Ecological Consequences of Ecotourism for Wildlife Populations and Communities

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Fig. 3.0 African elephants (*Loxodonta africana*), Amboseli National Park, Kenya. Photo credit Graeme Shannon

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3.1 Introduction

The individual ecotourist will probably only spend a comparatively short amount of time visiting a particular natural area, refuge, game reserve, or national park, with even less time in close proximity to wildlife. The temporary nature of these visits coupled with the spatial extent and apparent pristine environment of many natural areas can make it difficult to appreciate that tourism alone can drive discernible impacts on resident wildlife populations, particularly when these impacts are compared with seemingly more pressing threats such as habitat fragmentation, climate change, and illegal hunting. Indeed, ecotourism is based on the premise that the visitor values the chance to explore the natural world, to gain an appreciation and understanding of diverse habitats and native species, while also lending financial and political support for their continued protection [1]. Ecotourism is therefore commonly viewed as highly compatible with conservation objectives, and indeed it contributes a number of important benefits, including revenue generation, support for conservation, and educational opportunities for visitors and local communities [1].

Nevertheless, there is increasing evidence that human visitation to natural areas can have significant effects on the environment and the wildlife therein, especially when we consider the scale of visitation. A recent study estimated that globally, terrestrial protected areas receive eight billion visits per annum and generate approximately US$ 600 billion for local economies [2]. Visitation can also be highly concentrated; the busiest national park in the USA (Great Smoky Mountains National Park) attracts more than ten million visitors per year. This represents a significant source of potential disturbance to native wildlife, particularly as a result of the impacts associated with providing tourist infrastructure and access for large numbers of people to experience natural areas firsthand (e.g., extensive road networks).

Chapter 2 has highlighted a number of pathways by which the behavior and physiology of wild animals can be altered by the presence of humans. Though

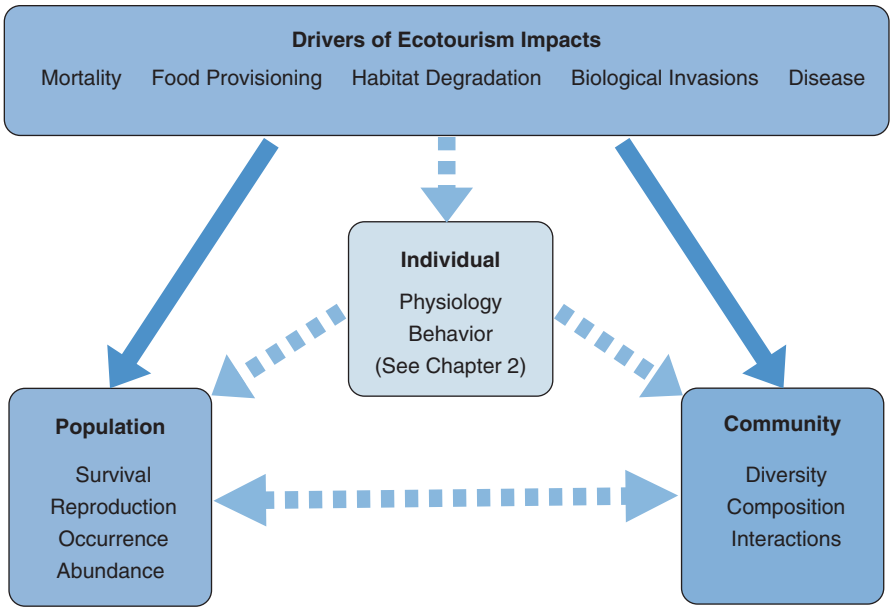

Fig. 3.1 A conceptual model demonstrating the drivers of ecotourism impacts and the effects that these can have at the individual, population, and community level. The solid arrows indicate how populations and communities can be directly affected by ecotourism, while the dashed lines represent indirect effects via changes in physiology and behavior (see Chap. 2), and interactions between the population and community levels

these shifts in behavior are often measured at comparatively short temporal scales, they may also have long-term effects with consequences for wildlife populations and entire ecological communities (see the conceptual diagram in Fig. 3.1 and a glossary of terms in Text Box 3.1). For example, the displacement of a red deer (*Cervus elaphus*) from a grazing site by hikers [3] may seem like a minimal impact if it is assumed that the animal will return to its natural behavior once the disturbance has passed. However, this brief disturbance may have long-term consequences if it occurs frequently, reducing the amount of time the animal spends foraging for important nutritional resources, or if the animal avoids the area, reducing the habitat available to the red deer population. Indeed, exploring these impacts over longer periods and broader scales can be challenging due to the multitude of interacting factors that dictate the reproductive success and survival of individual animals. However, there is a growing body of scientific literature on the effects of ecotourism on wildlife, which is beginning to reveal that behavioral shifts can accumulate over time and have the potential to adversely impact animal populations in the long term.

Box 3.1: Glossary of key terms in the conceptual model

Drivers of Ecotourism Impacts

Mortality: death of an individual animal as a result of ecotourist activity

- Examples: vehicle collisions; trampling; intentional killing of dangerous animals or pests

Food Provisioning: providing food to wildlife as a result of ecotourist activity

- Examples: attracting charismatic animals for viewing (e.g., bears, sharks); unintentional feeding (e.g., garbage)

Habitat Degradation: reduction of the amount and quality of wildlife habitat as a result of ecotourist activity

- Examples: use of limited resources (e.g., water); construction of infrastructure; fragmentation of habitat; human waste and litter; chemical, light, and noise pollution

Biological Invasions: introduction of non-native species as a result of ecotourist activity

- Examples: introduced weeds, domestic animals (e.g., cats, dogs), other animals (e.g., zebra mussels)

Disease: introduction of diseases via ecotourist activity that may infect native plants and animals

- Examples: primates, coral, sudden oak death

Population: a group of organisms in the same species in a given locality

Survival: the probability of survival of an individual animal, a critical determinant of population dynamics

- Examples: mortality; survival rate

Reproduction: the probability of having offspring, a critical determinant of population dynamics

- Examples: mating success; nest success; number of offspring produced

Occurrence: the probability that an animal will occupy a given area

- Examples: geographic range; population distribution; habitat use

Abundance: the number of animals in a population

- Examples: population size (number of individuals); population density (number of individuals per unit area)

***Community**:* assemblage of interacting species in the same locality
Diversity: the number of species in a given area

- Examples: species richness (number of species); species diversity (number and relative abundance of species)

Composition: the identity of species in an ecological community

- Example: catalogue of species

Interactions: interactions between species

- Examples: predator-prey interactions; competition between species; food web dynamics

A recent systematic review documented 274 scientific papers published between 1981 and 2015 on the effects of recreational activities (including ecotourism) on wildlife. Fifty-two percent of the results reported from these studies focused at the individual level in terms of behavior and physiology [4], whereas 48% of the results focused on effects at the population (e.g., survival, reproduction, occurrence, and abundance) and community level (e.g., species diversity, composition, and interactions, Fig. 3.2a). Of these studies investigating the population- and community-level effects of recreation, 35% detected negative effects (i.e., decreased species diversity, survival, reproduction, occurrence, or abundance), while only 6% found positive effects; 59% found no effect or unclear effects (Fig. 3.2b). More than 68% of these studies were conducted in Europe and North America, while South America, Asia, and Africa accounted for only 20%. Birds and mammals represented almost 80% of the research effort, with the majority of work conducted in terrestrial environments (71%). The growing interest in the effects of ecotourism on wildlife, including the ecological effects at the population and community levels, is also highlighted by a number of other recent reviews [5–8].

In this chapter we will delve further into the larger-scale and longer-term ecological effects that can be driven by human visitation. We focus on how human presence itself can have behavioral and physiological impacts (reviewed in Chap. 2) that scale up to affect wildlife population dynamics and community structure. We

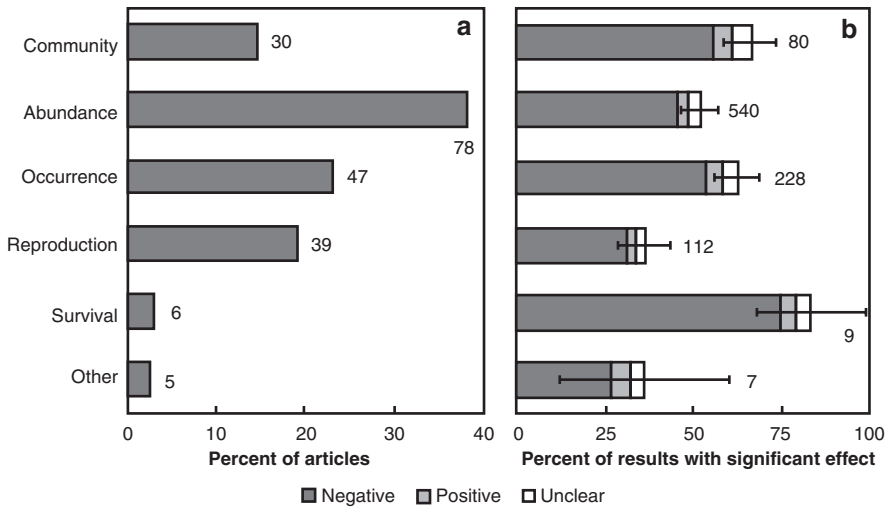

Fig. 3.2 (**a**) The number of scientific papers exploring population and community-level effects of recreation (including ecotourism) on wildlife from 1981 to 2015 [4]; the number of articles is given next to the bars and (**b**) the percentage of results from these studies that indicated a significant effect (the number of results is given next to the bars). Error bars show standard error for the sum of all effects. Unclear responses are those that were unable to be classified as positive or negative effects of recreation (e.g., a change in species dominance index) or results with nonlinear responses (e.g., highest reproductive success at an intermediate level of human recreation)

also explore several impacts of ecotourism, including mortality, food provisioning, habitat degradation, introduction of non-native species, and transmission of disease (Figs. 3.1 and 3.3, Text Box 3.1). A greater understanding and appreciation for how visitation and human activity can affect wildlife will help managers to identify areas of conflict and mitigate potential impacts, while still providing access for visitors.

3.2 Scaling Up the Behavioral and Physiological Effects of Human Presence

In Chap. 2, Geffroy et al. outlined a number of key behavioral and physiological responses of wildlife to the presence of ecotourists. These behavioral and physiological effects can, in turn, influence population and community level metrics through their effects on reproductive success, survival, abundance, species diversity, and the interactions among species.

Research on cetaceans offers some of the best evidence for the scaling up of short-term behavioral impacts of ecotourism to longer-term population level effects. Watching marine mammals has been one of the most successful sectors of the ecotourism industry over recent decades, with an estimated US$ 2.1 billion of income generated in 2008 by tour operators across 119 countries ([9]; and see Chap. 6). While there is no doubt that many cetaceans are faring better since the ban on commercial whaling in 1986 and the shift toward nonconsumptive use, there is growing

Fig. 3.3 Impacts on wildlife associated with ecotourism that can result in population and community-level effects: (**a**) long-term behavioral shifts driven by human presence that may include avoidance or increased vigilance (photo credit Graeme Shannon); (**b**) direct mortality, for example, as a result of vehicle strike (photo credit fishermansdaughter CC BY); (**c**) food provisioning, which is particularly popular for attracting top predators such as sharks (photo credit Joi Ito, CC BY); (**d**) habitat degradation associated with tourist infrastructure and access to protected areas (photo credit Grand Canyon National Park, CC BY); (**e**) biological invasion of non-native species, such as the zebra mussel (photo credit Tom Britt, CC BY), (**d**); (**f**) transmission of human diseases to vulnerable populations, including the mountain gorillas of central Africa (photo credit Henrik Palm, CC BY)

concern about the potential impacts of whale watching [10]. Research on dolphins in Shark Bay, Australia and Fjordland, New Zealand have demonstrated that repeated visitation causes not only short-term shifts in behavior but also long-term changes in social structure and a decline in local abundance [11, 12].

Behavioral avoidance of recreationists that translates to changes in population distribution and abundance has also been documented for many bird species [5]. Winter recreational activities drive significant impacts on population abundance and species diversity in sensitive alpine species [13]. For example, black grouse (*Tetrao tetrix*) in the Swiss Alps experienced a 12% reduction in available wintering habitat and a 36% decline in abundance as a result of activity associated with winter recreation [14, 15]. Nesting shorebirds and seabirds are also particularly vulnerable to disturbance by human tourist activity in coastal areas with effects on their distribution, particularly for species that nest on the ground in the open. However, even nocturnal storm petrels (*Hydrobates pelagicus*) that nest out of sight in cavities experienced higher nestling mortality with greater visitation, implying that noise and odors associated with human presence may drive population-level responses [16]. Likewise, juvenile hoatzin (*Opisthocomus hoazin*) in the Amazonian rainforest exposed to tourists experienced significantly altered stress responses and lower survival compared to those on undisturbed nests, even though adults appeared tolerant of ecotourists [17]. Tourist presence was linked to reduced body mass, a key indicator of survival in fledgling yellow-eyed penguins (*Megadyptes antipodes*) in New Zealand [18]. However, it is important to highlight that human presence does not always impact distribution and abundance, even for shorebirds such as the black-tailed godwit (*Limosa limosa*) that are thought to be easily disturbed [19].

It is well known that the decline of top predators can have cascading effects on lower trophic levels [20]. Similarly, the disproportionate effects of ecotourists on a particular species may impact other taxa in the ecological community. In some cases, disturbance-sensitive predators may simply avoid areas with human activity, thereby creating what is known as a predator shelter or human shield for prey species [21, 22]. This pattern has been seen in large herbivores in Yellowstone and Grand Teton National Parks, where moose (*Alces alces*) selected calving sites close to paved roads [23], while elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) behaved as though they perceived reduced predation risk near a major road [24]. Indeed, comparatively benign activities (e.g., cycling, hiking) in prime habitat may well tip the balance in favor of the more tolerant herbivore species, while driving the displacement of predators that require extensive ranges and are often already compromised by habitat fragmentation [21, 22].

In addition to providing a potential predator shelter for prey species, a recent paper suggests that the habituation (or reduced responsiveness over time) of prey to human activity may lead to reduced responses to predators, causing increased boldness, decreased vigilance (or watchfulness), and greater vulnerability to predators over time [25]. Although there has been only limited empirical exploration of this hypothesis, urban foxes (*Vulpes vulpes*), blackbirds (*Turdus merula*), and pigeons (*Columba livia*) that were habituated to humans were less responsive to predators [26–28]. Ultimately, this greater susceptibility to predators (and also human hunters) could impact individual reproduction, survival, population dynamics, and community structure. Indeed, a study on captive-bred swift foxes (*Vulpes velox*) demonstrated that bold behavior was a good predictor of mortality after release into the wild [29].

Though the presence of ecotourists can negatively affect disturbance-sensitive predators, these predator shelters can have a positive effect on the survival of endangered prey species. For example, the presence of tourists on beaches benefits hawksbill sea turtles (*Eretmochelys imbricata*) in the Caribbean by reducing the activity of introduced mongooses that predate on hatchlings [30]. Thus, the challenge is to identify the optimal level of beach use that maximizes turtle survival, while avoiding negative disturbance to this critical habitat. Interestingly, the benefits of human presence can also extend to large predators, such as grizzly bears (*Ursus arctos horribilis*) that are generally considered sensitive to human disturbance. The presence of tourists increased the feeding of female bears and cubs on salmon by displacing aggressive males that tend to dominate the best feeding sites [31]. This sex difference in tolerance of human activity results in important nutritional benefits for the survival of female bears and their young in hibernation.

The presence of humans can also benefit some wildlife populations and their habitat by deterring illegal hunting/harvesting and logging [32]. Sea turtles, in particular, have benefitted from ecotourism, which has enabled greater offspring survival because of the presence of humans, intent on viewing, and protecting turtles. However, the role of ecotourism and the presence of humans have been shown to play only a secondary role in the successful protection of threatened great apes, which rely on effective law enforcement first and foremost [33].

3.3 Mortality

The death of an individual animal as a result of tourist activity is perhaps the most direct way human visitation can negatively impact wildlife populations. Though definitions of ecotourism generally exclude forms of consumptive recreation, such as hunting and fishing [1], inadvertent killing of animals has the potential to be severely detrimental to populations of rare species. One of the most common methods by which animals are killed by tourists is through vehicle collision. For example, the upgrading of a road entering the Cradle Mountain—Lake St Clair National Park in Tasmania led to a dramatic rise in the numbers of eastern quoll (*Dasyurus viverrinus*) and Tasmanian devils (*Sarcophilus harrisii*) killed by cars. In fact, the quoll population became locally extinct and had to be reintroduced following successful efforts to reduce vehicle collisions [34]. Meanwhile, the mortality of nocturnal birds such as nightjars and spotted eagle owls (*Bubo africanus*) due to vehicles traveling at night through Kruger National Park in South Africa has been of concern for a number of decades [35].

In many coastal marine habitats, a rapid increase in the numbers of recreational boats has resulted in greater numbers of animals injured or killed by boat strikes [36]. Sea turtles and dugongs (*Dugong dugon*) appear to be particularly vulnerable due to their comparatively slow movement and preference for swimming close to the surface [37]. Legislation and awareness campaigns can be successful in reducing wildlife-vehicle collisions [38], but the effectiveness of these approaches outside of protected areas is less clear, particularly given the challenge of enforcement.

Apart from vehicle collisions, direct trampling can also inadvertently lead to animals being killed. There is strong evidence to suggest that the disturbance associated with ecotourism on beaches, which provide key habitat for nesting bird species, can result in reduced survival of young, particularly as a result of mortality due to trampling [39]. In addition, studies have also shown that tourists walking in the intertidal zone can drive significant declines in mussels and barnacles, while delicate corals on tropical shores can be even more vulnerable, suffering major damage as a result of trampling [37].

There are also cases of deliberate killing of wildlife connected to ecotourism. Such incidents generally occur around hotels and resorts and concern the presence of potentially dangerous animals, such as venomous snakes or mosquitos [40]. However, the widespread use of pesticides can have a negative impact on the populations of nontarget species, including popular taxa such as butterflies that ecotourists are keen to observe [40]. Finally, the habituation of animals to ecotourist activities can result in animals becoming vulnerable to persecution from other nontourists that consider the animals either a nuisance or a highly prized resource. For example, fishermen in a number of countries were reported to have killed dolphins that learned to associate with humans and ultimately became a tourist attraction [41]. Similarly, there is evidence that primates habituated for tourist viewing are at greater risk from poaching than non-habituated individuals [42, 43].

3.4 Consequences of Food Provisioning

Attracting charismatic species, such as large carnivores, for ecotourists to view at relatively close quarters is a popular and highly lucrative industry. For example, nightly bear shows at the garbage dumps in Yellowstone National Park were very popular with tourists during the early twentieth century. Indeed, the grizzly bear population in Yellowstone declined significantly after the closure of these dumps in 1970 and 1971 [44], while a number of habituated animals reportedly moved into campgrounds and tourist areas, increasing the risk of human-bear conflicts. Food provisioning is still used occasionally for tourists to observe black bears (*Ursus americanus*) in North America [45] but remains controversial due to the potential impacts on the target species and possible risks for tourists seeking close encounters with dangerous animals. A black bear feeding station in Quebec, Canada, altered the long-term movement, habitat selection, and densities of animals, which could result in greater human-bear conflict [45]. Elevated densities of animals due to food provisioning can also have implications for the transmission of disease, such as tuberculosis in white-tailed deer (*Odocoileus virginianus*) [46]. At tourist-fed sites, southern stingrays (*Dasyatis americana*), usually solitary foragers, had artificially high densities and experienced greater parasitism, lower body condition, and more injuries, potentially impacting survival and reproductive success in the long term [47].

Although active food provisioning of large mammals in natural areas is now less common and often discouraged (although see [42]), the situation is quite different

in marine habitats. Shark diving, for example, has become particularly popular over the past few decades, generating hundreds of millions of dollars in revenue every year [48]. Cage diving operations can alter the long-term use of specific sites by great white sharks (*Carcharodon carcharias*), which may alter predator-prey dynamics [49], while also potentially increasing the chance of divers, beachgoers, and swimmers being attacked [50].

Food provisioning can also occur in an uncontrolled or unintentional manner, when for example, ecotourists feed wild animals directly (e.g., primates [50, 51]) or when waste is disposed of inadequately [44]. Animals can become reliant on this readily available resource, such that they no longer search for their own food, which can have population consequences (e.g., as seen with the decline in Yellowstone's grizzly bears once the food source was removed; [44]). The health of Barbary macaques (*Macaca sylvanus*) fed by tourists was negatively impacted in the long term [51], while the unregulated feeding of sea lions (*Zalophus californianus*) at haul-out sites in the USA has led to a number of attacks on tourists, likely driven by an increase in boldness and aggression at the population level [50].

While the majority of the literature focuses on the negative aspects of food provisioning, it is important to note that there have been a number of positive examples, in terms of benefits to the species and conservation more generally. A recent review outlined the conservation benefits associated with the popularity of shark diving [48]. Supplemental feeding has also been successfully used to promote the recovery of the endangered Mauritius kestrel (*Falco punctatus*) [52] and dwindling vulture populations that benefitted from widely used "vulture restaurants" [53]. Nevertheless, there can be unintended consequences of supplemental feeding that have the potential to alter population and community dynamics through increased competition (e.g., the endangered blackbuck *Antilope cervicapra* was negatively impacted as a result of elevated densities of other herbivore species after provisioning), altering predator-prey relationships (e.g., sharks were attracted to food leading to greater number of attacks on dolphins) and advancing the timing of reproduction (e.g., a range of fed-bird species laid their eggs earlier) [50].

3.5 Habitat Degradation

Although one of the goals of ecotourism is to protect natural habitat, there are a range of environmental costs associated with providing large numbers of visitors with access to natural areas, which include the use of limited resources (e.g., water), construction of infrastructure, fragmentation of habitat, human waste and litter, and chemical, light, and noise pollution. All of these can reduce habitat quality, with negative impacts on wildlife, especially in close proximity to tourist infrastructure. Indeed, habitat loss and degradation has been identified as the primary threat to biological diversity worldwide [54].

Successful ecotourism efforts draw high numbers of tourists that can lead to concerns over physical and chemical habitat degradation. Direct physical impacts like trampling can alter vegetative cover, leaf litter, and soil composition, thereby

degrading habitat and, for some animals, destroying physical shelter from high temperature, desiccation, and predation [55]. The infrastructure associated with ecotourism, including roads, recreational trails, and resort development, is another source of physical habitat degradation, as it reduces and fragments wildlife habitat [13, 56, 57]. Indeed, in endangered urban forests in Australia, the level of fragmentation caused by recreational trails was similar to that caused by urban development itself [57]. Such habitat fragmentation is known to have negative consequences for wildlife by restricting animal movement and severing landscape connectivity, critical to the persistence of wildlife populations and a vital component of biodiversity conservation [54, 58]. Solid waste and chemical pollution in air and water also pose a serious threat to wildlife [59]. Though little is known about the relative contribution of ecotourism to these forms of pollution, it is likely relatively minor compared to urban and industrial sources of pollution [55]. That said, it is estimated that tourism (transport and activities) accounted for 5% of global anthropogenic CO_2 emissions in 2005 [60].

The infrastructure and activities associated with ecotourism also introduce light pollution into habitats, with effects on wildlife that are just beginning to be explored. Artificial light can negatively affect populations by disorienting animals (e.g., hatchling sea turtles on natal beaches), by "trapping" nocturnally migrating birds that only travel in the dark, and by reducing the reproduction of nocturnally mating animals (e.g., frogs; [61]). Some animals are repelled by light pollution thereby reducing the habitat available to them, while others are attracted to it, sometimes fatally, as documented in nocturnal seabirds [62]. Artificial lighting can also alter predator-prey relationships by increasing the foraging of diurnal animals at night, reducing the foraging of nocturnal animals, and in some cases concentrating predation in localized areas by attracting prey (e.g., moths) to light sources [61]. Lighting can also affect the vertical distribution of aquatic invertebrates in the water column, which may have ecosystem effects by increasing algal abundance and reducing water quality [61].

Noise is a form of pollution that has received increasing attention over the past two decades for its impacts on a wide range of terrestrial and aquatic wildlife [63]. Ecotourism can generate substantial amounts of noise, particularly as a consequence of vehicle use. There are also disturbances associated with subtler noise sources, such as the conversation of tourists who are in close proximity to wildlife [64] and mobile phone ringtones. Introduced anthropogenic noise can mask important sounds that animals rely on for finding mates, locating prey, avoiding predators, parent-offspring interactions, and territorial defense; it can also startle or threaten animals, distract attention away from approaching danger, and cause physiological stress. Although the most well-documented responses to noise are behavioral, several studies have also demonstrated that continued exposure can affect survival and reproduction [63]. For example, chronic road noise can lead to reduced pairing success, fewer eggs, and smaller young among birds [65–68]. Noise in prime stopover habitat reduced the ability of migratory birds to gain body condition, which is vital for survival during the next stage of their journey [69]. On the other hand, noisy conditions can improve the reproductive success of prey species, by providing a shelter from disturbance-sensitive predators, which has the potential to alter dynamics of ecological communities [70].

3.6 Biological Invasions

People visit natural areas from diverse locations, presenting a significant opportunity for non-native organisms to be transferred from one environment to another. A recent meta-analysis demonstrated that the abundance and species richness of non-native species are significantly higher in tourist areas compared with control sites, a relationship that holds for both terrestrial and aquatic habitats [71]. The majority of invasive species transferred via tourism are plants that have been moved inadvertently as seeds on belongings, shoes, or clothing. For example, Arctic species such as chickweed (*Stellaria media*) and yellow bog sedge (*Carex* sp.) were found on the clothing of tourists and researchers visiting Antarctica [72]. The zebra mussel (*Dreissena polymorpha*) is a prime example of an animal introduced as a result of ecotourism. Originally native to Russia, this species has spread rapidly through waterways in US and Western European protected areas, with recreational boating being implicated as a key vector [71]. Their voracious feeding reduces the amount of microorganisms available to other aquatic species that rely on this food source, and they attach themselves to other native mussel species (i.e., biofouling), which exacerbates susceptibility to environmental stressors and extirpation. The ease with which boats can transfer non-native species (e.g., the stalked benthic diatom *Didymosphenia geminata* in New Zealand [73]), coupled with the high visitation rates in many marine protected areas, presents a major risk to effective conservation at these sites [71].

Tourism can also indirectly lead to the introduction of non-native species through infrastructure (e.g., hotels and lodges) that is staffed by people who bring domestic animals with them, such as cats and dogs. Domestic cats are highly effective predators, and their release into the environment can have potentially catastrophic impacts on native prey species [74]. Likewise, dogs are considered a threat to biodiversity by directly killing, transmitting disease to, and outcompeting native wildlife [75]. Although the role of ecotourism in the spread of domestic animals is small compared to the number of free-ranging cats and dogs living in local communities, it can exacerbate the problem and increase exposure of wildlife to non-native species within natural areas.

3.7 Disease

Just as ecotourists can present a major route for the introduction of non-native species, they can also serve as vectors of potentially deadly microorganisms and parasites. The desire for interactions with wild primates has generated a profitable ecotourism industry, which many believe is crucial in securing funding for conservation efforts and protection for primates from poaching. Nonetheless, these benefits must be balanced against the increased risk of disease transmission that could have catastrophic impacts on remaining wild populations when primates are in close proximity to humans [76]. Humans are direct vectors for a number of diseases that can be harmful to wildlife, particularly primates, which are susceptible to similar

diseases because they are closely related in evolutionary terms. There is now considerable evidence to suggest that a range of respiratory diseases (e.g., influenza, common cold, pneumonia), measles, and stomach parasites have been transmitted from humans to chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) on multiple occasions, particularly affecting individuals that are habituated to human presence [76, 77]. For example, the Taï chimpanzee research project in Ivory Coast experienced five distinct outbreaks of human respiratory diseases over a period of 7 years with mortality rates of the affected groups reaching 19% [77]. Strict hygiene protocols and vaccination requirements must be enforced to reduce the risk of disease transmission, while field methods are urgently required to treat and vaccinate wild apes [77].

Outside of primates, there has been limited research on the spread of disease from tourists to wildlife. A study conducted in Thailand demonstrated that coral species exhibit elevated levels of disease near highly used dive sites, likely because tourism drives stressors, such as increased sediment, nutrient enrichment, and physical damage that increase the incidence of coral disease [78]. Additionally, the dramatic rise in human visitation to Antarctica has been identified as a potential threat to penguins, because limited previous exposure to pathogens due to geographical isolation and the extreme climatic conditions of the Antarctic have likely made penguin species immunologically naïve to diseases such as influenza and salmonella [79]. Evidence from zoos supports this, with captive penguins being highly susceptible to a number of infections. Thus, ecotourism combined with other stressors, like a changing climate and increased pollution, may further exacerbate the vulnerability of penguins to a potential disease outbreak.

Given that rare and endangered species are often confined to protected areas and exist in comparatively small, isolated populations, the threat of disease to their long-term existence is very real. Ecotourists may also inadvertently introduce a deadly pathogen indirectly on boots or clothing. In such cases, bacteria or viruses released into an environment where there is no natural resistance can quickly spread through naïve populations. For example, heavily used trails in central California had much higher numbers of *Phytophthora ramorum*—a pathogen that causes sudden oak death—in the soil compared with areas that were off the trail, suggesting that the dispersal of the pathogen was driven by human activity [80].

Conclusions

We have outlined how ecotourism and associated activities can have a variety of ecological consequences for wildlife. In summary, there is substantial evidence to indicate that ecotourism is not a benign activity with negligible disturbance but can in fact have major implications for the reproductive success, survival, and long-term viability of a number of populations of species, particularly those that are rare, geographically isolated, and/or sensitive to disturbance. These impacts are driven by the indirect effects of human presence on the abundance, distribution, reproductive success and survival of species that are disturbance sensitive. Visitors can also have direct effects, which include causing mortality, providing

artificial food resources to encourage sightings of elusive species, contributing to habitat degradation and fragmentation, introducing non-native species, and being vectors for disease. Ultimately, this can have far-reaching impacts across the ecosystem, generating cascades that ripple throughout the food web. Despite the potential impacts we have reviewed, tourism remains a key source of revenue for conservation and provides important experiences for people to become advocates for wildlife, while educating them about threats to biodiversity. There is no doubt that tourism can be a vital tool in successful conversation, but the potential negative impacts associated with human presence need to be understood and managed sustainably in concert with the myriad of other factors that threaten the long-term persistence of wildlife.

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