CellPress

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.

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.

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 fish[i].

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

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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 (*Sphenicus 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.

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.

Domestication and Antipredator Behavior

Domestication involves cognitive processes such as tameability and the reduction of aggression, fearfulness, and sensitivity to environmental variation [14]. These processes also occur when animals interact with humans in the wild. Domestication can lead to a progressive loss of antipredator behavior (e.g., [15]). An iconic study of domestication comes from Belyaev's pioneering work on silver foxes (*Vulpes vulpes*). After almost 35 generations of captive handling, 80% of the handled foxes were significantly more docile and responded less fearfully to novel stimuli than nonhandled control lines [16]. Importantly, these behavioral responses were transduced at the physiological level (there was a decrease of corticosteroid production) and accompanied by important physical changes (loss of pigmentation, development of floppy ears, and shorter tails) [16].

In salmonids, domestication also led to reduced physiological and behavioral responses to predators [17,18]. For instance, seventh generation juveniles of domestic Atlantic salmon (*Salmo salar*) had reduced heart rates and lower flight responses to simulated predator attacks than wild salmon [17]. More importantly, when placed in seminatural conditions, the first and the second generation of hatchery-reared juveniles from wild salmon had a significantly reduced antipredator response, compared with their wild counterparts [18].

Similarly, a study recently reported that after only one generation of laboratory breeding, stickleback (*Gasterosteus aculeatus*) were much less responsive to simulated predatory attack when compared with their wild counterparts [19]. Studies such as these highlight the essential role of experience in shaping antipredator responses and that these antipredator responses could be strongly altered within the lifetime of an individual (i.e., early in the domestication process). Nonetheless, we also may have strongly directed responses that are associated with the history of a population [19], and that might persist under relaxed selection [20].

Parental rearing patterns, which sometimes change under domestication, can also influence antipredator behavior. For instance, when compared with goose-raised geese, hand-raised greylag geese (*Anser anser*) suffered higher mortality when exposed to predators and had lower glucocorticoid metabolites (a proxy for physiological stress) in response to social density, handling, and predator stress [21]. In addition, geese were less vigilant and selected less safe nest boxes in which to lay their eggs (J. Hemetsberger, PhD thesis, University of Vienna, 2002). Moreover, a number of studies have shown that rats (*Rattus norvegicus*) that had early experiences with human handling had decreased fearfulness and modified how they coped with stressful situations in adulthood [22].

Livestock depredation by wild mammalian predators (e.g., pumas *Puma concolor*, jaguars *Panthera onca*, and wolves *Canis lupus*) has traditionally been associated with distance to the forest edge, cattle density, and cattle age [23,24]. However, recent evidence also noted that selection for docility impairs antipredator behavior when facing wolves [25]. It should be noted that this behavior was not assessed directly in this study, but rather indirectly through the facial hair whorl pattern [25], which is a phenotypic trait associated with vigilance in cattle.

Hence, there is evidence that domestication directly selects for less wary and bolder individuals that could then suffer higher predation in the wild (Figure 1A, Key Figure). This could also have consequences for animal conservation since early experience (or lack of it) with humans or natural predators can also influence reintroduction success [26]. Although there are, to the best of our knowledge, no studies directly linking human-mediated boldness resulting from domestication to increased predation risk in a reintroduction context, studies have shown that variation in temperament can influence survival in released animals. Bold (including those that were bold

Glossary

Behavioral spillover: a suite of covarying behaviors that is adaptively selected in one context but maladaptive in another context [79].
Behavioral syndrome: a suite of correlated behaviors across situations [80].
Boldness: the way in which an individual and/or population responds to threatening situations. Bolder individuals take more risks [32].
Domestication: the process by which a wild species becomes adapted to humans in captive environments by means of genetic changes and developmental or behavioral changes reinforced every generation [14].
Ecotourism: travel to natural areas in ways that are designed to conserve the environment and improve the well-being of local people.
Flight initiation distance (FID): the distance between the predator or threatening stimulus and prey when the prey begins to flee [35].
Habituation: decreased responsiveness of individuals caused by repeated exposure to a stimulus [81].
Human shield: prey species use humans as shield from natural predation [61]. This could happen in both relatively wild and urban areas.
Human-mediated behavioral spillover: when animals habituated to humans benefit by exhibiting behaviors in close vicinity with tourists (either to acquire food or receive passive protection from predators), but these behaviors become maladaptive when humans leave the area (e.g., the behaviors might increase predation risk).
Individual behavioral reaction norm: the set of behavioral phenotypes that a single individual produces in a given set of environments [82].
Nature-based tourism: travelling in natural places, although not necessarily in a responsible way (see ecotourism).
Personality: consistent individual differences in behavior over time and/or context [59].
Safe-habitat hypothesis: hypothesizes that abundance of native predators decreases in urban areas, reducing predation risk and, consequently, the antipredator behavior of their prey [46].

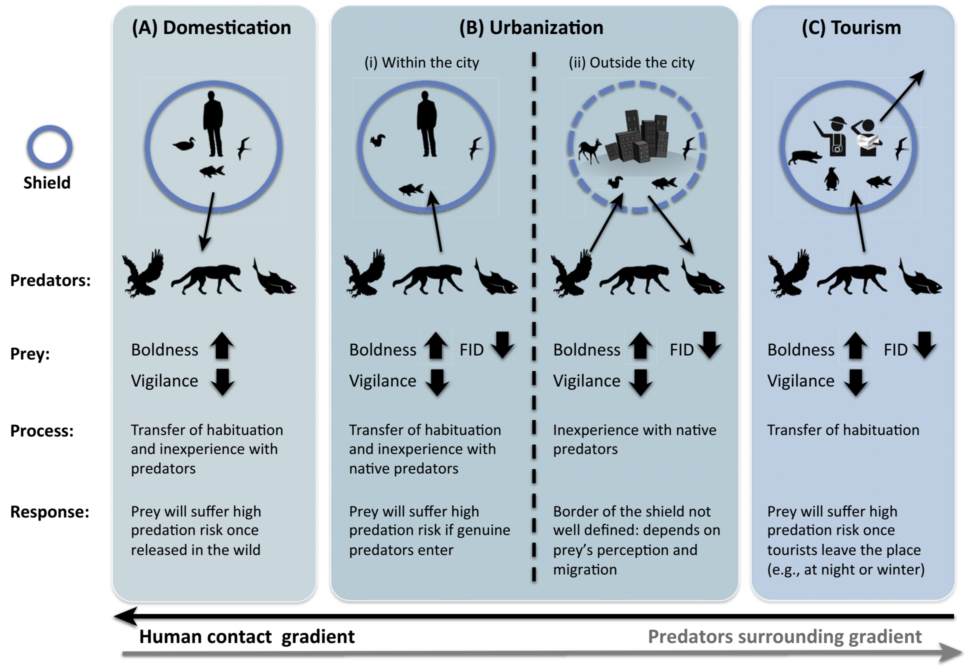

Figure 1. Animals Respond to Human Presence along a Gradient from Domestication to Nature-Based Tourism. (A) During domestication animals become tamed and remain close to humans. This involves a decrease of fearfulness at both behavioral and physiological levels. Such animals are bold towards humans and can suffer enhanced predation risk if released in natural areas. (B) During urbanization (i) within the city, animals can either become bold, or already bold animals are attracted to the city because of the human shield and habituation to humans. These animals will suffer high predation risk if predators enter the city, since they are less alert. A human shield also exists (ii) outside the city (e.g., in rural areas), such that the antipredator vigilance of a prey is attenuated and animals will suffer predation according to their risk perception. (C) When tourists contact wild animals, they create a temporal shield and a boldness syndrome mainly as a result of habituation (through presence alone and/or by food provisioning), mimicking what happens during domestication and with urbanization. This can create individuals more susceptible to predation when tourists leave (see Figure 2). Abbreviation: FID, Flight initiation distance.

towards humans) captive-bred swift foxes (*Vulpes velox*) suffered much higher mortality than their shyer conspecifics upon release to a natural, predator-rich environment [27].

To conclude, antipredator responses may be modified by experience and thus the specific response to predators could be lost or modified by domestication (Figure 1A). Such changes may happen quickly, within a single generation (this is also referred to as 'experience adaptive development' or 'experience adaptive programming'; see [28]), and have fitness consequences.

Urbanization and Antipredator Behavior

Characteristics of Antipredator Responses

Not all species successfully colonize urban habitats [29,30]. Yet urbanization shares similar features with taming processes in terms of the cognitive and physiological traits favored by selection, such as reduced fearfulness, increased aggressiveness, and reduced levels of circulating corticosteroids [31,32]. Species often have reduced **flight initiation distances (FID)** in urban areas when compared with rural areas [33], and the presence of artificial feeding sites also can reduce FID [34]. Importantly, FID is one metric by which individuals (and species) can be compared with respect to their boldness [35].

Urbanization: the process by which animals and plants modify their behavior and physiology to urban environments, with the change from ancestral rural to recent urban environments being the relevant transition [53].

When approached by humans, the average FID of fox squirrels (*Sciurus niger*) was almost seven times smaller in urban areas than in rural areas [36]. For 48 European bird species, FID was on average two times smaller in urban areas when compared with rural areas [31], suggesting that boldness is associated with urbanization. It is worth noting that some species inhabiting urban environments have greater FIDs compared with their rural counterparts, but these urban populations suffer higher predation by sparrowhawks (*Accipiter nisus*) when compared with rural populations [37]. If these species are preferentially targeted by sparrowhawks in towns, then this would explain their higher FIDs (towards humans) in urban areas. Nevertheless, it is difficult to disentangle causes from consequences since species with short FID (e.g., towards humans) could also suffer higher predation resulting from their lower overall reduced fearfulness [38,39]. Hence, it is likely that both predation pressure (which increases FID) and acclimation to urban area (which decreases FID) shapes the FID response of different species towards humans within towns.

Currently, it is not known whether only bold individuals from different species are able to successfully colonize urban areas, or if individuals that settled in cities become bold as a result of rapid behavioral adjustments [40]. Using relative brain size as a proxy for behavioral flexibility [41], one study found that brained species are highly variable in their FIDs and are also more likely to become successful urban colonizers [42]. However, two recent studies did not confirm the effect of relative brain size on urbanization either at the intraspecific or interspecific level [43,44]. Regardless, living in urban areas is associated with a number of cognitive modifications. For example, the structure of communication is modified [30], animals encounter new foraging opportunities [45], and animals reduce their FID in response to humans [37–39].

Human Shields around Urban Areas

Predators can avoid areas with human presence as a result of the so-called '**human shield**' effect [46]. This human shield effect is part of the **safe-habitat hypothesis** [47] that describes how predators are more likely to be absent in urban areas. Such safe habitats have a variety of consequences. For instance, nest predation is drastically decreased inside barns and sheds where predators fear to go compared with adjacent outdoor areas [48]. Human shields and safe habitats effects are important because they can provide a relatively safe area for potential prey [49], making them less vigilant and more likely to allocate their time on fitness-enhancing activities, such as foraging [50]. Human shields can partially explain why prey could be safer in urban areas if urbanization reduces predator presence and diversity [51] and also provides refuge from predators [52]. However, the safe-habitat hypothesis should be treated with caution because some generalist predators, such as cats, do extremely well around humans and tend to be abundant in urban areas [38].

Ecological Consequences: Two Causes, One Possible Outcome

Because habituation-like processes are a widespread mechanism driving human tolerance in many species (but see Box 1), this raises the question of whether habituation to humans can be transferred to genuine predators (Figure 1Bi). This question has been investigated in fox squirrels where individuals that were part of a population habituated to human presence (shown by a decreased FID) were also less responsive to different predator vocalizations, compared with rural fox squirrels [36]. Although this result should be interpreted with caution (as a result of pseudoreplication, i.e., the statistical unit is 'block' within one population), this is the first, and possibly the only, documented case of transfer of habituation between humans and native predators for fox squirrels in a field setting [36].

Møller and Ibáñez-Álamo [53] also found that urban individuals of 15 bird species wriggled, pecked, and bit less when removed from mist nets than rural individuals, suggesting relaxed antipredator behavior in cities. The mechanisms underlying these responses are difficult to isolate. Is the relaxation of antipredator behavior (shorter FID) in urban areas attributable to human shields (Figure 1Bi,ii) and thus reduced predation risk? Or, is this change caused by habituation to nonthreatening stimuli? It is possible that both processes occur simultaneously and hence increase prey vulnerability to predators (Figure 1B). Conducting experiments with predators that are recolonizing urban areas (e.g., foxes in London [54]) might offer an opportunity to disentangle these mechanisms.

Tourist Exposure and Antipredator Behavior

Human presence might thus act in two nonmutually exclusive ways: (i) indirectly, by creating a human shield that relaxes antipredator behavior of prey; and (ii) directly, such that docility and boldness emerge from repeated interactions with nonthreatening humans and these responses are then transferred to other more-threatening sources (i.e., genuine predators or wildlife poachers) resulting from a **behavioral spillover**.

Human Shields in the Wild: An Indirect Pathway

In contrast to domestication and urbanization where exposure to predators is likely reduced, nature-based tourism occurs in the wild, often in relatively intact predator communities (Figure 1C). Nonetheless, extensive human visitation to a wild location could create a temporary human shield. In this sense, human presence has been shown to reduce the probability of encounters between vervet monkeys (*Chlorocebus pygerythrus*) and predatory leopards (*Panthera pardus*) [55]. In another, more recent example, tourist presence (using car traffic as a proxy) also sheltered both pronghorn (*Antilocapra americana*) and elk (*Cervus elephus*) from predators in Grand Teton National Park [56]. This modified prey behavior: pronghorn and elk spent significantly less time in alert postures, more time feeding, and were in smaller groups in the areas with many tourists compared with the areas with fewer tourists [56]. Human presence also directly affects risk perception to terrestrial predators in samango monkeys (*Cercopithecus mitis erythrarcus*), who usually spend more time foraging on the ground around humans [57]. The indirect pathway assumes a process that is similar to relaxed selection where individuals that temporarily live without predators have reduced antipredator defenses (Box 2). This might lead to increased predation when humans leave the place (e.g., at night or winter; the indirect pathway in Figure 2).

Box 2. Permanent versus Temporary Human Shields

Tourist or other human presence can create a human shield (habitat free of predators) that can relax antipredator behavior during the lifetime of an individual. Antipredator behavior in predator-free environments is often lost [92] and could occur relatively quickly (e.g., less than 130 years in tammar wallabies *Macropus eugenii* [93]). We note that the taming process relaxes antipredator vigilance [94], but this selection process occurs over several generations. Similarly, urbanization relaxes antipredator vigilance (and more general wariness) because individuals assess reduced risk when protected by human presence. Both domestication and urbanization can create more lasting human shields, while nature-based tourism can create a temporary, although effective [57] shield.

In the case of hunting, animals might have relaxed antipredator behavior when not hunted. This has been seen during periodically fishing closures where individuals decrease their wariness (as shown by shorter FIDs) and suffer higher capture rates when fishing is reinstated [95], as well as when mammal poachers are temporarily absent. With respect to human shields linked to tourism, the core question is to determine whether the temporary presence of humans is sufficient to either permanently reduce antipredator abilities or reduce them for a sufficiently long time so that the population suffers.

Although this has never been formally tested, it is conceivable that animals living around substantial and invasive tourism can indeed modify their perceptions so that human presence is associated with safety. Nevertheless, the intensity of nature-based tourism usually changes according to the season, and predator presence can vary accordingly. For instance, animals might not encounter usual threats for some months (e.g., during spring and summer tourist seasons), while they would have to face high predation risk in other periods (e.g., during the fall and winter). Hence, the main question is to understand how fast antipredator behavior can be lost, or reduced, under temporarily relaxed predation pressure.

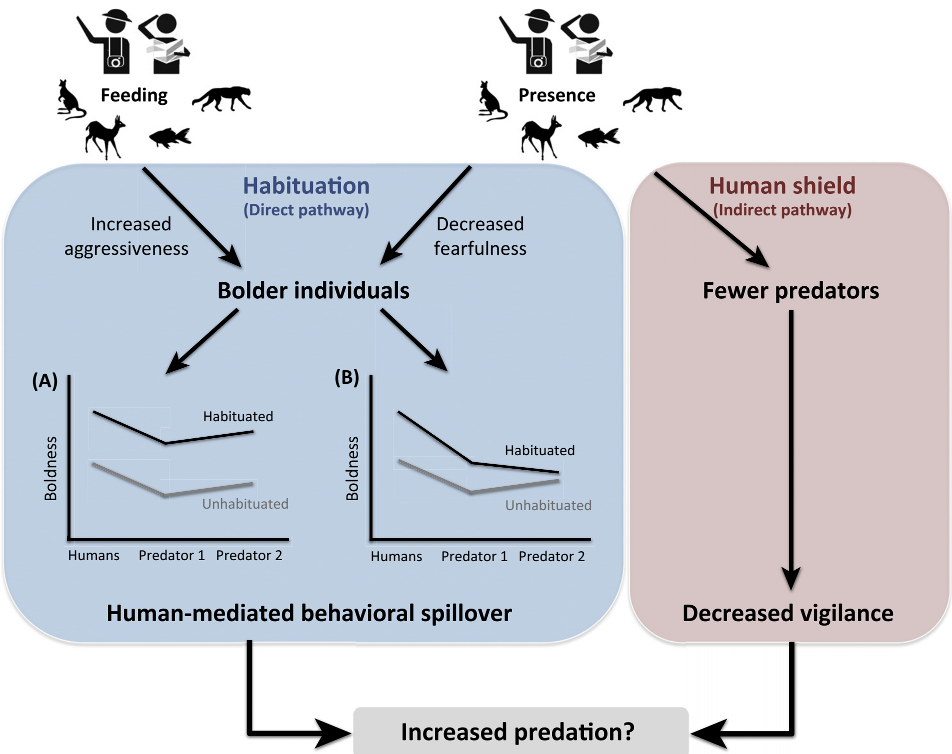

Figure 2. The Link between Intensive Wildlife-Based Tourism and Natural Predation. Both indirect (through decreasing vigilance) and direct (through increased boldness) pathways would enhance predation risk. The indirect pathway (salmon colored) assumes a process related to relaxed selection where individuals found in predator-free habitats lose (previously learned or even evolved) defenses against predators temporally pushed away. The direct pathway (blue colored) assumes that docility and boldness emerge from interaction with nonthreatening humans and these are transferred when encountering more-threatening species. (A) Similar behavioral reaction norms for animals unhabituated and habituated to human presence as a function of different contexts (humans or predator types). (B) Different behavioral reaction norms for animals unhabituated and habituated to human presence as a function of different contexts (humans or predator types). Note that habituated animals are bolder towards potential threats, either genuine predators or wildlife poachers.

Increased Tolerance to Humans: A Direct Pathway

As shown by the urbanization examples described earlier, the presence of humans can have unanticipated effects on prey antipredator behavior, even in the wild. For instance, some animals habituated to tourism presence and/or provisioning become bolder and/or more aggressive [1,5,6]. Can boldness and aggressiveness be repeatable over time and/or across contexts? This key question has been partly answered by studies that show repeatable behavioral traits [58,59] and by those showing that animals reduce flexibility with experience [60,61]. If the development of **personality** is affected by early experiences, and animals then find themselves in a relatively directed trajectory based on those early experiences, exposure to benign humans can create potentially maladaptive traits or syndromes (Box 3).

At the physiological level, there are proximate processes acting through the hypothalamic–pituitary–adrenal (HPA) axis that might reduce overall responsiveness to humans over time, and we know that early experiences modify HPA sensitivity over longer periods [62]. Exposure to tourism reduces stress-induced corticosteroid production in some species [63] and could increase it in others [10]. Nevertheless, the process of habituation to human presence from tourism decreases corticosteroid production over time [64].

Box 3. A Human-Mediated Behavioral Spillover

Both environmental [96] and early social experiences [97] can influence how an individual typically behaves, including how they respond to novel situations. Naïve juveniles generally are more wary and have greater FIDs in response to humans than adults [36], suggesting an habituation-like process where adult individuals became less wary after having multiple encounters with nonthreatening stimuli, such that their reaction norm decreases over time (e.g., leads to a decrease of corticosteroids throughout ontogeny in response to tourism [64,87]). This highlights the importance of early experiences in shaping behavioral traits ('experience adaptive development' or 'experience adaptive programming' for captive individuals [28]) that become progressively fixed with age (see [61] and references therein).

Antipredator behavior, such as FID, could be considered a personality trait in some species since there can be a very high temporal repeatability (e.g., $R = 0.84 - 0.92$ in burrowing owls *Athene cunicularia* [98]). The emergence of such personality traits has been explained in the context of fitness trade-offs, whereby a given behavior could be advantageous in one situation while it would not be in another. In Namibian rock agamas (*Agama planiceps*), bolder males had greater access to food, but they also suffered increased tail loss when compared with shyer individuals [99]. When a **behavioral syndrome** has adaptive consequences in one context but maladaptive consequences in another (e.g., with and without a predator present), the term 'behavioral spillover' is used. North American fishing spiders (*Dolomedes triton*) with high level of voracity in foraging (resulting in high fitness) and mating contexts (resulting in low fitness) were also bolder in a context of a simulated predatory attack (resulting in low fitness) [79]. In summary, if habituation to humans leads to a general decrease in fearfulness, this habituation might also lead to inappropriate (perhaps fatal) behavior in other contexts, such as being bold in the presence of predators, resulting in a 'human-mediated behavioral spillover'.

While boldness could be the result of human habituation, and behavioral spillover could enhance predation risk, the direct link between both is more difficult to establish, since it would mean that animals that become bold and aggressive towards humans (e.g., through habituation) transfer their habituation to real predators (Figure 1C). This pathway may seem unlikely at first glance, because it would mean that humans are classified into the same category as nonhuman predators and we know that many species are able to discriminate predators from nonpredators [65], as well as to discriminate among different predators based on their level of threat [66]. Moreover, we also know of at least two studies that found that human habituation enhanced predator discrimination [50,67]. Nevertheless, neither of these studies formally tested for a transfer of habituation, but rather capitalized on how individuals around humans were more tolerant of humans and then asked how the ability to discriminate between potential predators and nonpredatory species was effected by human exposure. As with squirrels that were less responsive to predator vocalizations in urban areas [36], a transfer of habituation can also have occurred in blackbirds (*Turdus merula*) exposed to tourists in parks [68]. Blackbirds decreased their FID with increased exposure to humans (consistent with an habituation-like process). In addition, blackbirds from high visitation areas had shorter FIDs in response to a novel, threatening stimulus (cars) [68]. Nevertheless, a possible caveat to this study relies on the fact that the authors did not take into account pseudoreplication (i.e., subsamples within parks and individuals that could have been sampled more than once) in their statistical analysis. Regardless, as we summarize in Figure 2, individuals might differentiate predators but have an overall reduced response to them following human habituation.

Hence, the main question focuses on the nature of the **individual behavioral reaction norm**. Specifically, how do bolder animals respond to humans and to predators? Indeed, independently of the underlying process involved in the presence of bolder individuals in areas with people (including tourists), if individuals become more tolerant to predators (Figure 2A,B) their vulnerability will be enhanced. This is an empirical question worthy of study, which could be tested by designing experiments similar to those used in the blackbird study [68] and the squirrel study [36], but in wild areas with real predators.

Apart from natural predators, another important issue concerns wildlife poachers who might also benefit from tourist-habituated wildlife. It is not currently clear whether or not animals are able to distinguish legal hunters from tourists. This distinction might be tightly associated with cognitive capacities of the species and the type of hunting. For instance, elephants (*Loxodonta africana*) are able to distinguish hunters (Maasai men) from nonhunters (Maasai women and children) based on their voices [69]. Mouflon (*Ovis gmelini musimon*) readily identify noisy hunting with hounds [70], while more silent spearguns might not be well detected by fish [71]. Regardless, we could view wildlife poaching as a form of 'cheating' in cases where a population has habituated to benign human presence and then individuals are caught off guard by a poacher. Viewed this way, a small degree of very successful poaching can be tolerated before individuals in a population learn to associate humans with enhanced risk resulting in higher capture rates [72,73]. For instance, gorillas (*Gorilla gorilla graueri*) habituated to tourist presence fled more slowly and did not readily attack or hide, when a poacher approached, when compared with nonhabituated gorillas [72]. This has also been observed for wild Barbary macaques (*Macaca sylvanus*), which are extremely habituated to humans, and which are easy targets for poachers [73].

Concluding Remarks

We know that humans are able to drive rapid phenotypic change in other species [74]. If individuals selectively habituate to humans – particularly tourists – and if invasive tourism practices enhance this habituation, we might be selecting for or creating traits or syndromes that have unintended consequences, such as increased predation risk (Figure 2). Even a small human-induced perturbation could affect the behavior or population biology of a species and influence the function of the species in its community [75]. Such cryptic function loss and the associated reduction in functional diversity are considered to be among the most significant concerns for ecosystem stability [75]. Exposure to humans can also reduce phenotypic variation and behavioral plasticity. Since behavioral plasticity might mirror genetic diversity, ecotourism could also drive the loss of genetic diversity. The effect might even be greater if human-linked perturbations affect keystone species or individuals [76,77]. Owing to the plethora of impacts nature-based tourism has on wildlife, it could well be added to the list of drivers of human-induced rapid environmental change (HIREC), which already includes habitat change, pollution, exotic species, human harvesting, and climate change [78]. Our review highlights numerous unanswered questions (see Outstanding Questions) that could be tested with the ultimate goal of better understanding whether and how habituation to human presence creates deleterious effects to wildlife.

Outstanding Questions

Are humans always initially perceived as predators?

How often does habituation explain tolerance?

How do bolder animals respond to humans and to predators?

Under what conditions do animals transfer habituation from humans to real predators?

Which intrinsic factors explain variation between species in human-oriented boldness? In other words, why do some species acclimate well to human presence while others avoid humans?

Is the **human-mediated behavioral spillover**, influencing antipredator behavior, affected by predator origin (i.e., native or alien species)?

With respect to human shields linked to tourism, the core question is to determine whether the temporary presence of humans is sufficient to either permanently reduce antipredator abilities or reduce them for a sufficiently long time to drive population decline.

Given temporal variation in risk, how fast can antipredator behavior be lost, or reduced, under temporary relaxed predation pressure?

How often does human presence reduce vigilance by distracting prey and diverting their attention?

What are the evolutionary responses of animals to nature-based tourism?

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Resources

[i] www.turismo.gov.br/turismo/noticias/todas_noticias/20131112.html

References

1. Knight, J. (2009) Making wildlife viewable: habituation and attraction. *Soc. Anim.* 17, 167–184
2. Balmford, A. *et al.* (2015) Walk on the wild side: estimating the global magnitude of visits to protected areas. *PLoS Biol.* 13, e1002074
3. Prideaux, B. and Cooper, M. (2009) *River Tourism*, CABI Publishing
4. O'Connor, S. *et al.* (2009) *Whale Watching Worldwide: Tourism Numbers, Expenditures and Expanding Economic Benefits, A Special Report from the International Fund for Animal Welfare*, International Fund for Animal Welfare
5. Ikuta, L.A. and Blumstein, D.T. (2003) Do fences protect birds from human disturbance? *Biol. Conserv.* 112, 447–452
6. Webb, N.V. and Blumstein, D.T. (2005) Variation in human disturbance differentially affects predation risk assessment in Western Gulls. *The Condor* 107, 178–181
7. Lloyd, J. and Ajarova, L. (2005) Chimpanzee habituation for tourism. In *World Atlas of Great Apes and their Conservation* (Caldecott, J. and Miles, L., eds), pp. 76–77, University of California Press
8. Gaspar, C. *et al.* (2008) Feeding sites frequentation by the pink whipray *Himantura fai* in Moorea (French Polynesia) as determined by acoustic telemetry. *Cybium* 32, 153–164
9. Albuquerque, T. *et al.* (2014) In situ effects of human disturbances on coral reef-fish assemblage structure: temporary and persisting changes are reflected as a result of intensive tourism. *Mar. Freshw. Res.* 66, 23–32

10. Ellenberg, U. *et al.* (2007) Elevated hormonal stress response and reduced reproductive output in yellow-eyed penguins exposed to unregulated tourism. *Gen. Comp. Endocrinol.* 152, 54–63
11. McClung, M.R. *et al.* (2004) Nature-based tourism impacts yellow-eyed penguins Megadyptes antipodes: does unregulated visitor access affect fledging weight and juvenile survival? *Biol. Conserv.* 119, 279–285
12. Higham, J.E.S. and Shelton, E.J. (2011) Tourism and wildlife habituation: reduced population fitness or cessation of impact? *Tourism Manage.* 32, 1290–1298
13. Reynolds, P.C. and Braithwaite, D. (2001) Towards a conceptual framework for wildlife tourism. *Tourism Manage.* 22, 31–42
14. Price, E.O. (ed.) (2002) *Animal Domestication and Behavior*, CABI Publishing
15. Kohane, M.J. and Parsons, P.A. (1989) Domestication: evolutionary change under stress. *Evol. Biol.* 23, 31–48
16. Trut, L.N. (1999) Early canid domestication: the farm-fox experiment. *Am. Sci.* 24, 124–129
17. Johnsson, J.I. *et al.* (2001) Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 58, 788–794
18. Jackson, C.D. and Brown, G.E. (2011) Differences in antipredator behaviour between wild and hatchery-reared juvenile Atlantic salmon (*Salmo salar*) under seminatural conditions. *Can. J. Fish. Aquat. Sci.* 58, 2157–2165
19. Wund, M.A. *et al.* (2015) The evolution of antipredator behaviour following relaxed and reversed selection in Alaskan threespine stickleback fish. *Anim. Behav.* 106, 181–189
20. Blumstein, D.T. (2006) The multi-predator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology* 112, 209–217
21. Hemetsberger, J. *et al.* (2010) Influence of socially involved hand-raising on life history and stress responses in greylag geese. *Interact. Stud.* 11, 380–395
22. Macrì, S. and Würbel, H. (2006) Developmental plasticity of HPA and fear responses in rats: a critical review of the maternal mediation hypothesis. *Horm. Behav.* 50, 667–680
23. Palmeira, F.B. *et al.* (2008) Cattle depredation by puma (*Puma concolor*) and jaguar (*Panthera onca*) in central-western Brazil. *Biol. Conserv.* 141, 118–125
24. Carvalho, E.A. (2015) Modeling the risk of livestock depredation by jaguar along the Transamazon highway, Brazil. *Basic Appl. Ecol.* 16, 413–419
25. Flörcke, C. and Grandin, T. (2013) Loss of anti-predator behaviors in cattle and the increased predation losses by wolves in the northern rocky mountains. *Open J. Anim. Sci.* 3, 248–253
26. McPhee, E. (2004) Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biol. Conserv.* 115, 71–77
27. Bremner-Harrison, S. *et al.* (2004) Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*). *Anim. Conserv.* 7, 313–320
28. Mason, G. *et al.* (2013) Plastic animals in cages: behavioural flexibility and responses to captivity. *Anim. Behav.* 85, 1113–1126
29. Phillips, B.L. and Suarez, A.V. (2012) The role of behavioural variation in the invasion of new areas. In *Behavioural Responses to a Changing World: Mechanisms and Consequences* (Candolin, U. and Wong, B.B.M., eds), pp. 190–200, Oxford University Press
30. Slabbekoorn, H. (2013) Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* 85, 1089–1099
31. Møller, A.P. (2010) Interspecific variation in fear responses predicts urbanization in birds. *Behav. Ecol.* 21, 365–371
32. Lowry, H. *et al.* (2013) Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549
33. Magle, S. *et al.* (2005) Behavioral responses to repeated human intrusion by black-tailed prairie dogs (*Cynomys ludovicianus*). *J. Mammal.* 86, 524–530
34. Møller, A.P. *et al.* (2015) Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* 6, 8
35. Cooper, W.E., ,, Blumstein, D.T., eds (2015) *Escaping from Predators: An Integrative View of Escape Decisions*, Cambridge University Press
36. Mccleery, R.A. (2009) Changes in fox squirrel anti-predator behaviors across the urban–rural gradient. *Landscape Ecol.* 24, 483–493
37. Møller, A.P. (2008) Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* 63, 63–75
38. Møller, A.P. *et al.* (2008) Risk taking by singing males. *Behav. Ecol.* 19, 41–53
39. Møller, A.P. (2014) Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* 27, 1105–1113
40. Sol, D. *et al.* (2013) Behavioural adjustments for a life in the city. *Anim. Behav.* 85, 1101–1112
41. Sol, D. *et al.* (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proc. R. Soc. B: Biol. Sci.* 272, 1433–1441
42. Carrete, M. and Tella, J.L. (2011) Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS ONE* 6, e18859
43. Dale, S. *et al.* (2015) Commonness and ecology, but not bigger brains, predict urban living in birds. *BMC Ecol.* 15, 12
44. Møller, A.P. and Erritzøe, J. (2015) Brain size and urbanization in birds. *Avian Res.* 6, 1–7
45. Sol, D. *et al.* (2012) Unraveling the life history of successful invaders. *Science* 337, 580–583
46. Berger, J. (2007) Fear, human shields and the redistribution of prey and predators in protected areas. *Biol. Lett.* 3, 620–623
47. Valcarcel, A. and Fernández-Juricic, E. (2009) Antipredator strategies of house finches: are urban habitats safe spots from predators even when humans are around? *Behav. Ecol. Sociobiol.* 63, 673–685
48. Møller, A.P. (2010) The fitness benefit of association with humans: elevated success of birds breeding indoors. *Behav. Ecol.* 21, 913–918
49. Waser, N.M. *et al.* (2014) Coyotes, deer, and wildflowers: diverse evidence points to a trophic cascade. *Naturwissenschaften* 101, 427–436
50. Coleman, A. *et al.* (2008) Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)? *Biol. Lett.* 4, 250–252
51. Shochat, E. *et al.* (2006) From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* 21, 186–191
52. Møller, A.P. (2012) Urban areas as refuges from predators and flight distance of prey. *Behav. Ecol.* 23, 1030–1035
53. Møller, A.P. and Ibáñez-Álamo, J.D. (2012) Escape behaviour of birds provides evidence of predation being involved in urbanization. *Anim. Behav.* 84, 341–348
54. Bateman, P.W. and Fleming, P.A. (2012) Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23
55. Isbell, L.A. and Young, T.P. (1993) Human presence reduces predation in a free-ranging vervet monkey population in Kenya. *Anim. Behav.* 45, 1233–1235
56. Shannon, G. *et al.* (2014) Behavioral responses associated with a human-mediated predator shelter. *PLoS ONE* 9, e94630
57. Nowak, K. *et al.* (2014) Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* 25, 1199–1204
58. Dall, S.R.X. *et al.* (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* 7, 734–739
59. Fürtbauer, I. *et al.* (2015) Personality, plasticity and predation: linking endocrine and behavioural reaction norms in stickleback fish. *Funct. Ecol.* http://dx.doi.org/10.1111/1365-2435.12400
60. Bergmüller, R. and Taborsky, M. (2010) Animal personality due to social niche specialisation. *Trends Ecol. Evol.* 25, 504–511
61. Groothuis, T.G.G. and Trillmich, F. (2011) Unfolding personalities: the importance of studying ontogeny. *Dev. Psychobiol.* 53, 641–655
62. Mirescu, C. *et al.* (2004) Early life experience alters response of adult neurogenesis to stress. *Nat. Neurosci.* 7, 841–846

63. Romero, L.M. and Wikelski, M. (2002) Exposure to tourism reduces stress-induced corticosterone levels in Galapagos marine iguanas. *Biol. Conserv.* 108, 371–374
64. Shutt, K. *et al.* (2014) Effects of habituation, research and ecotourism on faecal glucocorticoid metabolites in wild western lowland gorillas: implications for conservation management. *Biol. Conserv.* 172, 72–79
65. Belton, L.E. *et al.* (2007) Do Cape ground squirrels (*Xerus inauris*) discriminate between olfactory cues in the faeces of predators versus non-predators? *Afric. Zool.* 42, 135–138
66. Liesenjohann, T. and Eccard, J.A. (2008) Foraging under uniform risk from different types of predators. *BMC Ecol.* 8, 19
67. Carrasco, M.F. and Blumstein, D.T. (2012) Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. *Ethology* 118, 243–250
68. Rodriguez-Prieto, I. *et al.* (2009) Antipredator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* 20, 371–377
69. McComb, K. *et al.* (2014) Elephants can determine ethnicity, gender, and age from acoustic cues in human voices. *Proc. Natl. Acad. Sci. U.S.A.* 111, 5433–5438
70. Marchand, P. *et al.* (2014) Impacts of tourism and hunting on a large herbivore's spatio-temporal behavior in and around a French protected area. *Biol. Conserv.* 177, 1–11
71. Januchowski-Hartley, F.A. *et al.* (2012) Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. *Mar. Ecol. Prog. Ser.* 469, 113–119
72. Kasereka, B. *et al.* (2006) Vulnerability of habituated Grauer's gorilla to poaching in the Kahuzi-Biega National Park, DRC. *African Stud. Monogr.* 27, 15–26
73. Ménard, N. *et al.* (2014) How tourism and pastoralism influence population demographic changes in a threatened large mammal species. *Anim. Conserv.* 17, 115–124
74. Hendry, A.P. *et al.* (2008) Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* 17, 20–29
75. McConkey, K.R. and O'Farrill, G. (2015) Cryptic function loss in animal populations. *Trends Ecol. Evol.* 30, 182–189
76. Bond, W.J. (1994) Keystone species. In *Biodiversity and Ecosystem Function* (Schulze, E.D. and Mooney, H.A., eds), pp. 237–253, Springer
77. Modlmeier, A.P. *et al.* (2014) The keystone individual concept: an ecological and evolutionary overview. *Anim. Behav.* 89, 53–62
78. Sih, A. (2013) Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85, 1077–1088
79. Johnson, J.C. and Sih, A. (2005) Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behav. Ecol. Sociobiol.* 58, 390–396
80. Sih, A. *et al.* (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* 19, 372–378
81. McFarland, D. (1993) *Animal Behaviour: Psychobiology, Ecology and Evolution.* (2nd edn), Longman Scientific and Technical
82. Dingemanse, N.J. *et al.* (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89
83. Frid, A. and Dill, L.M. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11
84. Holmes, N.D. (2007) Comparing king, gentoo, and royal penguin responses to pedestrian visitation. *J. Wildl. Manag.* 71, 2575–2582
85. Bejder, L. *et al.* (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Mar. Ecol. Prog. Ser.* 395, 177–185
86. van Heezik, Y. and Seddon, P.J. (1990) Effect of human disturbance on beach groups of jackass penguins. *S. Afric. J. Wildl. Res.* 20, 89–93
87. Walker, B.G. *et al.* (2006) Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conserv. Biol.* 20, 146–154
88. Fowler, G.S. (1999) Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biol. Conserv.* 90, 143–149
89. Viblanc, V.A. *et al.* (2012) Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC Ecol.* 12, 10
90. Li, C. *et al.* (2011) Quantifying human disturbance on antipredator behavior and flush initiation distance in yellow-bellied marmots. *Appl. Anim. Behav. Sci.* 129, 146–152
91. Ellenberg, U. *et al.* (2009) Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. *Anim. Behav.* 77, 289–296
92. Lahti, D.C. *et al.* (2009) Relaxed selection in the wild. *Trends Ecol. Evol.* 24, 487–496
93. Blumstein, D.T. *et al.* (2004) A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* 110, 919–934
94. Beauchamp, G. (2015) *Animal Vigilance,* Elsevier
95. Januchowski-Hartley, F.A. *et al.* (2014) Fishery benefits from behavioural modification of fishes in periodically harvested fisheries closures. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 24, 777–790
96. Hensley, N.M. *et al.* (2012) Personality and habitat segregation in giant sea anemones (*Condylactis gigantea*). *J. Exp. Mar. Biol. Ecol.* 426–427, 1–4
97. Geffroy, B. *et al.* (2014) The link between social network density and rank-order consistency of aggressiveness in juvenile eels. *Behav. Ecol. Sociobiol.* 68, 1073–1083
98. Carrete, M. and Tella, J.L. (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* 6, 167–170
99. Carter, A.J. *et al.* (2010) Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behav. Ecol.* 21, 655–661