host) populations, and explicitly link this to host-pathogen dynamics.
Regulating zoonoses	Amphibian larvae (*Polypedates cruicger, Bufo melanostictus, Ramanella obscura, Euphlyctyis cyanophlyctis*)[3] Sri Lanka; Lab experiment 	Amphibian larvae feed aggressively on dengue mosquito (*Aedes aegypti*) eggs.	Lab-based experiment that does not account for alternative food availability that can dilute predatory effects. No direct quantification of human well-being. For example, lack of analyses on cost savings associated with vector control or reduced infection rates in humans as a result of amphibian predation of mosquito eggs.	Conduct field studies on amphibian larvae gut content across a variety of geographic areas subject to mosquito-borne diseases. Investigate whether predation of larvae by amphibians results in lower densities of adult mosquitos. Quantify how many human lives amphibian communities could affect.
Regulating zoonoses	Old world vultures (*Gyps spp.*)[4] India	Vulture declines are linked to increased feral dogs that cause rabies.	Potential benefit inferred from correlation (cause and effect not established).	Must identify other potential factors implicated in vulture declines and rule them out. Compare with vulture population trends in areas in which feral dogs have not increased.

				
Increasing agricultural output	Barn owl (*Tyto alba*)[5,6] California, USA 	Barn owls consume >99% crop pests and reduce rodent density by over 33% in alfalfa fields.	No demonstration of increased crop yield. No calculation of cost savings from pest species consumption.	A controlled replicated experiment may be feasible to demonstrate a causal link between barn owls and increased crop yield. Calculate cost savings through work-hours, chemical control, and trap costs saved from pest predation by owls.
Increasing agricultural output	New Zealand falcon (*Falco novaeseelandiae*)[7] New Zealand 	New Zealand falcons reduce the presence of four crop-raiding bird species, increasing profit margins in wineries from US$234-326/ha.	Geographically- limited case study.	Replication in other areas and other systems required to better establish generality. Include calculations on work-hours saved by having falcons present on wineries.
Increasing agricultural output	Dingo (*Canis lupus dingo*)[8] New South Wales, Australia 	Dingoes increase gross profit margins by reducing the density of kangaroos, which compete with cattle.	Geographically-limited case study based on a metamodel.	Fieldwork needed to show that forage availability is proportional to kangaroo density. Must account for both forage quantity and quality effects. Include calculations on work-hours saved. Conduct exclusion experiments. Are the results similar to the metamodel?
Increasing agricultural output	Thirteen frog species (*Bufonidae, Microhylidaae, Ranidae, Rhacopphoridae*)[9] Chitwan, Nepal	Frogs increase the number of rice seedlings and stem width of rice plants by consuming leaf rollers (*Cnaphalocrocis medinalis*)	No calculation of increased crop yield or cost savings from pest species consumption.	Demonstrate crop yield increases when frogs are present, ideally using field experiments. Calculate cost savings through work-hours, chemical control, and trap costs saved from pest predation by frogs.

				
Waste removal	Egyptian vulture (*Neophron percnopterus*)[10] Socotra, Yemen 	Vultures dispose of >22% of organic waste.	Clearer link to human well-being needed, such as disease implications and cost savings of waste scavenging. Small spatial scale.	Test water sources near waste dumps with and without vulture access. Additionally, assess costs of waste removal. Quantify how organic waste has negative impacts on humans.
Waste removal	Spotted hyena (*Crocuta crocuta*)[11] Tigray, Ethiopia 	Nearly 90% of studied hyenas were located at waste dumps.	Human benefit inferred from hyena abundance at waste dumps. Clearer link to human well-being needed, such as estimation of waste removal, disease implications, and cost savings. Small spatial scale.	Conduct diet analysis similar to Gangoso and colleagues[10], but take additional steps to address costs of waste removal and/or human disease implications.
Reducing species abundance that cause human injury/death	North American cougar (*Puma concolor*)[12] Eastern USA 	Potential recolonization of cougars over 30 years would curtail deer-vehicle collisions by 22%, saving 155 human lives, 21,400 injuries, and US$2.13 billion.	Human benefit based on a projected recolonization scenario for the eastern USA.	Account for the costs of cougar recolonization, such as increased incidences of livestock predation. Do the benefits on human well-being outweigh the costs?

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