

Review

How Nature-Based Tourism Might Increase Prey Vulnerability to Predators

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Tourism can be deleterious for wildlife because it triggers behavioral changes in individuals with cascading effects on populations and communities. Among these behavioral changes, animals around humans often reduce their fearfulness and antipredator responses towards humans. A straightforward prediction is that habituation to humans associated with tourism would negatively influence reaction to predators. This could happen indirectly, where human presence decreases the number of natural predators and thus prey become less wary, or directly, where human-habituated individuals become bolder and thus more vulnerable to predation. Building on ideas from the study of traits associated with domestication and urbanization, we develop a framework to understand how behavioral changes associated with nature-based tourism can impact individual fitness, and thus the demographic trajectory of a population.

How Might Nature-Based Tourism Influence Wildlife Behavior?

Nature-based tourism (see [Glossary](#)) and **ecotourism** have both become very popular leisure activities that constitute a business worth millions of dollars annually [1]. Terrestrial protected areas around the world receive approximately 8 billion visitors per year [2]; a number that is greater than each human on earth visiting a protected area once a year. Marine and inland waters also attract millions of tourists annually [3]. More invasive wildlife tourism, such as that in which visitors closely observe or swim with marine mammals, increased 30% between 1998 and 2008, involving 13 million people annually [4]. Inland waters also attract tourists, with, for instance, 242 000 people that, in 2012, swam along a riverine trail in Bonito (Center-West Brazil) to observe fish¹.

However, these interactions between wildlife and humans, even when the welfare of animals is considered, often change the behavior of wild animals. For example, it is well documented that individuals of many species that have benign interactions with humans undergo **habituation**-like processes leading to some degree of human tolerance [5,6]. Nonetheless, although frequent, tolerance is not a necessary outcome and the development of tolerance is influenced by various factors ([Box 1](#)).

Reserve managers or ecotourist providers may explicitly habituate animals so as to ensure client satisfaction. For instance, Ugandan park rangers habituated chimpanzees through daily visits in Kibale National Park so as to improve the quality of chimpanzee-watching ecotourists [7].

Food provisioning by tourist operators and guides has also led to documented changes in behavior. For instance, previous studies have shown that individuals learn to anticipate feeding

Trends

Nature-based tourism has become a very popular leisure activity in the past years and is a substantial conservation issue because it modifies the behavior and community structure of animals.

Nature-based tourism might modify behavior in ways similar to that seen in domestication and urbanization, as well as modify the population dynamics of species.

Domestication and urbanization reduce the fearfulness and antipredator behavior of animals around humans attributable to both habituation towards humans and displacement of predators.

Nature-based tourism could negatively influence behavioral responses to predators. This could happen indirectly, where human presence decreases the number of predators in a given area, and more directly, where individuals become bolder following habituation, resulting in a boldness syndrome that could increase vulnerability to predators.

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Box 1. What Governs Habituation-like Processes?

We assume that most individuals will respond to their first human encounter as an acutely stressful experience and therefore interpret humans as potential predators [83]. It is worth noting that species seemingly vary in how they deal with exposure to a first human (i.e., boldness at the species level [84]). Following this initial encounter, if the response to humans declines over repeated exposures, then the animal may accurately be described as having habituated to humans. By contrast, if the responsiveness is enhanced with repeated human exposure, then the animal could be described as having sensitized to humans. Both habituation and sensitization occur over time and lead to different degrees of tolerance. Because tolerance is measured at a point in time, we can view it as a behavioral 'state' (see [85] for a systematic review of the use and misuse of habituation, tolerance, and sensitization). While some species appear to go through habituation-like processes when facing chronic human exposure, other sensitize to increased human presence. This could happen, even in closely related species. For instance, jackass penguins (*Spheniscus demersus*) [86] and Magellanic penguins (*Spheniscus magellanicus*) [87] appear to habituate to human presence, while yellow-eyed penguins (*Megadyptes antipodes*) sensitize and thus are disturbed by humans [10]. Which variables drive habituation-like processes? In the Magellanic penguins, for instance, the rate of habituation depends on the intensity of tourist visitation [88], a variable that also has been observed to drive habituation in other species (e.g., Mediterranean mouflon [70]). The type of stressor (i.e., approach or capture [89]) and the type of tourism are also important factors that influence the degree of habituation (pedestrians, cars, bikes, horses [90]). Spatiotemporal variables such as time of the day, season (influencing reproduction, territoriality, migration), and food availability have been identified as important as have life history traits of a species such as the duration of parental investment and body size [12]. At the intraspecific level, sex, temperament, and previous experience with humans affect whether yellow-eyed penguins habituate or sensitize to repeated human visitation [91]. Calm individuals were more likely to habituate, as were females.

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events (e.g., [8]) and that provisioning food might increase aggression within and between species, resulting in wounding [1]. In addition to the short-term behavioral changes, aggregation following feeding events could also modify community structure by affecting species distribution, diversity, and richness [9].

The ultimate consequences of this increased tolerance to humans are diverse. Indeed, human presence has been shown to impair different fitness-related traits such as reproduction [10] and offspring provisioning [11]. To better understand how tolerance emerges and how it may influence fitness, we need to step back and develop a more fundamental understanding of how animals respond to humans.

How do Animals Respond to Humans?

Animals can interact with humans in three main ways: (i) they can be forced to interact through a taming process that ultimately may lead to **domestication**; (ii) they can move to or remain in a location where humans are settled (e.g., by **urbanization**); or (iii) they can passively interact with humans as a consequence of ecotourism or nature-based tourism. Although these three types of interactions act at different spatiotemporal scales (i.e., local versus landscapes and evolutionary versus ephemeral), they all involve similar cognitive processes – habituation or sensitization leading to approach or avoidance [12] – to the same nonthreatening stimulus (humans). Importantly, the outcome of these interactions could then influence the outcomes of predator–prey interactions. In this sense, habituation is often seen as synonymous with taming [1], as it would 'increase the ease of observation of animals by making them unnaturally tame to approach by humans' ([13], p. 35).

We develop a framework that identifies how antipredator behavior can be modified following human exposure in different contexts and how that might be deleterious for wild animals when facing natural predators or when humans hunt or illegally poach them. This framework links processes that occur over the short term (i.e., habituation) and longer term (i.e., domestication) to those that occur when animals interact with humans in both urban and more natural areas. It highlights how selection for **boldness**, which might result from interacting with humans, can make those individuals particularly susceptible to predation.

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