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**REVIEW**

# Contextual influences on animal decision-making: Significance for behavior-based wildlife conservation and management

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## Abstract

Survival and successful reproduction require animals to make critical decisions amidst a naturally dynamic environmental and social background (i.e. "context"). However, human activities have pervasively, and rapidly, extended contextual variation into evolutionarily novel territory, potentially rendering evolved animal decision-making mechanisms and strategies maladaptive. We suggest that explicitly focusing on animal decision-making (ADM), by integrating and applying findings from studies of sensory ecology, cognitive psychology, behavioral economics and eco-evolutionary strategies, may enhance our understanding of, and our ability to predict how, human-driven changes in the environment and population demography will influence animal populations. Fundamentally, the decisions animals make involve evolved mechanisms, and behaviors emerge from the combined action of sensory integration, cognitive mechanisms and strategic rules of thumb, and any of these processes may have a disproportionate influence on behavior. Although there is extensive literature exploring ADM, it generally reflects a canalized, discipline-specific approach that lacks a unified conceptual framework. As a result, there has been limited application of ADM theory and research findings into predictive models that can enhance management outcomes, even though it is likely that the relative resilience of species to rapid environmental change is fundamentally a result of how ADM is linked to contextual variation. Here, we focus on how context influences ADM, and highlight ideas and results that may be most applicable to conservation biology.

**Key words:** animal behavior, anthropogenic change, context, decision-making, wildlife management

## INTRODUCTION

Animals make many decisions each day. They may decide whether to forage in a certain area based on the expected rewards of doing so traded off against any risks of doing so. They decide when to look for predators, when to run, when to hide and when to sleep. On a good day, they may make decisions about whom to mate with and how much energy to allocate to a given repro-

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ductive event. However, these decisions are not made in a vacuum. Environmental and social context is an integral part of animal decision-making (ADM) because the adaptive value of decisions varies based on context. Thus, as humans change the environment and demographic structure of animal populations, humans change the context under which decisions are made. Here we define context as the environmental and social background conditions that animals experience, including changes in the characteristic trait values of contextual features (e.g. resource quality and availability, and population density).

Correlations between anthropogenic change and changes in behavior and population dynamics have been broadly documented (Parmesan & Yohe 2003; Crutzen & Stoermer 2006). However, these correlations have mostly been noted without explicit consideration of how the ADM process links environmental change to changes in behavior and population dynamics (but see Sih *et al.* 2010, 2011; Robertson *et al.* 2013). Numerous examples of maladaptive behavioral responses to a human-modified environment have been documented. From sea turtles [*Caretta caretta* (L., 1758) and *Chelonia mydas* (L., 1758)] being misdirected by artificial lighting (Tuxbury & Salmon 2005), seabirds and condors [*Gymnogyps californianus* (Shaw, 1797)] eating plastic trash (Houston *et al.* 2007), to kangaroo rats [(*Dipodomys stephensi* (Merriam, 1907)] digging burrows along roadside berms (Shier *et al.* 2012), the literature is replete with examples of behaviors generated by evolved ADM that no longer works. Some authors have adopted the prognosis that the discipline of behavioral ecology is undergoing a slow death as the environment in which animal behavior has evolved has been altered so drastically that behavior and decision-making under study no longer reflect current adaptive value and function (Caro & Sherman 2012).

However, what mechanisms are responsible for these bad decisions? Is it that in the current environment a cue no longer consistently represents the resource it once had? Is information integration more challenging amidst a more cluttered background? Do the decision rules long used to guide search strategies and resource choice set them up for "failure" in a modified landscape? Is it a combination of sensory mismatch, cognitive overload and a now-ill-fitting decision rule? Because ADM is inherently mechanistic (Blumstein & Bouskila 1996), explicit study of decision-making as a whole can provide a ready framework from within which to identify critical sensory (reviewed in Sih *et al*. 2010), cognitive (reviewed in Greggor *et al.* 2014), learning (reviewed in Schakner & Blumstein 2013) or strategic processes that may be disproportionately responsible for generating behavior, and ultimately influencing demography and population dynamics (Anthony & Blumstein 2000).

Sih *et al.* (2010) provide a mechanistic framework, founded in signal detection theory (Wiley 2006), to examine how mismatches between evolved cue-response systems may influence ADM and, thus, determine the susceptibility of some species to the negative effects of rapid environmental change [as exemplified by the jewel beetle, *Julodimorpha bakewelli* (White, 1859)], erroneously mating with brown glass bottles; Robertson *et al.* 2013). This cue-response framework can facilitate the development of explicit, quantitative predictions regarding both short and long-term impacts on animals inhabiting degraded or disturbed habitats when behavior is predominantly generated by a species stereotypic response to external stimuli. This framework also provides a model from which to approach the extraction of findings from other disciplines focused on ADM to conservation research and management.

Beyond the mechanisms of sensory inputs and cognitive processing, decision rules that link assessment to the ultimate fitness payoff shape the role of information gathering and resource sampling (Luttbeg 1996). Thus, decision rules may also fundamentally influence how contextual variation influences ADM and may have a disproportionate influence on behavioral responses to environmental change. For example, species that use character-trait threshold or absolute valuation (Jennions & Petrie 1997) to evaluate options may be influenced by changes in context in a different way than those that use comparative evaluation (Reaney 2009), consensus (Sumpter & Pratt 2009), sequential sampling (Luttbeg 1996) or a "best-of-N" strategy (Janetos 1980) (Table 1). Species using absolute or threshold valuation may pay increased search costs when confronted with changes in resource availability. If the trait-value criteria become rare because of anthropogenic changes, these search costs could have profound effects on fitness; in theory, animals could keep searching forever if the (optimal) criteria no longer exist in the current environment. For example, Whitehead *et al.* (1997) suggest that the dramatic depletion of large male sperm whales (*Physeter macrocephalus* L., 1758) in the southeastern Pacific has resulted in a persistent reduction in pregnancy rates because females of the species pass up the relatively common smaller males in their search for the now-rare largest males. Thus, a threshold-based decision rule has

**Table 1** Glossary of terms commonly used by behavioral ecologists to describe the decision rules that guide ADM across choice domains (i.e. for mate search, movement, predator avoidance and resource acquisition)

| Term | Definition | Example | Fitness implications in rapidly altered social context |
|---|---|---|---|
| Absolute valuation | Decision is based on a trait meeting a specific criteria value | Male must weigh 350 kg | ●Increased search costs if large males have become rare<br>●Reduced fitness due to lost reproductive opportunities |
| Comparative valuation | Simultaneous, relative valuation of a trait based on 2 or more options | Female simultaneously compares the attributes of 2 or more males | ●"Fixed" search cost<br>●Potential for reduced fitness if sub-par male traits confer reduced trait value to offspring |
| Best-of-N | Sampling of a fixed number of options. Chooser bases decision on best "quality" option sampled. | Female evaluates 4 males, chooses to mate with the largest of them | ●"Fixed" search costs<br>●Potential for reduced fitness if male traits are subpar |
| Threshold | Sampling of options continues until a threshold value of a particular trait is identified. | Male must weigh *at least* 350 kg | ●Increased search costs if large males have become rare<br>●Reduced fitness due to lost reproductive opportunities |
| Sequential sampling | Sequential assessment of options. | Female compares the attributes of 2 or more males in turn | ●Search costs dependent upon whether female uses a best-of-N, absolute or threshold strategy for mate choice<br>●Potential for reduced fitness if sub-par male traits confer reduced trait value to offspring or if search costs increase due to deplete population density or male quality |
| Consensus | Social animals choose between a number of options and follow the option with the most "votes" | Swarming or flocking species | ●Population density influences the speed and accuracy of decision-making |
| Heuristic rules of thumb | Fast and frugal approach to information gathering | Decisions made on incomplete information | ●Search costs reduced<br>●Incomplete assessment of mate quality may result in erroneous decisions |

We provide working examples of decision rules for a generic animal in the context of mate search/mate choice, illustrating how different rules influence the process of decision-making when the social context has rapidly changed, and suggest the potential fitness implications associated with these decision rules operating in an altered context.

intensified the population losses initiated by the rapid and large-scale human harvest of the species.

By contrast, the decisions made by species using comparative or sequential strategies may make "the best of a bad situation" (Dawkins 1979), settling for the best of the available options. This may have positive effects on fitness if it saves significant search costs, but could also result in maladaptive decisions that reduce survival or population growth. For example, if, during dispersal and habitat selection, an animal settles for the best available habitat of the "*N*" habitats sampled, they could end up settling in habitat associated with extremely low fitness (*sensu* "ecological traps," Battin 2004). This illustrates how changing environmental context can alter the fitness associated with different ADM mechanisms, with implications for population-level performance. Thus, the relationship between ADM and anthropogenic environmental change is likely to be of concern to conservation biologists and wildlife managers.

The relative importance of animal behavior to conservation biology is still, and somewhat surprisingly, debated (Caro & Sherman 2012); however, the potential for behavior-based studies to both reveal and address anthropogenic impacts has been broadly demonstrated (Blumstein *et al.* 2003; Blumstein 2006; Fernández-Juricic *et al.* 2005; Shier & Swaisgood 2012), if not fully realized (Caro 2007; Berger-Tal *et al.* 2011). We contend, however, that by considering the varied components of ADM as integrated parts, each potentially having a different influence on behavior, we can enhance our ability to predict the impacts of anthropogenic environmental change on animal populations.

## THE ANIMAL DECISION-MAKING PROCESS

Blumstein and Bouskila (1996) outline a generalizable mechanistic framework and standardized terminology for the ADM process. Taken together, the ADM process includes sensory, cognitive and behavioral actions. ADM begins with the acquisition of information via sensory inputs (i.e. stimulus filtering and perception). Evaluation of information gained through perception occurs via higher-level cognitive processes that result in an "informational state." Decisions are made based on the informational state, and result in behavioral actions that change (or maintain) the state of the organism. Ultimately, the outcomes of actions taken are re-evaluated, thereby consolidating experience into information that can influence future decisions (Fig. 1). Each step of the process may also be influenced by both the state of the receiver (Blumstein & Bouskila 1996), and the environmental or social context (Danchin *et al.* 2004).

Disparate scientific disciplines have approached the study of ADM in very different ways, and the resulting discipline-specific technical lexicon reflects the lack of a common theoretical framework or empirical synthesis (Sanfey 2007). Psychological studies of ADM have used both cognitive approaches (Lebiere & Anderson 2011) and behavioral economic theory (Bateson 2002) to construct paradigms that guide both experimental design and the interpretation of results. Cognitive approaches investigate the higher-level mental processes that underlie information acquisition and the role cognitive traits play in generating behavior (Dukas 2004). The behavioral economic approach is founded in stripping away context to expose underlying optimization processes (Real 1991). However, in nature, decisions are not made in a void (Rosati & Stevens 2009), so it is easy to appreciate that contextual variation is a constant and pervasive feature of ADM, and is, in fact, an important source of valuable information (Danchin *et al.* 2004).

Behavioral ecological approaches typically frame ADM in optimization strategies that reflect adaptive decision-making (McNamara & Houston 2009). In contrast to the behavioral economic approach, behavioral ecologists have incorporated a functional perspective, integrating contextual complexity and interpreting results in the context of adaptive trade-offs (Dill 1987). Behavioral ecological studies focusing on deci-

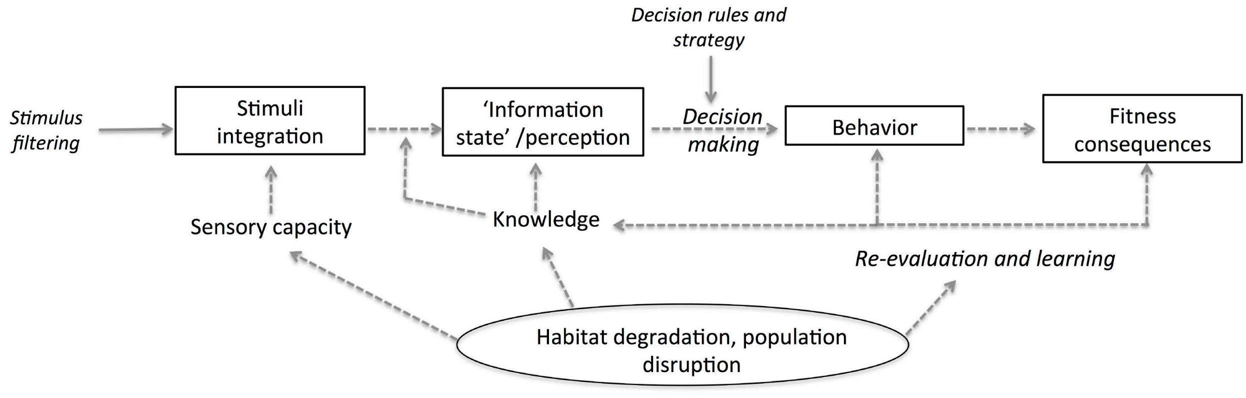

**Figure 1** Stages of the decision-making process (modified and expanded from Blumstein & Bouskila 1996). Context may influence each stage of the decision-making process. Personal information may have influence over all stages once a stimulus has been integrated. Sensory capacity, selection on the sensory apparatus and experience are part of the prior, and the posterior is formed after the evaluation process.

sion–rules examine the framework that governs information acquisition and option evaluation. For example, Janetos (1980) and Janetos and Cole (1981) tested models of decision rules animals may use when searching for resources and noted that animals either search for and evaluate all possible options, or that they may sample a subset of options and choose the best among them (e.g. "best-of-*N*" strategy). Heuristic models of ADM (Hutchinson & Gigerenzer 2005) are based on the idea that there are costs and time constraints on decision-making in nature. Thus, whether decision rules are fundamentally economic or ecologically optimized, information-gathering shortcuts (or "rules of thumb") are the rule, rather than the exception.

There is an extensive literature of empirical and theoretical research explicitly focused on ADM in the disciplines of sensory ecology, cognitive psychology, behavioral economics, behavioral ecology and evolutionary biology. However, there has been little intellectual exchange between these disciplines, and, as a result, a unified conceptual framework is lacking, thus limiting the application of research findings to conservation and wildlife management. Here, we review ADM theory, and describe some of the fundamental concepts guiding the study of ADM in varied disciplines. We provide definitions for terms commonly used among disciplines, and we explore the influence of context on the ADM process across choice domains (e.g. mate search, foraging, predator avoidance and settlement) and discuss the potential implications and applications of contextually modulated ADM for wildlife management and conservation. We suggest that to most effectively inject ADM into conservation research, an integrative approach should be taken and the synergy between different stages of the ADM should be considered. This approach should make it possible to identify the components of ADM that are disproportionately responsible for generating observed behavior and fitness changes, and results may then be used to mitigate conservation challenges.

## A BRIEF SURVEY OF ADM THEORY: FROM SIGNAL DETECTION TO HEURISTICS

### Signal detection theory and sensory ecology

Signal detection theory (SDT) provides a quantitative framework for assessing cue-response systems, by measuring the information-bearing content of a cue or signal against any aspect of the background that may obscure signal reception (often referred to as "noise") (Wiley 2006). Adapted from statistical decision theory (McNamara & Houston 1980), SDT can be explicitly used to predict how an organism's response will change in association with cue/signal strength or other measurable characteristics. For example, Ord and Stamps (2008) used this framework to demonstrate how the use of an alert display by *Anolis* lizards enhanced the efficacy of information carrying visual displays, increasing the chances of successful signal reception at greater distances. As a result, explicit predictions could be made regarding the signal strength required to successfully communicate with conspecifics under varying environmental conditions.

Within the SDT framework, context is included as a fundamental driver of cue-response relationships, and, thus, it can be readily utilized to examine the influence of human-driven environmental changes on ADM. In the context of animal conservation, SDT has been increasingly used empirically (Erbe & Farmer 1998), or invoked in theoretical discussions (Sih *et al.* 2010) and in the interpretation of otherwise descriptive findings (Nie *et al.* 2012). For example, Sih *et al.* (2010) provide examples of cue-response mismatches resulting from anthropogenic changes to the environment and theoretically demonstrate how SDT can be used to explicitly predict the strength and direction of these changes.

Signaling in communication systems is an area where anthropogenic alteration of context may disrupt signal transmission, with important consequences for mating, competition, and social integration/stability. Wollerman and Wiley (2002) tested the influence of background noise on signal reception in tree frogs (*Hyla ebraccata* Cope, 1874), demonstrating that female responses to calls from males were prone to error in the face of even moderate background noise. Erbe and Farmer (1998) took an applied approach, using this framework to examine how noise from different types of ocean vessels influenced conspecific signal detection in beluga whales [*Delphinapterus leucas* (Pallas, 1776)]. The authors apply their results within the context of shipping management, and make policy recommendations based on the predictable impact of different classes of ocean vessels on beluga communication. Airborne or waterborne pollutants may similarly disrupt chemical communication. For example, female swordtail fish (*Xiphophorus birchmanni* Lechner & Radda, 1987) show diminished preferences for conspecific males and are more likely to hybridize in the presence of pollutants associated with agricultural runoff and sewage (Fisher *et al.* 2006). Similarly, anthropogenic alteration of substrates important for chemical signaling may impede efficient communication to the detriment of mating or other important social functions. Nie *et al.* (2012) found that giant pandas [*Ailuropoda melanoleuca* (David, 1869)] selected scent mark sites based on optimal topographic, microhabitat and substrate surface characteristics. They suggest that "signaling habitat" should also be preserved alongside foraging and other resource habitats, because anthropogenic alteration of panda habitat may reduce signal transmission detection probability, increase energetic output and impede mating. These predictions could be explicitly tested empirically using SDT.

## Cognitive constraints and experimental psychology

Optimality models aside, animals do not possess perfect information about their world and many studies have sought to understand the constraints limiting information acquisition and ADM. Cognitive constraints, a frequent subject of study among experimental psychologists, can be defined as "limits on memory and neuronal processing of information" (Real 1991) and, from the ADM perspective, result in imperfect integration of all possible information-bearing stimuli (Lebiere & Anderson 2011). These limits may be determined by physical properties that limit perception (e.g. acoustic frequency or light wavelengths) or by processing limitations that constrain the quantity of information that can be handled.

Psychophysical and behavioral studies have demonstrated that cognitive constraints are an essential factor in the adaptive evolution of ADM and, thus, profoundly influence the information utilized for decision-making (Dukas 2004). For example, female mate choice in Tungara frogs [*Engystomops pustulosus* (Cope, 1864] is dominated by a preference for males with more complex calls (Bernal *et al.* 2009). However, Akre *et al.* (2011) demonstrate that the perception of calling complexity is constrained by Weber's law, and accordingly find that it is the ratio of male calling complexity between competing males, and not complexity per se, that defines attractiveness. Thus, if the number or quality of males is reduced due to human activities females may choose males subjected to less rigorous competition. Chan *et al.* (2010) found that hermit crabs [*Coenobita clypeatus* (Fabricius, 1787)] exposed to expanding images of an aerial predator were distracted by boat noise, as measured by a delay in their behavioral response to the expanding predator stimulus. When the crabs were exposed to an additional stimulus (flashing lights), the predator avoidance behavior was further delayed; although these investigators did not measure fitness impacts it is not unreasonable to extrapolate these findings to infer population-level impacts from higher predation levels in the presence of chronic disturbance. These results demonstrate potential cognitive constraints on information processing, and illustrate how anthropogenic stimuli may influence ADM by reducing cognitive efficiency. Similarly, Teixeira *et al.* (2007) review the many ways that biological stress may impede conservation translocations, emphasizing how stress impairs cognitive processes and decision-making.

## Rational decision-making and behavioral economics

Economic theory has had a profound influence on the study of ADM (McNamara & Houston 1996; Bateson 2002) and was developed out of expected utility theory. Expected utility theory, as applied to ADM, dictates that a decision maker will choose an option based on the product of its usefulness and its associated risk. A central prediction emerging from behavioral economic theory is that ADM will be "rational"; in other words, the choices that animals make will be "consistent across contexts" (Schuck-Paim *et al.* 2004, p. 2305). Conversely, decisions that are intransitive or that vary across contexts are termed "irrational."

Notably, however, irrational ADM has been widely documented in diverse taxa (Shafir 1994; Bateson 2002). Within the behavioral economics literature, irrational ADM has been described as "anomalous" (Waite & Fields 2000), expressed only under specific circumstances (Houston 1997), or interpreted as reflecting cognitive biases (e.g. Waite & Fields 2000). However, a growing body of literature suggests that an adaptive or ecological perspective lies at the heart of this seeming irrationality (Haselton & Buss 2009; Johnson *et al.* 2013) and that cognitive or ecological constraints on ADM are the rule rather than the exception in nature (Janetos 1980), and greatly influence how information is gathered and used.

We are unaware of examples in the literature where behavioral economic studies of ADM have been directly applied to wildlife management or conservation. However, results may be broadly applicable if their interpretation is reframed within the millieu of rapid environmental change. For example, Schuk-Paim *et al.* (2004) found that adding an irrelevant decoy to a set of food options influenced foraging choices in starlings (*Stur-*

*nus vulgaris* L., 1758). However, this influence was dependent upon the state of the chooser. Thus irrational decision-making in this context reflected the contextual influences on decision-making that may be driven by changes in body condition, degraded public information or socially acquired information.

We suggest that information regarding the resilience of ADM in a rapidly changing environment may be reflected in contextual influences on otherwise rational decisions. Although, it is likely that the stripped-down laboratory setting of most behavioral economic studies of ADM, coupled with the exclusion of context, has left behavioral economics ill-adapted to conservation, there are valuable concepts for conservation behavior when one explicitly integrates anthropogenic changes and ADM. These concepts should be informative regarding the degree of resilience of species to anthropogenic environmental changes, particularly from lessons learned from studies demonstrating "irrational behavior," which provides greater understanding of animals' ability to alter decision rules when the relative value or availability of resources change (*sensu* McNamara *et al.* 2014).

## Heuristics, strategy and behavioral ecology

Unlike behavioral economists, behavioral ecologists have historically been interested in the evolution of *adaptive* ADM (Dill 1987). Rosati and Stevens (2009) argue that natural selection does not result in animals that "adhere to economic theory" and acknowledge that the growing body of evidence suggests an adaptive role for contextual variation, and not an error producing one. Another perspective on adaptive ADM suggests that while strategic ADM may result in erroneous choices, the costs of bad decisions are often negligible (Waite & Field 2000). In situations where the fitness pay off is higher, animals should be more inclined to take risks in ADM, thus producing more "errors" (Houston 1997) and so, on average, there is a net gain. Furthermore, the pervasive context-driven asymmetry between the costs associated with false positive and false negative errors may drive the adaptive value of ADM errors (Johnson *et al.* 2013). Adaptive ADM incorporates the dynamic nature of the environment, including the variability of context, personal information, individuality and time, presuming that the trade-offs between costs and benefits inherent to optimal ADM are expressed in context (Lima 1989).

McNamara *et al.* (2012) suggest that irrational ADM is more appropriately interpreted as "strategic", reflecting the imperfect nature of information gathering in natural settings. These ideas are consistent with the constraints on ADM outlined by Janetos (1980) and Janetos and Cole (1981) (e.g. time, memory and mobility) and recast the information "skimming" associated with heuristic characterizations as tactical "cherry picking." McNamara *et al.* (2012) further argue that making decisions quickly is an adaptive strategy that reflects a *cumulative* rationality, shaped by experience and the real world constraints of incomplete information and little time to act.

Heuristics (Hutchinson & Gigerenzer 2005) are cognitive processes that provide a shortcut to ADM via gathering partial information from all that is available. By limiting the amount of time and energy, involved in information gathering, it has been suggested that the "fast and frugal" character of heuristic approaches enhances ADM efficiency but limits accuracy (Gigerenzer & Gaissmaier 2011). Because it is impossible for an animal to sample all possible options (Janetos 1980), mechanisms that promote the use of "rules of thumb" or comparative valuation may be adaptively advantageous (Bouskila & Blumstein 1992). In this regard, a heuristic approach to information gathering may be adaptive, or be representative of general ADM processes that function across choice domains. Regardless, the accuracy of decisions made using a heuristic approach may be compromised if the information available in the environment is no longer a good predictor of what, on average, will enhance fitness. This is well illustrated by the potential costs of erroneous decisions made while inspecting predators, a risky strategy employed by prey species to gain fitness-enhancing information about potential predators (Fishman 1999). Inter-population variation indicates that prey co-evolved with dangerous predators display greater caution when inspecting predators (Magurran 1986). Species that have evolved in a context that promoted risk taking may be more vulnerable in human altered landscapes, such as those with more dangerous introduced predators or habitat modifications that reduce escape options and increase vulnerability. In these human-modified landscapes the consequences of once-adaptive information acquisition strategies may entail greater than historical risk, with errors having profound impacts on fitness.

## Synthesis and summary of animal decision-making approaches and the role of context

Common questions emerge by taking a broad view of ADM. Does environmentally-driven variation in behavior result from sensory constraints? And if so, how? Do cognitive constraints limit animals' ability to retrieve salient information when confronted with irrelevant environmental stimuli? Are strategic decision rules obsolete when the demography of a population has changed dramatically? If constraints on information gathering are the rule, rather than the exception, will contextual changes render the information landscape inadequate to make critical decisions that will, on average, enhance fitness? McNamara and Dall (2010, p. 231) suggest that functional approaches to studies of ADM, as exemplified above, would be enhanced by the "judicious application of economics theory," and by taking an explicit information approach (Stephens 2007). The same can be said for incorporating the other, rather compartmentalized, disciplines we have discussed here.

Signal detection theory provides a framework within which to make predictions regarding how changes in external stimuli may influence behavior via the capacity of a species' sensory apparatus. Cognitive psychology provides a body of literature that tests the constraints on information processing, after signals are received. Information theory provides an adaptive framework within which to assess the overall performance of a dynamic chain of elements. Heuristic and strategic approaches to the study of ADM reflect the real world limits on information acquisition and overarching strategies that may enhance fitness over the course of an animal's lifetime. Taken together, these concepts are consistent with adaptive theories of ADM and provide a balanced framework from which to consider the contextual modulation of ADM processes in animals. The extent to which these varying processes are utilized will influence how organisms respond to rapid environmental change, and will determine whether these responses are adaptive or maladaptive. The different approaches to studying these processes related to ADM will yield different sources of information and, collectively, provide a new toolbox that can be applied to understanding, predicting and mitigating animals' fitness-reducing responses in a changing world.

## CONSERVATION APPLICATIONS AND IMPLICATIONS

### Overview

The scale, pace and pervasiveness of anthropogenic influences on natural systems is unprecedented (Crutzen & Stoermer 2006). Habitat loss, habitat fragmentation and habitat degradation may drive changes in resource availability or resource quality and influence the ecological context in which animals make critical conditions. Selective harvesting may drive changes in population density and age/sex structure that ultimately influence the social context in which animals make critical decisions (Molnár *et al.* 2008) or render evolved search strategies inefficient or maladaptive (Sih *et al.* 2011). For example, Lamberson *et al.* (1992) found that search-efficiency declined significantly in northern spotted owls [*Strix occidentalis caurina* (Xantus De Vesey, 1860)] when the population size fell below a certain threshold. Habitat degradation via noise (reviewed in Patricelli & Blickley 2006), light (reviewed in Longcore & Rich 2004), and chemical pollutants (Fisher *et al.* 2006) may also reduce the efficacy of signals, or availability of public information, and so influence the quality, accuracy and availability of information used for social ADM (Bateson 2007). Changes in body condition, driven by changes in resource availability, may also influence decisions guiding risk-taking and parental investment (Coleman *et al.* 1985) because animals in poorer condition may prioritize survival over reproductive or foraging needs. Together, these effects demonstrate the dynamic nature of social context (including the interaction between habitat degradation and social context) and the potential for shifts in social context to drive species depletion.

While incorporating ADM theory into conservation is not a new idea (e.g. Swaisgood 2007), it is infrequently applied and more rarely integrated across scales. However, recent reviews demonstrate growing interest in conservation relevance of some ADM processes (Sih *et al.* 2010; Schakner & Blumstein 2013; Greggor *et al.* 2014), and there are some notable examples of the application of ADM, either implicitly or explicitly, to behavior-based wildlife management. Application of ADM processes appears to be most common in the contexts of habitat re-colonization, conservation breeding and in applying an individual, process-based approach to projection models (Table 2). These examples demonstrate that understanding ADM, including the sensory, cognitive, strategic and learning processes that govern each stage of the process or guide how information is used, may enhance both applied conservation management and our understanding of how disturbance will influence critical behavioral domains and, ultimately, individual fitness and population dynamics.

There is also a rich literature documenting empirical studies, across these disciplines, where contextual influences on the varied stages of ADM have been iden-

**Table 2** Representative studies where animal decision-making (ADM) rules were explicitly identified and applied to conservation/ management research

| Application | Conservation/ management concern/ goals | Aspect(s) of ADM incorporated | Reference |
|---|---|---|---|
| IBM | Habitat use by caribou (*Rangifer tarandus*) in areas industrialized by oil and gas | Risk aversion | Semeniuk *et al.* (2010) |
| IBM | Impact of recreationist activity on blue butterfly (*Lycaeides melissa*) | Reproductive success and habitat choice | Bennett *et al.* (2013) |
| IBM | Habitat selection by white fronted geese (*Anser albifrons*) | Foraging decisions | Amano *et al.* (2006) |
| IBM | Habitat loss and shorebird mortality | Density dependent mortality | Goss-Custard *et al.* (2002) |
| PM | Population growth rates | Social modulation of social interactions | Sutherland and Norris (2002) |
| PA | Noise masking of intraspecific communication in beluga whales (*Delphinapterus leucas*) | Conspecific signal detection | Erbe and Farmer (1998) |
| PA | Noise masking of intraspecific communication in avian communities | Conspecific signal detection | Halfwerk *et al.* (2011) |
| CA | Degraded habitat, translocation | Use of public information | Ward and Schlossberg (2003) |
| CA | Temporal variation in settlement decisions by loggerhead shrikes (*Lanius ludovicianus*) | Use of public information | Etterson (2003) |
| CB | Mate choice in captive pygmy rabbits (*Brachylagus idahoensis*) | Manipulation of familiarity via neighbor swapping | Martin and Shepherdson (2012) |
| CB | Mate choice in captivity in harvest mice (*Micromys minutus*) | Olfactory manipulation of mate choice | Roberts and Gosling (2004) |

Applications reflect the inclusion of behavior in individual based modeling (IBM) or predictive models of population dynamics (PM), the use of psychophysics (i.e. using behavior to measure physical capacity, as in a standard hearing test) to assess the impact of anthropogenic stimuli (PA), the use conspecific attraction to influence settlement (CA) or the inclusion of ADM theory into captive breeding programs (CB).

tified (Fig. 2a–u). However, generally speaking, these studies stop short of integrating findings derived from other stages of the ADM process. Indeed, integrating previously disparate findings within a broader ADM framework is especially relevant to conservation biologists now, given the increasing availability of powerful computing platforms and theoretical developments in modeling approaches (Grimm *et al.* 2010; Traill *et al.* 2014). Given the challenges of applying adaptive management approaches to conservation dependent species (Sutherland 2006) the capacity *model* species' response to predicted contextual shifts in the absence of empirical data is exceptionally important. Emerging opportunities to incorporate findings across disciplines include the study of conservation dependent species where research is occurring across scales, as is commonly the case when both conservation breeding and translocation are priority components of conservation programs. These "bookends" of conservation efforts drive the need to understand the mechanisms of successful breeding (e.g. relative importance of sensory cues and mate valuation) and the social and ecological needs to support settlement, reproductive success and survival in the wild.

In the following sections, we highlight some prominent themes in conservation, and discuss where aspects of ADM have, and could, be applied in order to both better understand why populations are not thriving, and to develop management tools to enhance conservation and mitigation efforts.

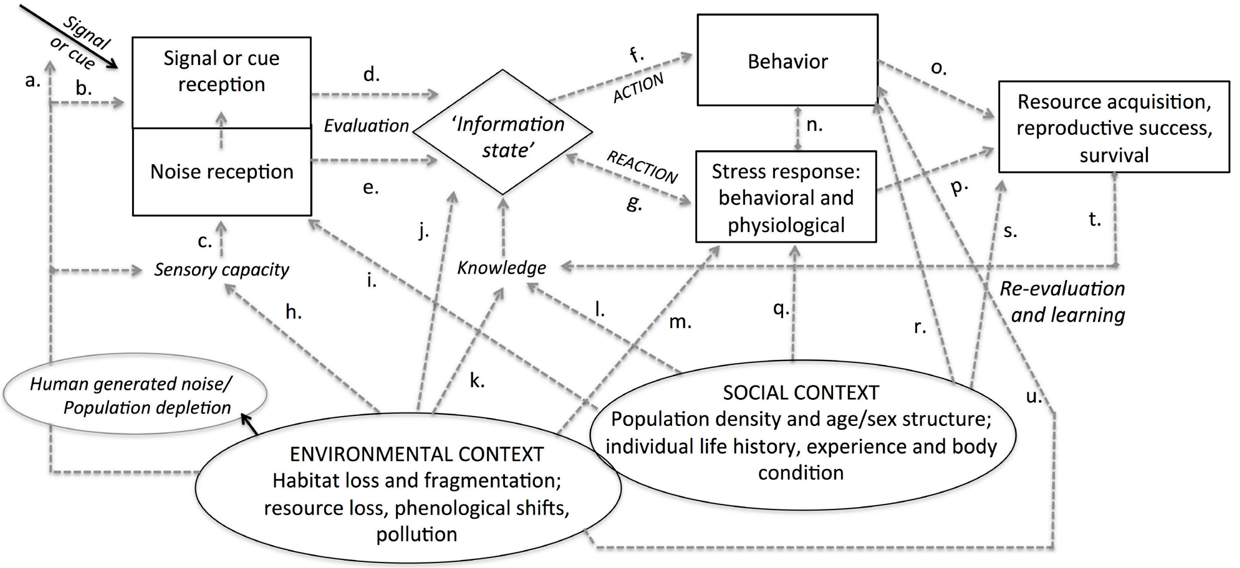

**Figure 2** Illustration of the decision-making process, integrating examples where the varied stages and processes, from signal generation in noise or depleted population, to biologically significant effects from anthropogenic disturbance, have been examined. This figure is expanded from Figure 1, and includes studies from varied disciplines. Integration of animal decision-making (ADM) components in the same system could be integrated to improve the predictive value of models, and assess the disproportionate influence of different stages on the ADM process in the face of rapid contextual variation, both social and environmental. (a) Brum (2004); (b) Lohr *et al.* (2003); (c) Gerstein *et al.* (1999); (d) Akre *et al.* (2011); (e) Frid & Dill (2002); (f) Shier *et al.* (2012); (g) Rolland *et al.* (2012); (h) Delaney *et al.* (1999); (i) Lengagne (2008); (j) Chan *et al.* (2010); (k) Tozer *et al.* (2012); (l) Betts *et al.* (2008); (m) Martinez-Mota *et al.* (2007); (n) Bales *et al.* (2006); (o) McPhee (2004); (p) Texiera *et al.* (2007); (q) Saltzman *et al.* (1994); (r) Whitehead *et al.* (1997); (s) Martin & Shepherdson (2010); (t) Doligez *et al.* (2004); and (u) Wolf *et al.* (1997).

## Ecological traps

The ecological trap concept, in which animals display an active preference for lower-quality habitat conferring lower fitness (Battin 2004), provides a number of examples that demonstrate both the influence of context on ADM and the relevance of ADM to conservation. Without an understanding of ecological trap theory and the mechanisms of ADM that explain it, conservation practitioners may inadvertently set ecological traps for species they are trying to manage, or, conversely, miss opportunities to manipulate ADM and enhance fitness. For instance, the creation of artificial burrows has been adopted as a "quick-fix" for the loss of fossorial mammal-engineered habitat for burrowing owls [*Athene cunicularia hypugaea* (Molina, 1782)]. This conservation-dependent species readily uses these artificial burrows (Belthoff & Smith 2003), but little research has addressed the optimal placement of burrows to provide other resources that the owls require. If burrowing owls' settlement decisions are guided primarily by burrow availability (historically indicating that the habitat also supports fossorial mammals and possibly predictive of other habitat factors important to burrowing owls, such as prey availability) then owls may be deceived into settling in an ecological trap with insufficient food. Thus, a better understanding of ADM may better attune managers to the possible deleterious consequences of their actions.

Ecological traps provide examples of how context influences ADM at the levels of sensory integration, cognitive mechanisms and the evolutionary strategies employed (Battin 2004). For instance, if contextual cues no longer provide reliable information about habitat or resource quality, previous ADM strategies that would "on average" be fitness enhancing, may now be maladaptive. If habitat cues are no longer efficiently transmitted or received, then animal decision-makers will miss out on high quality resources (i.e. "perceptual traps"; Patten

& Kelly 2010). In cases where sensory mismatch drives the development of ecological traps, this understanding can be used to manipulate habitat choices to reduce evolutionary traps by either masking or amplifying salient cues according to management goals. Furthermore, the relative or perceived value of cues, target resources or habitat features may also be manipulated using approaches and concepts from behavioral economics.

## Conspecific cueing

The use of socially-acquired public information by colonial nesting and territorial species has prompted the strategic use of decoys to attract animals to ecologically appropriate, yet underutilized, habitat (Fletcher 2006), and in some cases to avoid ecological traps. While numerous applications of varied types and configurations of decoys have been successfully used to trigger settlement decisions, there are cases where they have not been successful, even when species are colonial (Ahlering *et al.* 2010). These mixed results suggest that a more detailed understanding of the interaction between decision strategies, cognitive constraints, and environmental context, could enhance the success of using conspecific attraction as a management tool (Patten & Kelly 2010). For example, Loukola *et al.* (2012) demonstrated that older male great tits (*Parus major* L., 1758) were more likely to use social information for nest site selection than younger males (Fig. 2p). This effect, when integrated into an applied management strategy, can be used to enhance the success of re-colonization strategies.

The use of social information may also differ between age or sex classes. For example, Forsman *et al.* (2008) found that older male great tits (*Parus major*) were more likely to use public information when choosing a nest site than younger males. A better understanding of contextual influences on ADM in relation to conspecific cueing may also help avoid misguided approaches when using this potentially powerful conservation tool. If animal settlement decisions are based upon an integrated index of several ecological factors important to fitness, the risk of luring animals to ill-suited habitat is less than if animals are using conspecific cues as the only or primary cue to habitat quality. Here again, understanding the role of sensory integration and resource valuation may be essential to fully realize the potential conservation applications of conspecific cueing.

## Conservation breeding

Conservation breeding is an area of applied conservation management that has integrated decision theory, either implicitly or explicitly, to increase the success rate of pairings, and often this has involved contextual or sensory manipulation (Swaisgood & Schulte 2010). Because breeding pairs in captivity are often identified based on genetic considerations, an understanding of ADM, and how it is contextually modulated, can be a powerful tool to promote both breeding success and the genetic health of small populations. For example, Martin and Shepherdson (2012) showed that various measures of reproductive success in the pygmy rabbit [*Brachylagus idahoensis* (Merriam, 1891)] were socially modulated; females increased fitness when allowed to mate with familiar or preferred males. Integrating these social influences on reproductive success with necessary genetic management can greatly improve the long-term success of conservation breeding programs (Martin-Wintle *et al.* 2016).

In another example, Fisher *et al.* (2003) hypothesized a simple decision rule guiding mate choice in the asocial pygmy loris (*Nycticebus pygmaeus* Bonhote, 1907). While not explicitly identified as such, the decision rule the authors tested was a "best-of-*N*" strategy. Fisher and colleagues utilized scent as a proxy for the presence of conspecifics and manipulated the perceived social environment of estrus females, familiarizing each with a genetically preferred male (via scent) so that she "chose" him when she was ready to mate. This type of adaptive management strategy can be applied to species that use comparative valuation to choose between potential mates. For example, mate "choice sets" can be manipulated to ensure that a genetically appropriate mate is preferred. Furthermore, stimuli that indicate receptivity can be manipulated to prime sexual motivation in otherwise unmotivated animals (Swaisgood *et al.* 2000). In either of these applied contexts, the integration of the information content of sensory cues and the decision rule underpinning mate choice enabled efficient manipulation of potential breeders in this conservation breeding program.

## Translocation

The success rate of translocation is generally low (Fischer & Lindenmayer 2000). However, a number of studies have demonstrated how the integration of decision theory may enhance the likelihood of success. Specifically, socially-modulated ADM has been incorporated into translocation efforts for solitary species, such as the Stephen's kangaroo rat (*Dipodomys stephensi*) and black rhinoceros [(*Diceros bicornis* (L., 1758)]. In the case of the kangaroo rats, Shier and Swaisgood (2012) found that after translocation, settlement decisions were socially modulated and that fitness increased when individuals were translocated with neighbors. Neighbor-translocated kangaroo rats established territories closer to the release site and had higher survival rates and greater reproductive success than those that were translocated without neighbors. Similarly, black rhinoceros translocated with unfamiliar conspecifics into smaller reserves met with less success than those released into larger reserves with lower social density, due to the effects of excessive social conflict not found in stable groups of rhinos (Linklater & Swaisgood 2008). Socially-modulated ADM offers a plausible explanation of these results, because rhinos appear to make decisions about escalated fighting based on the degree of familiarity with others as well as their social density. Here, an understanding of how rhinos use sensory cues to acquire social information was integrated into the experimental design and was fundamental to developing an understanding of how settlement is socially-modulated in the species.

### Projection models

Integrating behavioral decision rules into projection models of population abundance and persistence has been underutilized. However, the growing use of behavior-based individual-based modeling (IBM) provides a coherent and valuable framework (Goss-Custard *et al.* 2006) to incorporate multiple aspects of ADM, from sensory constraints to overarching decision rules, into projection models. For example, Croft *et al.* (2012) developed an IBM to explore the influence of social group size on collision risk to address management concerns regarding the rate of fatal interactions between wildlife and wind turbines. Using the IBM approach, these authors identified interactive effects, (between group size and social interactions) that influenced both navigational efficiency and group cohesion, and suggested that these results would be essential for developing effective and protective management strategies for birds in the face of this growing sector of the energy industry.

Incorporating behavior rules into projection models is not limited to the IBM approach. For example, Molnár *et al.* (2010) developed an encounter rate model for polar bears (*Ursus maritimus* Phipps, 1774) to predict how female mate searching efficiency would be influenced by climate change-driven habitat fragmentation. In their mechanistic model, they found that reductions in mating success were nonlinearly sensitive to varying degrees of reduced search efficiency. While this work did not integrate a decision rule per se, the sensitivity of varying degrees of mate search efficiency suggest that the accuracy of projections could be enhanced by an understanding of the decision rules and cognitive constraints governing mate search in the species. For example, if male bears use an absolute or threshold decision rule to locate females that are in adequate body condition (via chemical cues; *sensu* Gosling *et al.* 1996), then the influence of reduced body condition or population depletion on mate search could be more pronounced than if they used a comparative or "best-of-*N*" strategy. For this species, identifying the mechanisms of mate search is essential because many populations have experienced changes in the operational sex ratio due to selective harvest (Molnár *et al.* 2008), and reductions in body condition due to sea ice loss. Generally speaking, an understanding of the decision rules animals use to choose between potential mates, and the sensory and cognitive mechanism they use to acquire and evaluate information regarding conspecifics may enhance the accuracy of predictive models, and generate insights as to which aspects of environmental degradation pose the greatest conservation threats.

## CONCLUSIONS

The study of ADM has emerged in disparate academic fields that include signal detection theory, cognitive psychology, behavioral economics and behavioral ecology. While the distance between these fields is great, and the context in which each has addressed the same overarching process differs in terms of its approach, overriding themes emerge from all, and these themes offer valuable insight into the ADM process. Context is clearly important; however, limitations on sensory input and processing may also influence ADM. Identifying how fundamental principles interact with contextual themes may have tremendous value in conservation and enhance the success rate of behavior-based management strategies, by providing targeted, and quantitative predictions for both behavioral and larger scale changes in the face of environmental change.

The potential for behavior-based studies to both reveal and address anthropogenic impacts is clear, as demonstrated by both a rich literature documenting both correlations between human generated changes in the environment and changes in behavior (Warren *et al.* 2006), and the application of animal behavior theory to conservation management (Ahlering *et al.* 2010). Likewise, incorporating ADM theory into conservation biology could refine our understanding of how anthropogenic stimuli and activities will influence species over time, and may also provide mitigation tools that can be applied to conservation management (Sih *et al.* 2011). Mitigation tools can be developed based on an understanding of what aspect (sensory, cognitive or ecological) of the decision-making process primarily drives behavioral responses and, ultimately, larger scale patterns.

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