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Habituation and sensitization: new thoughts about old ideas

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People have written about habituation, a process that leads to decreased responsiveness to a stimulus, as well as its counterpart, sensitization, or an increased responsiveness to a stimulus, for over 2000 years. And, while intensive research in the last century has led to well-supported generalizations about mechanisms of habituation, we have not developed a 'natural history' of habituation and tolerance that would help us predict, based on life history and natural history variation, how species will respond to humans and anthropogenic stimuli. The need for predictive models has never been greater. In this essay I will review generalizations about these learning processes and point out how a clear understanding of mechanism can be used to inform wildlife management and generate testable management interventions. I will also highlight unanswered questions about habituation and sensitization, and establish the groundwork for developing a natural history of habituation and tolerance.

> *There once was a shepherd boy who was bored as he sat on the hillside watching the village sheep. To amuse himself he took a great breath and sang out, 'Wolf! Wolf! The Wolf is chasing the sheep!'*
>
> **(Aesop ca. 5th Century BC)**

Habituation is a process that leads to decreased responsiveness to a stimulus with repeated presentation and is often adaptive in that it makes it less likely that individuals will respond to harmless stimuli. Found throughout the animal kingdom, some plants have also been shown to habituate (Jensen, Dill, & Cahill, 2011). However, habituation may also have consequences. Aesop recognized the consequences of habitation 2500 years ago when he noted that the boy who cried wolf would ultimately be ignored when he needed help to fend off a real wolf.

Habituation's counterpart is sensitization—the increased responsiveness to a stimulus with repeated presentation. Sensitization may be adaptive if it helps animals avoid potentially risky or costly situations. Being sensitized to the sound of bees may help elephants avoid getting their sensitive trunks stung (sensu King, Douglas-Hamilton, & Vollrath, 2007), and may help allergic humans avoid an anaphylactic reaction. But it too may be costly. For instance, while drug addiction is usually thought to involve some degree of tolerance to drugs, indeed, it also involves sensitized responses that can be used diagnostically because greater salience is attached to the drugs and drug-associated cues (Steketee & Kalivas, 2011). Living without risk is impossible (Sagarin et al., 2010), and the public may become sensitized to real or manufactured threats repeated by the press (e.g. consider the U.S. government assertions that Iraq had weapons of mass destruction, or the American response to Ebola cases being treated in the United States in September–November 2014). Over-reacting to risk can lead to costly foreign policy mis-steps and costly public health responses.

Wildlife managers and conservation biologists care deeply about these processes because there is variation in the degree to which species' tolerate humans and our various associated stimuli (Blumstein, 2014). Tolerance is seen when animals permit closer approaches by humans without overtly responding or fleeing (e.g. Herrero, Smith, DeBruyn, Gunther, & Matt, 2005; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015). This tolerance may emerge from habituation-like processes or from more tolerant animals settling in areas where they encounter humans, while less tolerant ones actively avoid humans (e.g. Samia et al., 2015). We may see apparently tolerant animals because of a lack of resources elsewhere, resulting in dwindling resources within a patch, increased competition for remaining resources and increased tolerance to disturbance (e.g. Owens, 1977). Thus, tolerance in these cases does not indicate habituation, so it is essential to understand when habituation occurs. However, not all species tolerate increased human exposure; some species apparently sensitize to humans and

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thus may avoid or have heightened escape responses to them as human activity increases (e.g. Blumstein, 2014).

There are several main areas of wildlife management/conservation that can benefit from a deep understanding of these processes and their outcome—tolerance or susceptibility with respect to humans. The first area is attempting to reduce human–animal conflicts through the use of animal repellents. In this case, habituation can severely reduce the effectiveness of the management plan as has long been known by managers. The second concerns cases where the goal of the manager is to habituate animals to anthropogenic activities. The third deals with the transferability of habituation from humans to other potential predators, a behavioural strategy that, if common, could have unfortunate conservation outcomes. While managers work to address these issues on the ground, greater communication and collaboration with behavioural biologists might lead to novel management strategies (Blumstein & Fernández-Juricic, 2010).

First, wildlife–human conflict situations require managers to decrease tolerance of animals to humans and human-related stimuli so that animals avoid humans and our resources. These situations are commonly seen when bears (Elfström, Zedrosser, Støen, & Swenson, 2014), birds (Belant, Seamans, Gabrey, & Ickes, 1993) and rodents are attracted to human garbage, or when ungulates and primates eat crops (Naughton-Treves, 1998; O'Connell-Rodwell, Rodwell, Rice, & Hart, 2000), and when marine mammals eat fish from human fisheries (Northridge, 1991). However, a state of increased tolerance may emerge from habituation-like processes that follow repeated exposure to potentially alarming stimuli or repellents and that render them ineffective.

Second, anthropogenic human disturbance may scare or otherwise interfere with animals' behaviour (Klein, Humphrey, & Percival, 1995; Steven, Pickering, & Castley, 2011). A variety of factors may modify behaviour including experience with more humans, or human development or activities, even seemingly benign ones like ecotourism and bird watching. Thus, when the goal is to not lose species as human impacts increase, we may aim to increase tolerance of animals to humans. The problem, however, is that not all species habituate.

In the remainder of this essay, I will more formally define habituation, sensitization and tolerance. I will review generalizations about these processes. I will then discuss why these processes are important to wildlife managers and conservation biologists, because not all species habituate and tolerance based on observed behaviours may not be benign, and how and why one way to study them capitalizes on quantifying the flight initiation distance in response to approaching humans. Then, I will outline a research programme by which we can develop a natural history of habituation and discuss future research needs.

THE RULES OF HABITUATION

Habituation has been formally and comprehensively reviewed by Rankin et al. (2009). Habituation has been studied for over a century and in their authoritative review, Rankin et al. defined habituation as '…a behavioral response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue' (page 136). In more general terms, habituation is a type of 'single-stimulus' learning that allows animals to avoid costly responses in situations where there is no benefit from responding to repeated stimulation.

Bejder, Samuels, Whitehead, Finn, and Allen (2009) systematically reviewed how these terms are used (and misused) in the wildlife management literature. They quoted Nisbet (2000, page 315) who wrote that 'Habituation and sensitization are processes, that occur over time, and that predict changes in tolerance (i.e. the intensity of disturbance that an individual tolerates without responding in a defined way)'. Viewed this way, tolerance is a 'state', and changes in tolerance reflect prior experiences. Managers typically measure tolerance in human impact studies, but it is the processes of habituation, habituation-like processes or sensitization or the differences in habitat-selection among individuals that ultimately lead to differences in tolerance.

Rankin et al. (2009) made a number of generalizations about habituation. I will focus on a number of these because knowledge of them can help design protocols to enhance or inhibit habituation and habituation-like processes. After this brief summary, I will attempt to apply some of these insights to concrete management problems.

First, regarding habituation, there should be a nonlinear asymptotic decline in the frequency or magnitude of a response with repeated or ongoing stimulation. After some time or number of repetitions, we should not expect more habituation. From a wildlife manager's perspective, animals that habituate should do so predictably to repeated exposure to anthropogenic stimuli.

Second, there can be spontaneous recovery (to prestimulus levels) if the stimulus is withheld, which means that if habituation is a goal, some degree of repeated stimulation is required. From a manager's perspective, intermittent exposure to anthropogenic stimuli, with long intervals between exposures, may not lead to habituation (Rodríguez-Prieto & Fernández-Juricic, 2005).

Third, after a series of stimulus repetitions and spontaneous recoveries, habituation becomes more rapid. This means that animals are likely to learn to rehabituate more quickly with prior experience. From a manager's perspective, if habituation is desired, intense bouts of experience with anthropogenic stimuli that are separated in time will ultimately lead to habituation. However, this raises concerns when the goal is to prevent animals from eating at dumps or other localized sources of food if individuals visiting them are intermittently hazed (e.g. Werner & Clark, 2006).

Fourth, more frequent stimulation leads to more rapid habituation, which means that if habituation is the objective of exposure to stimuli, short intervals between exposures to stimuli will be particularly effective.

Fifth, repeated stimulation after the asymptote has been reached may delay spontaneous recovery. Mangers thus may face problems when they seek to haze animals away from specific areas because repeated stimulation will maintain habituated responses.

Sixth, stimulus strength is important: 'weaker' stimuli lead to more rapid habituation while 'strong' stimuli might not result in habituation. This means that lower-intensity stimuli (amplitude, size, colour, etc.) may be more effective if the goal is to habituate animals to anthropogenic stimuli.

Seventh, it is possible for animals to dishabituate or have their response recover. One important factor that influences dishabituation is the presentation of another 'strong' stimulus. This is an important characteristic because, as Rankin et al. (2009) note, it is the only characteristic that ties a proximate mechanism of habituation to its ultimate benefit—habituating to innocuous stimuli while maintaining the ability to respond to novel stimuli.

Eighth, even though a stimulus may cause dishabituation, repeated exposure to that stimulus may lead to habituation. Again, from a manager's perspective, if habituation is desired, these are important characteristics to know, but they also create real challenges when trying to haze animals away from specific resources.

Ninth, habituation can be transferred from one stimulus to another. Such transfer of habituation has important implications because it is a fundamental way that we can identify the natural categories into which animals classify stimuli (e.g. categorical perception, Harnad, 1987). If, for example, by habituating to humans, a particular prey also habituated to another terrestrial, mammalian predator, say a fox (*Vulpes* sp.), we would infer that humans and foxes are perceived similarly. There are some data that suggest that after habituating to benign humans, animals may transfer their response to humans to their natural predators (Mccleery, 2009), but more data are needed to understand how widespread this is and the conditions under which it emerges (Geffroy, Samia, Bessa, & Blumstein, 2015). However, by habituating to benign humans, animals are certainly more vulnerable to humans with consumptive intent (Geffroy et al., 2015). This may be a real problem in protected areas that are subjected to wildlife poaching—such as the Virunga National Park gorillas, *Gorilla gorilla*, in the Democratic Republic of Congo (Kasereka, Muhigwa, Shalukoma, & Kahekwa, 2006). Herrero et al. (2005) and Smith, Herrero, and DeBruyn (2005) noted that brown bears, *Ursus arctos*, habituate to bears as well as humans, and the fact that bears habituate to other bears may predispose them to habituate to humans.

Tenth, there is the potential for long-term habituation to stimuli. From a manager's perspective, this may be a desirable feature, if the goal is to reduce human impacts on wildlife, or it may be a very undesirable feature, if the goal is to repel animals by using some sort of hazing device (http://icwdm.org/ControlMethods/Hazing.aspx accessed 24 February 2015). Developing hazing devices to protect wildlife has been an active area of applied research. Indeed, preventing large carnivores from eating livestock has led to the creation and evaluation of disruptive stimuli (such as fladry, small flags tied to fence lines, and a variety of noise makers that are triggered by a predator's presence), as well as aversive stimuli (such as training collars and the deployment of painful stimuli; e.g. Shivik, 2006). Shivik (2006) reviewed the effectiveness of various tools used to manage human–carnivore conflicts and found that although many became ineffective rather rapidly, some worked to various degrees on different carnivores (e.g. Shivik, Treves, & Callahan, 2003). Effectiveness wanes over time as animals learn to ignore relatively benign threats. Thus, currently available repellents may be best suited for relatively short periods of application in relatively high-risk situations (Shivik, 2006).

WHY MECHANISM MATTERS

A state of tolerance could be developed by habituation and habituation-like processes. However, apparent tolerance to human disturbances could also be caused, as Bejder et al. (2009) pointed out, by displacement, whereby individuals vary in the degree of disturbance they are able to tolerate and that they sort themselves out according to this variation in disturbance tolerance. In this case, we would see spatial variation in behavioural (or physiological) responses that do not result from habitation. Because habituation, as a mechanism, has certain characteristics, knowing when habituation is the mechanism responsible for tolerance could have important management implications if the goal is to either increase the degree of habituation or to delay the onset of habituation.

There are least two other processes that could lead to spatial variation in tolerance (Bejder et al., 2009). First, there could be physiological differences caused by repeated exposure to disturbances, which can affect the sensitivity of animals to similar disturbances, for example, deafening that results from prolonged exposure to loud noises. Second, there could be ecological traps that may affect certain individuals or those in certain locations. Van Horne (1983) pointed out that habitat quality should not be inferred from the distribution of animals, but rather where individuals have the greatest fitness. Later, Gill, Norris, and Sutherland (2001) noted that animals may be lured to areas with a particular resource even though their fitness is lower in that patch because of human disturbance. They cautioned that inferring suitable habitat from relative abundance is fraught with risk. Bejder et al. (2009, page 182) summarized aptly: 'mechanisms that do not involve true habituation are unlikely to denote natural or beneficial outcomes for wildlife affected by disturbance'. Thus, it is essential to understand the conditions under which true habituation, rather than other mechanisms that might explain apparent tolerance, occurs and the conditions under which it does not.

APPLICATION: PREVENTING HABITUATION

While aversive conditioning has been used by wildlife managers for years (e.g. Kloppers, St Clair, & Hurd, 2005; Leigh & Chamberlain, 2008), when the goal is to manage human–wildlife conflict from the position of reducing the likelihood of habituating to repellents, fear conditioning may be a particularly promising technique (Schakner & Blumstein, 2013, 2016). Indeed, the ultimate goal of using potentially harmful and aversive deterrents, like very loud and painful sounds, should be to not have to continually use them. Thus, creating anxiety that leads to avoidance of a contested area or resource should be an effective and more welfare-friendly/ethical strategy.

Unlike habituation or sensitization, which are examples of single-stimulus learning where stimuli are not paired with other predictive stimuli, fear conditioning is a method of associative learning that pairs a painful or startling unconditioned stimulus (US) with a benign stimulus (CS) that ultimately predicts the US. If applied successfully, a few pairings of the benign stimulus with the painful/aversive stimulus creates fear or anxiety in the target subjects when they experience the benign stimulus. While additional presentations of the painful/aversive US may be needed to prevent extinction of responses to the benign CS, fewer presentations are needed overall than when the US is repeatedly presented alone. True fear conditioning is not simply aversive conditioning because true fear conditioning ensures that the aversive stimulus is sufficiently painful/aversive so as to cause an unconditioned startle response. What is needed is to develop and properly evaluate fear-conditioning protocols to create effective and welfare-friendly/ethical deterrents.

APPLICATION: PROMOTING HABITUATION

There are a variety of situations where we might wish to promote habituation. For instance, if wildlife–human interactions are inevitable (a new hiking trail is being built, a formerly closed area is opened up to ecotourists, etc.), might there be ways to habituate wildlife to increased expected exposure to humans? The list of Rankin et al.'s (2009) generalizations offers great promise for management interventions. But, aside from researchers habituating animals to observer presence (e.g. Goodall, 1986), and studies that have demonstrated that habituation might extend to the specific location from which a disturbing stimulus approaches an individual (Raderschall, Magrath, & Hemmi, 2011), I am aware of no experimental studies that have tried to apply them in a management context specifically to habituate animals to anthropogenic disturbance. Some observational studies suggest that bears concentrate near concentrated food sources (natural or artificial), first habituating to each other, and then to people (e.g. Herrero et al., 2005). The lack of experimental studies is striking in part because treatments of post-traumatic stress disorder (PTSD) in humans, as well as behavioural therapies to reduce phobias, both involve repeated exposure to benign stimuli with the aim of reducing responsiveness to them (e.g. Wilson, Friedman, & Lindy, 2001). There is potentially much to learn from human therapies that could be applied to wildlife management.

By contrast, there are many studies that have reported differences, both over time and space, as a function of exposure to specific human-related stimuli (e.g. Li, Monclús, Maul, Jiang, &

Blumstein, 2011; Viblanc, Smith, Gineste, & Groscolas, 2012). It is essential, from a management perspective, to recognize that overt behavioural tolerance may not equal physiological tolerance (e.g. Ellenberg, Mattern, & Seddon, 2013) and, whenever possible, it is essential to try to study both the overt behavioural responses and less overt physiological ones (e.g. Tarlow & Blumstein, 2007).

APPLICATION: EVALUATING HABITUATION TRANSFER

It is possible that under certain conditions animals that habituate to humans become more vulnerable to predators (Geffroy et al., 2015). Formally, the transfer of habituation from one stimulus to another type of stimulus means that the two stimuli are categorically classified into the same class of stimuli (Harnad, 1987). While humans and coyotes may indeed both be members of a category of terrestrial mammalian predators, many species have sophisticated and nuanced predator discrimination abilities (e.g. Liesenjohann & Eccard, 2008; Relyea, 2003). Thus, some degree of habituation among very similar types of stimuli might be expected, but we may not generally expect that, by habituating to humans, prey will suddenly become vulnerable to other predators unless human presence creates a human shield (Berger, 2007), which reduces all threats on animals (Geffroy et al., 2015).

We asked whether dik-diks, *Madoqua guentheri*, a small African ungulate that is eaten by about 36 species of mammals and birds, transfers habituation from humans to predators in a situation where there was no strong human shield. To do so, we broadcast jackal, *Canis adustus*, calls and birdsong within about 0.5 km of human habitation and >0.5 km from human habitation. We assumed that dik-diks living within 0.5 km of humans were habituated to humans. We found that human-intolerant dik-diks, those living >0.5 km from humans, were unable to discriminate between the sounds of predators and benign sounds. From this we concluded that ecotourists at more pristine places are likely to disturb animals and interfere with their risk assessment (Coleman, Richardson, Schechter, & Blumstein, 2008).

From first principles, one might initially assume that animals that are not overtly persecuted by people and that have large home ranges that includes human areas should be tolerant of, and possibly habituated to, human presence throughout their home range. However, we often find that context is very important for habituation, so one might also assume that nonpersecuted individuals might habituate to the specific areas where human disturbance is present. We asked whether mule deer, *Odocoileus hemionus*, that are not hunted during the summer discriminate yellow-bellied marmot, *Marmota flaviventris*, alarm calls from white-crowned sparrow song, *Zonotrichia leucophrys*, within 0.5 km of human habitation and >0.5 km from human habitation. Similar to our dik-dik results, we found that deer were able to discriminate the sounds when they were tested within 0.5 km of human habitation but not when they were tested >0.5 km from human habitation, where they were generally more responsive to our presence (Carrasco & Blumstein, 2012).

I acknowledge that there are a number of factors other than learning processes—most are in some way related to the location of valuable resources—that could explain location-specific differences in tolerance to humans. Nevertheless, does 0.5 km have some special meaning? Studies of how mule deer respond to approaching humans (i.e. flight initiation distance, FID, the distance at which an individual flees an approaching person) identified a threshold somewhere between 300 m and 700 m, whereby they fled sooner after becoming alerted when they were farther from human settlements than they did when they were closer to human settlements (Price, Strombom, & Blumstein, 2014). Similarly, western gulls, *Larus occidentalis*, showed a rapid increase in flight initiation distance as human visits to a beach declined (Webb & Blumstein, 2005). And, in another study, where a fence restricted human access to the birds on the other side, four species of shorebirds were more tolerant of human approach in areas where they had been exposed to ecotourists and less tolerant in an adjacent area on the other side of the fence. Indeed, there were no significant differences in FID between the fenced side of the wetland and a nearby wetland that was closed to the public (Ikuta & Blumstein, 2003).

Humans may also shield prey from specific predators that are less tolerant of humans in specific locations. Such human shields change the behaviour of some ungulates (e.g. Berger, 2007; Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014) and primates (e.g. Nowak, le Roux, Richards, Scheijen, & Hill, 2014) and may help drive trophic cascades (e.g. Waser et al., 2014). Therefore, the human shield effect is important to consider when trying to understand the conditions under which animals become tolerant of humans, whether via habituation or other mechanisms (Geffroy et al., 2015).

There is a growing literature on the spatial ecology of fear (e.g. Brown, 1999; Brown & Kotler, 2007; Ditchkoff, Saalfeld, & Gibson, 2006; St Clair, Found, Gangadharan, & Murray, 2016; Zimmermann, Nelson, Wabakken, Sand, & Liberg, 2014), and much could be gained by more detailed studies of risk assessment in an explicitly spatial context. The goal would be to understand the extent to which ecological, morphological, behavioural and life history factors influence spatial tolerance of, and possibly habituation to, humans. From first principles it will likely depend on a species' perceptual active space (e.g. Lima & Zollner, 1996; St Clair et al., 2016) and home range size. Spatial detection maps, which reflect areas around an animal where the probability of threat detection are higher based on the visual system configuration, define the perceptual active space (Tyrrell & Fernández-Juricic, 2015). Once these are understood, we might expect that species that have large home ranges and that habituate to humans at a specific location may be more likely to transfer that perceived safety to other parts of their home range. However, what is completely unknown is how site-specific risk factors may directly or interactively influence the spatial ecology of fear. For instance, if a specific habitat type (e.g. dense cover) is associated with increased predation risk, are animals equally likely to be tolerant in or to habituate to these specific areas within a human-dominated landscape? More studies are thus warranted.

APPLICATION: UNDERSTANDING ANTHROPOGENIC DISTURBANCE

There are many situations where the establishment of hiking trails, roads or human development leads to the loss of intolerant species. How can we develop a better understanding of which species are likely to be more or less tolerant to human disturbance? And, more importantly, can we distinguish a change in tolerance from other factors, such as successful avoidance (i.e. modifying resource use around humans; Zimmermann et al., 2014), as the driver of coexistence or the failure to coexist with humans? I focus on insights from studies generated by quantifying flight initiation distance because these studies provide a large comparative data set that allows us to draw generalizations.

We know that humans change the behaviour of animals, and a key to understanding how they do this is to view people as predators (Frid & Dill, 2002). We know that when predators approach, animals often flee and hide from them. Thus, the distance at which an animal flees an approaching person (FID) can be used to quantify perception of predation risk and it can aid in wildlife management.

FID should, and does, vary quite dynamically (Cooper & Blumstein, 2015; Ydenberg & Dill, 1986). So, before we embark on comparative studies, we should have some confidence that FID is a species-specific trait. Blumstein, Anthony, Harcourt, and Ross (2003) studied Australian shorebirds at six sites that varied in rates of human visits and they found that FID varied in eight species, but with no significant interactions across sites. This means that flighty species were relatively flighty wherever they were studied and it provides some assurance that FID can be viewed as a species-specific trait. Subsequent studies have identified some phylogenetic signature of FID (e.g. Møller & Garamszegi, 2012; Møller, Samia, Weston, Guay, & Blumstein, 2014), which provides additional support for the hypothesis that FID can be viewed as a species-specific trait for comparative study. Importantly, and somewhat intriguingly, a phylogenetic signal in FID is not always found (e.g. Cooper, Pyron, & Garland, 2014; Symonds, Weston, Robinson, & Guay, 2014).

There is a huge literature on FID, mostly focused on birds (Møller, 2015), mammals (Stankowich & Reimers, 2015) and lizards (Cooper, 2015; Samia, Blumstein, Stankowich, & Cooper, 2016), that has identified a variety of extrinsic and intrinsic factors that influence FID (Stankowich & Blumstein, 2005). For instance, body size (Blumstein, 2006) and starting distance or alert distance (Blumstein, 2003, 2010; Samia & Blumstein, 2014; Samia, Nomura, & Blumstein, 2013) explain a considerable amount of variation in FID: large animals and animals that alert and flee at greater distances when approached. While a relatively small comparative study found no effect of eye size on FID (Blumstein, Fernández-Juricic, LeDee et al., 2004), another study using a larger sample found that birds with larger eyes flee at greater distances (Møller & Erritzøe, 2010). Thus, some evidence suggests that aspects of vision influence FID. Species that eat live prey have larger FIDs than those that do not (Blumstein, 2006), as do cooperative breeders. Species that begin reproducing at later ages (Møller & Garamszegi, 2012), that live in more open habitats (Møller & Erritzøe, 2010; but see; Blumstein, 2006) and that have faster basal metabolic rates (Møller, 2009) all flee at greater distances.

Remarkably, however, most of these studies have not followed marked individuals. Since one of the key questions is whether individuals habituate or not to repeated disturbance, this is a major shortcoming in our knowledge about how FID can be used to inform management. To determine whether individuals habituate to repeated approaches, it is essential to study marked individuals.

Over the past decade, we have studied FID in a marked population of yellow-bellied marmots studied at the Rocky Mountain Biological Laboratory, the site of a long-term research project that began in 1962 (Armitage, 2014; Blumstein, 2013). Marmots were experimentally approached one or more times annually. After controlling for a variety of other factors that influence FID, we found that older marmots, but not pups, allowed people to approach them more closely after repeated approaches and thus showed evidence of habituation-like processes.

Carrete and Tella (2010, 2013) repeatedly measured FID in individually marked burrowing owls, *Athene cunicularia*. They estimated the repeatability of FID, which is a measure of intra-individual consistency, and found that there was substantial repeatability (0.84–0.92). They also found significant interindividual variation in FID that was maintained over repeated experimental approaches. Thus, some owls failed to habituate. They hypothesized that more sensitive owls settled in places with less human disturbance, while more tolerant owls were able to coexist with human disturbance (Carrete & Tella, 2010).

In addition, some species may sensitize. In a study of 14 species of California coastal chaparral birds, only four species had significantly different FIDs when studied in areas with relatively more human visits than in areas that were less frequented by humans. However, and somewhat unexpectedly, these four species had greater FIDs when they were exposed to more people (Blumstein, 2014). The other 10 species had no significant differences in FID as a function of quantifiable differences in human visits. What could explain this apparent sensitization?

According to the dual process theory of habituation, an observed behaviour after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves & Thompson, 1970). Virtually nothing is known about the conditions under which sensitization dominates habituation in the wild.

I suggested that the perhaps species living in limited habitats (e.g. wetland fragments) may be more likely to habituate than those living in more contiguous habitats (e.g. chaparral) because those that live in remnant fragments may have already gone through a sorting process that eliminated less tolerant species or individuals (Blumstein, 2014). I called this the ‘contiguous habitat hypothesis’ and suggested that it needs proper testing by evaluating it in other habitats, with more species, and different types of disturbance. Indeed, the importance of contiguous habitat may also vary by whether a species is a generalist or a specialist, with specialists tolerating more disturbance in fragmented landscapes because they have no other options than to tolerate disturbance.

CONCLUSIONS: DEVELOPING A NATURAL HISTORY OF HABITUATION

> *A fox who had never yet seen a lion, when he fell in with him for the first time in the forest was so frightened that he was near dying with fear. On his meeting with him for the second time, he was still much alarmed, but not to the same extent as at first. On seeing him the third time, he so increased in boldness that he went up to him and commenced a familiar conversation with him.*
>
> **(Aesop ca. 5th Century BC)**

I suggest that we must develop a natural history of habituation and processes that lead to tolerance. What would this look like? I suggest we want to try to predict how species will respond to humans and our stimuli. We know that not all species habituate. Why? What future research is needed to develop better predictive models? Developing a full-blown natural history of habituation must be integrative in scope (it must be based on a wide range of physiological stress responses) and requires greater knowledge of all of species' sensory abilities. It would also require understanding all sensory abilities. Such data are not currently available across a wide range of species living in a variety of habitats and under a variety of anthropogenic disturbances. Thus, for a first stab, I will restrict it to insights that can be gained by studying FID.

We know that large species have greater FIDs than small species (Blumstein, 2006) and that body size is also a key predictor of the magnitude of habituation-like responses seen (Samia et al., 2016). Thus, large species might simultaneously be more likely to be initially disturbed by humans engaged in benign activities, but paradoxically, they might also be more likely to habituate to reduce the costs associated with disturbance. If large species pay a relatively larger cost of disturbance, then they should gain a relatively greater benefit from habituation. This hypothesis requires proper testing.

Life history and natural history variation may also be important predictors of the degree to which species habituate to and tolerate human disturbances. We know that sociality and other life history factors influence FID (Blumstein, 2006) and this in turn should select for greater benefits from habituation.

We must also understand past selection. Sih (2013) emphasized that decision rules that animals employ are the result of past selection. The degree of match between current and historical threats should permit us to understand how and when species may (or may not) habituate to or more generally tolerate specific types of disturbance. Truly novel disturbances may be more difficult to tolerate than those that share features with other known threats. And, truly novel disturbances might also lead to a level of tolerance (possibly via habituation) that, at some point, could prove lethal (e.g. animals adapting to frequent vehicle traffic, the novel disturbance, but then unable to respond adequately to instances of direct vehicle approach at moderate to high speeds in marine, terrestrial or airborne situations).

We must develop a better understanding of the spatial scale of habituation. It can be stark (e.g. with a fence), or gradual and occur over several kilometres. Does body size, acting through home range size and, therefore, through expected experience, influence the spatial scale of habituation? Or, might habituation be very site specific, which means that individuals are differentially tolerant to humans in different locations. Studies are needed to disentangle these alternative hypotheses in more than one species.

Similarly, the contiguous habitat hypothesis must be tested. Does the degree of habitat continuity really predict whether species habituate or not? Has a ‘filtering’ process occurred in fragmented habitats? Future studies in different systems will let us know more about the generality of the hypothesis.

Ellenberg, Mattern, and Seddon (2009) noted that sex, temperament and previous experience with humans affect whether yellow-eyed penguins, *Megadyptes antipodes*, habituate or sensitize to repeated human visits. Calm individuals were more likely to habituate, as were females. Are such patterns generalizable? Does this mean that certain types of individuals will be systematically more disturbed by human activities than others? Such studies are urgently needed because differential disturbance potential will change the mix of personality types in the population and this may affect population persistence.

We must develop a better understanding of the fitness consequences of habituation to humans. Are the results from dik-diks generalizable to other species? Is there any evidence that habituating to humans makes species more vulnerable to natural predators? Fortunately, to date, evidence for this is scarce, but that does not mean that it never happens.

We must develop a better understanding of individual differences in risk tolerance. Adopting a framework to study phenotypic plasticity gives us two ways to quantify individual tolerance: individuals may differ in their expected value (estimated with a best linear unbiased predictor, BLUP; Henderson, 1975), or they may differ in the slope at which they habituate (e.g. Dingemanse & Dochtermann, 2013). What are the patterns that different species show? Are there any generalizations that can be made about these patterns? What explains variation in these patterns?

Managers should try to apply insights from this corpus of knowledge to solve applied problems. However, to advance the field, applications should be in the context of adaptive management experiments (Walters & Holling, 1990; see also; Blumstein, 2007). Blumstein and Berger-Tal (2015) outlined a workflow through which behavioural ideas could be tested to see whether they can successfully be used to solve management problems, and if so, then their comparative efficacy can be evaluated. By including comparative efficacy evaluation, the relative utility of behavioural interventions can be compared to more traditional wildlife management interventions. In the context of managing human–wildlife conflicts, more stimuli (both in quantity and quality) may be more disturbing and hence, more effective, as might stimulus location and timing (also see Conover, 2002). And, while fear conditioning seems to offer great promise, it is essential to properly evaluate fear-conditioning paradigms to reduce human–wildlife conflict.

Bejder et al. (2009) noted the importance of developing and applying models based on individual decisions. To do so we must identify key internal and external factors that influence risk assessment. Meta-analyses of FID (Møller, 2015; Samia et al., 2015; Stankowich & Blumstein, 2005) and comparative analyses (e.g. Blumstein, 2006; Díaz et al., 2013; Møller et al., 2014) are good first steps.

It is, however, important to realize that results from comparative analyses that include a diversity of species with a broad range of trait values (e.g. body masses) might not apply at the intraspecific level. For instance, while body mass explains much of the interspecific variation in FID, body mass variation does not significantly explain variation in FID among individually marked, yellow-bellied marmots (Petelle, McCoy, Alejandro, Martin, & Blumstein, 2013). One likely explanation is that the range of variation within a species is substantially less than that found between species. If generally true, one must be somewhat sceptical about using the results of comparative analyses to identify key factors that influence a given species' behaviour without validating them in species of interest. Nevertheless, state-based models and approaches may be particularly important since they put decisions into a life history context by which individuals must trade off starvation versus predation risk (e.g. Gill et al., 2001; Rhoades & Blumstein, 2007). And, Sih (2013) makes a strong case for focusing on individual decisions in situations where there has been human-induced rapid environmental change (HIREC).

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