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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

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