Cognition-centered conservation as a means of advancing integrative animal behavior

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Abstract

The field of conservation has recently seen a shift towards the integration of behavior into the context of preserving biodiversity. We contend that this integration has been one-sided, typically done to improve conservation outcomes while ignoring the potential benefits that conservation has to the field of behavior itself. We propose that conservation provides a strong selective framework in which to investigate the origin and maintenance of behavior as well as a forum to examine the interdisciplinary nature of animals' cognitive responses to their environment. Using ectotherms as models, we argue that by engaging conservation, behaviorists have the opportunity to generate novel hypotheses, test established hypotheses in novel ways, and engage in collaborations central to the goals of integrative animal behavior.

Running title: The role of conservation in behavior

Introduction

Conservation biology is a composite discipline uniting such disparate fields as ecology, physiology, genetics, and mathematics with the end goal of protecting, preserving, and promoting biodiversity. This interdisciplinary approach stems from the inherent complexity of the challenges facing biota in peril [1**]. For over a decade, the field of conservation has seen a shift towards the integration of behavior into the context of preserving biodiversity [1-3]. This ‘conservation behavior’ approach considers individual patterns of activity with respect to the environment and assumes that animals respond dynamically, altering decisions in light of experience [4, 5]. Although not without criticism, conservation behavior has made valuable headway in enhancing conservation strategies (for full discussion, see refs. [6-9]).

Recently, several authors have proposed a conceptual unification of the basic principles of behavioral decision-making within the practice of conservation [10-13]. This approach aims to provide a deeper understanding of how animals use cognition to evaluate and respond to changing environments. Cognition, as defined in recent studies (e.g., [12**]), encompasses “all processes involved in acquiring, storing, and using information from the environment” [14, 15]. Greggor et al. [12] recently addressed the specific benefits of incorporating cognition into the field of conservation as a means of resolving some problematic behaviors observed in conservation efforts (Fig. 1). Further, Greggor et al. [12] directly link conservation and behavior by defining cognitive phenomena as part of the central mechanism of animal behavior. They diagram how incorporating cognition into a wide range of conservation strategies might increase conservation successes. Similarly, Schakner et al. [16] call for specific plans to “develop realistic and effective guidelines” for the application of these cognitive mechanisms in conservation.

Like Greggor et al. [12] and Schakner et al. [16], we embrace this approach. However, we emphasize that the value of integrating behavior into conservation is not unidirectional—the field of behavior can also benefit from considering conservation, especially when viewed through the lens of cognition. Behavior has certainly had a substantial impact on conservation, but we contend that the benefit of conservation to the discipline of behavior has yet to be fully realized (Fig. 1). Herein, we illustrate the value of conservation for advancing the field of integrative animal behavior (hereafter IAB) using ectothermic vertebrates (i.e., fish and herptiles) as model systems. While we propose that conservation science performed on all taxa has the potential to further the field of IAB, fish and herptiles possess certain attributes which allow us to best highlight this relationship. First, these taxa are particularly susceptible to global climate change [17]; they are thus frequent and relevant subjects of conservation efforts. Second, recent work suggests that these taxa possess brains that are structurally (e.g., [18]) and biochemically (e.g., [19]) far more advanced than previously thought [20, 21]. Similarly, increasing evidence supports advanced cognitive abilities in these taxa [22], including complex spatial abilities [23, 24] and advanced capacity for learning and memory [25*, 26]. Thus, ectothermic vertebrates represent ideal taxa through which to examine the ability of conservation to advance IAB.

Conservation as a means of advancing integrative animal behavior

Behavior is complex, influencing and being influenced by numerous phenomena across levels of biological complexity, from cells to communities. To obtain a complete understanding of the importance of behavioral processes in biological systems, we must broaden our mindset and expand our conceptual approach. Specifically, in a recent White Paper, Rubenstein et al. [27**] suggest that a fully integrative model of animal behavior must address Tinbergen's four questions in a dynamic and interdisciplinary manner. We contend that integrating conservation science into the field of animal behavior represents a particularly effective way of facilitating this integration. Considering behavior in light of conservation will provide the field of animal behavior with 1) a strong selective framework in which to investigate the origin and maintenance of behavior and 2) a forum to unravel the interdisciplinary nature of the complex biotic and abiotic interactions that influence the animals' cognitive response to their environment (Fig. 1). Thus, we see conservation as a means of advancing the discipline of IAB by providing the opportunity for testing current hypotheses, generating new hypotheses, and engaging in the type of collaborations and training that are central to integrative animal behavior (Box 1), all goals recently emphasized as pressing for the future of the field [27]. Although many studies have used behavior to improve conservation success, we highlight examples of conservation studies that have generated advances in field of behavior.

Conservation benefits the conceptual relevance of behavioral studies

Addressing behavior within the context of conservation stands to enhance IAB by refining our understanding of the context in which animals interact with their environment within a strong selective regime. Conservation explicitly considers the selective pressures that shape cognitive behaviors – these are often the factors driving population declines – thereby revealing elements relevant to the evolution and maintenance of such behaviors (Fig. 1). Animals inhabiting challenging and/or changing environments exhibit high levels of cognition and flexibility, as well as in the morphological correlates that underlie these processes [28, 29*]. Although the overall severity of an environment often predicts the cognitive ability of animals living therein, the rate of change within that environment might also be an important factor. Studying how environmental change affects the cognitive abilities of animals [29-32] and how these abilities manifest during such change will enhance our insight into how behavioral processes evolve.

For example, identifying the characteristics of invasive species and understanding the responses of native species to the community-level impacts of invasive species are important goals in conservation [33]. Predator-prey interactions are among the most central of these, but how these interactions evolve is unclear. Studying invasive predators from a conservation perspective can provide IAB with a framework to understand how species interact with novel stimuli/species and how learning evolves in changing systems. Caller and Brown [34] investigated the origin and maintenance of aversion behavior in the native crimson spotted rainbow fish (*Melanotaenia duboulayi*) to the introduced, toxic cane toad (*Bufo marinus*). Fish sympatric with toads demonstrated a pre-existing

aversion to toxic tadpoles, while fish from a naïve population learned to avoid tadpoles following repeated, direct exposure. This ability to learn seems to be, at least in part, a function of selection over multiple generations rather individual experiences. Successive laboratory work documented the ability of both populations to develop an avoidance of food pellets when presented alongside distasteful ones, but only the fish sympatric with toads decreased feeding on the distasteful items. These results not only inform conservation practice, but importantly, they shed light onto the means by which natural selection can shape learning in a predator-prey context.

Similarly, navigation and its sensory underpinnings are commonly studied, but investigating their evolution have proven difficult. By using a long-term fishery harvest dataset and drawing comparisons between behavioral patterns and harvest rates, Putman et al. [35**] were able to explain evolutionary shifts in salmon migration (*Oncorhynchus* spp.). Changes in the geomagnetic field accounted ~ 44% of the historic variation in migration routes of salmon. Likewise, Brothers and Lohmann [36] used a long-term record of nesting sites to address the evolution of natal homing behavior by loggerhead sea turtles (*Caretta caretta*), an endangered species. Over 19 years, fluctuations in the spatial distribution of turtle nests mirrored fluctuations in Earth's magnetic field, confirming that young turtles imprint on the magnetic field of their natal area and return to the site using this information. These results have obvious implications for managing protected populations, but also bring new insights into our basic understanding of animal navigation and the importance of learning in animals' responses to long-term changes in environments, insight that would not have been possible had the authors not addressed navigation outside of conservation.

Conservation also offers an ecological context that explicitly considers larger-scale interactions and the natural history of the focal organism, all facets recently identified as central to the future of IAB [27]. Conservation, by the very nature of its goals, takes an integrative perspective, providing the framework for behavior to better understand how animals respond to dynamic environments. Successful conservation, therefore, inherently integrates phenomena at the level of the individual (i.e., behavior and its proximate underpinnings), population (e.g., species interactions and population viability), and community (e.g., species composition, abiotic interactions) [37]. Thus, conservation can provide a broader, more integrative perspective to questions in and studies of animal behavior.

Sign stimuli, for example, are among the best studied of behavioral mechanisms, but their role in nature and their implications for the animals ecology remains poorly understood. Conservation can change the way we think about even the fundamentals of behavior. For example, Bostwick et al. [38] applied studies of sign stimuli to develop a shark model to decrease sea turtle by-catch in commercial fisheries. In doing so, they not only succeeded in reducing turtle by-catch, they increased our breadth of knowledge of the ecologically-relevant, anti-predator perception of sea turtles. Similarly, Connette and Semlitsch [39] investigated the context-dependence of animal movements by studying translocations in salamanders. They compared the movement strategies of salamanders in both open and forested habitats, and found that behavioral triggers interact with context to drive

salamander movements. Likewise, Emer et al. [26] expanded our understanding of sign stimuli in terms of the operant conditioning of wild Burmese pythons (*Python molurus bivittatus*), a particularly troublesome invasive species. Snakes were successfully trained to associate an extremely small food item (an atypical behavior given their natural history) with a visual stimulus, and to perform a conditioned task to earn the food reward. By working within a conservation context (attempting to find a solution to collect snakes) with a strong knowledge of the animal's natural history, Emer et al. [26] generated results that challenged conventional thinking and expanded our understanding about the range of behaviors possible through operant conditioning. Both of these studies emphasize the importance of using the conservation approach to enhance the ecological context of even basic behavioral phenomena.

Conservation advances the intellectual framework of the discipline of behavior

The recent drive to make animal behavior more integrative is in part motivated by the goal of understanding the evolution and maintenance of behavior by working across multiple levels of biological analysis, using diverse methodologies, and thinking across conceptual and theoretical paradigms [27]. The outcome of such integration will ideally be both paradigm-shifting (generating novel hypotheses) and paradigm-reinforcing (testing the robustness of current hypotheses) [27]. Conservation science, given its inherent taxonomic breadth, integrative nature, and strong selective viewpoint, stands to provide IAB with a forum to advancing the field of behavior in these ways (Fig. 1).

For example, conservation efforts expand how animal behaviorists ask questions about patterns of learning and critical learning periods, even when such efforts fail. For example, despite addressing issues of physiology and habitat quality, Pérez-Buitrago et al. [40] found that the majority of headstarted Mona Island Iguanas (*Cyclura cornuta stejnegeri*) failed to establish territories upon release. Likewise, Knox and Monks [41] reported virtually no sightings of translocated jeweled gecko (*Naultinus gemmeus*) when animals received no post-translocation care. These two studies, although conservation failures, drive the study of behavior by implying a role of learning in adult survival and providing the opportunity to generate hypotheses about the nature of learning. Indeed, Knox and Monks tested this idea by penning geckos for several months post-translocation, allowing them to learn their new surroundings; this greatly increased subsequent sightings [41]. Taken together, these studies expand the research mindset of IAB by highlighting the importance of taxonomic breadth and natural history when considering the role of experience and cognitive phenomena. Moreover, this work highlights the need to consider ontogeny in studies of learning, as jeweled geckos can clearly learn well into adulthood, suggesting a broad learning period in this species.

By contrast, our work on Eastern painted turtles (*Chrysemys picta*) challenged the contexts within which the field considers learning and expanded the contexts and taxa in which we investigate critical learning periods [25]. Utilizing two common conservation techniques – translocation [42] and rapid wetland drainage [43] – we monitored movements of turtles as they sought new habitat when their pond was drained. Rather than documenting only the movements of experienced adults, as is typical of

conservation studies, we examined the role of learning in navigation by tracking both experienced and naïve (translocated to site) turtles at different developmental stages. Our results demonstrate that learning is necessary for navigation – only resident adults and juveniles < 3 year-old successfully found water. Moreover, this learning is constrained by a critical period, as naïve turtles ≥ 4 years-old failed to locate permanent water. Although movement is commonly measured in both conservation and behavior, conservation provided the strong selective regime (the pond draining) and provided the opportunity to focus on learning and its ontogeny (to understand the variation in navigation success), providing the framework to generate hypotheses about the selective conditions under which learning itself might evolve.

Conclusion and prospectus

Integration is the future of animal behavior [27]. We propose that the conservation mindset provides the means to fully realize this integration. Conservation scientists approach threats to biodiversity by incorporating theories and concepts from disparate fields to find novel ways to conserve biodiversity. The solution-based “crisis” nature of the field demands that researchers consider the interactions of species under strong selection and in complex, often rapidly changing environments. Thus, the conservation perspective ensures that behaviorists use a broad and integrative research framework, not inherently present in other related fields (e.g., ecology, physiology, and genetics). Some of these features are present in these individual fields, but only conservation inherently incorporates all of these aspects simultaneously.

Although some researchers already combine conservation and behavior, this is typically done to improve conservation outcomes (e.g., [9, 12, 44]). Rather, the field of behavior should be receptive to the idea that conservation can benefit us, not only in terms of contextualizing behavioral studies, but more deeply by shifting our collective way of thinking towards the integrative approach. In this regard, even “failed” conservation studies can be informative for behavior (e.g., [41]), as the value of the conservation perspective to behavior is the mindset, not the dataset. Finally, the field of conservation provides a meaningful background to investigate the core skills of IAB [27] (Box 1).

Overall, our goal is to highlight opportunities to expand the discipline of animal behavior by providing the contextual and conceptual framework to generate novel hypotheses and novel ways to test established hypotheses. In doing so, we empower IAB to more fully address the role behavior in biological systems. Given the current and predicted future rates of biodiversity loss [17, 45], we will suffer no shortage of opportunities to engage in conservation. We encourage those in the field of animal behavior to actively consider the incorporation of conservation into their research paradigms. Whether through active collaboration, the consideration of conservation literature, or the utilization of conservation models, the conservation mindset can help behaviorists achieve integration in their own research.

Conflict of interest

None declared.

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Figure Legend

Figure 1. The disciplines of behavior and conservation are inherently linked, conceptually complimentary, and mutually beneficial.

Behavior benefits conservation (bottom): Studies of behavior provide the theoretical framework to elucidate key aspects of cognition, including perception, habituation, and learning. By considering fully how animals perceive and respond to new and changing environments, cognition provides solution for problematic behaviors in conservation, thereby leading to more successful conservation outcomes. Following Greggor et al. [12].

Conservation benefits behavior (top): Likewise, embracing a conservation mindset provides simultaneous insight into elements central to the study of integrative behavior, including an ecological framework (e.g., natural context, natural and life history, biotic/abiotic interactions), evolutionary implications (e.g., selection pressures, static/labile responses, evolutionary constraints) and proximate mechanisms (e.g., physiological, developmental, neurological, genetic) all within extreme, variable environments. The nature of the state in which species are studied in conservation, along with the very broad and integrative nature of the field itself, can facilitate a shift in the field of animal behavior towards the integrative approach.

Box 1. Conservation provides the opportunity to achieve the core competencies for the integrative study of animal behavior.

Rubenstein et al. [27] recently emphasized the importance of an integrative approach to animal behavior and delineated seven core competencies aimed at facilitating future collaboration between colleagues from disparate fields (see below). Conservation mirrors these core competencies by combining these tools across all levels of biological organization, thereby providing an excellent opportunity for the next generation of animal behaviorists to engage and train in these core competencies. This type of training can often be done simultaneously within the context of a single study paradigm, thereby embracing and capitalizing on the integrative approach. Here, we provide these core competencies in IAB with explanation of the approach taken by conservation and examples of accessible resources for further investigation of the topic.

-Quantification of behavior – the field of conservation behavior emphasizes the need to precisely define and measure behavior [4].

-Ecology/evolution – these basic tenets of biology feature prominently in conservation studies, especially those focused on habitat, population viability, biodiversity, and the interaction of multiple species [4].

-Mathematical theory – mathematics plays an integral role in many aspects of conservation from gene flow to population viability analyses [46, 47].

-Statistics – conservation relies heavily on multivariate and Bayesian statistical approaches to address hierarchical models, infer complex patterns in population fluctuations, and analyze population viability datasets [48, 49].

-Computational methods – the field of conservation relies heavily on computational and spatial models to predict changes in biodiversity, species movements, and the response of species to climate change [46, 50].

-Genetics/genomics - population genetics, molecular ecology, and systematics contribute heavily in conservation with applications in detecting hybridization, documenting genetic structure, and quantifying genetic variation in small or endangered populations [51].

-Physiology/mechanism – the field of conservation physiology seeks to understand and predict how organisms respond to environmental change using mechanistic responses across levels of biological organization [52, 53].

Figure