Conservation Biology

Contributed Paper

A systematic survey of the integration of animal behavior into conservation

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Abstract: *The role of behavioral ecology in improving wildlife conservation and management has been the subject of much recent debate. We sought to answer 2 foundational questions about the current use of behavioral knowledge in conservation: To what extent is behavioral knowledge used in wildlife conservation and management, and how does the use of animal behavior differ among conservation fields in both frequency and types of use? We searched the literature for intersections between key fields of animal behavior and conservation and created a systematic heat map (i.e., graphical representation of data where values are represented as colors) to visualize relative efforts. Some behaviors, such as dispersal and foraging, were commonly considered (mean [SE] of 1147.38 [353.11] and 439.44 [108.85] papers per cell, respectively). In contrast, other behaviors, such as learning, social, and antipredatory behaviors were rarely considered (mean [SE] of 33.88 [7.62], 44.81 [10.65], and 22.69 [6.37] papers per cell, respectively). In many cases, awareness of the importance of behavior did not translate into applicable management tools. Our results challenge previous suggestions that there is little association between the fields of behavioral ecology and conservation and reveals tremendous variation in the use of different behaviors in conservation. We recommend that researchers focus on examining underutilized intersections of behavior and conservation themes for which preliminary work shows a potential for improving conservation and management, translating behavioral theory into applicable and testable predictions, and creating systematic reviews to summarize the behavioral evidence within the behavior-conservation intersections for which many studies exist.*

Keywords: captive breeding, conservation behavior, dispersal, foraging, heat map, invasive species, learning, reintroduction

Un Censo Sistemático de la Integración del Comportamiento Animal a la Conservación

Resumen: *El papel de la ecología conductual en el mejoramiento de la conservación y el manejo de la fauna ha sido sujeto recientemente a muchas discusiones. Buscamos responder dos preguntas fundamentales acerca del uso actual del conocimiento conductual en la conservación: ¿Hasta qué punto se utiliza el conocimiento conductual en la conservación y manejo de la fauna y cómo difiere el uso del comportamiento animal, tanto en frecuencia como en tipos de uso, entre las áreas de conservación? En la literatura buscamos intersecciones entre áreas clave de la conservación y el comportamiento animal y creamos un mapa sistemático de calor (es*

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decir, una representación gráfica de los datos en la que los valores se representan con colores) para visualizar los esfuerzos relativos. Algunos comportamientos, como la dispersión y el forrajeo, se consideraron como comunes (media [SE] de 114.38 [353.11] y 439.44 [108.85] artículos por celda, respectivamente). En contraste, otros comportamientos como el aprendizaje y las conductas sociales y anti-depredadores se consideraron como raras (media [SE] de 33.88 [7.62], 44.81 [10.65] y 22.69 [6.37] artículos por celda, respectivamente). En muchos casos, la detección de la importancia del comportamiento no se tradujo en una herramienta aplicable de manejo. Nuestros resultados presentan un reto a las sugerencias previas de que existe poca asociación entre las áreas de la ecología conductual y la conservación y revelan una variación tremenda en el uso de diferentes comportamientos dentro de la conservación. Recomendamos que los investigadores se enfoquen en examinar intersecciones sub-utilizadas de temas de comportamiento y conservación para los que el trabajo preliminar muestre un potencial para mejorar la conservación y el manejo; traduzcan la teoría conductual a predicciones aplicables y evaluables; y creen revisiones sistemáticas para resumir la evidencia conductual dentro las intersecciones de comportamiento-conservación para las que existen muchos estudios.

Palabras Clave: aprendizaje, comportamiento en la conservacion, dispersion, especies invasoras, forrajeo, mapa de calor, reintroducción, reproducción en cautiverio

Introduction

When faced with the challenges of wildlife conservation and management, conservation practitioners should have access to an extremely diverse and constantly evolving toolkit of expertise that includes population dynamics, computer modeling, genetics, remote sensing, social sciences, and law. Behavioral ecology is one such important tool. An animal's behavior lies at the center of gene-environment interactions, and, as such, it serves as a mediator between an animal's fitness and anthropogenic disturbances (Berger-Tal et al. 2011). Many wildlife managers explicitly appreciate this role and have been using their knowledge of animal behavior to manage species for decades (e.g., Geist & Walther 1974; Harcourt 1999). But within the scientific community, attention to the potential role of behavioral ecology in conservation has greatly increased in the past 10–15 years, and the use of animal-behavior knowledge in conservation came to be known as conservation behavior (Blumstein 2001). Several recent books and various publications in journals aim to raise awareness among wildlife managers to the advantages of using the existing theories of behavioral ecology to improve conservation (e.g., Clemmons & Buchholz 1997; Festa-Bianchet & Apollonio 2003; Blumstein & Fernández-Juricic 2010; Greggor et al. 2014).

Although there are cases in which knowledge of animal behavior cannot inform the protection or recovery of species, either because it is not relevant to the problem or because it is not cost-effective (Blumstein & Berger-Tal 2015), the direct link between animal behavior and fitness makes behavioral-ecology knowledge an important tool. However, in many cases, conservation practitioners do not apply knowledge from behavioral ecology in their management plans, or they consider it only after a problem has emerged, resulting in setbacks, which in many cases can lead to the failure of management efforts (Knight 2001; Blumstein & Fernández-Juricic 2004). In an attempt to evaluate the success of the emerging field of conservation behavior in resolving such setbacks, some authors have assessed the integration of behavioral ecology into conservation and management by searching the academic literature for combinations of derivatives of the words *behavior* and *conservation* and analyzing whether reported trends have changed in the last decade (e.g., Angeloni et al. 2008; Nelson 2014). These authors concluded that currently there is little association between the fields of behavioral ecology and conservation biology and that attention to the potential role of behavioral ecology in conservation has not had an impact on conservation and management. However, their use of such a narrow subset of search terms is questionable.

We aimed to answer 2 foundational questions about the utility and actual use of knowledge of animal behavior in conservation. First, to what extent is behavioral knowledge used in wildlife conservation and management? Second, how does the use of behavioral knowledge differ among conservation fields in both frequency and types of use? For types of use, we distinguished between the relevancy of behavior to underlying conservation problems that stem from anthropogenic threats and the use of behavioral knowledge to support conservation action or solutions.

To answer these questions, we searched the literature for intersections between key fields in 2 disciplines, animal behavior and conservation biology. From the number of papers at each of these intersections, we created a systematic heat map to visualize relative development. We used the map to identify probable gaps in research and to delineate possible priorities for future research.

Methods

Choosing Behavioral and Conservation Themes

We designed this study in a workshop setting during which we chose 10 behavioral categories and 16 conservation themes to serve as the foundation for our heat map of the use of animal-behavior knowledge in conservation (Supporting Information). We chose behavioral categories to span the entire life history of most species and included categories that operate at very different spatial and temporal scales. For instance, we included learning, which operates continuously and variably at the scale of individuals, and dispersal, which typically occurs only once or twice during the lifetime of an individual and over large temporal and spatial scales. We did not assume the categories were mutually exclusive; an animal might learn while dispersing or use prior learning to inform dispersal. We separated conservation themes into conservation problems and conservation and management solutions. Conservation problems were conventional anthropogenic threats to wildlife discussed in most textbooks (e.g., fragmentation or pollution) (e.g., Groom et al. 2006). We used the diversity of expertise among us to develop a list of search terms for each of the behavioral and conservation categories (Supporting Information).

Extensive Survey to Construct the Heat Map

The 10 behavioral and 16 conservation categories formed a grid map of 160 cells in which each cell represented an intersection between one behavioral and one conservation category. For each cell, we searched the ISI Web of Science database using the combinations of the search terms we developed to identify published studies that included one or more terms from each of the associated behavioral and conservation categories in their titles, abstracts, or keywords. The search was conducted from March to September 2014 and covered the years 1900–2014. We searched in the following journal categories: ecology, zoology, biodiversity conservation, multidisciplinary science, biology, and evolutionary biology. We restricted our search to these categories because preliminary searches showed that adding other journal categories greatly increased the number of irrelevant papers; the addition of novel, but relevant, papers summed to $<1\%$ of those already detected.

To evaluate the performance of our search terms in the restricted subject categories, we read the abstracts of 50 randomly selected papers (or, if the cell contained fewer than 50 papers, we read the abstracts of all papers in the cell) in each of the 160 intersecting cells and identified the papers that did not use our search terms in behavioral or conservation contexts. We used this information to revise our search terms by removing, adding, or revising terms and excluding certain phrases, words, or journals from the search. We then repeated the search with the revised search terms and sampled 20 additional, randomly selected papers for each cell. Again, we identified the irrelevant papers and used them to revise our search terms. We repeated this process until our sample contained $\leq 10\%$ irrelevant papers. Our method did not include relevant work that was not searchable in the database (e.g., unpublished reports, MS theses, and PhD dissertations), and we expected our systematic search to reveal relative, not absolute, measures of activity among cells. Because we did not consider our disciplinary categories to be mutually exclusive (above), we permitted papers to appear in more than one cell in accordance with search results.

We used a χ^2 analysis to compare the number of behavioral-related publications related to conservation threats and the number of publications related to conservation solutions. To determine whether the results were indeed related to the use of behavior in conservation, we repeated the comparison but omitted the behavioral search terms; that is, we compared the total number of papers on conservation threats with the number of papers on conservation solutions.

Results are presented as means and standard errors (SE) unless stated otherwise.

We acknowledge the caveat of only using academic peer-reviewed papers for our analysis. Most managers and wildlife biologists do not publish their work in academic journals, and a large part of the references in conservation action plans comes from unpublished materials or gray literature (Linklater 2003). Thus, our result may be indicative of the integration of behavioral ecology into conservation research but should be treated with caution when applied to conservation practice.

Intensive Survey to analyze target cells

To explore the nature of the connections between behavioral and conservation themes, we investigated 2 of the 160 cells by reading each of the papers contained in them. The 2 areas selected were the intersection of learning and invasive species (60 papers) and the intersection of learning and captive breeding and reintroduction (92 papers). For each paper, we categorized the publication type (behavioral, conservation and management, ecology, or a multidisciplinary journal), the taxonomic focus (mammals, birds, amphibians, etc.), the strength of the link between disciplines (offered as context, explicit potential identified, explicit use identified), and the type of linkage made between disciplines (behavior as a source of vulnerability to an anthropogenic impact, behavior-based management action, behavior as an indicator for anthropogenic impact or management success [Berger-Tal et al. 2011]).

Results

The heat map showed tremendous variation in attention to animal behavior by researchers (Fig. 1). The number of papers in each cell ranged from 0 to 4692 (mean [SE] = 195.21 [45.04]; median = 36). Cells that included the behavioral themes of dispersal and foraging were the most

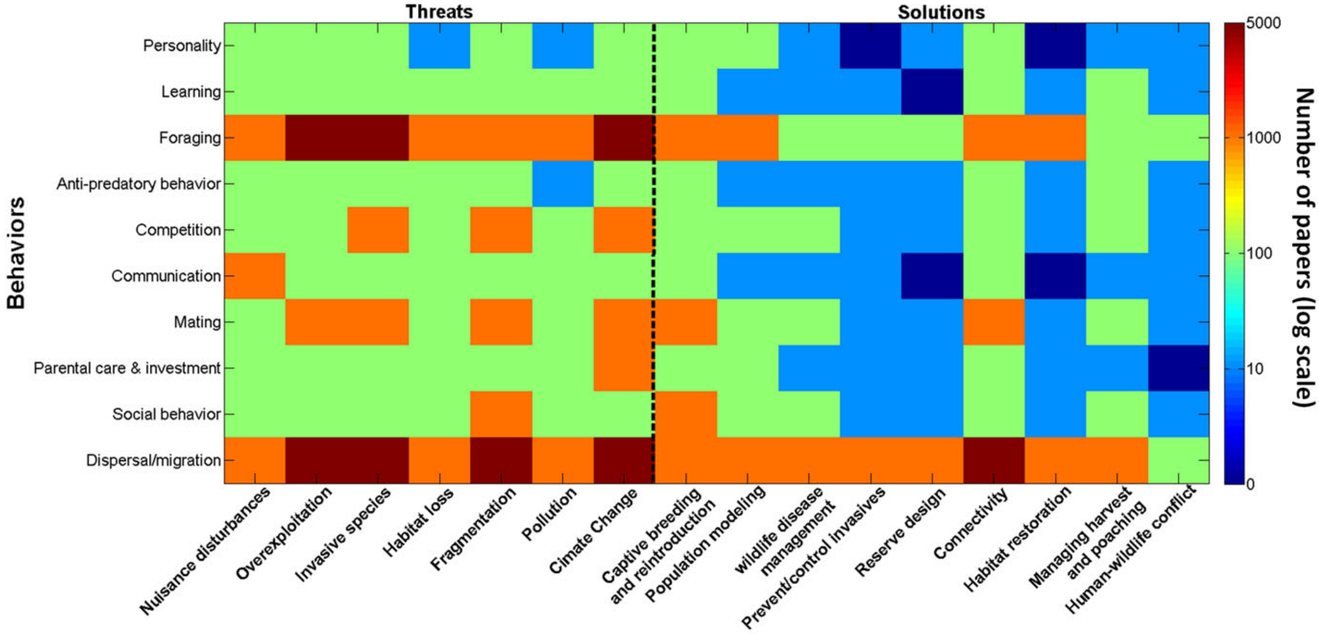

Figure 1. The number of papers found in a search of the ISI Web of Science database for intersections between animal behaviors search terms (rows, 10 categories) and conservation themes search terms (columns, 16 categories divided to threats and solutions). The number of papers is represented by color; hotter colors represent a larger number of papers (color scale is logarithmic).

populated, with 1147.38 [353.11] and 439.44 [108.85] papers per cell, respectively. In contrast, cells containing other behavioral topics such as personality, learning, antipredator behavior, and social behavior yielded far fewer papers. The average number of papers per cell for these behavioral themes was 13.25 [3.43], 33.88 [7.62], 44.81 [10.65], and 22.69 [6.37], respectively.

Another contrast shown by heat mapping is that the threats side of the map contained many more papers than the solution side of the map ($n_{\text{threats}} = 20{,}780$, $n_{\text{solutions}} = 10{,}413$; χ^2 test, df $= 1$, $p < 0.001$; Fig. 1). However, this simply reflected the difference between all papers discussing the problems caused by anthropogenic threats to species and papers discussing solutions to those problems ($n_{\text{threats}} = 69{,}112$, $n_{\text{solutions}} = 31{,}772$; χ^2 test, df $= 1$, $p < 0.001$). The normalized heat map (Fig. 2), for which we calculated what proportion the number of papers in each cell represented out of the total number of papers in the appropriate conservation theme, all but eliminated the differences between threats and solutions. Conservation-solution papers represented 23.95% of the total number of all conservation papers, whereas the number of papers that included both a solution term and a behavioral term represented 33.29% of all papers with intersecting conservation and behavioral terms (χ^2 test, df $= 1, p < 0.001$).

The more intensive analyses of the cells that intersected learning behavior with invasive species or reintroduction programs demonstrated some of the subtleties of how behavioral information is used in conservation contexts. Among the 60 papers addressing invasive species, 12% mentioned learning only in passing. The majority of the papers (73%) specifically discussed learning behavior in relation to invasive species, but only 15% of the papers provided advice that could be applied (Fig. 3a). Seventy-three percent of the papers identified anthropogenic effects on learning behavior, and 25% considered learning in behavior-based management action, whereas 1 paper (1.67%) considered learning an indicator of anthropogenic impact or management success (Fig. 3b). Almost half the papers were published in ecological journals, and the rest were relatively evenly divided between behavioral and conservation journals (Fig. 3c). The taxonomic distribution was relatively even among groups (Fig. 3d), with one notable exception: 27% of the papers discussed one species—the cane toad (*Rhinella marina*).

Twenty-eight percent of the 92 papers in the cell that intersected learning behavior with captive breeding and reintroductions identified explicit conservation actions related to learning behavior (Fig. 4a). This number is low considering the fact that almost all the papers (96%) addressed learning as a tool of behavioral-based management (Fig. 4b). Moreover, no papers considered learning as a behavioral indicator of either anthropogenic impact or management success (Fig. 4b). The majority of the learning and captive breeding papers were published either in ecological journals or in conservation ones

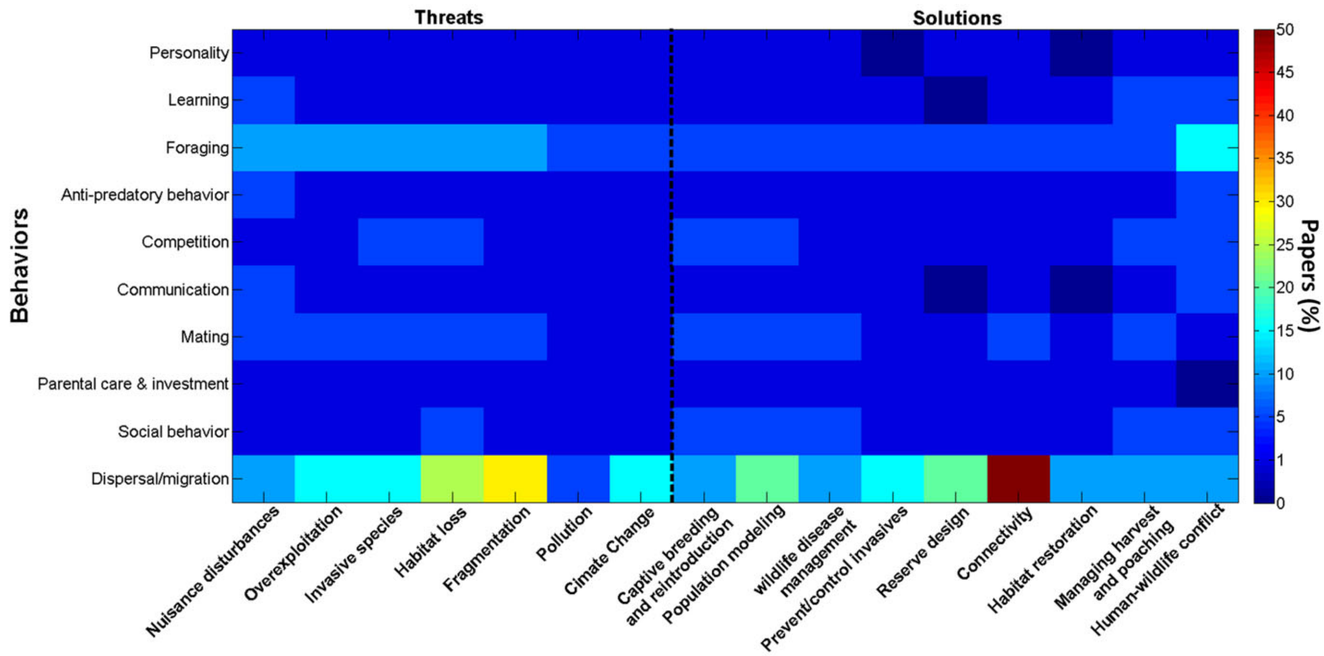

Figure 2. The relative use of behavior in the study of various conservation themes. Each cell represents the percentage of papers mentioning a behavior (rows) out of the total number of papers dealing with a conservation theme (columns); hotter colors represent a higher percentage.

(Fig. 4c), and most of them concentrated on birds or mammals (Fig. 4d).

Discussion

Our analyses revealed tremendous variation in attention by researchers, with some behaviors seemingly well integrated into management programs and others greatly underutilized. Movement behaviors such as dispersal and migration were, by far, the most mentioned among the behaviors we examined. One probable reason for that is that dispersal of individuals is a central part of population dynamics. The drivers of population dynamics are survival, reproduction, immigration, and emigration. Although many behaviors contribute to these factors, none contributes as directly as dispersal, and the term *dispersal* not only refers to the individual behavior but also to the processes of immigration and emigration.

Examples of the use of knowledge of dispersal in conservation abound. Dispersal behavior alone may determine the success or failure of reintroduction projects (Le Gouar et al. 2011). Consequently, many researchers have studied dispersal behavior both theoretically and empirically and used their insights to improve the probability of reintroduction success (e.g., Stamps & Swaisgood 2007; Trewenack et al. 2007). In Australia, understanding the dispersal behavior of the highly invasive cane toad has played an important part in identifying optimal locations for the creation of barriers that may reduce the toad's spread into Western Australia (Tingley et al. 2013).

The second most popular behavior in conservation studies was foraging. Foraging examples include the waggle dance of foraging honey bees (*Apis mellifera*), which is a reliable indicator of the quality of their environment in human-altered landscapes (Couvillon et al. 2014). Similarly, the foraging behavior of benthic fish in shallow lakes is an indicator of the ecosystem state and may be used as an early indicator of an approaching increase in turbidity (Persson & Nilsson 2007). The foraging behavior of marine species can be used in the design of or to improve existing marine protected areas to ensure their effectiveness (Thaxter et al. 2012; Chivers et al. 2013).

The least developed behavior in respect to conservation was animal personality, perhaps because, even in the behavior literature, the topic has become prevalent only in the past decade (e.g., Sih et al. 2004). It is less clear why the other behavioral topics were relatively undeveloped because they are well understood and are potentially highly relevant to conservation and management.

For example, animal learning has been studied for over a century (Dukas 2009) and has been central to some conservation projects. Knowledge of imprinting mechanisms has played a key role in the rearing of captive bred California Condors (*Gymnogyps californianus*), and the use of adult mentors to guide captive-bred juveniles has increased reintroduction success for this critically endangered species (Walters et al. 2010). Learning theory is also central to the development of efficient wildlife deterrents (many examples are in Conover [2001]) and training of vulnerable prey species to avoid novel predators

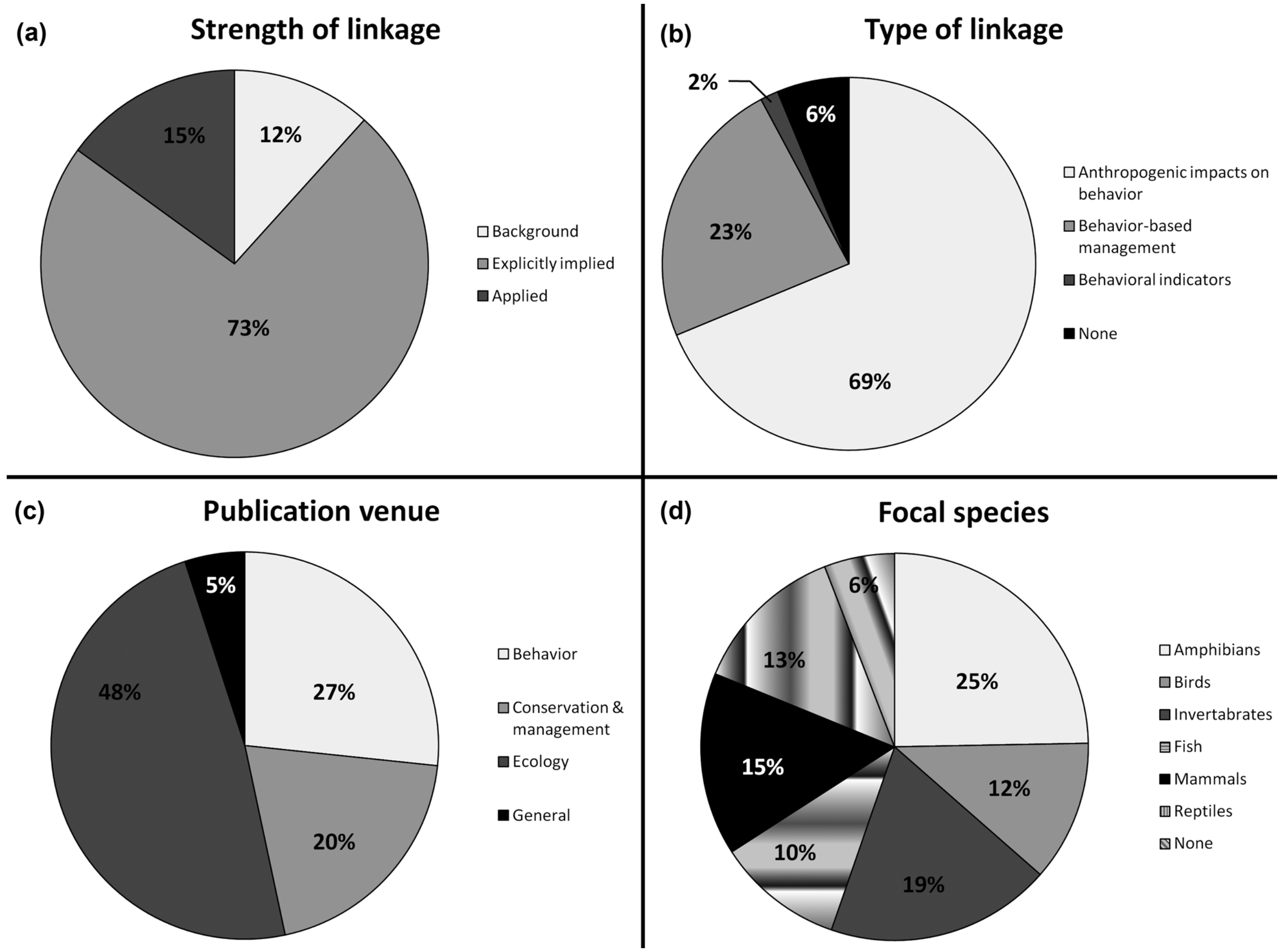

Figure 3. Results of the analysis of the 60 papers that included at least one learning behavior term as well as at least one term related to invasive species in their titles, abstracts or keywords (i.e., the learning-invasive species cell in our heat map): (a) strength of the link between animal learning behavior and the conservation problem, (b) type of link between animal behavior and conservation (Berger-Tal et al. 2011), (c) type of journal the paper was published in, and (d) taxon of the focal study species in the paper.

(Griffin et al. 2000). Despite these applications, learning was mentioned in 0.96% of the papers dealing with captive breeding and reintroduction and 2.03% of human-wildlife conflict papers (Fig. 2). Similarly, social behavior has strong theoretical foundations dating back decades (e.g., Wilson 1975) and appears to be a determinant of reintroduction success for several species (e.g., Shier 2006; Rowe & Bell 2007), as well as to have a fundamental connection to wildlife disease transmission (Altizer et al. 2003; Grear et al. 2010). Despite this fact, social behavior was only discussed in 1.45% of the papers on captive breeding and reintroductions and mentioned in only 2.15% of the papers studying wildlife disease management (Fig. 2). Hunting can have strong effects on animals' antipredator behaviors, which in turn may influence their fitness (Croes et al. 2007). Antipredatory behavior can also be used as a behavioral indicator. For example, the vigilance behavior of the Himalayan tahr (*Hemitragus jemlahicus*) has been used to monitor the elusive snow leopard (*Uncia uncia*) and has led to several rare sightings of this endangered predator (Ale & Brown 2009). Yet we could find only 19 papers at the intersection of antipredator behavior and human overexploitation, which constituted <0.2% of all overexploitation paper (Fig. 2). These examples tell us that learning, sociality, and antipredator behaviors have great potential as management tools that may significantly improve conservation and management programs but that this potential may, in many cases, remain unrealized.

Our heat map showed that the number of papers dealing with conservation problems greatly exceeds the number of papers reporting conservation solutions. This tendency of authors to report threats to biodiversity more frequently than discussing the solutions to

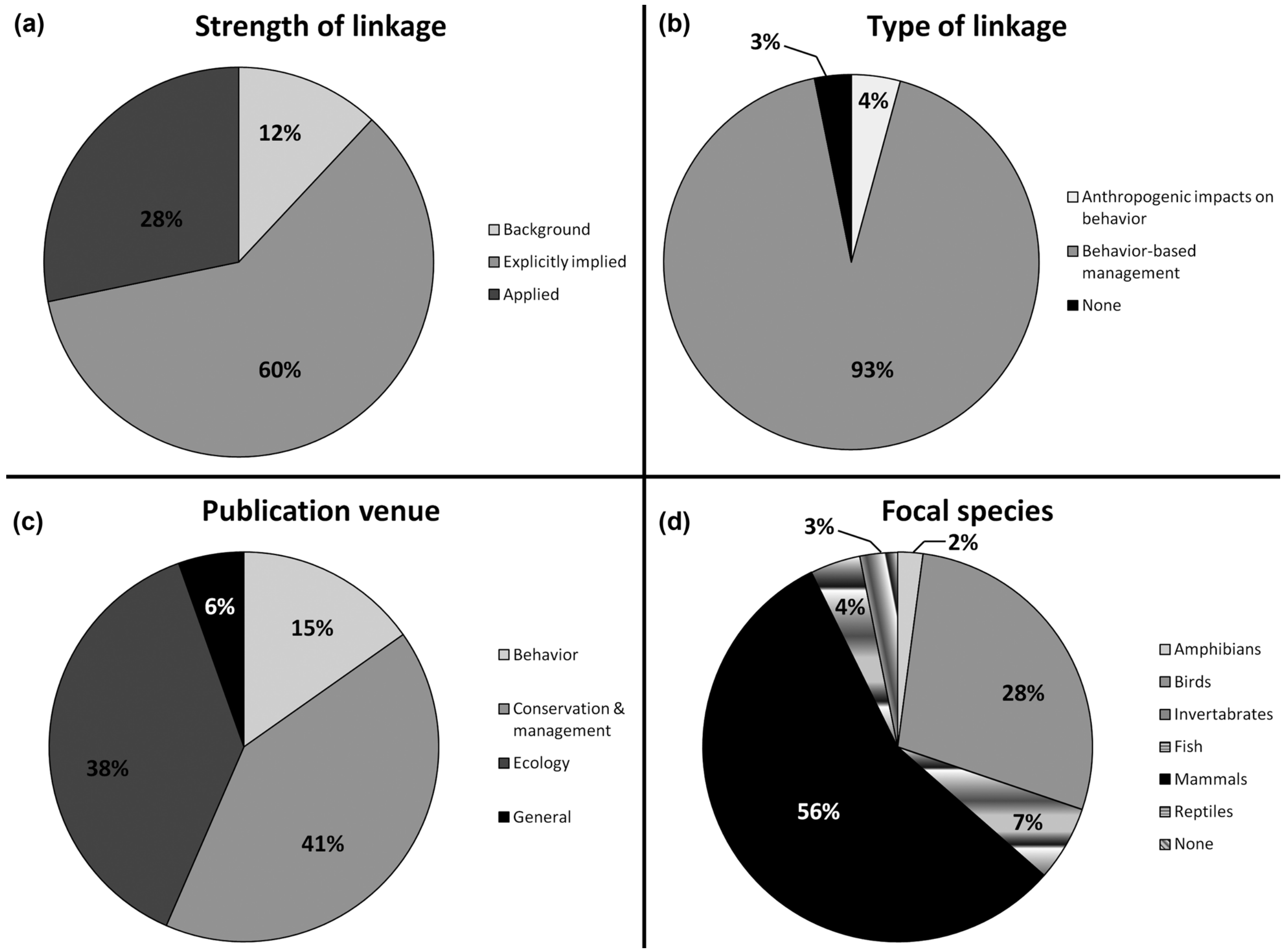

Figure 4. Results of the analysis of the 92 papers that included at least one learning behavior term as well as at least one term related to captive breeding and reintroductions in their titles, abstracts, or keywords: (a) strength of the link between animal learning behavior and the conservation problem, (b) type of link between behavior and conservation (Berger-Tal et al. 2011), (c) type of journal the paper was published in, and (d) taxon of the focal study species in the paper.

these threats has already been recognized as an international phenomenon that may hinder conservation success (Lindenmayer et al. 2013). Our findings indicate that the bias between studies of conservation threats and solutions was actually less when the behavior of animals was considered and that behavior was used in studies of conservation action more than expected. This suggests that behavioral research may have a potentially positive impact on conservation by supplying behavioral knowledge that could be used in promoting solution-based research. This is an important point indicating the maturation of the field of conservation behavior, often criticized for emphasizing implication while delivering few real applications (Caro 2007).

Our analysis of specific cells in which the topic of learning behavior intersected with the topics of invasive species and of captive breeding and reintroductions revealed that only a small percentage of the papers in the cells identified explicit conservation actions related to learning and that learning was used as an indicator in but a fraction of the papers. This is striking, especially in relation to reintroductions, given that a reintroduced animal goes through a learning process when released into a novel environment; therefore, the well-developed theory of animal learning is bound to provide critical indicators for subsequent reintroductions success (Berger-Tal & Saltz 2014). The use of postrelease behavior of reintroduced animals to assess reintroduction success is not novel (Owen-Smith 2003; Kemink & Kesler 2013), and our results may stem partly from semantics (i.e., authors who do not use the word *indicator* to describe the use of behavior to assess reintroduction success) and may be due to the fact that such indicators are usually manifested through movement or foraging behaviors and therefore these behaviors may be mentioned rather than learning. Nevertheless, our findings indicate that despite the importance of learning in determining the success of animals' adjustments to the wild, the large literature on learning theory is not presently considered when monitoring reintroduced populations. We also found a taxonomic bias; most of the learning-reintroduction papers concentrated on birds and mammals. This bias is representative of a greater trend of favoring birds and mammals across all conservation research (Clark & May 2002; Driscoll et al. 2014).

Our survey of the literature did not include reports, theses, and dissertations. We therefore believe it is safe to assume that our results represent an underestimation of the actual use of behavioral knowledge in conservation and management. Given the magnitude of differences we found among behaviors in the way they were considered in conservation, we do believe these differences reflect similar trends in the gray literature, at least to some extent. Nevertheless, expanding this work using additional and more inclusive databases is needed to accurately assess how prevalent these trends are in conservation practice (as opposed to conservation research).

Together, our results from the extensive analysis of the heat map and the intensive analysis of focal cells provide much information that is relevant to the debate about the utility of using behavior to improve wildlife conservation and management (e.g., Buchholz 2007; Caro 2007; Angeloni et al. 2008). Our results dispel the notion that a few simple terms can be used to identify or categorize the integration of the disparate literatures of these 2 disciplines. For example, studies that were based on summing the number of papers that used derivatives of the terms *animal behavior* and *conservation biology* (e.g., Linklater 2004; Angeloni et al. 2008; Nelson 2014) were unlikely to find most of the relevant literature, which compromises their conclusions that there is little association between the fields. Our results show that such associations are variable and nuanced. Although many behaviors appeared to be underutilized in conservation, other behaviors seemed to be well integrated. For example, over 45% of studies on connectivity (including studies on corridor design and management, and of barriers) also mentioned the behaviors of dispersal or migration. Similarly, dispersal was mentioned in $>25\%$ of studies dealing with fragmentation and $>10\%$ of invasive species studies. Almost 10% of overexploitation studies discussed foraging behavior, as did 11.5% of human-wildlife conflict studies (Fig. 2).

More importantly, our results shed light on the current gaps that may hinder the successful implementation of behavioral knowledge into conservation and management. Knowledge of animal behavior can be an extremely useful tool in conservation (Buchholz 2007; Blumstein & Fernández-Juricic 2010). However, behavioral ecologists must first consider the conservation problem and then select the most relevant tool to address that problem, acknowledging that the tool may not always be a behavioral tool. They must also share lessons from the application of behavioral research to make conservation practitioners more aware of behavioral tools. We therefore recommend the following.

Researchers should focus on developing explicit examples of how underrepresented behaviors can inform conservation. Our map showed a great inequity in the use of different behaviors in conservation and management. Cells with a low number of papers may have underutilized potential to improve conservation and management but may also have a low number of papers due to the papers' low applicability to conservation problem solving. Additional research is required to distinguish between these 2 types of cells, allowing for the development of novel and useful approaches to conservation on one hand and preventing a waste of resources on inefficient tools on the other hand.

Even within behaviors that are already widely considered in conservation and management, behavioral ecologists should make an effort to translate their theoretical knowledge into relevant and testable predictions that may be used to increase the success of adaptive-management programs; useful approaches to wildlife management (e.g., using the theory of density-dependent habitat selection [isodars] to detect ecological traps [Shochat et al. 2005]); and measurable behavioral metrics that can connect individual fitness to population status and predict demographic trends.

Conservation practitioners should work together with behavioral ecologists to create easily accessible and thorough systematic reviews and guidelines (Dicks et al. 2014) that will allow for the creation of evidence-based directories of potential and actual behavioral solutions to conservation and management problems. Being aware of the importance of behavior in conservation does not necessarily translate into efficient use of behavior in conservation. There are many cases where the potential of behavioral knowledge for conservation has been reported but no concrete and useful advice was provided. Managers can encounter various constraints and problems when attempting to apply behavioral principles, such as optimal foraging theory or associative learning, to real-life situations (Caro 2007; Schakner et al. 2014). For behavioral ecology to become an effective tool, behavioral ecologists must turn their implied insights into applied principles. Our heat map highlights the research areas that have been sufficiently studied to facilitate such systematic reviews and points out the areas where more research is needed before a systematic review can be conducted.

The burgeoning field of conservation behavior has been highly successful in raising awareness of the importance of behavior to conservation. However, a much greater emphasis on practical implementation is needed, and it is time to supply the tools that will allow managers to profit from this awareness.

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Supporting Information

A list of the behavioral categories and their search terms (Appendix S1), the conservation themes and their search terms (Appendix S2), and detailed results for all 160 intersections between behavioral and conservation themes (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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