

Evolutionary traps as keys to understanding behavioral maladaptation

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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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Introduction

Animals use environmental cues to guide their behaviors. The predictive value of those cues in accurately guiding behaviors, however, is a function of the historical correlation between the cues and the fitness value of responding to them. When rapidly changing environments decouple cues from their fitness correlates, animals can actually prefer to perform behaviors that are most likely to lead to reproductive failure or death. Evolutionary traps exemplify this severe form of behavioral maladaptation in which rapid environmental change triggers a mismatch between the perceived and actual fitness value of a resource or behavioral action [1,2]. For example, aquatic insects prefer to lay their eggs on man-made objects (e.g.

asphalt, glass buildings) where they fail to hatch because they reflect more polarized light, their primary habitat selection cue, than do natural water bodies [3,4,5].

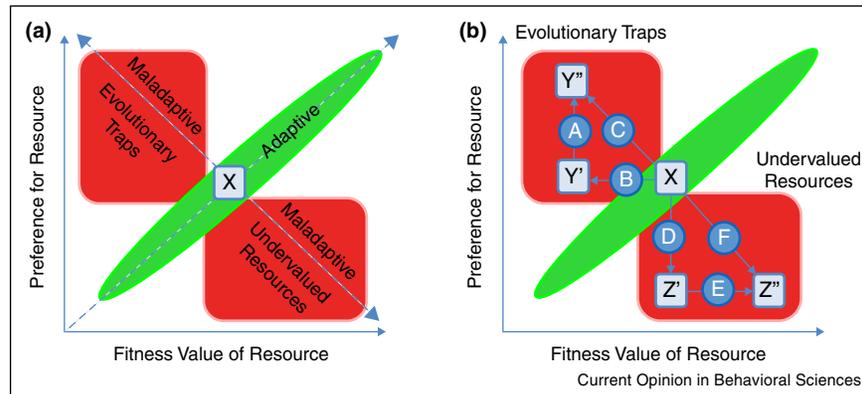
Evolutionary traps appear to corrupt a broad diversity of behaviors (e.g., mate and food choice and habitat selection—a.k.a. ‘ecological traps’, and navigation), affect a broad range of animal taxa, and be triggered by a diversity of environmental changes [6^{**}]. Traps therefore represent a theoretically fascinating phenomenon that occurs at the nexus of ecological, evolutionary, and behavioral sciences and have rapidly garnered attention in more basic [7^{**}] and applied behavioral and ecological sciences due to their potential to accelerate population collapses of native species [8,9,10,11,12^{*}]. The impetus for this paper is to address the frontiers of this cross-disciplinary phenomenon by illuminating where new knowledge is needed to inform and test basic theory, and facilitate further improvements in our ability to apply trap science toward the management of wildlife populations.

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

Figure 1



The adaptive vs. maladaptive preference–performance axes and the mechanisms that lead to evolutionary traps and undervalued resources. **(a)** Over evolutionary time, natural selection should lead to an alignment in the relative preference animals have for a resource (e.g. mate, food item, territory, point X) and its fitness value such that resources that garner greater fitness rewards are preferred over those with a lower fitness value (area of green ovoid). Rapid environmental change, however, may decouple this preference–performance correlation such that poor-quality resources appear more attractive than higher quality ones (evolutionary traps, top left square) or vice versa (undervalued resources, bottom right square). **(b)** Resources may be altered by making them more attractive (mechanism A, $Y' \rightarrow Y''$), less fitness-positive (mechanism B, $X \rightarrow Y'$), both simultaneously (mechanism C, $X \rightarrow Y''$), or both in sequence (A then B; B then A). In this way resource Y' becomes an 'equal-preference trap' relative to resource X, and Y'' becomes and 'severe' trap relative to X. In theory, these three trap mechanisms have opposite counterparts (D, E, and F) that lead to undervalued resources.

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 of 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 bakerwelli*), 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 green beer bottles unattractive. Supernormally 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 nest 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 oviposition 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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