

# Transgenerational Consequences of Human Visitation

# 4

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**Fig. 4.0** Ecotourist at hippo (*Hippopotamus amphibius*) pool, Laikipia District, Kenya. Photo credit Daniel T. Blumstein

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## 4.1 Introduction

Nature is rapidly changing as a consequence of human exploitation of natural resources, occupation of increasingly large areas for farming, industrial-scale forestry, and the huge worldwide fisheries industry, and the construction and growth of cities. Furthermore, humans reach even the most remote parts of the world in their quest for distant tourist attractions that include rare and pristine habitats that provide novel experiences for visitors. Ecotourism, defined as tourism specifically associated with natural resources, constitutes one such important source of change in how we exploit natural resources. Ecotourism has potentially profound consequences for the behavior of animals.

While ecotourism may benefit local communities economically, it may also have significant costs for such communities [1] and for the wild animals that are the focus of ecotourism [1]. The proximity of humans and their domesticated animals imposes strong natural selection on the behavior of wild organisms because some behaviors and some species are able to adapt to human exposure while others do not. Thus, animals in anthropogenically impacted habitats have only three options: adapt to human proximity, disperse to suitable areas away from humans (if available and suitable), or perish (e.g., [2, 3]). Numerous rare and undisturbed animal and plant populations on even the most remote islands around the world have gone extinct during the last century due to the presence of humans and their domesticated followers, such as dogs, cats, goats, and pigs, and also from the impact of wild species such as mice, rats, and numerous others (e.g., [4]).

In this chapter, I review the scarce and scattered literature dealing with changes in animal behavior across generations as a result of human contact, as well as critically assess the relative importance of their potentially underlying mechanisms.

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## 4.2 Changes in Animal Behavior as a Result of Human Proximity

Animals have repeatedly been shown to change their behavior in response to humans. Human proximity may result in reduced fear responses because animals experience reduced risks of predation around humans (e.g., [5, 6]). A classic example is the tameness of animals in urban environments, where individuals often stay put rather than fleeing when a human approaches them, which is the opposite of the ancestral behavior in natural or rural habitats [6]. Bird species that are the target of ecotourist activity or species that occur in areas frequented by tourists likewise show reduced flight-initiation distance (which is the distance at which animals flee when approached by a human) and flee shorter distances when disturbed [7–10] (but see also [11]) and reduced vigilance [12] (Fig. 4.1).

Numerous animals are adapted to human-impacted environments, but FID still varies with cost of fleeing related to food supply, and human-induced climate change affects perching behavior. Here I review such factors showing effects of humans on behavior thereby indirectly suggesting effects of ecotourism on behavior. In other



**Fig. 4.1** Tolerant Galápagos sea lion (*Zalophus wollebaeki*) resting on a bench near the main public pier, Isabela Island. Photo credit Daniel T. Blumstein

words, this provides a review of the underlying mechanisms and thus the evidence for effects of human contact, including ecotourism, on animal behavior (see also Chap. 2). A classic example has to do with barn swallows (*Hirundo rustica*), one of a number of species that have adapted to human proximity and now almost exclusively breed in association with humans and their habitation. Hence, it is surprising when such species still show dramatic changes in behavior across just a few generations. Barn swallows in a Danish breeding population showed a dramatic increase in flight-initiation distance from a mean of 5.1 m in 1984 to a mean of 15.9 m in 2013 [13]. This change was positively linked to increased spring temperatures that produced an earlier and larger peak in insect food availability.

Rapid changes should be generally expected. For instance, another example of rapid change in behavior across generations is a study of positions in the vegetation used by birds for singing. I investigated the position in the vegetation where a community of breeding birds was singing in 1986–1989 and again in 2010 [14], some 20 years after initial effects of climate warming. The choice of sites where animals display constitutes a compromise between transfer efficiency of the display to recipients and the costs of display in terms of exposure to predators. Singing birds' songs are best transmitted when they sing high up on exposed perches, the same position that may increase their vulnerability to predation. The change in where birds sang followed a period of climate change during which temperatures in spring increased

on average by 20% and precipitation had increased by 30%. Song post height chosen by singing male birds increased in species that had increasing population trends showing an effect of higher population density on the height at which males of different bird species sing [14]. There were additional effects of habitat and intensity of sexual selection on song post height in this study [14].

There are also examples of changes in fear response across generations. For example, large mammals within the Chernobyl Exclusion Zone have increased in abundance since 1986, when humans evacuated this large area due to radioactive contamination [15]. However, the behavior of animals has also changed. For example, two bird species, great tits (*Parus major*) and blackbirds (*Turdus merula*), showed reduced flight-initiation distance at sites in the Chernobyl Exclusion Zone with higher levels of radioactive contamination during the last 30 years [16]. In great tits, flight-initiation distance decreased from a mean estimate of 16.5 m to 2.2 m across a radiation gradient. Flight-initiation distance of blackbirds in the same area changed on average from 18.1 m to 1.4 m across the radiation gradient during the same period [16]. These examples provide evidence of rapidly changing antipredator behavior when the selective pressure changes.

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### 4.3 Mechanisms of Transgenerational Change in Behavior

Four possible mechanisms can explain why some animals are able to live in close proximity to humans, while others are not: microevolutionary changes, epigenetic changes, habituation, and phenotypic sorting (Table 4.1; [5]). I will define each below and note that while these theoretical alternatives are all viable possibilities, there are few documented cases that permit us to discriminate among them.

#### 4.3.1 Microevolutionary Changes in Behavior

Microevolutionary change is a modification in the genes responsible for a given behavioral or physiological trait (Table 4.1). Microevolutionary change in behavior implies directional selection on individuals with a specific allele (i.e., the variant located at a specific gene that expresses a specific behavior) with superior survival or reproduction and heritability (for which there is empirical evidence [13]), which results in a change in behavior over time due to the increase in frequency of specific genes conferring these advantages [13].

Two examples of reduction in flight-initiation distance may be attributed to microevolutionary change. First, animals on islands have lost or greatly reduced their fear of humans after divergence from their mainland ancestors that reacted to humans by fleeing [17–20]. Second, domesticated animals have likewise reduced their fear of humans in the process of domestication because animals that became associated with humans were more likely to survive and/or reproduce successfully [17, 21, 22].

**Table 4.1** Four different kinds of mechanisms underlying transgenerational changes in escape behavior and other types of antipredator behavior

Mechanism of change	Characteristics	Transgenerational change	Example	Suggestions for research
Microevolutionary change	Heritability, selection, and response to selection and temporal trends in change in antipredator behavior	Transgenerational change should be feasible but only reflect response to selection as predicted from the breeder's equation	Divergence in behavior between island and mainland populations	Selection experiments and experimental evolution experiments should change antipredator behavior in a predictable way
Epigenetic change	Change in antipredator behavior linked to structural change in DNA conformation or other change in transcription of genes (e.g., noncoding RNA)	Transgenerational change should be a consequence of change in epigenetic mechanisms	Divergence in behavior between urban and rural habitats	Experimental alteration of stress level and other factors inducing epigenetic changes should affect antipredator behavior
Habituation	Decrease in intensity of antipredator behavior as a consequence of repeated exposure to a nonlethal stimulus over time	Transgenerational change should only occur as a consequence of temporal trends in the number of repeated stimuli	Change in antipredator behavior over time	Tests for decrease in intensity of antipredator behavior of an individual following repeated exposure to stimuli
Phenotypic sorting	Nonrandom distribution of individuals based on their personality (e.g., bold and shy individuals)	Transgenerational change should only occur if the perceived risk in a given habitat changes over time	Systematic spatial differences in antipredator behavior	Experimental differences in perceived risk of different habitats should result in change in distribution of phenotypes

### 4.3.2 Epigenetic Changes in Behavior

Epigenetic changes are produced by modifications of genes, but these changes are not transmitted across generations in exactly the same way genes are (Table 4.1). Rather, epigenetic changes of the genome work by modifying how genes are copied by interfering with the process of DNA expression called transcription. Certain stressors, including environmental stressors, can lead to methylation (the addition of a methyl

group to DNA) of specific genes, which prevents these genes from being copied [23]. In some cases, these nongenetic modifications can persist for several generations. Regardless, these epigenetically modified genes may have behavioral consequences.

A recent study showed that DNA methylation affected exploration and novelty-seeking behavior in urban individuals of great tits but not among individuals living in nearby rural habitats [24]. The addition of methyl groups to DNA increased by 1–4% in urban compared to rural birds for all loci and tissues investigated [24]. Similarly, another study [25] showed that wariness of black swans (*Cygnus atratus*) was partly determined by a specific genotype associated with novelty seeking [26] and that individuals with warier behavior settled in less disturbed aquatic habitats than individuals seeking novel habitats. The DRD4 genotype that was modified is responsible for the gene involved in the dopamine receptor D<sub>4</sub>, which affects production of the neurotransmitter dopamine [26].

Rapid changes in antipredatory behavior in captive-bred birds have been documented to occur over just a couple of generations [27]. It is unlikely that these changes in captive-bred birds are the result of habituation, phenotypic sorting, or other phenotypically plastic responses because they have no known mechanisms of cross generational effects. Given the velocity at which these changes in antipredator behavior occurred, it was also unlikely caused by microevolutionary responses to selection, which leaves epigenetic changes in DNA transcription as the likely mechanism. And, if such changes in captivity occur in the wild, it is likely that ecotourists drive such epigenetic changes.

### 4.3.3 Changes in Behavior Caused by Habituation to Humans

Habituation arises as a consequence of repeated exposure to a stimulus, such as the close proximity of humans giving rise to ever-weaker responses over time in the absence of predation attempts (Table 4.1). Groves and Thompson [28], in their classical review of habituation, presented the dual-process theory of phenotypically plastic responses to repeated stimulation. Plasticity of behavior implies that the same individual may differ in behavior depending on its history of exposure to stimuli (e.g., the degree of repeated encounters with humans in the past). When animals are repeatedly exposed to a novel stimulus (such as well-meaning ecotourists in a pristine location), they may first respond aversively, but with repeated exposures, they may reduce the magnitude of their response and habituate. Neurophysiological experiments indicate that these two processes involved in habituation have separate and specific neuronal substrates implying that the two components of habituation are truly independent [28]. Blumstein [29] recently reviewed the habituation concept and concluded that intensive research has led to well-supported generalizations about mechanisms of habituation. A true “natural history” of habituation and tolerance that explains why some individuals, populations, and species become habituated and tolerant, while others do not, would help us predict how species respond to humans and anthropogenic stimuli. However, such a natural history has so far eluded scientific inquiry [29].

While habituation may result in a change in behavior, including fear responses of animals to humans, there is little evidence of habituation affecting fear response in standardized stimulus presentations in marked individuals ([5]; but see [30]). From an ecotourism perspective, habituation-like processes can allow animals to better tolerate humans, but it cannot be responsible for animal behavior changing across generations.

#### 4.3.4 Changes in Behavior Caused by Phenotypic Sorting

Phenotypic sorting occurs when individual animals that differ in their behavior (for instance, some individuals may be bold, while others are shy) are distributed non-randomly across habitats with different levels of human disturbance ([13]; Table 4.1). A large literature has documented the so-called temperamental [31] or personality [32] differences in a wide variety of species. These differences may lead to individuals differentially tolerating ecotourists (see also Chap. 2).

A classic example of phenotypic sorting is the distribution of gulls (*Larus occidentalis*) in the proximity of humans in California. Tame gulls are found near humans, whereas warier gulls are found at greater distance from humans [33]. Perhaps differences in behavior across generations due to phenotypic sorting could also explain differences in behavior of urban and rural animals [6].

While phenotypic sorting represents, at least theoretically, a feasible explanation for differences in behavior of individuals among sites, there are, to the best of my knowledge, no examples of phenotypic sorting changing the behavior of related individuals across generations. However, if certain types of individuals are more likely to be associated with humans, and these animals differentially survive or reproduce because of their tolerance to humans, there could be genetic changes in the larger population over time.

#### 4.3.5 The Biological Effects of Human Contact on Wild Animals

Many wild animals have become associated with humans to the detriment of animals and humans alike. As stressed above, frequent human exposure often results in a reduction or loss of fear responses of wildlife to humans, which can constitute a dangerous “ecological trap” [34, 35]. While reduction or loss of fear of humans may be beneficial for ecotourists whom usually seek close experiences with wild animals, it may be detrimental if these animals become more easily hunted for bush meat [1]. Human predation and exploitation of fishes and other marine species may explain increased fear in coral reef fishes, which are otherwise important resources for ecotourism [36].

Several of these species frequently exposed to humans are now known to be vectors of pathogenic parasites, such as rodents carrying hantavirus [37], bats carrying MERS virus [38], and Asian palm civets (*Paradoxurus hermaphroditus*) being the vector of SARS virus [39], all of which infect humans and have serious and even

lethal effects [40]. Such animals can be dangerous to humans because of their vector activity but potentially also to other animals that may constitute reservoirs of virus or because animals transmit viruses to novel hosts [38, 39].

A well-known example is the presence of antelopes, rhinos, giraffes, and numerous other species at waterholes in dry parts of Africa, which sustain a high population density at sites where density usually was consistently low [41]. Such a change in behavior can cause significant changes in habitat structure, such as change in density and composition of the vegetation, which previously only to a small extent was exploited by herbivores in the presence of artificial water bodies alone [41].

Another example is attraction to feeders or supplemental food, which occurs throughout the world [42] (Fig. 4.2). Because animals become aggregated at feeders, feeders may facilitate the spread of pathogens [42]. Feeders can also advance the timing of annual events such as migration, reproduction, and dispersal because such events are affected by body condition, which in turn is determined by food intake [42]. Feeders may also increase the rate of reproduction and the rate of survival with consequences for population density [42]. A particularly striking example of attraction to feeders is the feeding of great white sharks (*Carcharodon carcharias*) in South Africa, Australia, and Baja California as a means of attracting “extreme” tourists. Such attraction may prove fatal if shark feeding also results in the attraction of sharks to humans at nearby beaches.



**Fig. 4.2** Caribbean hermit crabs (*Coenobita clypeatus*) attracted to a garbage dump. St. John, Virgin Islands. Photo credit Daniel T. Blumstein



While effects of tourism on wildlife are well recognized in temperate countries (reviews in [43–45]), very little is known about whether visitors have any influence on rainforest animals, which constitute the majority of terrestrial animal diversity. The rare empirical evidence available indicates that even low numbers of visitors can change activity patterns of animals or cause rainforest animals to flee from potential foraging or breeding sites (e.g., [46–49]). Birds in tropical habitats are known to have much longer flight-initiation distances than conspecific or congeneric populations in the temperate zone [50]. Such dramatic differences in behavior between tropical and temperate zones are expected from life history theory (the theory dealing with the optimal timing of reproduction, clutch size, number of reproductive events, and the timing and rate of senescence) because animals in the tropics have low reproductive rates and high annual adult survival rates, while this is the opposite in the temperate climatic zones [50]. Such effects can reduce reproductive success and therefore hamper conservation goals in protected areas, even when ecotourism is supposed to protect such vulnerable species from human disturbance. Such antagonistic responses to human exposure provide the basis for potential conflicts between conservationists and the ecotourism industry. This may create trade-offs between conservation, on the one hand, and income from ecotourism on the other. That is because negative impacts on wildlife reduce both the value to ecotourists and the economic value of the visited area.

Despite several examples of human tolerance documented here, it is imperative to highlight that numerous animals living in the proximity of humans do not show reduced fear responses to humans. Many animals never managed to adapt to humans because they were all killed before they were able to change their behavior. The solitaire (*Pezophaps solitaria*), the dodo (*Raphus cucullatus*), the moas (Dinornithiformes), and numerous other animals on oceanic islands in the Pacific and the Indian Oceans belong to this category of species that were insufficiently afraid for their own good. Hence, there are clear limits to the ability for some species to adapt to rapidly changing environments when humans first arrive. Most such extinct species had large body sizes, which implies long generation times and little prospect for adaptation to rapidly changing human-impacted environments [51].

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#### 4.4 Future Directions

There are several examples of how animal behavior may reveal some of the intricacies of behavior to a recently altered human-impacted environment. A recent study showed that elephants (*Loxodonta africana*) can make subtle distinctions between language and voice characteristics of humans to correctly identify the most threatening individuals on the basis of their ethnicity, gender, and age [52]. In this study elephants were frightened by exposure to the language of one tribe that commonly kills or wounds elephants, while they reacted without fear when the scientists played back recordings of the language of another tribe that does not impose damage or death on elephants [52]. This study provided the first detailed assessment of human voice discrimination in a wild population of a large-brained, long-lived mammal,

and it highlighted the potential benefits of sophisticated mechanisms for distinction between different subcategories that differ in fear response within a single predator species. Given that humans have imposed strong selection pressures on animals, we can expect many other examples of animal antipredator behavior being influenced by interactions with specific groups of humans, such as different ethnicities, professions (farmers vs. pastorals), and humans engaged in different activities (hunters vs. birdwatchers).

Future prospects for research include the study of changes across generations in behavior in the tropics where most biodiversity is located and where the importance of habitat change and exploitation is likely to be the most dramatic during coming decades. Indeed, I urge biologists involved in ecotourism projects to monitor changes in fear responses of animals to humans over time before ecotourism begins and also after initiation of ecotourism activity. I also emphasize the importance of documenting not only the benefits of ecotourism but also the changes in associated costs, such as increased risks of hunting and the risks of disease transmission among animals and between animals and humans. Finally, I suggest that the exposure of rare animals to humans in an ecotourism context may result in increased levels of habituation over time that eventually may further endanger such species. Ecotourists may inadvertently transmit pathogens from domestic or pet animals to rare species in environments where such pathogens are otherwise absent. Likewise, habituation of rare animals to humans may result in loss or reductions of fear responses that would in turn result in an increase in risk of mortality due to hunting or poaching or capture for the pet trade.

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### Conclusions

I have reviewed a small but diverse literature on transgenerational changes in behavior with significant importance for assessment of the impacts of ecotourism and other kinds of human exploitation of wild animals. Such changes in behavior may be better documented in coming decades as more studies of behavior enter the stage with sufficiently long-time series to allow rigorous analyses of underlying mechanisms. Finally, ecotourism may, despite creating benefits for local communities, have a number of costly side effects for animals due to habituation to human exposure and proximity, eventually increasing the risk of transmission of pathogens and the risk of hunting, poaching, and capturing of wild animals for the pet trade. Some of these potential dangers can be mitigated if carefully monitored as a part of ecotourism.

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