Evolutionary traps are severe cases of behavioral maladaptation that occur when, due to human activity, the cues animals use to guide their behavior become uncoupled from their fitness consequences. The result is that animals can prefer the most dangerous resources or behaviors, even when better options are available. Traps are increasingly common and represent a significant wildlife conservation problem. Understanding of the more proximate sensory-cognitive mechanisms underpinning traps remains poor, which highlights the need for interdisciplinary and collaborative approaches to investigating traps. Key to advancing basic trap theory and its conservation applications will be the development of appropriate and tractable model systems to investigate the mechanisms that cause traps within species, and how mechanisms vary across species.

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Ecological traps vs. undervalued resources

The decoupling of behavioral preference with fitness performance that leads to traps has been universally associated with rapid environmental changes elicited by human activity [6**,13]. An evolutionary trap arises when a poor-quality resource or behavior becomes as, or even more attractive than another higher-quality one (Figure 1a). Animals so affected will either be unable to distinguish mate, food items or other options that differ in their fitness benefits (so-called ‘equal-preference traps’, Figure 1b, mechanism B), will actively prefer the worse option (a.k.a ‘severe’ traps’, [13], Figure 1b, mechanism A) or both (Figure 1b, mechanism C, A and B). Equal-preference traps occur when the quality of the resource and/or fitness outcome of a behavioral option is degraded, but the environmental cues associated with decisions have not been altered [14,15,16,17]. Severe traps occur when environmental cues are altered to make a resource more attractive, but also when the attractiveness of a resource is increased at the same time its fitness value is degraded (Figure 1b) [3,18,19,20]. To date, there currently exist more than 60 examples of evolutionary traps. The frequency of these three mechanisms appears to be roughly equal in nature, as do equal-preference vs. severe traps [6**].

Almost completely unknown from an empirical point of view is the maladaptive corollary to the evolutionary trap — the undervalued resource [21]. Undervalued
resources represent behaviors and resources (e.g. mates, habitats) that are of high fitness value, but that are relatively unattractive compared to alternatives (Figure 1a). Just as traps are falsely attractive, undervalued resources are falsely unattractive. While undervalued resources are intuitive explanations when animals fail to exploit suitable food supplies, habitats [22,23], or other resources, there currently exists no compelling evidence supporting their existence inconsistent with an adaptive explanation. Presumably, the general mechanisms by which traps are created have counterparts that create undervalued resources (Figure 1b), however, rigorous empirical tests are lacking. This is because robust evidence for this phenomenon would require evidence eliminating a broad range of adaptive explanations for why animals are failing to exploit a novel and apparently valuable resource, or even an experiment capable for forcing animals to exploit a resource they apparently avoid; both are challenging. As such, it is unclear if the conservation-relevance of undervalued resources meets or exceeds those of evolutionary traps.

**Exposing the sensory-cognitive underpinnings of traps**

Though the general pathways by which cue-environmental correlations become mismatched have been identified, understanding of the more proximate sensory-cognitive mechanisms remain unclear. Can the mis-weighting of cues in decisions be attributed to sensory organs being poorly designed to process novel types of information? Conversely, such organs may be relatively reliable in passing information on to the brain, but the algorithms for evaluating that information could become outdated and, therefore, corrupted. That exaggerated forms of evolved behavioral cues (a.k.a. supernormal releasers) commonly trigger abnormally intense behavioral responses has been known for almost 65 years [24], and this is a common mechanism by which evolutionary traps are triggered (degree of polarized light: [3]; prey abundance: [16]; mate size: [25]; nest site availability: [26].

Organisms commonly evolve the use of multiple cues to guide a single behavior, however, and in these cases it is less clear whether alteration of a single cue is always sufficient to trigger an evolutionary trap. Individual cues might be weighed equally or multiplicatively, and, at least for some organisms or behaviors, decisions may only be triggered via the conditional presence of multiple ancillary cues. Male Giant Jewel Beetles (*Julodimorpha bakeri*), for example, appear to use the size, color and texture of potential mates as cues to their suitability, and seem to prefer to mate with beer bottles, primarily because of their relatively large size compared to female beetles [27]. Yet, texture and size alone are insufficient to attract mates, as males find fresh beer bottles unattractive. Supernormal strong versions of individual cues can therefore increase preferences, however, these cues appear to be weighed in a conditional behavioral algorithm such that all cues must be present at some threshold level. Knowing which environmental cues are used to guide behaviors, how organisms weigh them, and the shapes of the resulting norms of reaction (e.g., unimodal vs. threshold) in behavioral response to increasing cue strength will...
be essential to understanding why traps occur and for devising strategies for dismantling them.

Implicit in a traditional sensory ecology point of view is the assumption that only evolved cues can guide focal behaviors. Yet, cues evolved for a specific purpose may be perceptually co-opted to elicit completely different behaviors in a novel context. For example, female zebra finches (Taeniopygia guttata) prefer males to whom white, feathered crests (but not those of any other color) have been added, and it is postulated that this is because wild females prefer to line their nests with white feathers [28]. Night-active aquatic insects, moreover, are attracted not only to water bodies or artificial polarizers illuminated by moonlight or artificial night lights (polarized light is an ooposition cue associated with water), but also to the artificial night lights themselves (which mimic the moon, a navigational cue) [29], such that they prefer to lay eggs on artificial polarizers under night lights [5,29]. These examples illustrate that cues from one behavioral context can trigger maladaptive behavior in a separate one, possibly because such cues have never before occurred in close spatial or temporal proximity. Natural selection may have never had an opportunity to shape cognitive systems to more carefully partition their interpretation within separate behavioral contexts. This represents an unappreciated potential mechanism by which maladaptive behavior, including traps, can be triggered. Indeed, that natural selection has repeatedly exploited such a mechanism of manipulation within the context of sexual selection [so-called ‘sensory traps’, [30]] suggests that this is a potential avenue by which behavior can be ‘hijacked’ by ecological novelty.

Are traps common and predictable?
The question of the ubiquity of evolutionary traps was first posed 10 years ago when a review of the literature surprisingly found only five examples that explicitly met the criteria for constituting a trap [13]. There currently exist over 60 examples meeting evidentiary criteria, yet it is unclear whether this growth is a consequence of the acceleration of anthropogenic habitat change, and/or if researchers are looking more carefully for the presence of traps because of increased awareness of the phenomenon. In fact, all of the aforementioned examples were the unintended results of human activity, but none were predicted by scientists. All were detected only after their creation. Perhaps one of the most central and unanswered questions in the subfield is, therefore, whether behavioral ecologists can predict the ecological or environmental conditions under which traps will occur. That all known aquatic insect taxa on earth have evolved the ability to locate water via their polarized light signature and so can be ecologically trapped by sources of polarized light pollution indicates that ecologically similar taxa can share behavioral susceptibilities that provide some predictability in where traps are likely to arise as a function of human development. Food subsidies, too, seem to be a common mechanism by which animals and their predators are both attracted to a common resource creating ecological traps [6]. General rules about susceptibility to traps may emerge as a function of ecological function, trophic level, degree of ecological specialization and habitat association, and this area bears investigation. Adaptation of a risk-assessment framework to predict activities that are likely to trigger ecological traps for at-risk species using extant knowledge of the behavior, life-history and habitat requirements [e.g. 31] is an important first step.

One potentially fruitful avenue for simultaneously enhancing our behavioral knowledge of species while addressing the efficacy of predicting traps is to begin to experimentally field test a broad diversity of species whose habitat choices, behavioral or life-history characteristics suggest a predisposition to being trapped. For example, Robertson et al. [32] developed an experimental field assay for evaluating the susceptibility of aquatic dipterans to evolutionary traps caused by polarized light pollution. They mapped behavioral reaction norms of attraction to the % of polarized light across values typically reflected by natural water bodies and those produced only by man-made objects. Results showed that while reaction norms differed in shape, susceptibility to evolutionary traps was taxonomically broad. A similar study shows that evolutionary traps created by polarized light pollution are more important during the day while, unexpectedly, both terrestrial and polarotactic aquatic insects are more attracted to evolutionary traps triggered by unpolarized light at night [33]. This type of field experimental approach can be adapted to map the reaction norms for multiple and diverse cue types, and expose susceptibility to trap conditions across diverse taxa.

Demographic consequences of traps
Demographic and eco-evolutionary simulations universally show that traps represent perhaps the most severe form of demographic sink, capable of rapidly crashing populations when trap conditions are sufficiently common, and preference for traps resources are higher [8,9,10,11,12+]. This and the increasing rate at which traps are being detected places evolutionary traps more centrally as a global-scale conservation problem. Indeed, studies of traps have focused heavily on birds and insects [34], but evolutionary traps may affect any taxa or biological system. There is increasing recognition among botanists that plants respond to ways analogous to animal behaviors [35] and so it is possible that plant species, too, may be susceptible to traps. Traps can act in concert with other stressors (e.g., habitat loss and fragmentation) and commonly affect already rare and/or endangered species [13,15,36,37,38]. Indeed, traps may have already been responsible for contemporary extinctions, but empirical evidence linking evolutionary traps to population declines is limited to three examples. Two studies demonstrated
population declines in endangered animals only after the creation of a local evolutionary trap [15,39]. More recently, continent-wide declines in honey bee populations have been linked to an evolutionary trap created by neonicotinoid poisons that bees preferentially consume [40,41].

Traps can clearly persist for multiple years at the same site [18,19,20] confirming that they need not be ephemeral in time or space. Yet, empirical demographic studies evaluating the ability of traps to drive population declines are desperately needed both to inform conservation efforts and ecological theory. Such studies will need to focus at broader spatial and temporal scales than existing, typically site-focused studies, and must explicitly consider the potential for learning or natural selection to facilitate "escape" from traps [10,11,42,43]. Behavioral ecologists could develop closer relationships with scientists and conservation practitioners who monitor populations and key demographic parameters to: 1) clarify the specific conditions that suggest the presence of an evolutionary trap, and 2) devise ways to gather ancillary data on behavioral preferences that can be used to test evolutionary trap-driven hypotheses.

**Conclusion**

Because the study of evolutionary traps is still in its infancy, scientists have focused heavily on satisfying the evidentiary criteria necessary to document their basic existence [13], and not necessarily the behavioral and demographic mechanisms generating them. Because the corruption of evolved sensory and/or cognitive mechanisms are common proximate triggers for traps, our ability to predict where, when, and why traps occur, how to eliminate them and mitigate their impacts, and even how to use them as tools in the control of invasive species will center around our ability to deepen our understanding of their mechanistic bases [44]. Model experimental systems for asking behavioral, demographic and applied questions in conservation science are desperately needed to move theory forward. Understanding if broader taxonomic groups share sensory-cognitive systems that are susceptible to corruption by particular types of ecological novelty would be especially valuable in resource management. Behavioral and conservation scientists will also benefit from adopting new approaches to locating, predicting and understanding traps such as landscape ecological methods [45], and experimental mapping of behavioral reaction norms [33,46], especially in relation to the careful measurement of the physical attributes of the visual, olfactory or other sensory signals animals are using to guide their behavior. And because behavioral maladaptation is driven by factors that shape both the reliability of information and how it is sensed and processed [7,47,48], sensory ecological perspectives that emphasize the design of sensory organs to gather information and recognize that non-human organisms rely more heavily on non-visual senses will be invaluable.

Collectively, these needs call for increasingly interdisciplinary collaborations and cross-cutting approaches that overcome disciplinary limitations [49].

**Conflict of interest statement**

Nothing declared.

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**References**


This review paper developed criteria for identifying evolutionary traps and found that over 50 empirical examples exist, affecting a broad diversity of taxa, corrupting a diversity of behaviors, and that were triggered by a wide range of human activities topped by the introduction of invasive species, but including ecological restoration activities. This effort provides guidance on how to apply signal detection and adaptive plasticity theory to identifying traps and investigating their mechanistic basis, and outlines ways to eliminate ecological traps based upon and understanding the their mechanistic causes.


This review provides a context and conceptual model for understanding why some individuals and species respond maladaptively to rapidly changing environments and ecological novelty while other show adaptive behavioral responses. It draws on several existing frameworks (i.e., ecological traps) and theoretical approaches (i.e. cost-benefit theory) to help behavioral scientists interpret existing variation in behavioral responses to novelty and to ask and answer new and innovative questions.


This first examination of the dynamics of metapopulations containing evolutionary traps agrees with earlier two-population models showing that traps most rapidly reduce metapopulations when they are a larger fraction of available habitat, when traps are more attractive and are most damaging for species with faster population growth rates. It breaks new ground in showing that trap habitats can help stabilize metapopulations and that natal-habitat preference exacerbates population declines.


This study uses a field experimental approach to partition the relative effects of two different types of light pollution cues in triggering evolutionary traps for two species of aquatic insects. Its illustration that distinct light pollution cues, evolved to guide different behaviors, can non-linearly react to increase the attractiveness of evolutionary traps is unique.


This is the first study to examine the degree to which a taxonomic group of species were susceptible to ecological traps associated with a single cause: Artificial sources of polarized light pollution like asphalt roads, solar panels or glass buildings. It mapped behavioral reaction norms of attraction in relation to variation in polarized light and found that 7 distinct species tested were most attracted to degrees of polarized light that exceed levels capable of being produced by natural water bodies and so were predisposed to being caught in ecological traps associated with artificial polarizers.


Nocturnally-active aquatic insects are attracted to unpolarized sources of polarized light (artificial night lights) and to artificial objects like asphalt or buildings that reflect and polarized that light. Because use of unpolarized light evolved within the context of navigation while attraction to polarized light pollution evolved within the context of oviposition behavior, it is unlikely how animals should weigh these two separate causes of ecological traps when they are placed in close spatial context. In contrast to terrestrial insects that were only attracted to sources of unpolarized light, aquatic insect taxa were attracted to ecological traps triggered by both unpolarized and polarized light pollution and different insects species maladaptively weighed these cues in diverse ways.


This review collects examples illustrating how taking a mechanistic approach toward understanding animal behavior, especially a sensory ecological perspective, is fundamental to solving management
problems. It provides a conceptual model for the application of this approach within the context of the field of conservation behavior.


The authors developed a novel method for visualizing ecological traps across large natural landscapes by combining a spatially explicit model of anthropogenic threats (poaching) to a large mammal, the Spectacled Bear (Tremarctos ornatus), with a habitat selection model based upon occurrence probability. The effort illustrated, counterintuitively, that habitat corridors between protected areas could actually enhance access to ecological traps. It also illustrated how even sparse monitoring data could be useful in identifying potential ecological traps.


