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Learning and conservation behavior: an introduction and overview

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3.1 CONCEPTUAL BACKGROUND

Learning is a key aspect of behavior that may greatly enhance the survival and fecundity of animals, especially in a changing environment. Wildlife conservation problems often involve increasing the population of threatened or endangered species, decreasing the population of species deemed over abundant or encouraging animals to move to or from certain areas. Learning is an example of reversible plasticity (for review see Dukas 2009), which typically remains open to change throughout life. Old associations can be replaced, relearned and reinstated, facilitating behavioral modifications across an individual's lifetime. Because learning is potentially demographically important, and because it can be used to modify individual's behavior, it may therefore be an important tool for conservation behaviorists (Blumstein & Fernández-Juricic 2010). Our aim in this chapter is to introduce the fundamentals of learning that will later be developed and applied in subsequent chapters.

Animal learning theory defines learning as experience that elicits a change in behavior (Rescorla 1988, Heyes 1994). There are three basic mechanisms, or types of experiences, that underlie animal learning. The simplest learning process is non-associative because it involves an individual's experience with a single stimulus. During this process, exposure to the single stimulus results in a change in the magnitude of response upon subsequent exposures to that stimulus. If the response increases, the process is called *sensitization*; if the response decreases, the process is called *habituation*. More complex associative learning mechanisms involve a change in behavior as a result of experience with two stimuli through *Pavlovian conditioning* (also referred to as *classical conditioning*),

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or the relationship between a subject's own behavior in response to a stimulus, which is called *instrumental conditioning*. Finally, learning can also occur as a result of interactions or observations with other individuals through *social learning*, but it is currently unclear whether social learning actually represents separate learning mechanisms than individual learning (Heyes 1994). Below we will describe these in more detail and outline the conditions that influence them. Later we will explain how knowledge of mechanisms of learning can be applied to wildlife management and conservation.

3.1.1 Non-associative learning: habituation and sensitization

3.1.1.1 What is it?

Single-stimulus learning is the simplest learning process and involves a change in the frequency or intensity of response to a stimulus. Non-associative, single-stimulus learning involving a reduction of a behavioral response to repeated exposure to stimuli that is not due to sensory fatigue is called habituation (Groves & Thompson 1970). Unlike generalized sensory adaptation or motor fatigue (which would exhibit generalized responses within a modality to stimuli), habituation is characterized by stimulus specificity, which can be tested by showing responsiveness to novel stimuli (Rankin *et al.* 2009). This specificity suggests the function of habituation is to filter harmless stimuli from novel stimuli (Rankin *et al.* 2009). In contrast to habituation, heightened responsiveness after repeated exposure is termed sensitization. According to the *dual process theory of habituation*, an observed behavior after repeated exposure to a stimulus represents the sum of the two underlying learning processes of habituation and sensitization (Groves & Thompson 1970).

3.1.1.2 Conditions influencing habituation

Generally, simple parameters such as intensity, modality and frequency influence single-stimulus learning in animals. More frequent exposure typically results in quicker or more pronounced habituation (Groves & Thompson 1970, Rankin *et al.* 2009). Correspondingly, repeated exposure to less intense stimuli results in a response decrement, whereas repeated exposure to higher intensity stimuli may either elicit no habituation or may result in sensitization (Groves & Thompson 1970, Rankin *et al.* 2009). After becoming habituated, withholding the stimulus results in a partial recovery in responsiveness, a process termed *stimulus recovery*. Response decrement exhibits specificity within a modality, which can be demonstrated by restored responsiveness to novel stimuli. During the course of habituation, the presentation of another, strong stimulus results in *dishabituation*, or restored responsiveness to a previously habituated stimulus. These behavioral characteristics of habituation have been clearly described in Groves and Thompson (1970), and since refined in Rankin *et al.* (2009).

3.1.2 Pavlovian conditioning

3.1.2.1 What is it?

Pavlovian learning is seen when individuals learn the relationship between two stimuli; it is also called classical conditioning and, broadly, is one type of associative learning (Mackintosh 1974, Dickinson 1980, Rescorla 1988). In this type of learning, a biologically relevant stimulus, called the *Unconditioned Stimulu*s (abbreviated US) is preceded by another stimulus, the *Conditioned Stimulus* (abbreviated CS). According to contemporary animal learning theory successful classical conditioning depends upon the contingency between the CS and US. This contingency can be positive, meaning that the US reliably follows the CS, or negative, meaning the CS reliably signals the absence of US. As a result of this pairing, animals are able to learn the relations between the two stimuli and generate an adaptive response (Dickinson 1980, Shettleworth 2010).

The capacity to learn about the relationship between two stimuli, such as sounds preceding the presence of a predator, or taste cues associated with edible food, is functional because it guides how an animal can adaptively respond to exogenous stimuli as well as anticipate future events (Domjan 2005, Shettleworth 2010). *Pavlovian fear conditioning* is an associative form of learning in which individuals are exposed to an aversive stimulus (US) paired with an innocuous stimulus (CS) (Fanselow 1984, Grillon 2008, Fanselow and Ponnusamy 2008). Once conditioning has occurred, exposure to the unconditioned stimulus generates fear reactions to the conditioned stimulus. For example, by learning the cues that predict a predator attack, prey are able to modify their behavior and reduce the probability of death (Domjan 2005). From this functional learning perspective, learning about the relationship between two stimuli influences the adaptive decision-making process and can modify an individual's behavioral response (Hollis 1982).

3.1.2.2 Conditions influencing Pavlovian conditioning

Functionally, there are particular conditions in which animals are able to learn patterns or relationships between stimuli in the natural world. The temporal relationship between two stimuli influences the conditioning process. Generally, a CS that precedes a US in time leads to more robust conditioning (Domjan & Burkhard 1986, Rescorla 1988). This is intuitive because in nature it is adaptive to learn the cues that precede consequences (i.e. certain tastes may precede sickness, or alarm calls are likely to precede predator presence).

The Rescorla-Wagner model (RW) is a generally accepted model for predicting the behavioral consequences and conditions driving associative learning between a CS and a US (Rescorla & Wagner 1972). According to the model, learning occurs as a result of the difference between what an animal expects to happen versus what happens. The RW model suggests that all learning curves are similar and asymptotic (Figure 3.1). For example, the first pairing of a CS (e.g. a neutral tone) followed by a US (e.g. a shock) is surprising, and results in a significant amount of learning (Figure 3.1). After subsequent pairings, the amount that is learned decreases because the US is less surprising when it follows the CS, resulting in a negatively accelerating curve. At the asymptote, the past experience with the CS/US pairing means that the CS accurately predicts the US, and thus little more is learned. According to the model, learning curves may differ in their slope, which is determined by the values of the rate parameters (i.e. magnitude of US or CS and US salience). In other words, some relationships can be learned more quickly than others (e.g., taste aversion or fear conditioning). The model can be used to help understand differences between species (Trimmer *et al.* 2012) and help explain differences in the speed of learning. For instance, the value of alpha (the CS learning rate) for auditory cues may be higher in one species than another, which will then lead to the former learning more quickly than the latter when an auditory cue signals something like the imminent delivery of food. The RW model produces idealized learning curves during controlled conditions. In the wild, differences in parameter values across species may explain observed patterns of learning in different situations, although this requires further study.

Conditioning also depends on the nature and relationship of the stimuli being paired. Conditioning experiments confirm that learning particular combinations of stimuli can be especially effective. For example, pigeons form effective associations when auditory cues are the CS preceding a shock and visual cues precede food (Shapiro *et al.* 1980). Taste aversion learning is

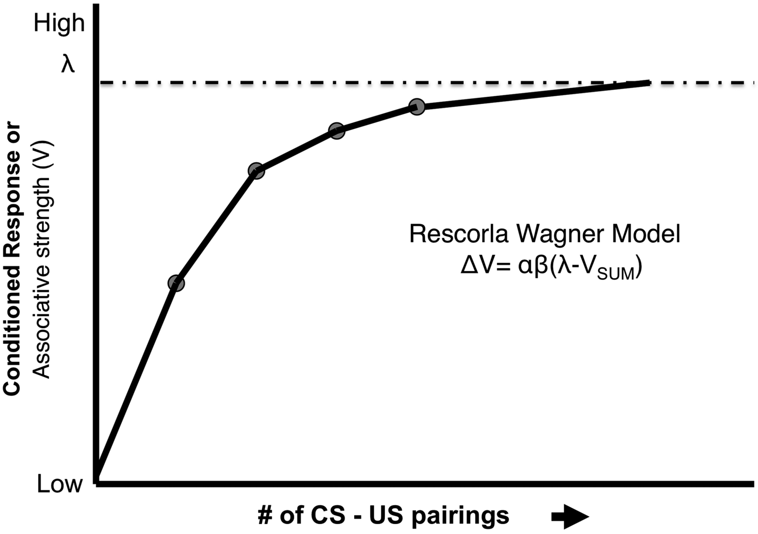

Figure 3.1: The Rescorla-Wagner model of learning. On the *y*-axis is the performance, which represents underlying learning (associative strength). The change in predictive value of a CS, ΔV is a result of the discrepancy between what is expected versus what actually happens ($\lambda - V_{SUM}$). and are learning rate parameters that correspond to salience of the αCS and βUS, and $V_{SUM\ I}$ is the sum of current associative strengths for all the CSs present. During the first few trials of CS/US (*x*-axis), the associative strength is large because the US is surprising. With subsequent trials, however, the associative strength decreases because it becomes less surprising. At the asymptote, the CS predicts the US with certainty, thus there is nothing more to be learned.

a well-known example of selective associations. In Garcia and Koelling's (1966) experiment, rats with two cues, taste CS and audiovisual CS, were then exposed to a nausea-inducing US or shock US. Shocked individuals associated the shock with the audiovisual cue and poisoned individuals associated the sickness with the taste cue (Garcia & Koelling 1966). There is also evidence of preparedness (Öhman & Mineka 2002), or evolved predispositions to associate particular stimuli (Griffin & Evans 2003). Animals form rapid associations between ecologically relevant CSs and certain aversive USs compared to fear-irrelevant CSs (Mineka & Öhman 2002).Examples include fearful responses to foxes (*Vulpes vulpes*), but not goats (*Capra hircus*), by tammar wallabies (*Macropus eugenii*) (Griffin *et al.* 2001), or fear responses to snakes but not flowers by primates (including humans) (Öhman & Mineka 2002). These, and many other examples (Domjan 2005) have suggested animals are predisposed to learn the relationships between evolutionarily relevant stimuli; findings which help develop an ecologically relevant perspective on general learning theory.

3.1.3 Instrumental conditioning

3.1.3.1 What is it?

In instrumental conditioning, the animal learns a relationship between an operant behavior and the consequence of that behavior, and behavioral frequencies are adjusted accordingly (Thorndike & Bruce 1911, Domjan & Burkhard 1986). This is a second type of associative learning. During conditioning, a stimulus, typically termed a *reinforcer* influences the likelihood of a response. Thus, behaviors followed by positive consequences will increase in occurrence, whereas behaviors followed by negative consequences will decrease. Functionally, instrumental conditioning is a mechanism that enables individuals to modify, shape or create complex patterns of behavior.

3.1.3.2 Conditions influencing instrumental conditioning

The rate of instrumental conditioning is influenced by the reinforcer type, the reinforcement schedule and the nature of the response (Domjan & Burkhard 1986). Generally, positive reinforcers, such as food or water, increase the frequency of a behavioral response, whereas negative reinforcers, such as shock or other pain-inducing events, decrease the frequency of a behavioral response. Similar to Pavlovian conditioning, instrumental conditioning depends on the temporal association between the reinforcer and response as well as on the contingency between the response and occurrence of the reinforcer. Finally, instrumental conditioning is limited by the degree that reinforced behaviors fit into an animal's natural behavior patterns, as well as the *belongingness* (the fit between the animal's behavior and stimuli used to reinforce them – e.g. Shettleworth 1975).

3.1.4 Social learning

3.1.4.1 What is it?

We use Hoppitt & Laland's (2008) definition of social learning as "the process through which one individual influences the behavior of another individual in a manner that increases the probability that the observer learns" (further reviewed in Heyes 1994, Galef & Laland 2005). Research has emphasized the adaptive value of social learning (Laland 2004, Rendell *et al.* 2010, Heyes 2012). Social learning can function as a multiplier, since new traits can spread more quickly socially than by individual learning alone. There is evidence that asocial and social learning rely on the same underlying associative and non-associative mechanisms (Heyes 1994, 2012).

For instance, stimulus enhancement has been proposed as a form of single-stimulus social learning. It occurs when a demonstrator's presence exposes an observer to a stimulus, resulting in an increase or decrease in responsiveness in the observer's interaction with that stimulus (Heyes 1994). From this perspective, stimulus enhancement may sensitize or habituate a response to a stimulus following an observer's interaction with a stimulus. For example, Heyes *et al.* (2000) found that rats observing conspecifics pressing a lever increased the probability of the observer interacting with that lever. It should be noted, however, that it is difficult to rule out associative learning in many cases of stimulus enhancement, because individuals may be learning to associate a location or stimulus with a reward (Hoppit & Laland 2008).

Observational conditioning is another form of social learning that, in this case, involves associative learning. Learning occurs when an observer's exposure to a demonstrator enables it to learn the relationship between two stimuli. For example, classic work by Mineka and Cook (1984) on rhesus monkeys (*Macaca mulata*) showed that naïve monkeys, when exposed to videos of wild monkeys responding fearfully to snakes, quickly learned the relationship between the fear response and the snake stimulus. In this experiment, the demonstrator monkeys' fear response is believed to be a US and associative learning occurs when paired with the snake, a CS.

Finally, observational learning occurs when an observer's experience with a demonstrator facilitates the observer's learning of a stimulus and response. For example, Akins and Zentall's (1996, 1998) work on Japanese quail (*Coturnix japonica*) used a two-action test to show observer quail learn to peck or step on a treadle based upon the demonstrator's action and the observed reward for that specific action.

3.1.4.2 Conditions influencing social learning

If we assume that asocial and social learning are governed by the same underlying fundamental learning mechanisms (Heyes 1994), then the conditions for both will be similar but with an added condition for social learning: the presence of conspecific or traces of conspecific stimuli. The components of an individual's social milieu provide opportunities for individuals to interact with and learn from conspecifics or traces of conspecifics (Coussi-Korbel & Fragaszy 1995). Variables such as rank, age, familiarity and social group size can influence how and from whom individuals learn, and this is termed directed social learning (Coussi-Korbel & Fragaszy 1995, Swaney *et al.* 2001, Nunn *et al.* 2009).

A given individual is not equally exposed to all animals in space and time (Cousssi-Korbel & Fragaszy 1995), so there is some uncertainty as to who can and should learn socially. Network-based diffusion analysis (NBDA) uses formal network statistics to test for social learning in social groups (Hoppit *et al.* 2010). NBDA tracks the passage of information along established social networks in animal groups (Franz & Nunn 2009) because behaviors are expected to be transmitted across existing social connections.

While social learning may be potentially adaptive, like many traits, whether or not animals that learn specific things enhance their fitness may depend on the specific situation. For instance, social learning may lead to animals acting upon outdated information because they copied demonstrators who had learned something that is no longer valuable, and making the outdated behavioral response last longer within the population despite being less valuable (for review, see Laland 2004, Rendell *et al.* 2010).

3.2 LEARNING AND CONSERVATION: HOW KNOWLEDGE OF LEARNING MECHANISMS MAY HELP SOLVE CONSERVATION PROBLEMS

With this fundamental review of learning behind us, we shall now go on to highlight some important conservation questions that will be enhanced by the study of learning. Many conservation and management problems can benefit from mechanistic insights into how animals respond to stimuli and learn about biologically important events. We organize this section according to the three conservation behavior themes (Berger-Tal *et al.* 2011, Chapter 1).

3.2.1 Theme 1. Anthropogenic impacts on behavior

3.2.1.1 What constrains animal learning in response to anthropogenic change?

Anthropogenic change may increase environmental variation and may create novel environments that animals may have not experienced before (Sih *et al.* 2011). When faced with variable environments, learning is an adaptive mechanism that permits individuals to acquire predictive information from local conditions to generate adaptive behavioral responses (Shettleworth 2010). But, there are constraints on learning, and there is variation in how species respond to environmental change (Sol *et al.* 2002). We divide constraints to learning into internal and external. Internal constraints are largely cognitive, while external constraints include the rapidity of the stimulus exposure, the magnitude of the consequence and its consistency over time.

Internal constraints Differences in underlying input mechanisms, such as a species' perceptual abilities, the attention an individual can allocate to a task, or an individual's motivation (Macphail & Barlow 1985, Shettleworth 2010, Heyes 2012) are likely to influence learning capacities.

Non-detectable stimuli can't be learned. Some anthropogenic stimuli may simply not be detected, such as glass windows by birds. An animal that relies on vision might not learn to avoid a highway, compared to an animal with acute hearing that is disturbed by distant sounds. Sensory disturbances vary (Lowry *et al.* 2011) and so does the combination of sensory modalities during association formation (taste precedes sickness, sound precedes pain, etc.).

The Rescorla-Wagner model predicts that novel or surprising unconditioned stimuli will be more effective at strengthening CS–US associations than those whose occurrence is not surprising. But this may be a double-edged sword to managers. Novel foraging resources, such as crops or fishing lines, can be attractive, highly rewarding and lead to accelerated learning of nuisance behaviors. By contrast, other novel anthropogenic disturbance stimuli are perceived as threatening, resulting in accelerated avoidance (Frid & Dill 2002). Thinking about stimuli with respect to their potential RW learning rate parameter values (such as salience, suprisingness, belongingness) may be a fruitful way to categorize anthropogenic stimuli, particularly if the goal is to train animals to selectively make associations or to train animals to selectively avoid resources.

Motivational mechanisms mediate an individual's tolerance for conspecifics, heterospecifics (including humans) or other potentially novel stimuli. Ultimately, motivational mechanisms will influence the stimuli an animal encounters, and how effectively they are conditioned. Neophobia is defined as a propensity to avoid novel stimuli (Greenberg 2003). Differences in neophobia may underlie the propensity to learn (Sol 2013). For example, there is evidence that urban zenaida doves (*Zenaida aurita*) that experience a highly dynamic environment, become less neophobic, learn faster and are more inclined to learn from conspecific demonstrators than less urbanized doves (Carlier & Lefebvre 1997, Seferta *et al.* 2001). Motivational mechanisms can also vary intraspecifically due to personality differences in boldness/shyness (Shettleworth 2010, Sih & Giudice 2012). In numerous species, such as guppies (*Poecilia reticulata*), trout, (*Oncorhynchus mykiss*) and black-capped chickadees (*Poecile atricapillus*), bolder or more exploratory individuals learn a conditioning or discrimination task more quickly than shy individuals (Dugatkin & Alfieri 2003, Sneddon 2003, Guillette *et al.* 2009).

Comparative studies in birds and mammals suggest that the correlations between brain size, learning and overall behavioral flexibility enable species to respond to novel ecological challenges (Sol *et al.* 2002, 2008). Generating behavioral flexibility through learning may enable individuals to modify, copy or create novel anti-predator responses (Berger *et al.* 2001), prey choice (Estes *et al.* 1998), or habitat selection (Doligez *et al.* 2002). Comparative approaches suggest that species with larger brains (relative to body size) have enhanced survival in novel, disturbed or dynamic environments (Sol et al. 2005, 2007, 2008; Amiel *et al.* 2011). Thus, while behavioral plasticity, generated by learning, is widespread in nature, there is variation in the degree to which animals can learn to respond to the new situations that are generated by anthropogenic change, and relative brain size is a rough index of this flexibility. Managers should be sensitive to this variation and future research should identify other correlates of flexibility. It is important to note, however, that the effect of brain size on behavioral complexity remains highly debatable (Healy & Rowe 2007), and no study that we know of has looked at the influence of brain size on the effectiveness of different learning mechanisms.

In some species, there may be a sensitive time period during which most learning about a particular biologically important process occurs (Hogan & Bolhuis 2005). The classic example is filial imprinting in precocial birds (Lorenz 1970). However, there is also strong evidence of sensitive periods for habitat (Davis & Stamps 2004) and sexual preferences (Bateson 1978). More generally, however, individuals at different life stages may be more or less likely to learn (Dukas 2008). Hawkins *et al.* (2008) demonstrated age dependent learning of predator cues in hatchery-reared salmon. Their results suggest heightened receptivity to learning predator cues during the life history stage at which juveniles would be undergoing a habitat shift and thus are particularly sensitive toward predation. Such variation in the ability to learn may allow young, but not older, animals to learn appropriate responses in an anthropogenically disturbed environment.

Learning during sensitive periods can be via individual associative learning mechanisms or via social learning from parents. These so-called parental effects may be obligatory for survival in some species. However, parental effects can also act as multipliers, spreading maladaptive behaviors through populations. For instance, wild black bear (*Ursus americanus*) cubs raised by garbage-pilfering sows were significantly more likely to rely on human resources (Mazur & Seher 2008).

Finally, managers should be mindful of sensitive periods to optimize reintroductions/translocations. For instance, if animals are to be moved to a new environment, pre-exposure to that environment (or certain characteristics of that environment, such as food sources) during a sensitive period may be essential for successful establishment. Much work remains to be done to provide concrete examples that can help inform management.

External constraints Learning is adaptive because it enables individuals to track environmental variation. We know that the type of reinforcer, the temporal relationship between the reinforcer and the consequence, and the magnitude of the consequence will all constrain the rate of learning (Shettleworth 2010). Positive reinforcers, such as food, safety or conspecifics tend to increase behavioral responses. Negative reinforcers, such as painful, noxious or distracting stimuli, may only require a single exposure to create long-term learning (Rau & Fanselow 2009).

Learning can only occur if the rate of learning is faster than the rate of environmental change (Johnston 1982). If anthropogenic change is too rapid, learning cannot occur and individuals in a population will be unable to modify their behavior and behaviorally track the changes. In such cases, given sufficient additive genetic variation, there will be strong selection against those animals with an inadequate behavioral response.

The magnitude of the consequence, the speed (rapidity) at which a stimulus reaches its full magnitude, and its consistency over time (anthropogenic noise, for instance, may cycle over 24 hours) will also influence learning. An event or stimulus that is always lethal will prevent any learning from occurring, whereas highly profitable food sources (such as crops or garbage cans), or painful/nearly lethal encounters, may stimulate rapid and complete learning after one or a few exposures. Intense stimuli with a rapid onset elicit startle responses (Yeomans *et al.* 2002). In organisms vulnerable to high-intensity acoustic stimuli, such as sea turtles or cetaceans, rapid onset exposures (seismic airgun arrays or sonar) may lead to sensitization of avoidance responses (Gotz & Janik 2011, DeRuiter & Doukara 2012).

3.2.1.2 Anthropogenic impacts on behavior: can we develop an evolutionary ecology of habituation?

A fundamental question in wildlife conservation and management concerns the causes and consequences of habituation and sensitization. Why do some species habituate, while others sensitize to anthropogenic stimuli? The "life–dinner principle" suggests that for a prey species, the costs of getting predated far outweigh the costs of missing a meal (Dawkins & Krebs 1979). From a life–dinner principle perspective, there is an asymmetry between the fitness costs of failing to detect a predator (Type 1 error) and over-reacting to non-threatening stimuli (Type 2 error).

Habituation to non-threatening stimuli is somewhat expected since anxiety or stress from over-generalized threat recognition may be costly in terms of energy or time allocated to unnecessary defenses (Blanchard 2008). We therefore expect animals to show an initial heightened response, followed by rapid habituation to repeated unreinforced exposures of even potentially threatening stimuli (Groves & Thompson 1970). Habituation is thus a mechanism to reduce the costs of false alarms (Thorpe 1956, Shalter 1984).

Remarkably, given how long we have known about mechanistic processes involved in habituation and sensitization (Groves & Thompson 1970), little is known about habituation in the wild, or what we will refer to as the evolutionary ecology of habituation. Perhaps this is in part because habituation has been extensively investigated under controlled experimental conditions. By contrast, in nature, an organism's environment is noisy and filled with threatening and non-threatening stimuli that occur in a variety of different contextual situations. To deal with this uncertainty, there is evidence that habituation under natural conditions is quite selective and enables individuals to learn what is not threatening (Deecke *et al.* 2002, Hemmi & Merkle 2009, Raderschall *et al.* 2011). In a series of studies of anti-predator responses in wild hermit crabs, Hemmi (2011) demonstrated that habituated responses are recovered when the same predator stimulus is presented at a different distance or angle. Similar to laboratory investigations of dishabituation, this study shows that in the wild even small changes in stimulus presentation can result in recovered responsiveness. Correspondingly, selective habituation is hypothesized to be the mechanism by which harbor seals (*Phoca vitulina*) discriminate between threatening and non-threatening killer whale (*Orcinus orca*) vocalizations (Deecke *et al.* 2002). Harbor seals responded with flight to playback of vocalizations from local marine mammal-eating killer whales and novel fish-eating killer whales, but not local fish-eating killer whales. These results suggest that the seals habituated to non-threatening local fish-eating killer whales, but were fearful to unknown vocalizations. This specificity of habituation makes sense in terms of the fundamental characteristics of habituation described in our introduction and illustrates its evolutionary context.

Ultimately, to develop a natural history of habituation we will need to understand what sorts of stimuli in nature lead to habituation and then understand what life history and natural history features are correlated with habituation or sensitization. As a step towards this, (Li *et al.* 2011) developed a mixed-modeling statistical approach to identify how different anthropogenic stimuli (people, people on bicycles, people in cars) influenced flight initiation distance decisions in yellow-bellied marmots (*Marmota flaviventris*). Flight initiation distance (FID) is a particularly sensitive assay for how animals respond to approaching threats, and animals repeatedly exposed to humans often tolerate closer approaches before fleeing.

The nature, spatio-temporal pattern and context of exposure to stimuli influence the rate of habituation and whether sensitization occurs. For example, yellow-eyed penguins (*Megadyptes antipodes*) show sensitized stress responses to tourists in Sandfly Bay (Ellenberg *et al.* 2009). The authors suggested that the unpredictable and abrupt behavior of tourists that ran, shouted and chased penguins prevented habituation and facilitated sensitization. During exposure to threatening stimuli, animals assess the type and risk of the threat, as well the contextual cues (whether or not escape was possible) and used these factors to generate an appropriate response (Blanchard 2008, Blanchard *et al.* 2011). Risk assessment studies using laboratory rats show that an individual's response is the result of the type and distance of threat, and the local environment, to produce the adaptive response (Blanchard 2008, Blanchard *et al.* 2011). In the wild, whether an animal habituates or not is likely to be influenced both by the immediate environment (for instance, is a safe place to escape available?) and its own locomotor abilities (can it escape?).

Species and individuals within species may vary in how quickly they habituate as a result of personality or sex differences (Rodríguez-Prieto *et al.* 2010a). In humans, personality traits such as extroversion and impulsivity are correlated with a faster startle habituation response (LaRowe 2006). This suggests that over time there will be a non-random distribution of personalities in response to anthropogenic disturbance. Thus, we can predict that more tolerant species or individuals will be able to colonize more disturbed areas (Carrete & Tella 2010).

Habitat availability may be another factor that influences the likelihood of habitation or sensitization. Blumstein (2013) proposed the "contiguous habitat hypothesis" to explain why some Southern California birds habituated while others sensitized. The contiguous habitat hypothesis predicts that species that find themselves in highly fragmented and rare habitats will be more likely to habituate to increased human disturbance. This might result from a process of sorting whereby individuals and species that were unable to tolerate increased disturbance have been eliminated while those that tolerated disturbance persisted in the patches. The net result would be that "tolerant" species will be found in this highly patchy habitat while those in more contiguous habitat might be more variable and indeed might respond to increased disturbance by sensitizing. If generally true, the hypothesis suggests that the opportunity to move within habitat patches will be more often associated with sensitization than situations where animals are so constrained that they have no other choices than habituation.

3.2.1.3 Novel mismatches between cues and fitness: is learning important?

Individuals may naturally learn to identify cues that help them detect suitable habitats in which they historically have had relatively high survival or reproductive success (reviewed in Davis & Stamps 2004, Stamps & Swaisgood 2007). In some circumstances, individuals may select suboptimal habitats because of a mismatch between the cues they evolved to evaluate and novel fitness consequences associated with those cues; this is referred to as an ecological trap (reviewed by Schlaepfer *et al.* 2002, Sih *et al.* 2011, chapter 4). Whether ecological traps are more or less likely in species that learn about their habitat (or other biologically important characteristics) is an open question. For instance, animals that disperse may rely on learning cues from their natal habitat to help them develop a template by which they can evaluate habitat quality and determine where to settle while dispersing (Davis & Stamps 2004). The degree that animals learn would influence how those cues can be manipulated.

We expect that associative learning mechanisms (e.g. Pavlovian and instrumental associative learning) should enable individuals to select suitable habitats if learning is a mechanism underlying habitat selection. Even if learning is not a natural mechanism, it might be possible to generate positive experiences to train animals to use a desired habitat and/or negative experiences to train animals to avoid a particular habitat. Stimuli such as tastes, smells or visual cues can give information on relative forage quality or risk of predation that will influence animal decisions.

Extensive work on learning and life skill training in hatchery-reared fish represents an important application of learning theory that has translated to applied value. Hatchery fish that learn life skills such as predator recognition, prey handling and foraging locations exhibit enhanced post-release survival (reviewed in Brown & Laland 2001, Brown *et al.* 2003, Hawkins *et al.* 2008). Additionally, social learning can act as a multiplier of these skills, facilitating quicker learning and transmission, which is more efficient for the aquaculturist whose aim is to produce animals that will survive upon release.

3.2.2 Theme 2. Behavior-based management: training for conservation

Knowledge of learning mechanisms is also of use to managers who wish to modify animal behavior. Training animals with basic learning mechanisms may help repel animals from human resources, attract them to particular habitats/regions or generate basic survival skills to enhance survival during translocations/reintroductions.

3.2.2.1 Teaching attraction

Animal learning principles can provide general rules on how animals can be taught specific behaviors or attraction to habitats as well as the conditions under which they may not be able to be taught. Positive reinforcers can be used to attract an animal, locate food source or increase the frequency of a particular behavior. Stimuli used for positive reinforcement include food, shade, odors, shelter or access to conspecifics. These stimuli can be manipulated to facilitate the learning of habitat preferences. Preferences can be taught via Pavlovian conditioning where the taste is associated with food quality or via instrumental means where, for example, animals are trained to use tunnels beneath freeways. Additionally, conspecific or heterospecific stimuli can act as positive reinforcers during food source localization or habitat selection (for review see Avarguès-Weber *et al.* 2013). The constraints to learning mentioned above similarly apply – there may be certain critical periods for learning to develop certain preferences.

3.2.2.2 Teaching avoidance

The creation of novel concentrations of resources, such as crops, garbage cans, fishing lines and domesticated livestock, provide motivation for animals to learn to exploit those resources, resulting in human/wildlife conflict. Since anthropogenic resources, such as fishing lines or crops, can reduce the costs compared to natural foraging, the motivation to form the association between humans and food reward is not only high, but learning is expected to occur quickly (Schakner & Blumstein 2013). Once learned, the association is difficult to break and thus management efforts require foresight and a preventative mindset. Since learning to acquire human resources involves associative mechanisms, there are points in the learning process that management efforts should target to be most effective in teaching avoidance: pre association formation, during association formation and post association formation.

Animals require a contingency to form an association between two stimuli or stimulus/response (Rescorla 1968). In the wild, animals can learn the association between human resources and the cues that reliably precede them. For example, marine mammals, such as sperm whales (*Physeter macrocephalus*), have learned to associate vessel sounds (CS) with a food reward (US: fish on line) (Thode *et al.* 2007). In order to form that association, the vessel sounds must reliably predict the food reward. Therefore, the most effective management of depredation is preventing animals from learning the depredative behavior in the first place by reducing the contingency between stimulus and reward. This can be accomplished by decoupling the spatio-temporal overlap between potential depredators and the human resources. For example, in the Gulf of Alaska, demersal longline fisheries management shifted from a 10-day derby-style fishing season (vessels catch a year's quota in a set period of time) to an 8-month-long individual fishing quota regime. As a result of the extended overlap between sperm whales and fishing vessels in space and time with the new quota fishing regime, there was ample opportunity for the animals to learn to exploit the resources and the whales are now attracted to boats setting and hauling in lines, which results in a loss of valuable fish (Hill *et al.* 1999). A lesson from this case study is that foresight may be necessary to prevent learning from occurring in the first place.

When innovators initially learn to depredate or crop raid, social learning can have a multiplier effect by spreading behaviors through populations quickly (Lefevbre 1995). In elephants (*Loxodonta africana*), for example, network analysis of crop raiders has demonstrated that the behavior appears to be socially learned through social networks (Chiyo *et al.* 2012). Correspondingly, social learning is believed to underlie the diffusion of depredation in sperm whales, killer whales and pilfering black bears (Whitehead 2004, Mazur & Seher 2008, Schakner *et al.* 2014). In these cases, it is important to know both the identity of innovators (age/sex) and the pattern of diffusion. This knowledge is useful to stop the spread of the behavior and for targeted repellents or removals of individuals.

Once the association between humans and food reinforcers has formed, management efforts rely on raising the cost to the individual depredator. Because the association is difficult to extinguish, management efforts must rely on forming new negative associations or on decoupling the contingency between humans and reward. Deterrents and repellents produce noxious, aversive or painful stimuli to prevent animals from interacting with human habitat or resources (Ramp *et al.* 2011). Here we suggest that associative learning may produce long-term learned avoidance.

During painful encounters, animals rapidly learn the cues, context or local conditions that are associated with that danger. This learning mechanism, i.e. fear conditioning, enables animals to learn from, respond to and detect danger. Repellents, therefore, should capitalize on insights from the fear conditioning literature to generate avoidance. The use of painful stimuli such as rubber bullets or electric shocks are widespread for eliciting avoidance, but their effectiveness can be short term or impractical, and this raises ethical issues (e.g. is it ethical to continue to do something that's both painful and ineffective?). However, painful deterrent stimuli may be an integral part of a fear-conditioning program. Once conditioning has occurred, exposure to the conditioned stimulus generates fear reactions.

During painful encounters, an animal's unconditioned response is different from the conditioned response. For example, rats exposed to shock (US) react with a burst of motor activity. In contrast, rats exposed to a stimulus that predicts shock (CS such as context or experimenter) evoke behavioral responses such as fleeing, hyper-vigilance or freezing. This suggests a conditioning approach may offer promise, especially if the conditioned response to the target CS is avoidance.

What cues animals pick up on to avoid an area remains an open question. For instance, it is known that animals learn to avoid environments, stimuli or conditions that are correlated with a decrease in fitness (i.e. death; Lima & Dill 1990, Frid & Dill 2002). Habitats, however, contain a suite of stimuli such as landscape features, conspecifics, heterospecifics and background sounds. During an aversive event (a predator attack), individuals likely associate features of the environment (such as open space or shadows) as well as other cues (such as predator scents). According to the Rescorla-Wagner model, contextual stimuli compete with the CS to predict the US. In contrast to simplified experimental conditions of context (a cage), the natural world is full of stimuli, and thus the animal may make associations between competing contextual cues and salient predator cues, This means that managers should use conditional stimuli that are obvious, discriminable and detectable, preceding the biologically relevant aversive stimuli, when designing and implementing repellents. If habitat avoidance is the goal, diffuse CS stimuli, such as a strobe or sound, can be implemented (Table 3.1).

A checklist for US and CS selection Effective deterrence relies on stimuli that are both aversive enough to cause rapid fear conditioning, and sufficiently aversive to prevent rapid habituation. To accomplish this, managers must tailor deterrent stimuli toward species-specific sensory modalities and sensory sensitivities. For example, sound is a fundamental channel for

Table 3.1. *Advantages and disadvantages of a variety of stimuli that can be used as both conditioned and unconditioned stimuli for management-based training.*

Stimulus	Advantages	Disadvantages
Conditioned stimulus		
Sound (e.g. Neutral tone)	Localized transmission	Non-target species impact
Light (e.g. Strobe light)	Discriminable	Limited to night or dark locations
Object (e.g. Flag or person)	Useful for place avoidance	Difficult to associate object with US
Chemosensory (e.g. Taste or scent)	Salient cue for food aversion	Limited to nauseating US
Unconditioned stimulus		
Pain (e.g. Electric shock)	Long-lasting associations after few exposures	Can cause physical damage
Distracting (e.g. White noise)	Wide-ranging	Impact non-target species
Ecologically relevant stimuli (e.g. Predator cue)	Species-specific	Rapid habituation
Frightening stimuli (e.g. Looming, novel or abrupt stimuli)	Can elicit fear responses	Rapid habituation
Nauseating (e.g. LiCl)	One trial learning	Unwanted prey avoidance

communication, foraging and predator detection in marine mammals and this makes it a useful modality in which to develop acoustic deterrents (Jefferson & Curry 1996). However, the input of aversive acoustic stimuli can impact non-target species, which should be considered during the development and implementation of acoustic deterrents (T. Gotz, pers. comm.). Deterrents can be modulated to match a species' sensory sensitivity while still being outside non-target animals' sensory range. Unconditioned stimuli that elicit pain must be practical as well and not cause permanent damage to the depredator. Finally, in social species, fearful responses by conspecifics can serve as a US (Mineka & Cook 1984).

There is evidence that CS which are natural precursors to US result in rapid and more durable associations (Domjan 2005). From this functional perspective, using biologically meaningful stimuli such as predator calls that precede painful stimuli may result in rapid and stronger associations. For example, Leigh and Chamberlain (2008) used barking dogs as a conditioned stimulus preceding rubber buckshot US on crop-raiding bears, which yielded stronger responses than non-conditioned individuals. A conditioned stimulus that precedes the US must be discriminable, salient and consistent. Additionally, the reinforcement schedule (how often to pair CS/US versus CS alone) can be modified depending on the nature of the conflict.

3.2.3 Theme 3. Behavioral indicators

Our final section is brief: there may be a variety of behavioral indicators that can be used to reflect an animal's past experiences, and knowledge of past experiences may be useful to wildlife management. The brevity of this section should not undermine its potential importance, and future research should focus on identifying other situations and indicators that can be used to inform management.

3.2.3.1 Flight Initiation Distance

As discussed above, in order to understand the behavioral imprint of humans, flight initiation distance can be used as a behavioral indicator of disturbance (see Chapter 11 for more details). Assuming that all else is equal between sites (e.g. Gill *et al.* 2001), the difference in FID between two sites can provide a measure of the degree to which humans have modified risk assessment. When measured longitudinally, FID can also be used as a proxy for habituation (Ikuta & Blumstein 2003, Rodríguez-Prieto *et al.* 2010b).

3.2.3.2 Socially learned traits

Socially learned traits can diffuse through populations. After reintroductions or translocations, social transmission can be used to track the spread of behaviors through groups. This may indicate how well reintroduced individuals are being incorporated or adapting behaviorally to life in the wild. In a well-documented case of reintroduction, captive-bred Arabian oryx (*Oryx leucoryx*) foraging behavior was suggested to have been influenced by interactions with conspecifics (Tear *et al.* 1997). Social learning is believed to have enhanced foraging behaviors of reintroduced individuals during periods of low food availability (Tear *et al.* 1997). This study suggests that after reintroduction/translocation, managers can probe individuals in a group to assess whether behaviors have spread indirectly through social transmission.

In several species, social learning underlies stable inter-population behavioral variation. Apes, songbirds and cetaceans are believed to exhibit long-term, socially learned traditions or cultures (Whiten et al. 1999, Rendell & Whitehead 2001, Laiolo & Tella 2007). Since these socially learned behaviors are often functional (i.e. they are foraging tactics or social signals with fitness consequences) these traits could be used to indicate population viability (Laiolo & Tella 2007, Whitehead 2010). Laiolo and Tella (2005, 2007) were able to use bird song (a socially learned trait) diversity to show that fragmentation has eroded both cultural and population diversity. These studies suggest that cultural diversity can be used as a proxy for population viability as well as a tool for targeting subpopulations likely to be threatened (Whitehead 2010).

3.3 SUMMARY

We believe that the fundamental mechanisms involved in animal learning are of practical importance to conservation/management practitioners and central to integrating behavioral ecology with conservation and wildlife management. The necessity of incorporating learning into conservation is further discussed in subsequent chapters. In Chapter 6, for instance, Fernández-Juricic describes how species-specific input channels and sensory systems influence the stimuli that will be learned, which can be applied to repelling or attracting animals. The role of learning in behavioral modification is further discussed by Shier in Chapter 10, including case studies involving reintroduction/translocations. From a broader perspective, learning is a mechanism of phenotypic plasticity, and the range and limits to plasticity in endangered and threatened species can be used to predict and manage species responses to anthropogenic change (Chapter 5).

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