# Physiological and Behavioral Consequences of Human Visitation

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**Fig 2.0** A mother lion (*Panthera leo*) taking care of her offspring and facing ecotourists at Phinda Private Game Reserve, South Africa. Photo credit Graeme Shannon

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## 2.1 Introduction

Imagine you are coming home after a successful foraging trip to the local grocery store and you find your front porch occupied by a pack of lions. Sightseeing lions, that is, apparently well fed and lazily dosing in the sun, but, well, with lions you never know! Would you get out of your car and just walk across that pack of lions to feed your hungry kids? Or would you rather stay in the car, lock yourself in where you feel safe? Maybe you feel a bit bolder after a little while and try to sneak into your house through the backdoor. Probably you will make this attempt with your heart in your throat and just bring in the bare essentials. When one of the lions notices you, and gets up to get a better look, you'd probably drop your bags and run for cover.

Just like you may be struggling to trust those front porch lions, many animals are suspicious of us. Wildlife generally perceives humans as potential predators. Not surprisingly so, really, since we've been hunting animals for food and for their products for thousands of years. Today, well fed by modern food production technologies, we now use some of these animals for pleasure and entertainment. But how should they know that we might mean no harm? We still smell like predators, and even a pleasant bouquet of rose perfume won't mask this from the sensitive nostrils of some animals. We are often noisy and colorful and thus very detectable. And we behave oddly too. Today, we hunt with cameras leveled chasing after a good shot to share with our friends via social networks. Not so long ago, we were out there with spears, guns, nets, and harpoons to feed ourselves and the world (indeed, we still do this in many places).

No wonder many animals respond in a strongly negative way to human presence. And even if you only observe subtle behavioral changes—such as increased vigilance—their heart rate is probably going through the roof. Increasing heart rate is a simple, yet important, physiological response that keeps animals prepared so that they can rapidly flee in case we changed our mind and spontaneously decided to pick them up for a nice family feed. The fact is that these normally adaptive behavioral and physiological responses are energetically costly. While a one-off visit may have limited impact, frequent human visitation may deplete energy reserves and reduce the likelihood that an individual survives or has sufficient energy to reproduce. This is mainly driven by physiological and behavioral modifications, and the long-term success of ecotourism ventures will thus depend on a sound understanding of these processes that could be used to inform management action. In the remainder of this chapter, we will examine such often unintentional and avoidable impacts of human disturbance on wildlife in more detail.

## 2.2 Physiological Responses to Human Visitation

### 2.2.1 Humans Are Perceived as Stressors

Facing a stressful event, we all respond using the same physiological mechanisms that are triggered at various intensities. Looking down a canyon, making an important presentation, or facing a dangerous predator will make your heartbeat increase and your face will flush with blood. These are the consequences of physiological mechanisms that are very similar among many species [1]. These responses help animals adaptively respond to the stressor and eventually to reset their physiology to a more normal physiological state. This process is called homeostasis. The first physiological response is linked to an increase in "stress hormones" such as catecholamines released within seconds to few minutes after the stressor and followed by the secretion of glucocorticoids in the plasma after several minutes [2, 3]. Secondary responses are related to a change in energy allocation, by inhibiting systems that channel energetic resources to growth or reproduction [4], in order to provide energy for (1) the cellular responses to the stressor, such as the production of protective molecules and the initiation of defensive mechanisms [5], (2) the increase of immune functions [6, 7], or (3) as a source of energy for a new energy-demanding behavior (e.g., an escape) [8]. Thus, during stressful events, energy is transferred from stored reserves and is released in the blood. At the same time, the cardiovascular and ventilatory systems are stimulated and transport oxygen to the organs to prepare them for escape.

Any situation that triggers these physiological responses can be considered a stressor, and therefore, many of these endpoints can be used as indicators to identify a stressful situation. Human visitation has been shown to trigger the stress response cascade in many species leading to higher levels of stress hormones after human encounters [9–11] (but see Tables 2.1 and 2.2). Stress hormones, more specifically corticosterone or cortisol, depending on the species, are frequently used as markers of physiological stress. They are easy to measure from blood plasma samples, and their levels are generally considered to provide an estimate of the intensity of anthropogenic disturbance (higher levels indicate higher disturbance) [12]. They can be estimated using noninvasive tools, since their levels or the levels of their metabolites in hair, feathers, feces, or even in the water for fish are reliable indicators of the overall secretion of stress hormones [13–17]. However, data resulting from these noninvasive techniques need to be interpreted with caution since they are the result of an accumulation over some period of time, making it difficult to disentangle the effects of different potential sources of stress. Studying other parameters of stress can validate hormonal results, and heart rate has been proven to be a reliable and precise measure of human disturbance [18]. Measuring heart rate during and after human presence allows quantification of the relative severity of different disturbance events [19–21].

Overall, human visitation can be considered a stressor for many wildlife species, eliciting physiological modifications such as the production of stress hormones and an increase in cardiovascular activity. These effects are, on their own, not harmful for the animal but part of the normal stress response. However, repeated exposure to a stressor, such as human visitation, can lead to long-term elevated stress levels, described as chronic stress, with eventually deleterious effects compromising an animal's homeostasis. Animals in a state of chronic stress can be expected to show impaired growth, reduced resistance to disease, and ultimately lower survival [22].

### 2.2.2 Effects of Prolonged Human Visitation on Basal Stress Hormone Levels

Under-regulated nature-based tourism often results in frequent and lasting disturbance impacts that may create chronic stress for wildlife. There have been a number of studies that compared basal glucocorticoid levels in populations living in tourist areas with those outside tourist areas. Interestingly, many studies did not find significant differences in baseline stress hormone levels in visited compared to non-visited zones (Table 2.1), and one study even showed decreased baseline levels in animals from visited zones [9]. On the contrary, other studies found increased glucocorticoid baseline values in animals exposed to frequent visitation [23–27]. This inconsistency between studies is partly linked to the diversity of species studied, highlighting that some species are more sensitive to human presence than others, but also to differences in tourism intensity and practices. Additionally, the methods by which stress hormones are measured may also account for differences between studies. Measurements in feathers or feces integrate stress hormones over a longer

**Table 2.1** Ratio of stress levels as inferred from measures of basal glucocorticoid (GC) levels in animals from human-visited and nonhuman-visited areas

| Common name | Species | Basal GC (visited/ unvisited ratio) | Measured in | References |
|---|---|---|---|---|
| Marine iguanas | *Amblyrhynchus cristatus* | NS | Plasma | [32] |
| Marine iguanas | *Amblyrhynchus cristatus* | NS | Plasma | [33] |
| Northern pintails | *Anas acuta* | NS | Plasma | [34] |
| Northern Bahamian rock iguanas | *Cyclura cychlura* | NS | Plasma | [35] |
| European storm petrel | *Hydrobates pelagicus melitensis* | NS | Plasma | [36] |
| Yellow-eyed penguins | *Megadyptes antipodes* | NS | Plasma | [37] |
| Hoatzin chicks | *Opisthocomus hoazin* | NS | Plasma | [38] |
| Magellanic penguins | *Spheniscus magellanicus* | NS | Plasma | [39] |
| Magellanic penguins | *Spheniscus magellanicus* | NS | Plasma | [40] |
| Magellanic penguins | *Spheniscus magellanicus* | NS | Plasma | [10] |
| Magellanic penguins | *Spheniscus magellanicus* | 0.57 | Plasma | [9] |
| Gentoo penguins | *Pygoscelis papua* | 1.5 | Feathers | [24] |
| African lions | *Panthera leo* | 1.7 | Feces | [25] |
| Barbary macaques | *Macaca sylvanus* | 1.18 | Feces | [26] |
| Capercaillie | *Tetrao urogallus* | 1.28 | Feces | [23] |
| Gorillas | *Gorilla gorilla gorilla* | 1.14 | Feces | [27] |

The values indicate how many times greater the basal GC of animals from visited areas is from the basal GC of animals from non-visited areas. In studies showing no significant differences, a ratio is not provided and replaced by NS time than those measured in the blood, and these feather and fecal measures often show increased stress hormone levels in visited areas.

It is, however, important to treat these baseline levels of stress hormones with some caution. Although high baseline stress hormone levels are reliable indicators of prolonged exposure to a stressor [28, 29], low baseline values can be misleading. Chronically stressed animals sometimes show low stress hormone levels as a result of the exhaustion or downregulation of their stress response system [30, 31]. In order to evaluate the actual physiological effects of human visitation, additional measures need to be considered. A common approach relies on the capacity to respond to a second stressor or a hormonal challenge, enabling to evaluate coping abilities of the animals.

### 2.2.3 Frequent Human Visitation Disrupts Coping Abilities

The capacity of animals to respond appropriately to stressors is an important ability that affects survival and reproductive success [41], since it involves a process of coping and restoring homeostasis. Investigating whether human visitation impacts these stress-coping abilities is essential for effective conservation management, and there have been a number of studies that contrasted tourist and non-tourist areas in animals' response to stressors.

Overall, studies have shown that the response to a stressor differs significantly in animals from tourist compared to control, unvisited areas (Table 2.2). Several of these studies identified a hypersensitivity of the stress response in animals repeatedly disturbed by human visitation, resulting in a significant stronger glucocorticoid response (GC ratio > 1 in Table 2.2). Thus, repeated human visitation can sensitize animals. Most of these results were obtained using the standardized stressor of capture and restraint, where previous experience with humans can significantly affect an animal's response. Consequently, the differences in glucocorticoid responses detected in these studies can partly reflect the changing perception of humans from a nonthreatening to a threatening stimulus. To test directly for physiological disruptions, researchers have used a technique that directly activates the stress axis (also called "HPA axis"), which is the set of glands involved in the production and degradation of stress-related enzymes by the hypothalamus, the pituitary, and the adrenal glands. This can be done by injecting adrenocorticotropic hormone (ACTH). Following this protocol, stronger stress responses were recorded in a bird (*Hydrobates pelagicus melitensis* [36]) and fish species (*Moenkhausia bonita* [42]) from tourist areas. This suggests that the change in stress sensitivity is not only the result of a change in the perception of humans as a threat but also an actual change in the physiology of the stress and coping response.

Conversely, other studies showed that repeated human exposure may lead to reduced stress responses to human visitation. But it is still uncertain if reduced stress responses are the result of habituation to humans, a change in the ability to physiologically respond to disturbance, or reflect differential sorting where more sensitive individuals leave the disturbed area (see Sect. 2.3.4 on animal personality).

**Table 2.2** Ratio of glucocorticoid (GC) levels of animals from human-visited and non-visited areas

| Common name | Species | Stressor | GC levels (visited/unvisited) after stressor | Measured in | Comment | References |
|---|---|---|---|---|---|---|
| Magellanic penguins | *Spheniscus magellanicus* | Capture and restraint | NS | Plasma | | [10] |
| Northern Bahamian rock iguanas | *Cyclura cychlura* | Capture and restraint | NS | Plasma | | [35] |
| European storm petrel | *Hydrobates pelagicus melitensis* | Human disturbance | NS | Plasma | | [36] |
| Magellanic penguins | *Spheniscus magellanicus* | Human visitation | 0.34 | Plasma | | [10] |
| Magellanic penguins | *Spheniscus magellanicus* | Human visitation | 0.50 | Plasma | | [9] |
| Marine iguanas | *Amblyrhynchus cristatus* | Capture and restraint | 0.54 | Plasma | | [32] |
| Magellanic penguins | *Spheniscus magellanicus* | Capture and restraint | 0.65 | Plasma | | [40] |
| Magellanic penguins | *Spheniscus magellanicus* | ACTH injection | 0.74 | Plasma | | [40] |
| Yellow-eyed penguins | *Megadyptes antipodes* | Capture and restraint | 1.43 | Plasma | | [37] |
| European storm petrel | *Hydrobates pelagicus melitensis* | ACTH injection | 1.47 | Plasma | No statistics | [36] |
| A small fish | *Moenkhausia bonita* | Capture restraint and ACTH | 1.85 | Water | | [42] |
| Marine iguanas | *Amblyrhynchus cristatus* | Capture and restraint | 1.92 | Plasma | In non-breeding animals | [33] |
| Hoatzin chicks | *Opisthocomus hoazin* | Capture and restraint | 2.01 | Plasma | In juveniles | [38] |
| Magellanic Penguins | *Spheniscus magellanicus* | Capture and restraint | 3.57 | Plasma | At hatch | [39] |

GC levels were measured soon after a stressful stimulus. The values indicate how many times the GC of animals from visited areas is larger than GC of animals from non-visited areas. *NS* nonsignificant

Reduced physiological capacity to respond to a stressor, as found in Magellanic penguins (*Spheniscus magellanicus* [40]), can cause catastrophic ecological consequences, leading to decreased abilities of animals to efficiently respond to life-threatening stressors, such as a sudden change in the environment or the presence of a predator [43]. More studies using nonhuman-related stressors are required to investigate if differences in stress responses are the result of habituation or modification of individual's abilities to mount an appropriate physiological stress response.

In conclusion, prolonged or repeated exposure to human presence can lead to physiological modifications. Some studies suggest that under-regulated tourism can increase the anxiety of animals toward humans and thus result in sensitization to human visits. In this case, animals perceive human visitation as stressful stimuli, and the accumulating impacts of repeated visitation can increase energy expenditure and ultimately affect individual growth, reproduction, and survival. Other studies described a decreased responsiveness of individuals caused by repeated exposure to humans: habituation. When habituation occurs, the impact of ecotourism seems less important. However, habituation is sometimes accelerated by feeding wild animals [44], leading to quantitative and qualitative modifications of their diet, illustrated by changes in their body condition. Investigating the effects of ecotourism on body condition is therefore part of an important area of research for studying the long-term effects of ecotourism.

### 2.2.4 Effect of Ecotourism on Body Condition

Where wildlife is fed to increase visibility, animals might be heavier compared to those not fed [26]. However, wildlife provisioning might also have long-term negative effects. For example, southern stingrays (*Dasyatis americana*) regularly provisioned with squids, a nonnatural diet, show a strikingly different blood fatty acid profile when compared with unfed animals, mainly characterized by a higher $n$–3 by $n$–6 polyunsaturated fatty acid ratio [45]. Since fatty acids are the main constituents of cellular membranes, such a change in fatty acids ratio can be expected to change cellular membrane permeability possibly impacting the proper functioning of cells [46].

The mere exposure to frequent human visitation might also lead to a decrease in body weight, through an increase of stress. For example, in the common wall lizards (*Podarcis muralis*), animals from tourist-exposed areas had relatively lower body masses in summer—the season with most human–animal interactions—compared to animals not exposed to tourists [47]. Similarly, juvenile hoatzin chicks (*Opisthocomus hoazin*) in tourist-exposed areas are smaller than undisturbed juveniles [38]. Yellow-eyed penguins (*Megadyptes antipodes*) exposed to under-regulated tourism fledged at significantly lighter body weights and, as a result, were less likely to survive their first year at sea [37]. Hence, an increase in energetic expenditure toward stress response mechanisms is often traded-off with the energy available for other essential functions, such as growth [48] and reproduction [4]. This is particularly concerning when animals are already working at their physiological limits, such as during migration or breeding. Indeed, lower body weight can reduce breeding success [49, 50] and the ability to survive predation or environmental challenges [51, 52]. Additionally, effects on body weight or body condition can be the results of a shift in the fine balance of the behavioral time budget, as described in the next sections. Disturbed animals in visited areas may spend more time being vigilant and less time foraging for food (see Sect. 2.3.2 on behavioral time budgets).

## 2.3 Behavioral Responses

### 2.3.1 Avoidance: Flight and Displacement

As highlighted in the previous physiological section, animals may perceive an approaching human as an immediate threat to their survival and react by fleeing the area. Animals might also simply avoid valuable areas when humans are present. Such areas were presumably chosen for good reasons, such as providing them with high-quality food and shelter. As a result, animals are displaced to areas of lower quality, foraging in patches with less food and possibly more predators. Furthermore, when animals flee from humans, they use up their limited energy stores while being unable to continue with activities such as feeding or grooming that are crucially important for their survival.

Thus, measuring the flight initiation distance (FID) is a common approach to assess the degree to which individuals are prone or averse to risks. In recent years, considerable research has quantified the FID of animals exposed to apparently non-threatening human visitation. Studies found that FID depends on many factors, including animal group size, individual size, age, experience, sex, starting distance of the intruder, and distance of the closest refuge [53, 54]. Furthermore, FID is species-specific. In some fish species, such as parrot fishes, FID to human approach is 0.5–2 m [55]. In some lizard species, FID varies between 2 and 10 m [56]. In South American fur seals (*Arctocephalus australis*), FID elicited by tourist approaches was 10 m [57], which is similar to that reported for northern elephant seals (*Mirounga angustirostris*) [58]. In birds of Eastern Australia, FID ranged between 2 and 150 m [59], and in Humboldt penguins (*Spheniscus humboldti*), FIDs of more than 200 m were observed [Ellenberg pers. obs.]. This highlights variable sensitivities to disturbance.

The intensity of flight response could also depend on the historical nature of the relationship between the focal species and humans, especially in a context of historic hunting as seen in penguins [60]. Fish from highly fished areas also tend to flee at longer distance than individuals of the same species in protected areas [61]. Hence, the optimal FID for a given species depends on disturbance history, but also on the cost/benefits balance, where readily leaving a “valuable place” increases energy expenditure but also reduces perceived predation risks.

Sometimes, avoidance is so pronounced that it becomes difficult to determine whether animals are even present. A very simple tool to circumvent this issue is quantifying animal footprints along tourist trails (Fig. 2.1). Fewer footprints mean

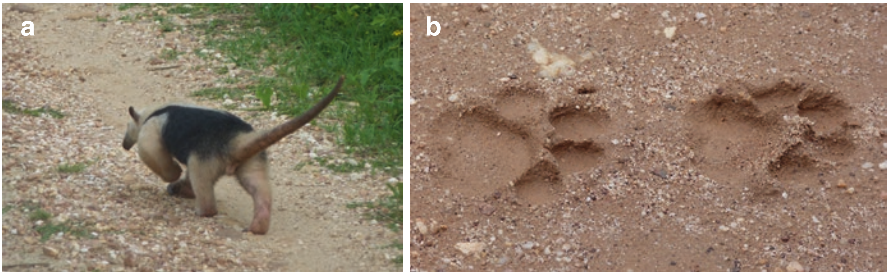


**Fig. 2.1** (**a**) Collared anteater (*Tamandua tetradactyla*) leaving delicate footprints and (**b**) footprints of a jaguar (*Panthera onca*) in the "Transpantaneira" tourist trail in Pantanal, Mato Grosso, Brazil. Photo credit Benjamin Geffroy

lower abundance of animals. This is an effective way to measure displacement of animals due to human presence, which is particularly useful for large mammals that are difficult to observe [62]. Remotely triggered infrared cameras are also often used to attest the presence of a given species. This was done in California, where a study detected that bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) avoid trails that are frequented by hikers and mountain bikers [63].

### 2.3.2 Behavioral Time Budgets

Being able to multitask is a gift that few possess. Thus, the time spent on one activity has consequence on the time available for other activities. The resulting "behavioral time budget" reflects these trade-offs between different activities. There are a number of studies that have shown that tourist presence modifies animal's time budgets, which then affects their energy budget.

Dolphins are good models for studying activity budgets. As flagship species, they attract many tourists and, depending on species, may interact directly with tourists. It was found that Australian bottlenose dolphins (*Tursiops australis*) might not perceive visitors as a threat, as long as swimmers approached from the side [64]. The time spent interacting with humans will nevertheless compromise the time available to forage and rest. This has been observed in many dolphin species (common dolphins *Delphinus* sp., dusky dolphins *Lagenorynchus obscurus*, and bottlenose dolphins), where individuals were shown to compensate by increasing feeding activities following human visitation [64–66], and is discussed more in Chap. 6. Hence, the exact timing of human activities need to be managed carefully to avoid lasting effects on dolphin behavior and ultimately body condition. Disruption of behavioral budgets is also the most consistent finding of studies that quantify whale-watching impacts [67]. In terrestrial mammals, such as elk (*Cervus canadensis*), an increase in travel time during the day has been observed in response to avoidance of humans [68]. Interestingly, travel time increased according to the noise produced by tourist activity, with all-terrain vehicle noise having the most negative effects [68].

Mediterranean mouflon (*Ovis* sp.) also shifts their circadian activity by becoming active nocturnal foragers, but only when tourism pressure is high [69]. In brown bear (*Ursus arctos*) not habituated to humans, a shift in activity patterns has been detected; unhabituated bears become almost exclusively nocturnal [70]. Interestingly, those habituated to humans do not shift their activity, allowing them to maximize foraging opportunities [70].

Similarly to activity, vigilance levels are affected by human presence. Animals look up both to monitor both members of their own species and to look for potential predators. Thus, changes in vigilance behavior can have negative consequences. By studying the behavior of Gentoo penguins (*Pygoscelis papua*) on Subantarctic Macquarie Island, researchers found that vigilance levels were lower in less disturbed areas [71]. As a result, frequently disturbed animals may be more vulnerable to predation [43] or poaching [70, 72]. A change in vigilance and activity patterns was also seen in samango monkeys (*Cercopithecus mitis erythrarcus*) that spend more time foraging near ground level when humans were present than in the absence of visitors, suggesting an artificially created human refuge where the monkeys "feel" safer around humans [73].

Overall, the modification of activity budgets strongly depends on visitor numbers. In some primates, the threshold number of tourists triggering a change in activity was 15 [74], while no differences are detected when only a few visitors (researchers in this case) are present [74, 75]. In Gentoo penguins, the time spent resting was similar on and off a research station although the number of people present was greater inside than outside the station [71]. In comparison, higher frequencies of visitation can lead to decreased resting behavior in marine mammals [76]. Time spent resting also decreased in elk, when both biking and hiking disturbances were intense [68]. These changes in behavior are usually reported when humans are noisy and are a source of disturbance. However, habituation to humans might reduce these effects, as observed in bears [70]. This habituation may be speeded up by providing food. However, provisioning can have negative consequences.

### 2.3.3 Behavioral Responses to Provisioning

Provisioning animals is commonly used to make them more easily observable, ultimately increasing their tameness [44]. This practice is often accompanied by behavioral changes in activity and aggressiveness. Activity budgets of bottlenose dolphin calves are indirectly impacted by the provisioning of their mother [77]. Calves born from provisioned mothers spend significantly more time foraging and less time resting than calves from non-provisioned mothers. The authors proposed that it could result from lower milk intake, reduced foraging abilities, or increased energy expenditures during the journey to reach the provisioning site.

In most provisioned sharks studied to date (tiger shark *Galeocerdo cuvier*, bull shark *Carcharhinus leucas*, and nurse shark *Ginglymostoma cirratum*), provisioning appeared to have only minimal effects on long movements, such as migration [77]. Indeed, for tiger sharks [74] and bull sharks [75], the time spent in tourist areas does not significantly differ from time spent in other areas. Both species engage in long-range movements to forage and reproduce, and both species visit reef regardless of feeding occurrence. However, other shark species that do not perform such large-scale migrations might instead become more sedentary due to provisioning [78]. There is an increase in daytime activity when tourism operators are diurnally present in fed whitetip reef sharks (*Triaenodon obesus*) that are, otherwise, nocturnally active [79]. Feeding has similar effects on other aquatic species (Fig. 2.2; see also Chap. 5). Some damselfish (e.g., *Chromis chromis*) reduce their home range when artificially fed by humans [80, 81]. In terrestrial animals such as African elephants (*Loxodonta africana*), the installation of artificial water points for conservation purposes allows ecotourists to observe large elephant aggregations, but it also modifies migration patterns and the location of resting places [82]. This appeared to have cascading effects on the vegetation, since elephants selected new places to rest and foraged on endemic plant species [82]. Artificial water holes also have consequences on sexual selection. For instance, female springbok preferentially (*Antidorcas marsupialis*) aggregate around novel water resources such as only strong males surround these artificially created areas [83].

Providing food to animals has been shown to increase aggressiveness and modify social structure in a variety of species [84, 85]. For example, pink river dolphins (*Inia geoffrensis*) become more aggressive when food is provisioned [86]. Aggression between conspecifics also occurred when food was delivered ad libitum

**Fig. 2.2** A tourist guide provisioning different fish species with corn, to satisfy snorkelers in a tributary river of Rio Cuiabá, Mato Grosso, Brazil. Photo credit Benjamin Geffroy

to southern stingrays. This was probably linked to overcrowding in a normally solitary species [87]. At the interspecific level, artificial aggregations at feeding practices were shown to lead to an increase in bites and chases between eagle rays (*Myliobatis australis*) and some stingrays [88]. This food provisioning attracts bolder animals [44, 87, 89] that may (un)intentionally target humans as potential prey or competitors. Not surprisingly, feeding operators delivering food to sharks have an increased risk of bite injuries [90].

Similar to pets receiving food every day at the same hour, provisioned wild animals associate humans with food. Some rays and sharks learn quickly to anticipate a food reward and arrive early and wait for food to be provisioned [78]. Changes in behavior associated with shark feeding have also been observed in whale sharks that progressively display vertical feeding behavior below tourist boats. These continuous contacts with humans lead to the progressive conditioning of animals to expect food from humans [91]. Food conditioning is also the main hypothesis explaining the presence of bears around human settlements [92]. Nevertheless, these are only proximate mechanisms, since food conditioning implies that a given bear was previously exposed to an accessible food source from anthropogenic origin. More generally, an individual's social status may also explain which bears will become associated with humans. Subadult and females with offspring will tend to avoid large dominant males by using areas surrounding humans as refuges [92]. Variation in personality also may help explain the differential distribution of bears [92] and other species (see Chap. 4). This has been shown in sharks, where some individuals are highly sedentary when food is provided, whereas others are less affected by provisioning practices [78]. Such individual variability is also observed for learning capacities [85], probably as a result of differences in personality traits.

### 2.3.4 Animal Personality

The recognition that individuals vary in consistent ways has generated considerable research interest [93, 94]. Statistically, individuality or "personality" is seen when the within-individual variation is less than the between-individual variation [93]. For example, a bold individual will remain relatively bold across different contexts and throughout time. Boldness, exploration, aggressiveness, and sociability/gregariousness are among the best studied personality traits [95, 96]. The response of a community to nonthreatening human exposure will differ according to the species and the type of disturbance but will furthermore depend on the degree of a species' personality types.

Current research often does not distinguish between whether individuals are tolerant toward humans due to individual habituation or because shyer individuals moved away from frequently disturbed areas [97]. It is quite likely that prolonged contact with humans would affect the composition of personality types in a population, selecting for either bolder or shyer individuals [43]. Changing personality types may have long-term consequences since different personality types vary in their reproductive success. For instance, bold and aggressive male zebra fish fertilize a greater number/proportion of eggs than shy fish [98]. Overall, it has been shown in a meta-analysis (including different taxa) that bolder individuals had higher reproductive success than shy individuals [99]. However, bold and aggressive individuals only do well under stable environmental conditions. When the situation becomes more challenging, it is often the shyer ones that are better able to adapt and find a way to survive, whereas bold individuals suffer higher mortality [99]. In the face of current rapid environmental change, it is essential to maintain diverse personalities to enhance adaptive capabilities of wild populations. Favoring one type of personality (e.g., bold over shy), either intentionally or unintentionally, will be risky for the long-term sustainability of populations exposed to ecotourism and thus the industry itself.

## Conclusions

In this chapter, we have shown how interactions with humans can systematically change the physiology and behavior of wildlife species. While some changes are transient, others may have long-term consequences. It is essential to realize that these effects are highly dependent on the species, the animal's life stage, the frequency and duration of visits, as well as the degree of human-wildlife interaction (Fig. 2.3). Hence, the "tipping point" where an animal will

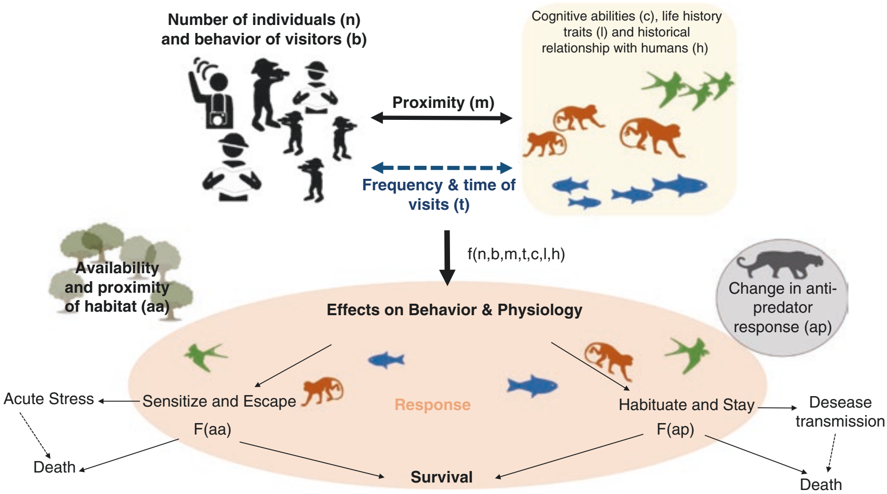


**Fig. 2.3** Human visitation can change the behavior and physiology of wildlife leading to sensitization or habituation. The impact of human visitation on wildlife is a function "f" of the number of humans; the proximity to the observed animals; the timing, frequency, and duration of the visits; and the escape capacity and behavior of the animals. Full arrows indicate very likely situations, while dashed arrows indicate possible outcomes. "F" relates to the *function*, such as effects on behavior and physiology are modulated as a function of the intensity of the different variables identified (*n*, *b*, *m*, *t*, *c*, *l*, *h*). Infographic developed by Benjamin Geffroy, Bastien Sadoul, and Ursula Ellenberg

suddenly change its physiological/behavioral state is difficult to estimate, even within a species. However, our global analysis reveals that, overall, when human visitation is an intermittent or rare event, an encounter with a visitor leads to physiological responses similar to those observed when facing an acute stressor, such as the presence of a predator. However, if visitor numbers reach a certain threshold, it can either lead to a state of chronic stress, with deleterious consequences for individual fitness, or to habituation of exposed individuals that results in a decreased stress response over time. However, increasing habituation to humans could have long-term negative effects if translated into higher tolerance around genuine predators [43]. The paucity of information on the effect of ecotourism on animal personality is a call for more research on individual responses. Although nature-based tourism undoubtedly has positive socioeconomic effects for some people, accumulating pressures of frequent visitation needs to be considered and managed carefully. It is essential, for both ecological and economical sustainability, to avoid or reduce any negative human impacts.

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