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CONCEPTS & THEORY

Harnessing knowledge of animal behavior to improve habitat restoration outcomes

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Abstract. Restoring degraded habitat to increase biodiversity is a global challenge. While habitat restoration for animals should lead to self-sustaining breeding populations of target species, often this does not occur. Understanding the factors constraining progress toward this goal and how these constraints can be overcome is vital. We use a review to highlight how insights from animal behavior can help plan restoration projects, and identify and ameliorate some of the reasons why restoration may fail to meet biodiversity goals. We present a decision tree to highlight how behavioral knowledge can identify and address two ways in which restoration can fail when: (1) target animals do not colonize restored sites and (2) they colonize restored sites but experience conditions that do not match their habitat requirements. Investing in the collection of behavioral information may be difficult for management agencies when funding is limited. We highlight when behavioral information is likely to be most important, and some of the practical considerations for its application in restoration projects. We conclude by identifying key knowledge gaps and future directions that can improve restoration outcomes for biodiversity by incorporating behavioral knowledge. Restoration is needed to ameliorate the effects of habitat loss, degradation, and fragmentation on fauna. Unfortunately, restoration does not always lead to the intended optimal outcomes for target animals. A greater consideration of animal behavior and its consequences can help during both the planning and evaluation of restoration projects. We hope to stimulate dialogue between restoration and behavioral ecologists to improve restoration outcomes for animals.

Key words: behavioral ecology; ecological restoration; ecological trap; fitness; habitat selection; monitoring.

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Introduction

Given the threats that habitat loss and degradation pose to biodiversity, the need to restore habitats is well established, as highlighted by the recent announcement of the UN Decade of Ecosystem Restoration (United Nations 2019). Habitat degradation and loss is the most common threat globally for birds, mammals, reptiles, and amphibians, and the second most common threat for fishes (World Wildlife Fund 2018). While restoration is often focused on plants (McAlpine et al. 2016), it is also required for animals.

Restoration for animals often emphasizes individual species and their specific habitat needs (McAlpine et al. 2016). Strategies often focus on altering structural elements (e.g., vegetation) assumed to provide the necessary ecological resources for animals, both in the cues they may use to select habitats, and those that they require for survival and breeding (Van Dyck 2012, Jones and Davidson 2016). By habitat, we are referring to the physical and biological features that collectively define the environment where a target animal species lives. Information about habitat selection and fitness is vital for assessing success of restoration (Hale et al. 2019*b*), especially when responses are unexpected. For instance, Willow flycatchers (*Empidonax traillii*) often fail to recolonize sites, regardless of habitat suitability, if these sites lack calling conspecifics (Schofield et al. 2018). Alternatively, restoration could create ecological traps (Robertson and Hutto 2006) where individual animals are attracted to restored sites but, once there, suffer reduced fitness (Hale et al. 2015, Hale and Swearer 2017). Be'er Sheva-fingered lizard (*Acanthodactylus beershebensis*) populations crashed when trees and shrubs were planted in their savannah habitat, mainly because these new structures provided perches for predatory birds (Hawlena et al. 2010). Traps clearly illustrate situations where a lack of knowledge about habitat-selection behavior led to unexpected failures in restoration.

There has been extensive work in developing the theory underpinning our understanding of habitat-selection behavior (Rosenzweig 1981, 1991, Morris et al. 2008), including describing the types of cues and sensory modalities animals may use (Huijbers et al. 2012) and illustrating how variability in habitat selection can translate into differences in individual fitness and the size of populations (Jenkins 2005, Arlt and Pärt 2007, Hale et al. 2008). However, while the need to consider animal behavior in restoration was recognized at least a decade ago (Lindell 2008) to our knowledge there has not been a quantitative assessment of how often habitat-selection behavior is considered in restoration projects. This prompted us to systematically select and review 256 restoration studies (Fig. 1). We found that habitat preference was measured in fewer than 20% of studies for most taxa, except for terrestrial mammals (45%). Restoration is most commonly assessed using indirect measures of fitness such as abundance (Hale et al. 2019*b*), which may not tell us whether habitat quality (supporting fitness) has been fully restored or whether restored sites are preferred over other habitats.

We highlight some of the ways that behavioral knowledge can help support restoration decisions and actions at the planning stage and to help identify and ameliorate causes of restoration failure. We present a decision tree (Fig. 2) which describes the steps from planning restoration projects to the eventual successful establishment of self-sustaining breeding populations of target animals (our definition of successful restoration). For each step, we outline reasons why restoration can fail (Fig. 2 S1–S5) and suggest solutions, building on previous studies that have described the steps in successful restoration (Bond and Lake 2003*b*, Miller and Hobbs 2007, Hale and Swearer 2017, Prach et al. 2019). While the structure of our decision tree is reactive in that we identify causes for failure and we propose solutions, the information we highlight about habitat selection and its consequences should also guide the design of restoration projects (i.e., in steps 1 and 2 in Fig. 2). In many cases, using this mode of thinking to help guide the planning stages of restoration may be more cost-effective than attempting to repair cases where restoration has failed. The scope of our review is primarily on in situ restoration for establishing breeding populations at individual sites rather than landscape-scale design, which aims to increase functional connectivity at larger scales (Thomson et al. 2009, McAlpine et al. 2016). Some information may be transferable, but landscape-scale design requires its own treatment to properly incorporate insights from behavioral knowledge, including ideas from landscape ecology.

Three reasons for restoration failure (implementation failure, lack of colonists, and inappropriate matrix; Fig. 2 S1–S3) have been discussed previously and are not influenced by the habitat-selection behavior of animals or its fitness consequences per se; these are presented for completeness but are not discussed in detail. We initially outline how a better understanding of habitat-selection behavior can help identify why animals fail to colonize restored sites (Fig. 2, step 4), and provide ways that this can be addressed. We then discuss reasons for failing to meet an

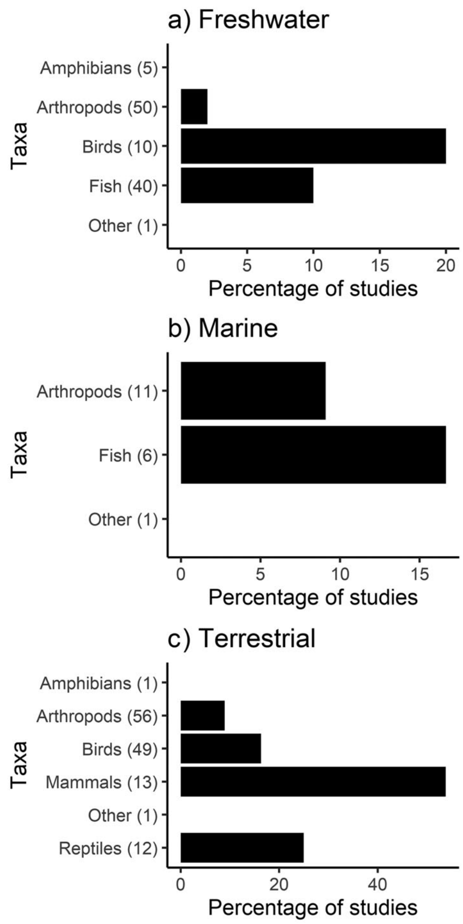

Fig. 1. Results of a quantitative assessment of the use of habitat-selection behavior in restoration. To identify relevant studies to review, we searched the Web of Science Core Collection database across all years using the following search term: (((biodiversity OR abundance OR density OR richness OR select* or choice* or prefer* or settle* or coloni* or recruit* or metamorph* or breed* or reprod* or growth* or fitness or surviv* or mortal* or death* or birth* or spawn* or matur* or condition or metamoph* or fidelity or population*) AND habitat* AND restor*)). From the initial 11,545 publications, we identified 256 empirical studies that (1) focused on responses of one or more animal species to restoration of habitat structure at local scales and (2) included a comparator against which responses could be assessed (i.e., monitoring sites before/after restoration, control vs. impact, before–after/control–impact). When there were multiple papers reporting on the same restoration project through time, we included only the most recent. For these 256 papers, we assessed whether authors considered habitat selection, which were those that compared relative preferences for restored vs. non-restored sites (i.e., a binary response), including both direct experimental tests (e.g., choice experiments) and observations made from survey data (e.g., higher densities of animals at restored sites). We present the percentage of studies that considered habitat selection across freshwater, marine, and terrestrial realms. The number in parentheses after each taxonomic group indicates the number of studies.

animal's habitat requirements (Fig. 2, step 5), and how behavioral information can help address this problem. We present an example to illustrate how the key principles can be considered, and then conclude by highlighting some important management considerations associated with incorporating behavioral knowledge into restoration projects.

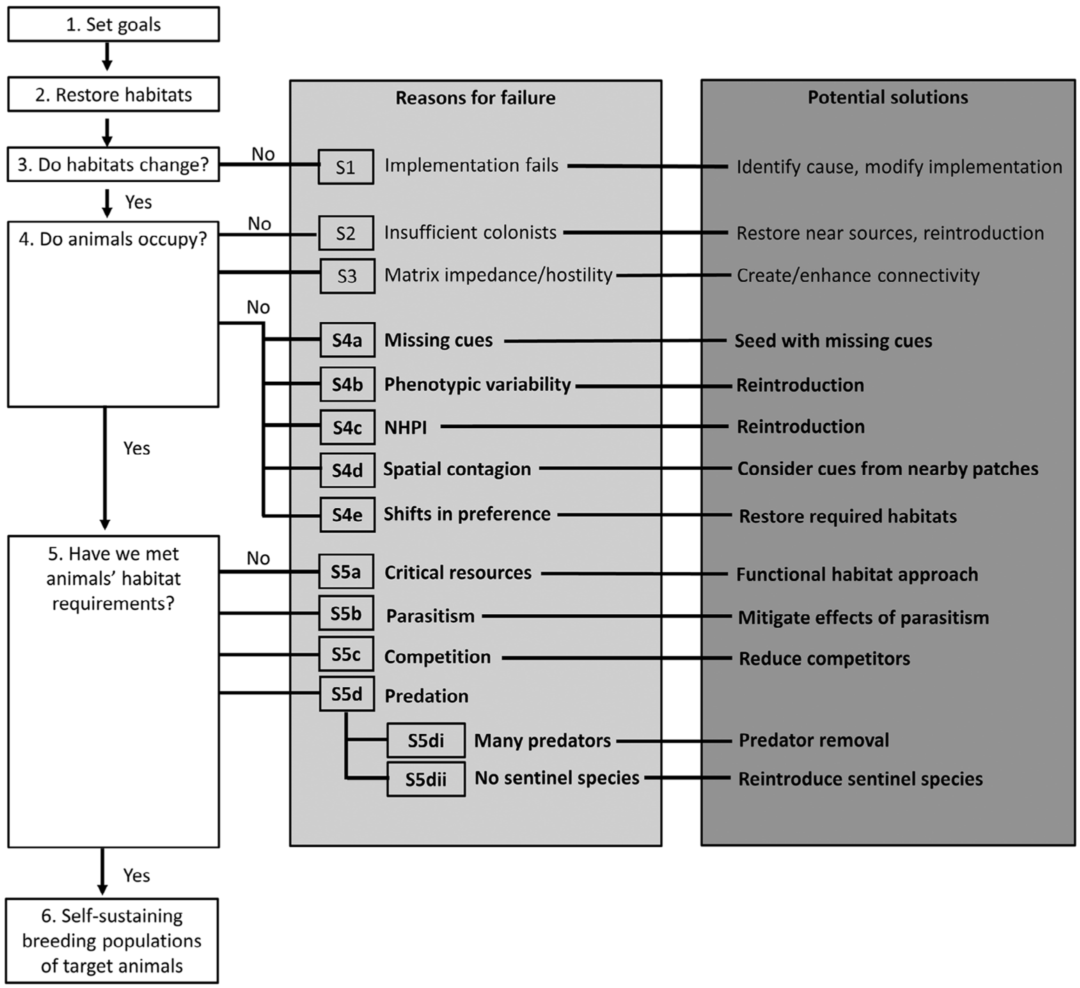

Fig. 2. A decision tree to illustrate how using behavior can improve restoration success. Restoration succeeds when target animals establish self-sustaining populations. Best-practice restoration projects will satisfactorily accomplish the following actions: (1) Goals are set; (2) restoration actions are implemented; (3) there are the desired changes to habitat structure; (4) animals colonize and occupy restored sites; (5) restoration provides animals' habitat requirements; and (6) recruitment occurs, leading to self-sustaining populations. We outline five ways (Situations S1–S5) that restoration can fail and propose response actions. Our focus is primarily on situations S4 and S5 (highlighted in bold), which relate to why animals might not occupy restored sites (S4) and reasons why animals that colonize restored sites may not survive and reproduce (S5). Animals will not colonize restored sites that lack habitat-selection cues (S4a). More complex aspects of habitat-selection behavior might limit occupation of sites if phenotypic variability in habitat preference means only some individuals colonize (S4b), animals avoid restored sites due to natal habitat preference induction (NHPI, S4c) and spatial contagion (S4d), or animals have shifting habitat preferences (e.g., through ontogeny (S4e). The latter scenarios (S5a–d) describe ways that restoration can fail if the habitat requirements of target animals are not met. Behavioral knowledge can inform potential solutions to mitigate these causes of failure, as outlined in the main text. The figure is intended to show a procedural flow of actions throughout the restoration process rather than being an exhaustive list of all reasons for failure and potential solutions. We define success as a binary outcome (i.e., yes/no) at each step for simplicity, but a more refined process (e.g., population viability analysis; Beissinger and McCullough 2002) would help determine the proportion of animals that must meet each step to produce self-sustaining breeding populations.

Do Animals Colonize Restored Sites?

Studies that examine animal behavior uniquely provide the information to understand the sensory mechanisms employed during habitat selection (Greggor et al. 2016). While these studies can guide restoration, the habitat-selection cues required by target species are often not considered in restoration planning or implementation (Fig. 1). Some species respond to a single cue detected using one sense (e.g., marine invertebrates that settle based on a chemical cue; Pawlik 1992), whereas others use multiple cues from several senses (e.g., marine fish that respond to visual, chemical, and auditory cues; Huijbers et al. 2012). While animals can use a diversity of biotic and abiotic cues, many respond to signals from conspecifics (Ward and Schlossberg 2004, James et al. 2015). For these species, the presence of conspecifics (or evidence they have been present, e.g., fecal pellets) is a key indicator of habitat quality. Given that target animals will not colonize restored sites in the absence of appropriate cues (Fig. 2 S4a), knowing which cues animals respond to (and how) can help understand why they may fail to colonize restored sites.

It is also important to consider how individual animals, even those from the same species, might differ in their responses to restoration. Phenotypic variation in habitat-selection behavior may mean that some individuals are more likely to colonize restored sites (Fig. 2S4b). Some animals exhibit consistent behavioral differences between individuals among ecological contexts and through time (Sih et al. 2004) or personalities. If movement and habitat selection are personality-dependent (Spiegel et al. 2017), bolder (neophilic) individuals may be more dispersive and so be more likely to encounter and occupy restored sites (Cote et al. 2010). However, more reticent (neophobic) individuals might avoid previously unencountered predators, food, or objects (Sol et al. 2011). Therefore, these individuals may not colonize restored sites, especially those that are very different to habitats they have inhabited previously. Phenotypic variability in behavior can have important ecological consequences (Sih et al. 2012); for example, aggressive and non-aggressive Western bluebirds (*Sialia mexicana*) settle into distinct breeding habitats (Duckworth 2006). While these differences could affect restoration outcomes depending on which habitats are restored, there has been little research on the implications of phenotypic variability in behavior for conservation and management (but see Merrick and Koprowski 2017). Given that there is no guarantee that the phenotype most likely to colonize restored sites is the best suited to these habitats—bolder individuals may be more susceptible to fitness costs such as increased predation risk (Kashon and Carlson 2018)—there is a need to determine the potential importance of different personalities in restoration.

Another reason why responses to restoration may vary is because of differences in natal experience. Natal experiences can be an important influence on habitat preferences because some individuals will only colonize habitats that are similar to where they were born (i.e., natal habitat preference induction or NHPI; Davis and Stamps 2004; Fig. 2 S4c). NHPI could cause individuals to avoid restored sites that are very different from their natal sites, similar to when relocated animals abandon release sites to search for habitats that they perceive to be more suitable (Stamps and Swaisgood 2007). To our knowledge, NHPI has not been considered in the restoration ecology literature despite being a potential explanation for why restored sites are not colonized.

The spatial context of habitat patches can affect how target animals perceive their likely suitability. For some animals, spatial contagion can be important, whereby the characteristics of nearby habitat patches influence how animals perceive a given focal patch (Resetarits and Silberbush 2016; Fig. 2 S4d). For example, habitat selection by mosquitos is affected by the presence or absence of predatory fish in nearby ponds (Resetarits and Silberbush 2016). If spatial contagion influences habitat selection, animals may avoid suitable restored patches that are surrounded by unsuitable patches (e.g., those with predators) or may colonize unsuitable restored sites surrounded by suitable habitat (Resetarits and Binckley 2009).

It is important to also be aware that both the habitat requirements and preferences of target animals are not static. Some species use different habitats as they develop and mature (e.g., fish; O'Connor et al. 2017) and the strength of their preference for restored sites might change

(Fig. 2 S4f). For example, livestock removal increases spawning of the common galaxiid (*Galaxias maculatus*; Hickford and Schiel 2014), a freshwater fish that spawns obligately in riparian vegetation in estuaries. Restoration will be more effective if one were to target estuarine spawning habitats rather than upstream areas where fish are present but in which they will not spawn. Colonization by target species may change through time as habitat elements develop (Vesk et al. 2008*a*). For example, different bird guilds will likely vary in when they colonize replanted sites based on the rate at which their habitat resources are established—shrub cover in the short term, then arboreal vegetation, and, eventually, some elements such as tree hollows and fallen timber that may take more than a century to develop (Vesk et al. 2008*a*, *b*). Collectively, these examples illustrate the diversity of reasons why animals, or the suitable animal phenotypes, may fail to colonize restored sites.

How could behavioral knowledge help ensure animals colonize restored sites?

A first step to ensure that target animals colonize restored sites is to identify the cues that they use to select habitats, and by using which senses. A useful starting point is to review the literature given that there is a wealth of published information about the cues or structural features that might be important for habitat selection and settlement of target species. This stage could also include the literature on reintroductions and translocations which may yield valuable information about which cues (or other factors) might affect whether animals remain at restored sites (Le Gouar et al. 2012). Enough may be known about target species that a restoration plan can be drafted based only on published information.

When there is insufficient published information about a target species, studies can be undertaken to examine habitat associations in the field (Bond and Lake 2003*a*). A more nuanced approach would be to examine habitat selection along chronosequences or among sites in different landscapes, and correlating preference with concurrently measured environmental predictors (e.g., conspecifics, predators, or vegetation). Pitman et al. (2018) used this approach to correlate oviposition preference of Monarch butterflies (*Danaus plexippus*) at 26 sites in three landscape types to abundances of predators, parasitoids, and parasites. Choice experiments can also be used to corroborate responses to key habitat elements. If we know which cues animals use, we can use this knowledge to ensure that these are provided during restoration (e.g., planting particular vegetation types that individual bird species use to select sites; Yen et al. 2011) or the cues could be emulated if missing (Fig. 2 S4a; e.g. playbacks of calling conspecifics for birds and amphibians; Ward and Schlossberg 2004, James et al. 2015).

How the different behavioral influences on habitat selection described here (Fig. 2 S4b–d) affect restoration is not well understood. As a first step, we need information about how often these factors are important, under what conditions, and how strongly they might affect habitat selection. While this information can be difficult to collect, a useful initial approach could include characterizing phenotypic variability in the habitat-selection behavior of target animals and generating a better understanding of the effects of natal experience and spatial contagion on habitat preference. Potential phenotypic variability in habitat selection can be explored by using choice experiments to measure habitat preferences (Hale et al. 2008) coupled with behavioral assays to explore whether these preferences depend on phenotypic traits. Individuals can be raised in controlled conditions and then exposed to choice experiments to test whether preference depends on natal experience (Ousterhout et al. 2014, Hale et al. 2019*a*). Mesocosm experiments can be used to examine effects of spatial contagion on habitat preference by manipulating the characteristics of focal patches and also their likely quality (e.g., by adding predators to nearby patches) and then measuring colonization rates (Resetarits and Binckley 2009, Resetarits and Silberbush 2016).

If these influences mean animals do not colonize restored sites, how can we manage them? In some instances, such as when phenotypic variability in behavior or NHPI may cause individuals to avoid restored sites (Fig. 2 S4b–d), it may be difficult to address directly these factors. Instead, habitat restoration may need to be coupled with reintroductions, where it is possible to either (1) habituate target animals to stimuli to reduce avoidance behaviors or (2) raise them in similar conditions to those they will subsequently experience at restored reintroduction sites. Overcoming avoidance from spatial contagion (Fig. 2 S4e) or shifts in habitat preference (Fig. 2 S4f) requires consideration of where restoration occurs within the landscape. If animals assess habitat suitability based on both focal and nearby habitats, better outcomes may arise by restoring sites adjacent to remnant patches that provide these landscape-level cues. Alternatively, it may be prudent to avoid restoring habitats in unsuitable landscapes (i.e., where there are no other suitable habitats to provide cues). Shifts in preference may require that restoration is undertaken at multiple habitats that collectively provide the conditions that target animals need to fulfill their life-history requirements (Schlosser 1995); this will be necessary if species have different seasonal or life history-based habitat needs.

Have We Met Target Animal's Habitat Requirements?

Restored sites need to provide the habitat requirements of target animals (e.g., food, shelter; Fig. 2 S5a) that ultimately allow them to survive and reproduce. While the focus is often on individual species, inter- and intra-specific interactions are important components of habitat suitability for target species. Behavioral knowledge will improve understanding of the potentially subtle ways that restoration might not meet habitat requirements through interactions such as parasitism, predation, and competition (Fig. 2 S5b–d).

Food-web theory can help identify the types of interactions that can influence restoration outcomes (Zanden et al. 2016) but considering the behavior of animals is also important. Prey species may benefit from predator-alarm signals produced by other syntopic prey, even those from different taxa (Hettena et al. 2014). If these other species are not present, then the habitat is less suitable (Gil et al. 2016). Other interactions, such as the behavior of ecosystem engineers, can influence habitat suitability for other species. Habitat restoration for the western burrowing owl (*Athene cunicularia hypugaea*) is more successful when vegetation management is combined with the translocation of California ground squirrels (*Otospermophilus beecheyi*), whose burrowing, incidentally, creates owl habitats (McCullough Hennessy et al. 2016).

Interactions among species can be even more complex, potentially involving multiple trophic levels (Zanden et al. 2016). These indirect behavioral interactions can also affect habitat suitability. Fear induced by the presence of large carnivores modulates the behavior of mesocarnivores, with cascading effects through food webs (Suraci et al. 2016). By simulating predation risk using large-carnivore vocalizations (dogs, *Canis lupus familiaris*), Suraci et al. (2016) showed that mesocarnivores (raccoons, *Procyon lotor*) foraged less and that the abundance of their prey (fish, intertidal invertebrates) increased. Multi-trophic level interactions in food webs have a rich history in ecology, and this insight needs to be incorporated into restoration studies.

Another important consideration is how restoration actions may result in the unintentional provision of habitat for non-target species, especially those that are non-native or invasive and may have deleterious impacts on for target animals. For example, forest restoration in Hawai'i increased biomass and abundance of Black rats (*Rattus rattus*), which pose a threat to native birds and plants (Shiels et al. 2017). Many invasive species have traits that allow them to preemptively occupy newly created habitat, and a key challenge is to determine how restoration can be undertaken to disbenefit non-target species in favor of native species (Bond and Lake 2003*b*). Information about the habitat requirements of natives and non-natives will help to inform these efforts.

How could behavioral knowledge help to identify what makes a suitable habitat?

Identifying the habitat elements that are most strongly associated with habitat suitability for a given animal species is important, so we can ensure restoration provides these elements. Ultimately, monitoring needs to then assess whether target animals use restored habitats and have improved fitness outcomes as a result.

Initially, it is important to identify the specific habitat elements that animals require. This information can be collected using the functional resource-based habitat method, which involves considering the resources that animals need in their life cycle such as food and shelter (Dennis et al. 2003). Fitness might be estimated among sites of differing condition or time since restoration, and these can be related to concurrent measures of habitat (e.g., vegetation type and cover, densities of predators, competitors, parasites) to identify the critical habitat elements (Selwood et al. 2009).

Some changes in behavior can be an indicator that fitness is likely to increase in restored habitats (Lindell 2008, Berger-Tal et al. 2011). Yet, restoration studies rarely measure behavioral responses as indicators and instead generally focus on changes in population size or community composition (Hale et al. 2019*b*). As above, comparing changes in behavior along a restoration chronosequence could be used to identify those factors that may be important determinants of fitness. Those behaviors that are likely to change following restoration are important to consider, such as oviposition by butterflies (*Plebejus icarioides* fender; Carleton and Schultz 2013) and feeding rates (e.g., Seychelles giant millipedes *Sechelleptus seychellarum*; Lawrence et al. 2013).

Identifying when these changes in behavior are expected to occur following restoration will inform expectations of the timing and nature of responses. Some behaviors might be immediate while others may lag well behind the implementation of restoration actions (Vesk et al. 2008*b*), leading to potentially non-linear temporal responses. Recognizing such temporal schedules can be used to manage stakeholder expectation. One would not expect birds that breed in tree hollows to use recently restored sites if hollows take decades to develop (Vesk et al. 2008*a*). Knowing when responses are likely to occur can help to guide the allocation of scarce resources in monitoring. In turn, ongoing monitoring of restoration projects will help to identify situations in which further actions might be necessary, such as managing predation, competition, or parasitism in restored sites if these are constraining desired outcomes (i.e., Fig. 2 S5b–d). Predator removal can increase hatching success and post-breeding population sizes of birds (Côté and Sutherland 1997) and could be used to increase success if predators are present at restored sites. Restoration actions for the endangered Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) will be more effective if predator management is undertaken concurrently to reduce densities of exotic domestic cats (*Felis catus*; Cove et al. 2018).

Practical Considerations in Using Behavioral Knowledge in Restoration

The behavioral elements we describe can be directly applied to restoration projects (Box 1).

Box 1.

An example of applying behavioral information in restoration: the Southwestern willow flycatcher

The information we present in our decision tree (Fig. 2) is intended to be general but can be adapted to identify and mitigate factors that constrain the outcomes of specific restoration projects. To illustrate, we cite work on the Southwestern willow flycatcher (*Empidonax traillii extimus*; Schofield et al. 2018). Californian populations of this species have declined due to massive habitat loss, and habitat restoration efforts are underway to create new habitat (Fig. 2, step 1). Often, these efforts are successfully implemented (steps 2–3), but birds do not occupy restored sites. For this species, a lack of vocalizing conspecifics (e.g., missing cues, S4a) is likely to be the cause. Schofield et al. (2018) conducted a field experiment, broadcasting flycatcher vocalizations in 14 meadows that had been restored (hydrological restoration through channel filling, plus livestock removal) but were unoccupied, and not broadcasting vocalizations in 19 unrestored control sites. These sites were located close to known breeding populations (so scenarios S2 and S3 were not likely to cause restoration failure). Flycatchers were seven times more likely to recolonize restored sites than controls following broadcasts. The restored sites were selected to have similar vegetation characteristics to known breeding sites to maximize the chance that the animal's habitat requirements are met (step 5). However, in the future, conspecific broadcasts need to be accompanied by monitoring to assess fitness (e.g., nesting success) and multi-year persistence (Schofield et al. 2018).

However, such projects are often limited by financial or human resources available for implementation, maintenance, and monitoring. What then, in practice, should be considered when deciding whether to incorporate behavioral knowledge in restoration projects?

Key consideration 1: When should we prioritize the use of behavioral information?

Behavioral knowledge can help inform all of the three broad phases of restoration (i.e., planning, doing, and evaluating; Prach et al. 2019). During planning, knowledge of behavior can help identify which habitat elements should be targeted. If we make the wrong decisions initially (e.g., by replanting plant species that will not provide required resources), it may be difficult, and more costly, to remedy such choices later in the restoration process. Using behavioral information from the outset may be more cost-effective than attempting to retrofit later.

We can use behavioral information, in particular knowledge of the habitat elements that are either used as cues or determine fitness, to select sites to restore (i.e., in the doing phase; Prach et al. 2019). Sites can be targeted that have some of these elements already, so restoration focuses on supplementing these, which may be more cost-effective than rebuilding much degraded habitats. Alternatively, information about which habitat elements are required may allow us to avoid sites that are so degraded that these elements will never, or take a very long time, to develop. As outlined above and elsewhere (Lindell 2008, Berger-Tal et al. 2011), behavioral indicators can also be used in the evaluation phase to help assess progress toward goals.

The costs and benefits of collecting the behavioral information or implementing the behaviorally informed solutions in Fig. 2 have not been quantified. Some solutions will be relatively inexpensive, such as providing missing habitat-selection cues by using conspecific playback recordings providing that this does not include the costs of preliminary research needed to determine that this is the essential cue, but other actions may be more labor- and resource-intensive, such as coupling restoration with reintroductions of target animals from captive-bred populations or with predator control. An important step is to consider the costs and benefits of different options, informed by knowledge of behavior. Whether to apply behavioral knowledge can be assessed by formal comparative effectiveness analyses (Blumstein and Berger-Tal 2015: Fig. 1), which outlines the relative costs and effectiveness of different conservation solutions.

Key consideration 2: How could behavioral knowledge be incorporated into resource-limited restoration programs?

Collecting detailed behavioral information at a wide variety of restoration sites in any system is likely to be logistically challenging. Instead, intensive research sites (i.e., where behavioral information is collected) could be embedded within a wider network of spatially extensive in situ monitoring locations, similar to multi-scaled environmental monitoring networks (Jones et al. 2010). These research sites can be used to collect information about habitat-selection behavior and the determinants of fitness, or to trial behaviorally informed solutions.

It is important to highlight that there are precedents where information about animal behavior is directly informing restoration. The Midland restoration project in Tasmania is one such example (Jones and Davidson 2016). In this project, information about the risk-sensitive movements of mammals and the subsequent fitness outcomes of such movements are being combined with occupancy modeling and landscape genetics to guide revegetation actions. Other examples from the broader field of conservation behavior (Blumstein and Fernandez-Juricic 2010) provide further evidence that using behavior in applied situations is feasible. In situ predator training has been shown to be a useful method to improve anti-predator responses of predator-naïve threatened bettongs in the Arid Recovery project (West et al. 2018) and to improve the success of translocations to areas with predators in predator-naïve Australian bilbies (Ross et al. 2019). Researchers working in the Banff National Park in Canada have been collaborating with management agencies to develop simple warning systems based on bear learning to reduce train collisions (St. Clair et al. 2019). The last example here is from a recent special issue that presents a range of recent studies illustrating the use of behavioral knowledge in conservation (Bro-Jørgensen et al. 2019). This compilation of examples, alongside the extensive reintroduction and translocation literature, shows that using such knowledge in restoration projects is also possible.

Key consideration 3: Can behavioral knowledge be misleading?

While behavioral knowledge can help guide restoration efforts, such data sometimes might provide misleading information. Careful consideration needs to be given to the methods that are used to collect behavioral information. Inferences about habitat preference from observational data (e.g., abundances, densities) can lead to incorrect conclusions because observed patterns can have other causes (e.g., differential mortality; Underwood et al. 2004). Foraging rate may be used as an indicator of success (assuming food is more plentiful) but foraging rate and habitat quality may not be positively correlated. European hare (*Lepus europaeus*) spend more time foraging in vegetation that contains relatively lower food quantity and quality when predatory red foxes (*Vulpes vulpes*) are present (Weterings et al. 2018). To reliably use behavioral indicators, we need to understand when these provide a meaningful representation of habitat quality.

Behavioral habitat-selection preferences can be misleading about habitat suitability, as the ecological trap literature demonstrates (Robertson and Hutto 2006). Assessing habitat preferences experimentally and measuring fitness directly provide the strongest evidence that animals prefer restored sites, and there are good fitness outcomes (Hale et al. 2019*b*). When proxies are used for the latter, it is important to determine how closely these are linked to fitness outcomes. For example, breeding behaviors can be weighted by how closely they are associated with ultimate breeding success (viz. production of independent young; Mac Nally 2007).

Key consideration 4: Adaptive management is critical

Restoration is an iterative process that involves periods of assessment of success, often within an adaptive management framework (Holling 1978, Prach et al. 2019). For simplicity, our decision tool presents information as a linear process. However, it is important that assessments are undertaken throughout the planning, doing, and evaluating phases of restoration and that management actions evolve throughout the life of individual projects. Behavioral knowledge can help in the planning stage and to redefine goals, targets, and indicators that are used with monitoring data.

Greater reporting of case studies showing the success or failure of different uses of behavioral information should be made available to help guide other projects. For example, this could be done in a similar way to those in *Conservation Evidence* (https://www.conservationevidence.com/), which is an online resource aimed at supporting decisions to help maintain and restore biodiversity. Once sufficient information becomes available, it can be assessed using systematic reviews and meta-analyses (Berger-Tal et al. 2018) to guide future restoration actions.

Conclusions and Future Research Directions

Habitat restoration is urgently needed but often fails to have desired fitness benefits for focal animal species. We suggest reformulating restoration goals for animals to ask: How do we restore habitats so that (1) target animals occupy them and (2) the restored habitats provide all the features that animals need for growth, survival, and reproduction? Greater insights into habitat-selection behavior and how habitat variation is related to fitness will help to increase restoration successes, but there are two key knowledge gaps that need to be addressed.

First, we need to better understand when investing in behavioral knowledge is warranted. To do so, we need information about how often restoration fails due to a lack of behavioral information compared with other constraints (e.g., influence of large-scale, long-term disturbances such as land use and climate change). Second, we must identify the major impediments to the integration of behavioral knowledge into restoration actions. Are the major obstacles due to (1) logistics (time, money, expertise); (2) knowledge gaps about animal behavior; or (3) management agencies considering other constraints on restoration to be more important? Answering these questions, coupled with improving knowledge of habitat-selection behavior and fitness outcomes, will mean that restoration projects will be more likely to lead to the establishment of self-sustaining populations of target animals. This in turn will help to limit and reverse the adverse effects of habitat loss and degradation on biodiversity.

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