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The Rules of Attraction: The Necessary Role of Animal Cognition in Explaining Conservation Failures and Successes

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conservation behavior, habituation, learning, memory, umwelt

Abstract

Integrating knowledge and principles of animal behavior into wildlife conservation and management has led to some concrete successes but has failed to improve conservation outcomes in other cases. Many conservation interventions involve attempts to either attract or repel animals, which we refer to as approach/avoidance issues. These attempts can be reframed as issues of manipulating the decisions animals make, which are driven by their perceptual abilities and attentional biases, as well as the value animals attribute to current stimuli and past learned experiences. These processes all fall under the umbrella of animal cognition. Here, we highlight rules that emerge when considering approach/avoidance conservation issues through the lens of cognitive-based management. For each rule, we review relevant conservation successes and failures to better predict the conditions in which behavior can be manipulated, and we suggest how to avoid future failures.

INTRODUCTION

The idea that knowledge of animal behavior can be applied to animal conservation and wildlife management is not new. In fact, decades of work have documented areas in which behavior is useful for understanding anthropogenic impacts (Candolin & Wong 2012, Wong & Candolin 2015) and enacting conservation interventions (Berger-Tal & Saltz 2016, Blumstein & Fernández-Juricic 2010). However, there are still novel insights emerging about the intersections between animal behavior and conservation. For instance, knowledge of an individual's position in a social network can explain disease transmission (Silk et al. 2017) and the socially learned spread of problematic behaviors, such as how to predate longline fisheries' catches (Schakner et al. 2014). Humans may overtly or accidentally modify social structure in ways that destabilize groups and drive population declines (Snijders et al. 2017). Individuals may differ systematically in the way they interact with their environment, which can have implications for population sustainability and management (Found et al. 2019, Merrick & Koprowski 2017). These topics, both old and new, can be generally classified into three main areas (Berger-Tal et al. 2011). Behavior can serve as an early indicator for monitoring population trends, help identify the mechanisms underlying population declines, and function as a tool when planning and executing conservation interventions.

Simply cataloging areas in which conservation behavior can be relevant to management action is not enough to influence conservation outcomes and decisions. Instead, research must be prioritized and evaluated in systematic ways and made available to managers and decision makers via open access means (Greggor et al. 2016). Conservation behavior can only be useful as a tool if it proves to be more effective and efficient than traditional management methodologies. Thus, recent work has focused on generating a series of systematic reviews to evaluate the relative efficacy of conservation behavior interventions and determine their utility across a range of contexts (Berger-Tal et al. 2019). Such reviews work on the underlying assumption that animals must behave in a predictable way for behavioral interventions to be effective. Therefore, understanding what drives behavior can be critical to making such predictions and generalizing results to new species and contexts.

To understand what drives animal behavior, we must understand animal cognition. Animal cognition is an umbrella term that covers the processes involved in perception, decision making, learning, and memory (Shettleworth 2010). Cognitive mechanisms create the rules and biases that guide behavior, which evolved as a result of the challenges of the ecological and social environment that animals face. Since the neuronal architecture necessary to support cognitive mechanisms is metabolically costly (Finlay et al. 2001), animals have evolved streamlined cognitive systems that allow them to perceive, filter, learn, and remember a subset of stimuli in their environment (Shettleworth 2010). These constraints make each species cognitively unique, just as it is morphologically unique. However, many species share similar cognitive mechanisms across disparate taxonomic groups, even with radically different brain structures (Bshary et al. 2002, Chittka et al. 2012, Emery & Clayton 2004, Marino 2002), which may allow for predicting behavioral responses across taxa. These cognitive rules can be applied in conservation (Greggor et al. 2014), and they are increasingly used to address and understand diverse conservation issues (e.g., Barrett et al. 2019, St. Clair et al. 2019, Proppe et al. 2016).

We live in a time of great change, and human-induced rapid environmental changes (Sih et al. 2016) have created novel stimuli and mismatched outcomes from what animals evolved to experience (Ehrlich & Blumstein 2018, Greggor et al. 2019, Robertson et al. 2013). These mismatches create inappropriate decisions and may produce wildlife conservation and management problems. We suggest that addressing these problems requires an explicit consideration of cognitive mechanisms. Below, we develop a framework for cognitive-based management to understand an important class of animal decision making and use it to interpret wildlife conservation actions.

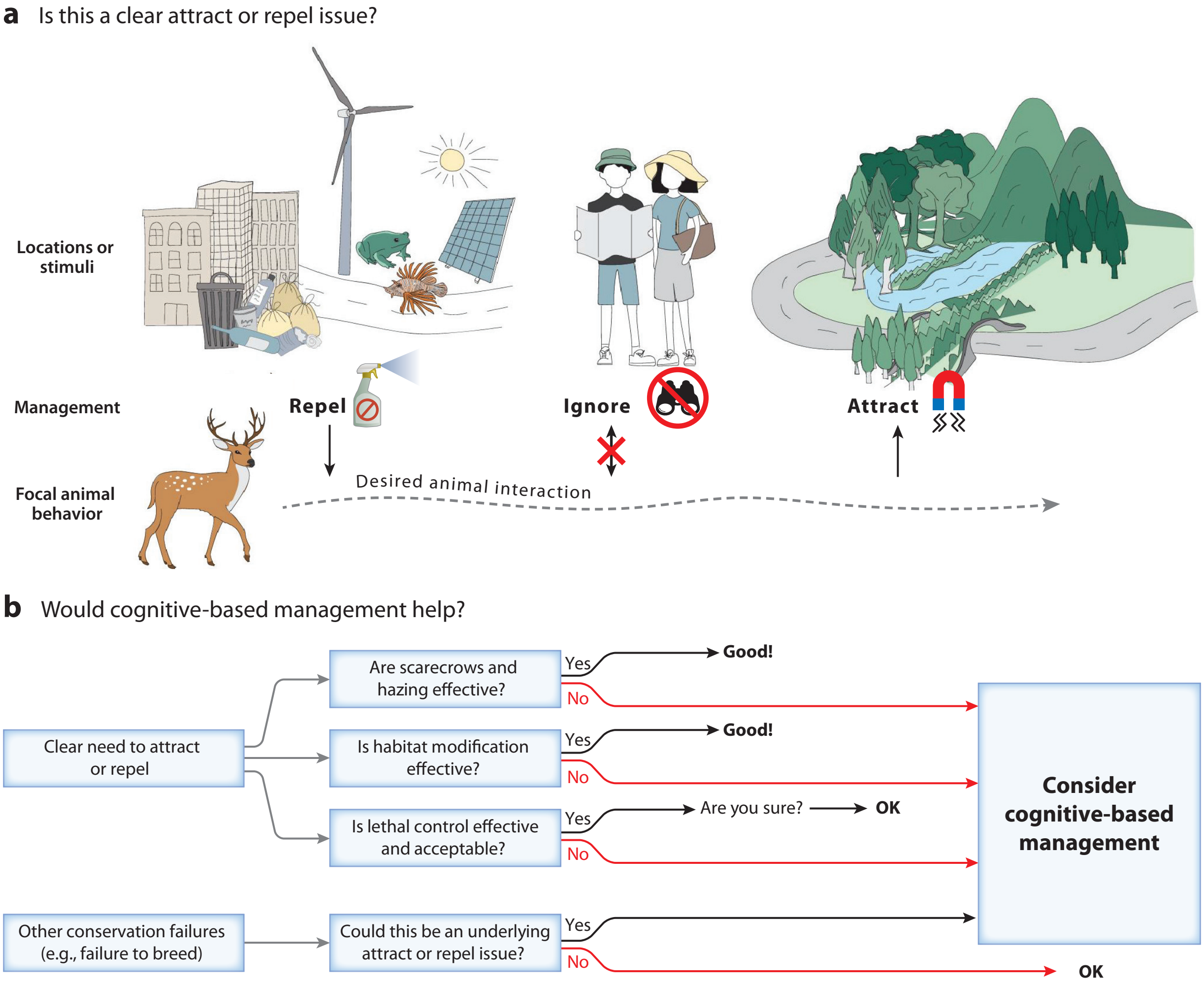

Figure 1

Attract/repel issues and the role of cognitive-based management. (*a*) Many conservation challenges can be defined along an approach/avoid continuum in which we want to repel animals from certain locations or stimuli (*left*, e.g., human settlements, garbage, roads, wind turbines, invasive predators and prey, and ecological traps such as solar panels). At the same time, we want animals to ignore other stimuli (*middle*, e.g., ecotourists) and be attracted to specific locations and stimuli (*right*, e.g., overpasses and high-quality habitats). (*b*) With these cases in mind, we can then decide if cognitive-based management is appropriate for managing the issue.

THE APPROACH/AVOID FRAMEWORK

Many challenges that the field of conservation behavior tackles can be defined as approach/avoid management, in which researchers and managers aim to either attract or repel animals from specific locations or stimuli (**Figure 1**). For example, researchers and managers may use their knowledge of animal behavior to understand why some animals are attracted to anthropogenic resources and to find efficient ways to reverse this attraction and encourage avoidance in order to reduce human-wildlife conflict (Appleby et al. 2017). Behavioral manipulations of approach and avoidance have been deployed in contexts that include attracting translocated animals to use high-quality habitats and avoid predators and ecological traps (Shier 2016), improving the usage of conservation corridors (St. Clair et al. 1998), training animals to avoid harmful invasive predators or prey (Griffin et al. 2000, O'Donnell et al. 2010), and reducing the risk of animal-vehicle collisions by encouraging animals to avoid approaching vehicles (Blackwell et al. 2016).

Viewing conservation challenges from an approach/avoid perspective can elucidate why some traditional conservation actions fail. For instance, interventions that focus on either repelling animals by altering population size {often using guns, fences, and poison [e.g., eradicating invasive house mice (MacKay et al. 2007)]} or attracting animals by altering the physical aspects of the environment (a build-it-and-they-will-come approach) often fail to efficiently manage these challenges. Such traditional approaches can sometimes even create unintended consequences, such as creating ecological traps (Hale & Swearer 2017), or actually worsen the problem they were intended to address. For instance, European badgers (*Meles meles*) are culled as a tactic to prevent the spread of tuberculosis (TB) to cattle (*Bos taurus*), yet studies have shown culling badgers can actually increase the prevalence of TB (Donnelly et al. 2006). Understanding what drives badger movement helps explain the reason for this increase: Removing badgers increases dispersal by neighboring individuals as they seek information about new territories. This dispersal facilitates an influx of new badgers carrying TB into areas with cattle, thereby transmitting the disease to uninfected farms (Woodroffe et al. 2006). Because badgers are attracted to vacant badger territories, programs such as badger vaccinations that prevent disease contact have been suggested as better alternatives.

To increase the success rate of conservation interventions, we need to understand why animals choose to approach or avoid certain stimuli. By considering how animals perceive stimuli, learn their properties, and consequently decide whether to approach or avoid them, managers will not only be able to better predict the ways human disturbance affect wildlife populations, but more importantly, they will be able to design more efficient ways to attract or repel animals to improve conservation outcomes.

In any conservation intervention, there are many ways to fail and only a few ways to succeed. Not all failures are attributable to behavior, but some are. Here, we reframe conservation and management interventions into an explicit approach/avoid framework and explain their failures and successes by examining them from a cognitive-based management perspective. To do so, we lay out the rules of attraction and repulsion and how they can be applied to improving conservation and management efficacy.

We organize the framework under different section headings that convey the cognitive steps information must take as it passes through the decision-making process. In order, animals must (*a*) perceive and attend to information, (*b*) process that information and react to it, (*c*) learn from the consequences of their actions, and (*d*) remember that information for future use (or fail to do so). Each step is subjected to different rules or biases that are outlined in subsections, and we suggest that understanding these rules and biases is key to understanding animal decision making. While dividing cognitive processes into discrete linear steps is convenient, it also simplifies reality; many of the rules we highlight could fit under more than one cognitive step. Our list of rules and choice of examples are by no means exhaustive but rather represent how a cognitive approach can be used to identify the mechanism underlying some common failures and may generate efficient alternatives that will increase the chances of conservation success. To help illustrate how a cognitive approach can generate novel solutions to conservation problems, each topic that we discuss links to a distinct part of the attract/repel workflow outlined in **Figure 2**. Key concepts or terms in **Figure 2** are referenced throughout the text, and relevant problem-solving steps are referenced with a number followed by the letter A for the attract workflow or R for the repel workflow. The same references are then used in **Figure 3** to walk through an illustrative example that applies the rules and workflow.

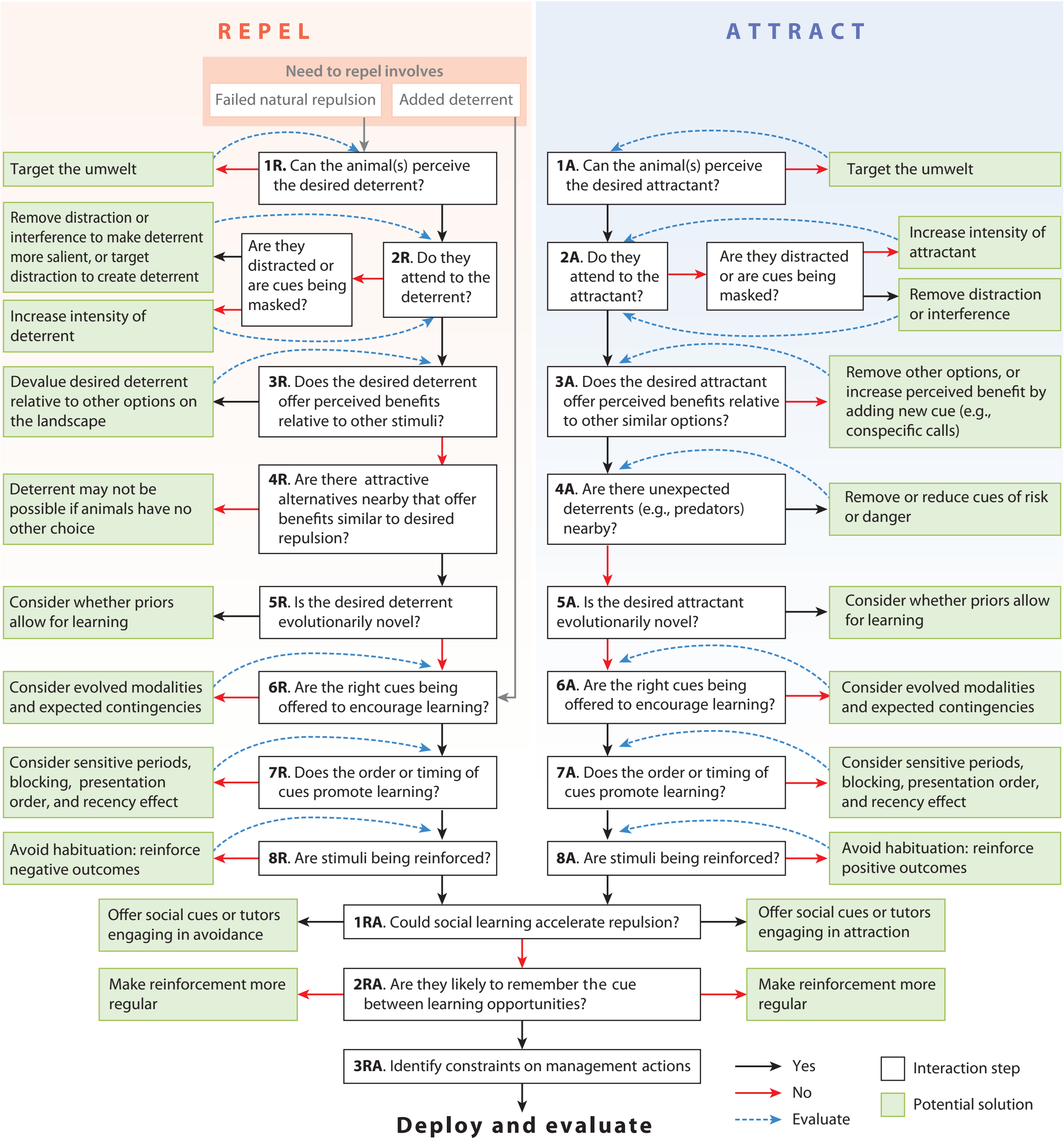

Figure 2

Workflow to address approach/avoidance issues in wildlife conservation and management with cognitive-based management. Many conservation problems can be boiled down to the need to attract or repel individuals, and different workflows are outlined for each one. At each logical interaction step in the cognitive process (*numbered, white boxes*), there are potential solutions (*green boxes*) for researchers and managers to consider that may help to troubleshoot issues with an intervention. After addressing the suggested solutions, the blue dashed arrows return the manager to reevaluate that step in the workflow. At the end of the process, using best-available knowledge, it is essential to identify other constraints on management actions and to deploy a cognitive intervention and evaluate its ultimate success or failure.

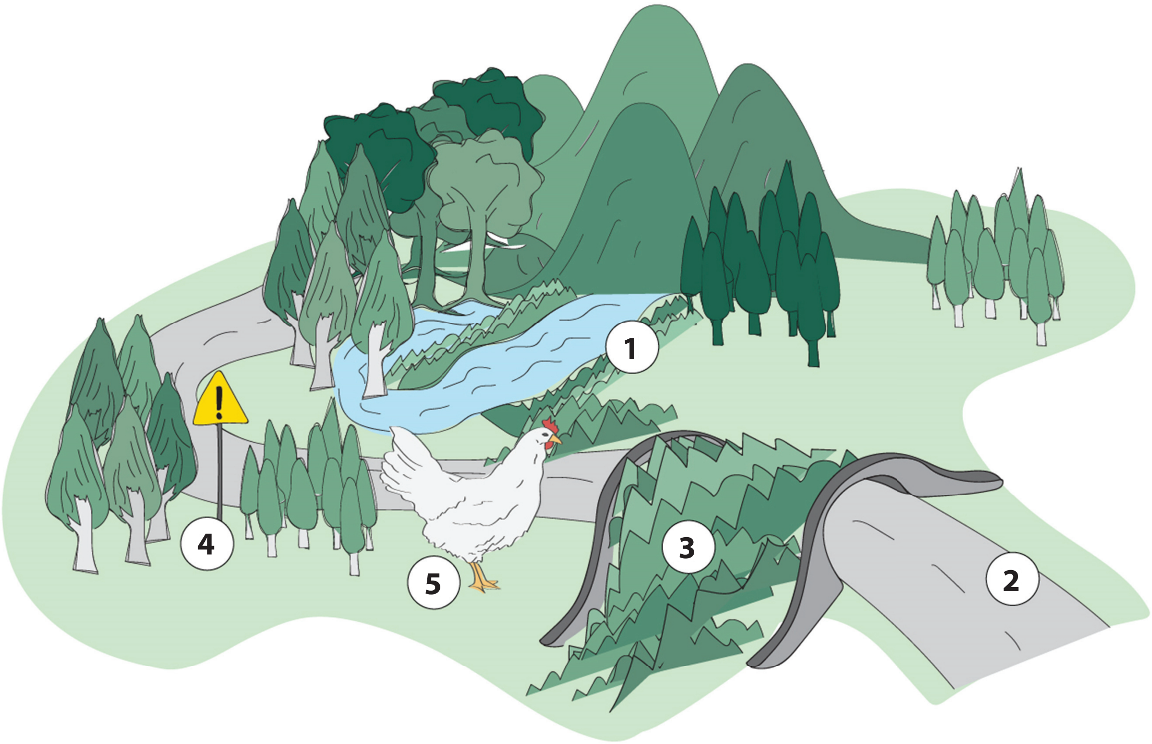

Figure 3

Why did (or didn't) the chicken cross the road? Number/letter combinations refer to the relevant boxes in **Figure 2**. ① Good habitat (attract): Can the chicken perceive the habitat (1A)? Does the chicken attend to the habitat, or is it distracted (2A)? Are there sufficient conspecific or habitat cues to alert the chicken that the habitat is better than its current location (3A)? ② Road (repel): Can the chicken perceive the road (1R)? Is it distracted from attending to the road, or are road-based cues being masked (2R)? Is the road an evolutionarily novel danger (5R)? Has the chicken successfully crossed the road before (7R)? ③ Overpass (attract): Is the overpass perceivable (1A)? Is the chicken distracted by the road and unlikely to attend to the overpass (2A)? Is there sufficient motivation for the chicken to leave its current patch (3A)? Does the overpass feel safe compared to the landscape (4A)? Has the chicken used the overpass before (7A)? Are other chickens using the overpass, and can the chicken perceive them (1R, 1A)? ④ Deterrent (repel): Is the deterrent perceivable and aversive, and does it target evolutionarily relevant fear stimuli (6R)? Is it sufficiently predictable to not result in habituation (7R)? Does the chicken associate the deterrent with the road (8R, 2R, 2A)? ⑤ The chicken: Does the umwelt of the chicken allow it to perceive desired attractants and deterrents (1A, 1R)? Does the evolutionary history or past experiences of the chicken allow it to learn about these new attractants and deterrents (6R, 6A)?

THE RULES OF ATTRACTION AND REPULSION

Perception and Attention

Animals must first perceive and direct their attention toward a given stimulus before they can respond to it. In addition to animals' morphological constraints on perception, there are also cognitive biases that shape how and what information animals take in from their surroundings.

Rule: The umwelt matters. Each species lives in a unique perceptual and cognitive world, termed the umwelt (Van Dyck 2012, von Uexküll 1909). Understanding how animals perceive the world differently than humans can help explain why they sometimes respond unexpectedly (from a human perspective) to stimuli in maladaptive ways (1A and 1R in **Figure 2**). For instance, animals can fall prey to ecological traps (attraction to harmful habitat) or perceptual traps (avoidance of good habitats) when they mistakenly categorize anthropogenic stimuli as an attractant or deterrent (Patten & Kelly 2010, Robertson et al. 2017). Misaligned attraction can happen in contexts including mating [buprestid beetles (Gwynne & Rentz 1983)], foraging [plastic ingestion (Wilcox et al. 2015)], and navigation [sea turtles disorientated by streetlights (Truscott et al. 2017)]. The most effective way to mitigate these perceptual errors may be to reduce the attractiveness of the luring cue or remove it from the environment (Greggor et al. 2019, Robertson & Blumstein 2019).

Understanding the umwelt and sensory ecology of species is also important when developing ways to encourage animals to avoid dangerous stimuli that they may otherwise not perceive. Bird collisions with wind turbines, buildings, and power lines and vehicular collisions with wildlife are all issues stemming from a lack of avoidance. Understanding what information and sensory modalities animals use to make decisions in the environment (e.g., sounds and smells) and the sensitivities of their sensory organs, including the temporal resolution and spatial aspects of their ranges, are key in designing attention-grabbing stimuli (Fernandez-Juricic 2016). For instance, Blackwell et al. (2012) studied Canada goose (*Branta canadensis*) vision with the goal of optimizing the frequency of lights on airplanes to reduce airstrikes by making them easier to perceive and hence, more salient. Relying on human-based assumptions about the salience of stimuli can lead to ineffectual conservation interventions. For example, some interventions have tried to prevent avian collisions by placing lights and potential attention-grabbing stimuli on human-made structures, as we would see them (Drewitt & Langston 2008). However, many bird species focus their attention toward the ground when in flight, suggesting that perceptual deterrents should instead be placed on the ground (Martin 2011). Although the effectiveness of ground-based deterrents is still inconclusive (Marques et al. 2014), they may be an alternative to consider when traditional deterrents fail.

Considering the umwelt of a species is an important step in management planning when trying to attract or repel animals. For instance, knowing that Asian elephants' (*Elephas maximus*) dominant sense is smell (Plotnik et al. 2014), one may predict that visual deterrents may be less effective than olfactory ones. That being said, even potent olfactory deterrents can become ineffective over time, due to downstream cognitive processes (see below).

Rule: Attention is finite. All animals are constrained in how they allocate their limited attention (Leavell & Bernal 2019). If an individual is focusing on detecting a predator, it cannot as effectively allocate cognitive resources to looking for food or mates. Much of approach/avoid management can be viewed as influencing whether animals direct attention toward certain stimuli. Thus, understanding how attention is influenced by environmental stimuli is often essential to predicting downstream decision making (2R and 2A in **Figure 2**).

The distracted prey hypothesis posits that any stimuli an individual can detect has the ability to capture attention and thus make it more difficult to allocate attention to other tasks (Chan & Blumstein 2011, Chan et al. 2010). Accordingly, disturbances such as anthropogenic noise are distracting enough that they influence risk assessment and foraging efficiency in animals such as hermit crabs [*Coenobita clypeatus* (Chan et al. 2010)], fishes (Hasan et al. 2018, Radford et al. 2014), and birds (Ware et al. 2015). If such distraction makes noisy patches less attractive, then distracting stimuli may be used to repel animals from undesirable locations.

When attempting to manipulate attraction by changing the quality of a habitat patch, it can be worthwhile to consider how target species' attend to and assess risk. Animals make many decisions to visit or avoid foraging or habitat patches based on how easily they can obtain information about risk. For instance, mowing grass at airports is typically done to repel birds by reducing patch quality, since it reduces food and protective cover, but for some species, such as common starlings

(*Sturnus vulgaris*), it can have the opposite effect when mowing enhances visibility and thus may lead the birds to perceive the patch as safer (Blackwell et al. 2013).

Unwanted stimuli can also cause interference or masking. Some natural interference is predictable (e.g., many visual cues cannot be perceived in the dark). In such cases, animals will have evolved ways to overcome perceptual interference (e.g., foraging during the day). Conversely, intermittent distraction, or masking that is due to anthropogenic disturbance, can create a greater interference. For instance, turbid waters can prevent attending to and subsequent learning about predatory cues (e.g., Ferrari et al. 2010), and anthropogenic noise can interfere with communication (Barber et al. 2010). However, interference can also be used as a management tool. For instance, broadcasting white noise can repel animals from a specific location by restricting their ability to communicate, making it harder for them to share information about risk. By interfering with birds' abilities to hear and respond to conspecific alarm calls, and thereby increasing birds' perception of danger, such risk-based management has shown promise in deterring birds from airports (Swaddle et al. 2016).

Decision Making

Once animals acquire information, they must act on it to make decisions. How animals evaluate conflicting information and weigh past versus present experiences contributes to the choices they make.

Rule: Decisions are economic. Animals' decisions are profitably viewed through an economic lens; those that have net benefits will be favored by natural selection. These decisions are also influenced by external context and internal state, which trade off against acquired benefits (Owen et al. 2017). For instance, the decision to remain in a foraging patch and accept some risk should be influenced by the presence of a predator (external context), hunger (internal state), and the amount of food in the patch (acquired benefit) (Berger-Tal et al. 2010, Brown & Kotler 2004). Thinking about how animals make decisions amid such trade-offs permits managers to engage in behaviorally informed approach/avoid management.

The economics of foraging decisions can be exploited in attract/repel contexts. For instance, invasive rats often eat the eggs of ground-nesting birds, driving massive population declines. On small islands, rats may be eliminated with intensive poisoning and trapping, but both methods can also affect nontarget species. In open mainland systems, reducing rat populations is even more difficult. By capitalizing on the economic nature of foraging decisions, Price & Banks (2012) successfully trained black rats (*Rattus rattus*) to avoid ground nesting birds. They put out artificial nests that contained either a quail (*Coturnix coturnix japonica*) egg and a plasticine egg or two plasticine eggs, along with bedding material and feces from real quail nests. They found that rats learned in 7 days that quail bedding was not predictive of eggs. When real eggs were put out a week later, predation on these nests was significantly reduced compared to those where rats learned that quail bedding was associated with foraging success. Therefore, reducing the profitability of quail egg foraging created an effective deterrent (3R in **Figure 2**).

Devaluing an attractant is not always easy. In theory, olfactory deterrents work by causing sensory aversion or physical pain, or by simulating an increased risk of predation, which makes a specific patch less profitable than an alternative patch (Parsons et al. 2018). However, such fear-based deterrents do not work in all situations. In Australia, much work has gone into creating nonlethal deterrents to prevent marsupials from eating restored postmining revegetation. Animals can be fenced out of revegetated areas, but this is very expensive. By contrast, bullets and poison are less expensive alternatives, but the public has demanded nonlethal options. Kangaroos (*Macropus* spp.) are less likely to forage on food placed next to experimentally deployed dingo urine (Parsons & Blumstein 2010). However, while this intervention may work in areas where there is sufficient alternative food, in the Australian arid zone, there is relatively little aboveground standing biomass. In such conditions, fear-based deterrents may never work because animals would not have other comparable foraging options (Parsons et al. 2018). Therefore, when attempting to repel animals, considering what alternative options animals have helps determine the relative trade-off they make with any given choice (4R in **Figure 2**).

When animals make decisions, their assessments of the state of the world are imperfect, and this uncertainty leads to systematically biased decisions (Marshall et al. 2013). Cognitive biases can be defined as "a consistent deviation from an accurate perception or judgment of the world" (Fawcett et al. 2014, p. 153). Some cognitive biases may be adaptive under ecologically relevant conditions and incomplete information, either as heuristic rules for computationally efficient decision making (i.e., such biases are the results of computational shortcuts to avoid processing limitations) (Haselton et al. 2016, Trimmer 2016) or as error-management tools when error payoff is asymmetrical (Bateson 2016, Haselton et al. 2016, Jefferson 2017, Trimmer 2016, Tversky & Kahneman 1974). One particular area in which cognitive biases may play an adaptive role is the well-known trade-off between exploration and exploitation (Addicott et al. 2017, Berger-Tal et al. 2014, Mehlhorn et al. 2017). To reduce uncertainty, individuals balance known resource exploitation with the time and energy devoted to exploring new resource patches (Bartumeus et al. 2016, Berger-Tal et al. 2014, Kembro et al. 2019, O'Farrell et al. 2019). Under certain conditions, cognitive biases may help maintain a beneficial exploration-exploitation balance (Berger-Tal & Avgar 2012) and thus should influence avoid-approach decisions (for example, in the context of conservation translocations) (Berger-Tal & Saltz 2014).

Rule: Not all cues are treated equally in making decisions. Habitat restoration is increasingly used to reverse habitat loss and biodiversity decline. A common notion in restoration ecology is that by recreating the habitat structure and fulfilling species' ecological requirements, animal species will colonize the restored habitat (Hale & Swearer 2017). However, species often fail to recolonize habitats, regardless of their suitability, unless these sites are paired with specific habitat-selection cues, such as playbacks of conspecific calls (Hale et al. 2020, Schofield et al. 2018) (3A in **Figure 2**). Viewing this issue through a cognitive lens clarifies the reason why. Animals do not react to all cues equally, and many species are primed to strongly respond to cues that, over their evolutionary history, have been reliable indicators of habitat quality, while ignoring other, less certain, cues. Since it can be difficult to assess the balance of resources and dangers via habitat-based cues, many animals instead rely on easy-to-obtain conspecific (or heterospecific) social cues. While broadcasting calls has been used successfully to attract animals on many occasions, it does not always work (Ahlering et al. 2010, Putman & Blumstein 2019), suggesting that the context of conspecific cues must be considered. Call type, timing, and amplitude may determine whether it is successful or not, as will the species' life history (e.g., social behavior and philopatry) (Nocera et al. 2006, Ward et al. 2010).

Attracting animals to desirable habitat can also be challenging if there are unexpected cues of danger (4A in **Figure 2**). For example, as part of their effort to ensure national-level connectivity between protected areas, the Israel Nature and Parks Authority designated an agricultural area at the southern edge of Mount Carmel, Israel, as an ecological corridor, to connect isolated populations of the endangered mountain gazelle, *Gazella gazella*. However, a camera-trap study revealed that despite the removal of physical barriers from the region, the gazelles did not use the corridor (Shamoon et al. 2018). Apparently, daytime human activity in the agricultural fields shifted golden jackal (*Canis aureus*) activity from day to night. Thus, the presence of human activity during the day, and the resulting increased levels of predator activity during the night, effectively excluded the gazelles from these areas, rendering them useless as an ecological corridor for this species (Berger-Tal & Saltz 2019, Shamoon et al. 2018). From a cognitive perspective, not all cues are created equally, and predator cues will often overrule positive cues that a habitat might offer. This is not only because of the high price that predator cues have associated with them but also because of the relatively high certainty of cost associated with such cues, compared with the uncertainty of benefits that may come from habitat cues (Johnson et al. 2013).

Learning

After an animal decides to respond to a stimulus, it may have the opportunity to learn about the outcome of its action.

Rule: Learning is Bayesian. To learn, animals need perceivable stimuli that are associated with reliable outcomes or states of the world. Reliability can be assessed through repeated experience, but individuals often have some prior expectation about the probability of an event occurring or the attractiveness or repulsiveness of a stimulus. We assume that these priors, which have been shaped by natural selection, are also forged by experience. Thus, animals should begin life with a predetermined initial estimate of their environment, which they later hone by incorporating experience. This process is called Bayesian updating and has profound implications for how easily animals learn, including in management contexts (5R and 5A in **Figure 2**).

Populations of tammar wallabies (*Macropus eugenii*), like those of many Australian mammals, have been decimated on mainland Australia following the European introduction of two novel predators: red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*). In a series of studies, Blumstein et al. (2000) showed that tammars have some innate predisposition to respond to foxes, possibly because they share features with thylacines (*Thylacinus cynocephalus*), a historically important marsupial carnivore. Griffin et al. (2001) then showed that tammars could be trained to significantly increase their escape responses to a taxidermically mounted fox after only four training trials. The presentation of the fox was immediately followed by the presence of a person dressed in a witch's costume and carrying a net. Tammars flee people with nets; thus, this was highly aversive. By contrast, tammars were unable to learn (at least using identical methods) to respond fearfully to a taxidermic goat (*Capra aegagrus hircus*) (Griffin et al. 2002). When interpreted through a Bayesian lens, tammars had some expectation that fox-shaped stimuli were to be avoided, and this was quickly honed with experience. By contrast, tammars' prior expectation was that a goat-shaped stimulus was benign, and thus it was harder for experience to modify this initial prior and learn to avoid the goat. Similar predator learning biases have been documented in species as diverse as fish and bush rats (*Rattus fuscipes*) (Carthey & Banks 2016).

Rule: Learning may be biased to focus on certain information. Not all information is equally likely to be learned. Over evolutionary time, certain types of information were more often associated with certain stimuli, which resulted in contextual learning biases. These biases are well illustrated by the psychological principle called the Garcia effect. Garcia et al. (1966) showed that rats easily learn to associate nausea with flavor—rats made nauseous after drinking flavored water avoid it in future—but do not easily associate a physical shock with drinking. By contrast, rats easily learned to avoid lights and sounds associated with shocks, but not if they were associated with later nausea. These types of biases can influence the success of managing attraction or avoidance and must be specifically targeted where necessary (6R and 6A in **Figure 2**). The case of human-bear conflict illustrates this dynamic.

Bears living around humans may learn that humans are a source of food, creating huge problems that range from bears eating out of trash receptacles to bears breaking into homes and cars (Can et al. 2014). The most effective nonlethal techniques deal with the human side of the conflict, by eliminating sources of food (e.g., educating people to store barbeques inside) and providing and enforcing the use of bear-proof trash cans. However, bears may still break into unattended homes and cars. Hazing by making aversive noises and shooting bean bags and rubber bullets at bears is often used to move animals out of an area of conflict. But hazing does not always work. St. Clair realized that learning is often limited by the evolutionary relevance of associations managers attempt to teach bears (e.g., avoid food source after physical pain) (C.C. St. Clair, personal communication). She and Lori Homstol experimented with letting bears (*Ursus americanus*) eat specific foods (e.g., apples or grain) laced with an emetic deworming drug used by veterinarians. Unfortunately, the bears were able to taste the emetic and quickly learned to avoid the treated foods. But the researchers found that if they presented treated and untreated foods together, the bears could not tell which caused their nausea and avoided both types in future (Homstol 2011).

Rule: The order of cues (and experiences) matters. Even for well-known examples of learning, such as the rapid learning that takes place when animals associate illness with food [i.e., conditioned taste aversion (CTA)], how cues are presented matters. In Australia, the poisonous cane toad (*Rhinella marina*) has invaded large swaths of the country, decimating mammal populations that unknowingly consume it. Because consuming the toad immediately kills animals, they cannot learn to avoid such dangers in the future. Researchers tried to help endangered northern quolls (*Dasyurus hallucatus*) avoid this fate by giving them sublethal experiences with small portions of toad meat, thereby successfully training them to avoid any future interactions with toads (O'Donnell et al. 2010). However, similar applications of CTA have failed in different systems. For example, to prevent coyotes (*Canis latrans*) from depredating livestock, managers put out nonlethal poison in baited, dead livestock, with the expectation that it would prevent coyotes from future attacks. While sometimes successful (e.g., Ellins et al. 1977), baiting dead livestock has not always curbed coyote attacks (Forthman Quick et al. 1985, Smith et al. 2000), even for individuals that had consumed the distasteful bait.

A potential reason for the differential effectiveness of these two interventions is that the strength of CTA does not override a main rule of learning: The order of cues (and experiences) matters (7R and 7A in **Figure 2**). The presentation of CTA could have worked for quolls because deciding whether to eat meat that smells like toad involves the same olfactory evaluation the quolls experience when seeking to ingest an actual toad. In contrast, some CTA programs for coyotes may have failed because as predators that chase down their prey, their decision to attack live, moving sheep occurs before the decision to scavenge on a dead, nonmoving sheep carcass (Snijders et al. 2019).

Alternatively, the differential effectiveness of these two interventions could stem from the role of prior experience. The quolls were able to form a new category of toxic thing because they were trained before having any experience with toads. In contrast, coyotes that may have previously experienced the rewards of attacking sheep would be unlikely to discount those highly rewarding experiences, despite having a negative experience. Unless they started having negative experiences every time they attacked sheep, they are unlikely to learn that the good thing is now bad. How many experiences they need would depend on how likely they are to discount negative experiences as bad luck (Greggor et al. 2019), a topic often considered widely in predicting responses to aposematic prey and undefended mimics (e.g., Lindstrom et al. 2004). These hypotheses need not be mutually exclusive; a combination of incongruent cues and prior experience may also be at play.

Rule: Sensitive periods matter. Beyond the order of cues, the timing of cue presentations within an individual's lifetime can matter (7R and 7A in **Figure 2**). Many species have sensitive periods during development when they are primed to learn certain information. The effects of sensitive periods are apparent in the unwanted dispersal away from release sites that plagues many conservation translocation programs (Berger-Tal et al. 2020). Long-distance movements soon after release can put animals in suboptimal habitat, isolate them from conspecifics, and put them beyond support structures for postrelease monitoring or feeding. One main driver of unwanted dispersal following translocations is natal habitat preference induction, a behavioral phenomenon that occurs when experience in animals' natal habitat affects their preference for postdispersal habitats, regardless of the actual quality of that environment in comparison to other available habitats (Davis & Stamps 2004, Stamps & Swaisgood 2007). The proposed mechanism for natal habitat preference induction is imprinting—a genetically canalized learning process characterized by a relatively short sensitive period occurring early in development, which has lasting effects and is almost irreversible (Bolhuis 1991). Thus, animals may be attracted to habitat cues they experienced during a sensitive period in their development and may disperse to find them if such cues are missing at the translocation release site. The issue is not limited to vertebrate translocation programs. For example, adult flax snails (*Placostylus ambagiosus*) dispersed outside the 7-m release area plots, with subsequent work demonstrating that they can go as far as 80 m away (Parris & Stringer 2010). While some adult snails ultimately survived, their numbers were too low for population recovery. Meanwhile, juvenile snails released under the same program did not disperse, presumably because they were still forming their habitat preferences. Understanding the window of sensitive periods is important in deciding when to release animals and in designing their prerelease environment.

Depending on the species, another important timing bias to consider when translocating species is the recency effect, which favors remembering recently presented information, thereby giving recent information greater weight when forming judgments (Shettleworth 2010). The recency effect is influenced by the amount of time animals spend in a habituation enclosure before being released. Habituation enclosures serve two main purposes in conservation translocations: (*a*) They familiarize animals with the habitat and the surroundings in a predator-free setting, and (*b*) they prevent homing attempts by fencing in animals at the release site until they develop an affinity for the location (Swaisgood & Ruiz-Miranda 2018). To successfully translocate animals, a manager must therefore correctly balance the recency effect with any habitat imprinting animals may have (e.g., by using habituation enclosures and ensuring that the release site contains cues from the animals' natal habitat). While evidence so far has been mixed about the benefits of habituation enclosures as a soft release strategy across species (Swaisgood & Ruiz-Miranda 2018), studies suggest that captive-bred animals fare better after spending time in habituation enclosures, due to their greater need to learn about the wild. For instance, burrowing owls (*Athene cunicularia hypugaea*) reared in breeding facilities were 20% more likely to remain at the release site and produced 50% more offspring after spending 2 weeks in a prerelease habituation enclosure than when released directly into the wild (Mitchell et al. 2011). In contrast, wild-translocated animals may need shorter habituation times or a harder release strategy, due to the increasing stress of prerelease holding (Swaisgood & Ruiz-Miranda 2018).

Rule: Be explicit about what you are teaching. While some learning mechanisms, such as imprinting on habitat or mate preferences, may occur only during sensitive periods, other types of learning, such as associative learning, can occur throughout life. A subset of associative learning, called fear conditioning, can be used when trying to repel animals away from an otherwise attractive stimulus. Fear conditioning occurs when a stimulus that has not been initially aversive [referred to as a conditioned stimulus (CS)] is paired with a highly aversive stimulus [referred to as an unconditioned stimulus (US)]. Fear conditioning differs from traditional management techniques that use aversive stimuli alone because it allows animals to anticipate danger and flee before encountering the negative consequences of the deterrent. For instance, a traditional deterrent approach might deploy acoustic deterrent devices (ADDs), which broadcast aversive auditory stimuli, such as painful or predator-like sounds, to repel animals (Götz & Janik 2013, Schakner & Blumstein 2013). ADDs may create ethical issues when they are strong enough to cause hearing damage and can be ineffective in the long-term, since animals often habituate to unreinforced predatory sounds (i.e., predatory stimuli in the absence of the predator) (Götz & Janik 2010, Schakner & Blumstein 2013). Fear conditioning has shown promise as an alternative, learning-based repellent technique. However, it can be challenging to apply because one must be careful that the intended CS and US are actually the ones being learned.

Scientists explored using fear conditioning to repel gray seals (*Halichoerus grypus*) from commercial fishing pens to negate the need for consistent ADDs. In ex-situ trials, they showed that it was possible to train the seals to avoid a formerly nonaversive tone (CS) that predicted the aversive ADD sound (US) (Götz & Janik 2011). Schakner et al. (2017) aimed to extend the application of fear conditioning to the field, to teach California sea lions (*Zalophus californianus*) to avoid two types of attractants: commercial live bait barges (where sea lions haul out and eat the bait) and sport fishing boats (where sea lions eat bait and captured fish off hooks). A rapid-onset, broad-spectrum sound was designed to elicit an aversive acoustic startle reflex. In both contexts, sea lions responded aversively to the startling stimulus. However, the startling stimulus alone was more effective than when paired with the CS on the bait barge, suggesting that while sea lions were fear conditioned, this was not an effective management strategy. Additionally, fear conditioning failed to deter sea lions from boats at sea. In both contexts, it appeared that sea lions learned rapidly to ignore an unreinforced neutral stimulus, even if it predicted the startling ADD. In neither case was the desired management outcome achieved.

An important cognitive lesson emerges from these failed attempts to repel animals. Blocking is a learning phenomenon whereby animals will learn about new stimuli in situations in which associations already exist, only if the new stimuli provide additional information (Shettleworth 2010). In this context, California sea lions had learned to associate the bait barges and fishing boats with food and bait barges with relatively safe haul-out sites. The novel contingency that was created during fear conditioning was an association between a highly aversive sound and a nonaversive sound, not the highly aversive sound and new information about the food or secure location. Thus, one must be very clear on what associations are being taught and ensure that they are properly aligned with the management problem (7R and 7A in **Figure 2**). Moreover, in some management situations, deterrents such as ADDs may be the only viable option until fear conditioning is properly developed, despite ADDs having potentially detrimental consequences. As lab-based applications of fear conditioning continue to be translated to the field, better guidelines will need to be developed to predict what cue variability matters and what cue-experience contingencies are most effective at eliciting continued aversion.

Rule: Stimuli should be reinforced. Animals will show reduced responses over time to repeated presentations of identical stimuli. Such habituation is a common problem when trying to deter animals from engaging with an otherwise attractive stimulus. While fear-related cues can strongly direct behavior initially, they can still require reinforcement of a negative outcome to retain their efficacy over time (8R in **Figure 2**). The battle against habituation is often fought when trying to induce animals to avoid areas where they disrupt or exploit valuable human resources, especially when interventions aim to use nonlethal deterrents. This strategy has led to tactics that broadcast conspecific cues of danger, since studies have shown that they are more resistant to habituation than other, more arbitrary loud sounds, such as gunshots (Bomford & O'Brian 1990; but see Biedenweg et al. 2011). For instance, many bird species produce alarm calls to communicate about danger. Humans often use these cues to deter animals from a particular location (e.g., agricultural fields) or resource (e.g., grain stores). Despite success over limited time periods (e.g., 6 months) (Spainer 1980), birds eventually learn to ignore these calls in the context of the deterrent if they are broadcast repeatedly (Bomford & O'Brian 1990). The same processes explain why predator models and scarecrows fail to be effective after time (Marsh et al. 1992), as is widely evident with the static, plastic great horned owl models employed unsuccessfully across rooftops in the United States, commonly seen with the very bird they are trying to deter (pigeons) sitting atop them. While delays in habituation are possible with varied sounds that include nonbiologically meaningful stimuli (Biedenweg et al. 2011), eventual habituation still likely occurs because reinforcement is necessary to retain the potency of repeated cues that occur over time in the same location. Although habituation is highly specific, especially toward predatory-type cues, it is unknown how habituation in contexts such as deterrents generalizes to reducing responsiveness to true threats (Blumstein 2016, Greggor et al. 2019). Therefore, the ecological costs of failed deterrents are mostly untested.

Researchers have tried to develop habituation-resistant deterrents for elephants, with some success. Elephants often create conflicts around agricultural communities, including trampling and eating crops. When farmers make noises to scare off elephants, they quickly habituate to these nonreinforced stimuli. Electrified fences have been used to deter elephants, but they require constant power and sometimes are destroyed by the elephants. However, African bush elephants (*Loxodonta africana*) live around aggressive bees and avoid getting their sensitive trucks stung by them. Playbacks of bee sounds cause elephants to both move away and warn others in their groups (King et al. 2007). Capitalizing on this naturally aversive stimulus, researchers set up a virtual fence comprised of beehives around crops (King et al. 2009). Elephants avoided these beehives, and the crops were not damaged. A cognitive interpretation of this effective deterrent suggests that since bees are highly aversive, the living bees created a potentially reinforced stimulus—which would be resistant to habituation, since elephants could actually get stung.

Rule: Social learning can be an accelerant. Social learning involves similar learning processes seen in individual learning, except that animals attend to cues created by other animals rather than those created by asocial circumstances (Heyes 2012). Social learning is also subject to a series of biases about who and when to copy (Rendell et al. 2011), which can be important to consider when addressing conservation issues (Greggor et al. 2017). Underappreciation of these influences on behavior can impact the outcome of conservation interventions because social learning can accelerate the spread of deleterious behaviors and be targeted for promoting others (1R and 1A in **Figure 2**). For example, social learning can be an accelerant to human-wildlife conflict and has been shown to increase the approaches of bears to human-produced food (Mazur & Seher 2008) and to explain the rapid increase in catch depredation by sperm whales along longline fisheries (Schakner et al. 2014). In such situations, understanding the role of social learning may also help de-escalate conflict when particular individuals can be targeted to help stem the spread of information or influence group behavior (Swan et al. 2017). For instance, considering the social spread of salmon depredation behavior in California sea lions (*Z. californianus*) allowed researchers to model the relative effectiveness of culling offending animals (Schakner et al. 2016).

Memory

Animals can only use previously learned information upon reencountering a stimulus if they remember information obtained from prior experience. The duration of memories varies by their type, their content, and the species involved.

Rule: Animals are more likely to remember survival-relevant information. Memory is under similar natural selection pressures as learning and favors the retention of survival-relevant information. For instance, many fishes learn to recognize predators, retaining a memory after only a single experience (e.g., Ferrari et al. 2008). Antipredator training retention may last at least 2 months in fish (Chivers & Smith 1994) and at least 3 months in some birds (de Azevedo & Young 2006). Some species revisit specific foraging patches at specific times of the year throughout their lives, an observation that suggests lifelong learning. Developmental stage may also influence memory duration: Wood frog (*Rana sylvatica*) embryos responded to learned predation-related cues for >5 weeks, while wood frog tadpoles responded for only 10 days after training (Ferrari et al. 2019). Importantly, the duration of memory can influence the efficacy of learning in management contexts (2R and 2A in **Figure 2**).

Following translocation into the wild, many individuals are killed by predators (Swaisgood & Ruiz-Miranda 2018). This can create both a management problem (failure to establish a new population) and an ethical problem (sending out individuals to likely death). Prerelease predator training has been proposed as a way to reduce predation risk for translocated animals. Whether by directly training animals to associate predatory stimuli with fear (reviewed in Griffin et al. 2000, Shier 2016) or by creating situations for in situ learning where animals are housed with low densities of their predators for a period of time before release (Moseby et al. 2016), a key factor is how long animals retain their lessons about fearful stimuli.

In conservation translocations, the lessons may only have to help animals survive their initial forays into the new environment. Often, animals scatter upon release and have to find safe and productive areas to live. Individuals are most vulnerable to predators during this initial postrelease settlement (Berger-Tal & Saltz 2014), which can occur, depending on the management strategy, outside their sensitive period for risk assessment. Once in a safe location, they can maximize their chances of surviving based on their own experiences. Thus, associative lessons need to last sufficiently long so that animals are released with the memories fresh. However, this may sometimes be challenging when releasing animals from habituation enclosures, since their time in the enclosure may cause the memories of the antipredator training to decay (Bell 2016). To avoid this problem, managers may need to consider reinforcing the antipredator training inside the habituation enclosure, when feasible, or, alternatively, translocating animals directly from areas in which they are living in the presence of predators (whether naturally or by human design).

CONCLUSIONS

We have taken an explicitly cognitive approach to understanding and predicting animals' decisions about approach and avoidance. By providing a mechanistic basis for behavior, we hope to have created levers that managers can use to attract and repel target animals, which we illustrate through a series of troubleshooting steps (**Figure 2**). This approach, however, highlights some key unknowns.

We know very little about perceptual processing in the vast majority of species. Audiograms, which define a species' auditory sensitivity, have been developed for a fraction of known vertebrate (e.g., Fay 1988) and invertebrate species. A detailed understanding of visual spectral sensitivity has been mapped in few species, and very little is systematically known about the vast majority of species' olfactory sensitivity. Given our general lack of understanding of specific sensitivities, we are often unable to evaluate or justify using surrogate species as guides. Yet, since understanding a species' umwelt is the first step in cognitive-based management, researchers and managers must allocate efforts to understanding relevant perceptual processes if they are to lead to successful wildlife interventions.

Optimal decisions depend on context. While behavioral and evolutionary ecologists have a rich tradition of studying context, managers must realize that identifying key contextual modulators of behavior is an essential task. Context is pervasive in influencing every cognitive step. Context may influence what is learned or how quickly something is learned. And, because learning and memory are adaptive solutions that are themselves the product of natural selection, context should influence how long lessons are retained.

We have not focused on a potentially obvious issue with approach/avoidance: how animals deal with novelty. The effects of the fear (neophobia) and attraction (neophilia) to novelty can have consequences. On initial interactions with stimuli, neophobia and neophilia can determine responses. However, we still lack research into the long-term effects of neophobia and neophilia as novelty subsides (Greggor et al. 2019). We chose not to include novelty responses here because their long-term effects are not yet well articulated with respect to specific conservation interventions.

While we know much about learning and memory from over a century of laboratory studies, we lack an understanding of these cognitive processes in the field (Blumstein 2016, Thornton et al. 2014). For instance, we do not know whether habituation rates differ between modalities, which has implications when deciding what cue type to use for repellents. And, while there are some select instances where multi-modal deterrents have worked under field conditions (e.g., Smith et al. 2000), there is not yet sufficient evidence to prove that unreinforced multi-modal stimuli will delay habituation.

As we learn more about how to manipulate approach/avoidance decisions, the integration of this knowledge into interventions needs to take an evidence-based approach (Blumstein & Berger-Tal 2015, Blumstein & Fernández-Juricic 2010, Greggor et al. 2016). The effectiveness of cognitive-based management must be evaluated alongside other techniques. Additionally, the welfare consequences for using cognitively informed interventions should be considered, since they may comparatively reduce the need for lethal interventions, reduce bycatch, and improve survival for translocated species. Ultimately, we hope that the cognitive framework developed here will help focus research and lead to more effective interventions that preserve biodiversity.

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