

Trojan Females and Judas Goats: Evolutionary Traps as Tools in Wildlife Management

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Evolutionary traps occur when rapid environmental change causes animals to prefer poor-quality resources (e.g., habitats) or behaviors over higher-quality ones that lead to greater survival or reproductive success. Here, we bring together science from the pest-control, eco-evolutionary, and conservation communities to outline how evolutionary traps can be repurposed to eliminate or control pest species. We highlight case studies and devise strategies for the selection of appropriate cues to manipulate, traits to target, and mechanisms to use in setting evolutionary traps that will most rapidly reduce animal abundance while preventing evolutionary escape. Approaches to setting evolutionary traps have been diverse but uneven with respect to principles that would make them more effective, such as strengthening resource preference, triggering out-of-context behaviors, and targeting underexploited sensory modalities. We find that evolutionary traps are demonstrably effective and unique tools with high target-species specificity that are deployable in concert with more traditional approaches.

Keywords: ecological trap, conservation behavior, pest control, invasive species, maladaptation

Evolutionary traps are cases in which rapidly changing environments cause animals to prefer resources or preferentially execute behaviors with poor fitness outcomes (Schlaepfer et al. 2002, Robertson et al. 2013). Traps occur when the environmental cues that animals use to adaptively guide their behaviors become associated with resources (e.g., habitats, mates, or food) that are dangerous or otherwise reduce fitness relative to historical conditions (Schlaepfer et al. 2002, Robertson and Hutto 2006). This decoupling of cues from their fitness correlates creates a maladaptive preference–performance relationship such that traps, as their name suggests, lure animals to prefer to settle in locations rife with predators or disease (Weldon and Haddad 2005, Hawlena et al. 2010), to prefer genetically incompatible sexual partners (D’Amore et al. 2009), or to disperse away from the most suitable habitats (Tuxbury and Salmon 2005). For example, water is the primary natural source of horizontally polarized light, so most species of aquatic insects have evolved the ability to locate water bodies where they can lay their eggs using this unique cue (Horváth 2014). However, human-made objects such as solar panels, asphalt roads, and dark glass buildings are capable of polarizing a higher fraction of reflected sunlight than natural water bodies, such that these insects actually prefer to oviposit on artificial surfaces where their eggs perish despite the availability of nearby rivers and lakes (reviewed in Kriska et al. 1998, 2008, Horváth et al. 2010).

Whether evolutionary traps are habitats (Weldon and Haddad 2005, Robertson and Hutto 2006, Robertson et al. 2013), mates (D’Amore et al. 2009), food items (Firlej et al. 2010), human structures (Jeffres et al. 2012), or agricultural activities (Hedin et al. 2008), they have generally been associated with human-induced rapid environmental change (Robertson et al. 2013). They differ from similar eco-evolutionary phenomena (e.g., mimicry) in that the maladaptive behavior they create is an unintentional consequence of that change (box 1). And because traps attract animals away from more fitness-positive resources, traps act as attractive population sinks capable of rapidly reducing—and even extirpating—populations of affected species (Kokko and Sutherland 2001, Fletcher et al. 2012). Empirical examples of traps are emerging rapidly, and because they appear to negatively affect a broad diversity of taxonomic groups, traps have become recognized as a significant threat to the conservation of native species that act in conjunction with other better understood causes of population decline (e.g., habitat destruction and fragmentation; Kokko and Sutherland 2001, Robertson et al. 2013). However, in the same way that traps are a threat to native wildlife whose populations conservationists hope to stabilize, they also have the potential to be employed as tools in the management of species whose numbers need to be controlled or reduced (Duerr et al. 2007). Conventional approaches to the control of target species

Box 1. Definitions contrasting relevant eco-evolutionary phenomenon and wildlife management tools.

Deception: The transmission of misinformation by one animal to another, of the same or different species, in a way that propagates information that is not true. Because this transfer is intentionally—although not necessarily consciously—transmitted from a sender to a receiver, deception is a form of communication. Mimicry and camouflage are mechanisms of deception that enable animals to appear to be other than they are and so trigger temporarily maladaptive behavior on the behalf of the signal receiver.

Sensory trap: A phenomenon in which sexual preferences for mates originated in nonsexual contexts or as by-products of preferences that were co-opted by novel displays into favoring individuals that use the displays in mating. Because one sex is manipulating the sexual preferences of another, sensory traps are a form of communication. But because the offspring of successful mating will inherit the manipulative and newly successful trait, sensory traps cannot be said to be maladaptive.

Evolutionary trap: Any resource (e.g., mate, food, or habitat) or behavior that an organism finds equally or more attractive than other available resources or behaviors despite a reduced fitness value (Schlaepfer et al. 2002). Traps occur when rapid environmental change (human induced or otherwise) decouples the correlation between the environmental cues organisms have evolved to guide their behavior and the fitness value of those behaviors. Because there is no animal intentionally signaling deceptive information, traps are technically not forms of communication, although they result in maladaptive behavioral responses. The intentional deployment of traps as tools that signal information to animals and trigger maladaptive behavior can transform them into forms of deception.

Animal trap: A device used by humans to remotely catch an animal for a variety of purposes (e.g., food, fur, or pest control). If animal traps have properties (e.g., baits or colors) that cause animals to preferentially associate with them over other available resources, they may act as objects of deception or evolutionary traps. Animal traps will often have the same impact on individual trapped animals as will evolutionary traps, but the impacts on the focal animal population can differ. For instance, traps for sustainable harvesting would avoid reducing abundance of the trapped population, whereas evolutionary traps would not.

are often limited by cost, their efficacy at low target-species densities (Clout and Russell 2006), deleterious effects on nontarget species (Bergstrom et al. 2009), and loss of efficacy due to rapid evolutionary responses (Tabashnik et al. 2008), spurring strong demand for more targeted, efficient, and cost-effective approaches (Simberloff et al. 2005).

Perhaps one of the most successful conservation interventions of the last century, the eradication of over 230,000 feral goats from Pinta, Isabela, and Santiago Islands, Galápagos (Cruz et al. 2009), was accomplished through the strategic deployment of evolutionary traps. Efforts began with a phase of ground-based corralling and hunting that eliminated 84% of the goat population and an aerial hunting phase that eliminated a further 15%. Previous eradication efforts failed at this stage because animals are most difficult to detect when they reach low densities (Campbell and Donlan 2005) and eradication of every animal is essential. Both of the traps deployed by this intervention involved captured female goats fitted with radiotelemetry collars and released. Once released, the so-called Judas goats found other individuals by sight and smell and associate with these new social groups (Rainbolt and Coblenz 1999). After release, hunters repeatedly relocated Judas goats by ground or helicopter and killed associated conspecifics, further reducing the population to only approximately 1% of original numbers. The ability of Judas goats to attract conspecifics was subsequently enhanced by sterilizing them and putting them in chemically induced estrous (becoming Mata Hari goats, *sensu* Cruz et al. 2009), stimulating sex pheromone production to lure otherwise wary male goats, which would have continued to adversely affect native biota for years even if the goat population did not grow. Collectively, the sequential deployment of Judas and Mata Hari goats effectively

converted these individuals into attractive but dangerous conspecifics, leading to complete eradication of nearly a quarter million feral goats and a dramatic restoration of the ecological community.

Here, we outline a conceptual framework by which evolutionary traps can be repurposed as tools of deception to eliminate or control target species (figure 1). We use this empirical analysis to help guide strategies for the selection of appropriate cues to manipulate, the mechanisms to use and the traits to target that will most rapidly lead to reductions in target numbers, and to demonstrate how to strategically deploy traps without allowing populations to escape via learning or rapid evolution. We bring together the theory of evolutionary traps with science from the pest-control, ecological, and conservation communities to highlight case studies of target-species control that have successfully employed traps as tools and those that would have benefitted from more explicit use of the framework we highlight. We conduct a meta-analysis of the trap literature to ask whether particular anthropogenic causes or proximate mechanisms triggering traps are linked to more severe fitness consequences for trapped populations and so might represent more effective strategies for intentionally deploying evolutionary traps in the context of target-species control. Finally, we discuss how our approach differs from that of traditional wildlife management and biocontrol strategies, the unique implications of our approach, and critical caveats to the employment of the strategies we advocate.

How to set an evolutionary trap

The primary goal in intentionally creating an evolutionary trap is to attract an animal to a resource (e.g., mates or prey items) or situation that is as dangerous or fitness negative as



Figure 1. Species whose numbers have been, or could be, effectively controlled using evolutionary traps. A female mosquito (*Aedes stephensii*) engineered with a genetic drive to carry a gene that reduces the fertility of male offspring (Gemmel et al. 2013; top left; photograph: Stock.xchng/G. Bibor). An adaptation of the Trojan female technique has been highly effective in eradicating feral goats (top right) in the Galapagos Islands (Cruz et al. 2009; photograph: Stock.xchng/J. Bernalte). The numbers of Cane Toads (*Rhinella marina*) can be controlled via evolutionary traps that induce cannibalism of young (Crossland et al. 2012; photograph: Flickr/P. Kirillov) and by exclusion fencing of habitats at invasion hubs (Florance et al. 2011). Khan and colleagues (2008) identified trap crops that emit volatile organic chemicals that attract stem-boring insects such as the African maize stalkborer (*Busseola fusca*, bottom right; photograph: Creative Commons/B. Calatayud) to preferentially settle away from corn plantations.

possible by making it as attractive as—or even more attractive than—alternatives that are safer or of higher quality. Anglers employ this same technique in that the vast majority of worms are not associated with hooks, and artificial lures can be designed that are actually more attractive than any existing natural prey item. The cues that bait individuals need not simply be those associated with food items, though, but may be mating opportunities, apparent safety or shelter, oviposition sites, conspecifics, or other resources that directly or indirectly enhance fitness under typical circumstances. The mechanism of fitness reduction may be immediate mortality, but it need not be if less lethal or immediate declines in fitness are more effective or feasible in reducing population growth rates over a desired time span. Although

hunting and fishing are activities known to generate evolutionary trap dynamics, we avoid discussion of case studies in this area because the goals of these activities commonly focus on the sustained extraction of a limited resource rather than targeting population collapse.

The broad approach to intentionally setting an evolutionary trap in any one case follows from the three general mechanisms by which traps are known to be inadvertently created by human activity (Schlaepfer et al. 2002, Robertson and Hutto 2006, Robertson et al. 2013). All three increase the attractiveness of a resource or behavioral option relative to its fitness value, decoupling evolved correlations between preference and performance (figure 2a). First, one can introduce a new resource or alter existing environmental cues such

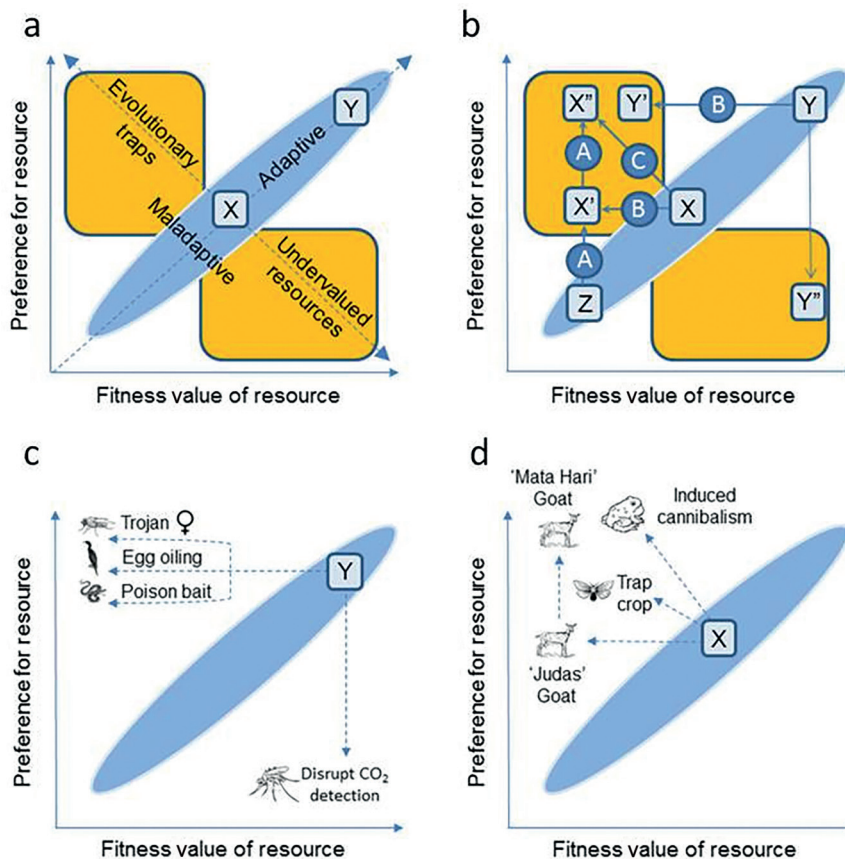


Figure 2. Conceptual models of strategic options for setting evolutionary traps for pest species. (a) Conservation interventions designed to improve resources for focal species will increase their performance value with the assumption that evolved and adaptive preferences will be correlated (“adaptive axis”). In creating traps for pest species, managers must decouple these preference–performance correlations along the “maladaptive axis” by devaluing existing resources (i.e., creating “undervalued resources,” bottom right) and overvaluing new or existing resources (i.e., creating evolutionary traps, top left). The boxes outlining the conceptual space in which traps and undervalued resources are actually maladaptive are only valid for any one case relative to alternative behavioral options an organism might select. In other words, a resource might be a trap in one environment but not in another because of the availability of higher-quality resources. (b) Broad strategies for setting evolutionary traps. Resource Z can be made more attractive, via mechanism A, such that this altered resource X' is now an equal-preference trap relative to resource X. If it is altered such that it becomes even more attractive (now X''), it will now act as a severe trap relative to resource X. The quality of a portion of resource X can also be degraded (becoming X') such that it becomes an equal-preference trap via general mechanism B. Actions making X more attractive while also reducing its fitness value result in a severe trap (X'') via general mechanism C. Degradation of even high-fitness-value resources (Y) can still lead to the creation of equal-preference traps (Y'), whereas making them less attractive can actually cause them to be avoided (Y''). Mechanisms A, B, and C, by which traps are created, all have equal and opposite counterparts by which higher-quality resources can be turned into undervalued resources (arrow on the bottom right). (c) Degrading the fitness values of existing resources (offspring viability, Duerr et al. 2007; prey items, Clark et al. 2012; mate quality, Gemmel et al. 2013) makes them look equally attractive but less valuable, causing them to act as “equal-preference traps” (top left). Chemicals that disrupt the ability of mosquitos to track hosts make available hosts hard or impossible to detect, reducing their apparent fitness value and creating an “undervalued resource” (Turner et al. 2011, bottom right). (d) Three methods of creating “severe” evolutionary traps. The targeted application of high concentrations of bufotoxin can induce preferential cannibalism of eggs and larvae by conspecific cane toad adults (Crossland et al. 2012, top right). Plants with a high diversity of focal volatile organic compounds surrounding food crops attract stem-boring moths away from crops but are unsuitable for larval growth (Khan et al. 2008, center). Goat eradication on the Galapagos relied on a two-stage evolutionary trap (Cruz et al. 2009, left). First, managers created a radio-collared Judas goat, which would locate and associate with conspecifics that would then be culled with firearms. When goat numbers became very low, hormone implants transformed Judas goats into Mata Hari goats, which emitted sex pheromones as they traveled through landscapes, enhancing conspecific attraction and concentrating remaining individuals for elimination (bottom right). The icons indicate the taxa of targeted pest species.

that a lower-fitness behavioral option appears as attractive as—or even more attractive than—a higher-fitness one (figure 2b, mechanism A). This occurs when artificial surfaces (e.g., asphalt or glass buildings) polarize reflected sunlight more strongly than natural water bodies do, causing aquatic insects to preferentially oviposit on objects where eggs fail to hatch (Kriska et al. 1998, 2008, Horváth et al. 2010). Second, one can reduce the fitness benefit associated with a preferred behavioral option (or one that is at least not avoided) without altering the associated environmental cues (figure 2b, mechanism B). This occurs when endangered bark beetles feed and oviposit in piles of timber that will later be collected and milled (Hedin et al. 2008). Finally, managers may take both approaches, simultaneously reducing the fitness quality of a behavioral option while altering the cue set to make it more attractive (figure 2b, mechanism C). Unnaturally abrupt forest–field transitions created by logging simultaneously become more attractive

to edge-associated birds and mammalian nest predators that hunt along ecotones, creating a trap via this mechanism (Weldon and Haddad 2005). Traps can be created by altering existing resources (e.g., host plants, habitat structure, or predator refugia) or by introducing entirely new resources (e.g., pheromone traps, poison bait stations, or sterile conspecifics) into an environment whose characteristics make them an evolutionary trap relative to available resources already in that environment.

Manipulation of behavioral cues

Human activities that have accidentally created evolutionary traps solely by reducing the fitness value of a resource (figure 2b, mechanism B) without altering its associated cues are commonly created through the introduction of exotic species (Hawlena et al. 2010) or agricultural activities (Powell et al. 2010). For example, a water reclamation and revegetation project conducted in the Negev Desert included the planting of trees where they had not historically been present. This attracted a predatory perching bird (*Lanius* spp.) that directly reduced populations of an already critically endangered lizard (*Acanthodactylus beershebensis*) whose habitat preferences were unrelated to the presence of trees (Hawlena et al. 2010). This mechanism leads to what are known as *equal-preference traps* (Robertson and Hutto 2006), in which animals are unable to distinguish between the unaltered resource and the degraded, but equally attractive resource or behavioral option. Approaches to intentionally setting these traps within the context of wildlife control often involve contaminating selective prey items with poisons (e.g., mammal-specific poisons) that are undetectable by the sensory systems of target species (figure 2c; Howald et al. 2007).

Invasive fish (e.g., sea lamprey, *Petromyzon marinus*) that parasitize and/or compete with native species (e.g., Asian carp, genus *Cyprinus*) and insects that act as disease vectors (mosquitos, superfamily *Culicoidea*) or parasites on endangered species (e.g., *Philornis downsi*) can be turned into equal-preference evolutionary “mating traps” through different forms of genetic sabotage. In these approaches, lab-bred and genetically altered but phenotypically indistinguishable individuals are released to breed with wild types but are either infertile (sterile male technique), unable to produce female offspring (daughterless technique, Thresher et al. 2014), or only produce sterile male offspring (Trojan-female technique; figure 2c; Gemmell et al. 2013). Other approaches include the application of oil to render already-laid bird eggs infertile such that females continue to invest in parental care (figure 2c; Duerr et al. 2007), as well as the application of (nonrepellent) pesticides to livestock, causing disease-carrying ticks (subclass *Acarina*) to die while attempting to feed on the treated livestock (Keesing 2013). Finally, Cruz and colleagues (2009) used this strategy by creating Judas goats in the first of their two-phase evolutionary-trap approach (figure 2d). Of course, the efficacy of deploying evolutionary traps to manage wildlife must be weighed against the time and labor costs of the trap, as

compared with an alternative control strategy. Some evolutionary traps involve high costs, such as the locating of bird eggs to be sterilized but not removed, in order to trap parents into investing futilely in reproduction (Duerr et al. 2007). But such evolutionary traps still might be more cost-effective than alternative methods.

Perhaps the most obvious approach to setting an evolutionary trap is to introduce attractive cues into an environment, triggering an adaptive behavior at an inappropriate time, place, or context such that it leads to reduced survival or reproductive success. Exaggerated forms of evolved behavioral cues (also known as supernormal releasers) that commonly trigger abnormally intense behavioral responses have been known for almost 65 years, and this is a common mechanism by which evolutionary traps are triggered (degree of polarized light, Kriska et al. 1998; prey abundance, Kloskowski 2012; mate size, D'Amore et al. 2009; nest site availability, Mänd et al. 2009). The selective harvesting of trees in forests creates an open, structurally heterogeneous, and food-rich habitat attractive to olive-sided flycatchers (*Contopus cooperi*) that attracts settling birds away from the relatively predator-free burned forests that are their more common historical breeding habitat (Robertson and Hutto 2007). Such accidental traps can be created by activities that increase the attractiveness of existing but also dangerous resources (human-made structures or habitats; figure 2b, mechanism A). Because preference for resource or behavior with a worse fitness outcome is a quantitatively more extreme degree of maladaptation than that of an equal-preference trap, these traps are known as *severe traps* (Robertson and Hutto 2006).

In the second phase of their goat-eradication approach, Cruz and colleagues (2009) fitted Judas goats with a hormone implant, causing the goats to release attractive sexual pheromones and turning these individuals from equal-preference traps into severe traps that they called Mata Hari goats (figure 2d). Because Mata Hari goats were constantly dispersing pheromones while grazing and moving throughout each island, they attracted males and their mixed-gender social groups from isolated and hidden locations, allowing managers to overcome the primary cause of failure in most previous attempts at island goat eradication: inability to locate and eradicate the last few wild individuals (Campbell and Donlan 2005). The use of species-specific synthetic chemical lures such as sex and aggregation pheromones, often in addition to food, has a long history in the control of species that are pests to timber (e.g., gypsy moth; Tobin et al. 2007) and agricultural crops (boll weevil; Brazzel and Hightower 1960). In this combined approach (figure 2b, mechanism C), animals are differentially attracted to a location where resources such as mates and food appear to be concentrated, but the animals are then trapped or poisoned *en masse*. In a more unusual example, Crossland and colleagues (2012) exploited the fact that invasive cane toads (*Rhinella marina*) are triggered by concentrations of bufotoxin to cannibalize conspecific eggs and larvae; the addition of supernormal concentrations of this toxin to ponds triggers

toad tadpoles to eat as many conspecific eggs and hatchlings as possible (figure 2d). This strategy effectively hijacks what is, presumably, a behavioral mechanism to reduce competition among offspring to intentionally cause massive reproductive failure in an invasive species (Crossland et al. 2011).

A potentially more robust alternative strategy to mass trapping with attractants (e.g., pheromones) is a push–pull approach that associates repulsive cues with a high-quality resource and attractive cues with a poor-quality one. For example, mountain-pine-beetle control can combine the permeation of ecologically valuable forest stands or species with an “antiaggregation” pheromone or repellent, whereas attractive and lethal pheromone traps are attached to peripherally located and less-valuable “trap trees” (Gillette et al. 2012). So-called “trap crops” employ a strategy of surrounding food crops with plantings of carefully selected nonfood plants that emit volatile organic compounds that pest insects use to identify suitable feeding and oviposition sites but that will not support larval development. Khan and colleagues (2008) created a particularly effective trap crop by first chemically isolating a diverse range of plant volatiles that attracted stem-boring moths, then identifying candidate host-plant species that were poor for their larval development and that emitted the greatest number of these attractive chemical cues (figure 2d). Broadly speaking, making poor-quality resources more attractive can be accomplished by the careful deployment of both attractive and repulsive cues designed to cause animals to undervalue high-quality resources and overvalue poor-quality resources and behaviors (figure 2a).

Disrupting information and triggering out-of-context behaviors

A corollary to manipulations that make poor-quality resources more attractive by altering their associated cue sets is blocking or interfering with the ability of organisms to get information that allows them to locate high-quality resources—or any resource at all. Information disruption (Lürding and Scheffer 2007) is often accomplished via the use of chemicals that disrupt the transmission of information, reducing the ability of affected organisms to identify predators (Scott et al. 2003), detect and locate mates (Park et al. 2001), or locate prey (Sherba et al. 2000). For example, carbon dioxide exhaled from a potential host is the most important sensory cue used by female blood-feeding mosquitos, but synthetic chemicals can trigger ultraprolonged activation of carbon-dioxide-detecting neurons, effectively chemically blinding mosquitos from locating humans (figure 2c; Turner et al. 2011). This approach to reducing the apparent attractiveness of high-quality resources (also known as undervalued resources; Gilroy and Sutherland 2007) is the corollary to creating an evolutionary trap and should be an equally effective tool, but empirical examples are limited.

It is commonly assumed that only evolved cues can guide focal behaviors, but in novel environments, the focal behavior of an organism can become maladaptive because it is

influenced by cues that evolved to guide other behaviors. 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 (Burley and Symanski 1998). Aquatic insects are attracted to oviposit on human-made objects that are stronger polarizers of light than natural water is and so appear as supernormally attractive false water bodies (asphalt, Kriska et al. 1998; solar panels, Horváth et al. 2010; glass buildings, Horváth 2014). But night-active aquatic insects are also attracted to artificial night lights that mimic their primary navigational beacon: the moon. When unpolarized artificial night lighting (a maladaptive navigational cue) is placed above artificial polarizing surface such as an asphalt parking lot (a maladaptive oviposition cue), evolutionary traps from two separate behavioral contexts interact. Insects prefer to lay eggs on artificial polarizers under unpolarized night lights, and unpolarized light appears to be a relatively more important cue than polarized light (Boda et al. 2014, Robertson et al. 2017).

These two examples illustrate that cues from one behavioral context can help trigger maladaptive behavior in a separate behavior context, most likely because these cues have never before occurred in close spatial or temporal proximity, so natural selection has never acted to shape cognitive systems to more carefully partition their interpretation within separate behavioral contexts. Practically speaking, these results indicate that when trying to create an evolutionary trap in a particular behavioral context, managers may be able to draw on candidate cues that have evolved to guide completely separate behaviors in order to increase the attractiveness of the trap they design. Over evolutionary time, exploitation of environmental cues from a variety of nonsexual behavioral contexts in attracting mates has been a common and potent mechanism in the evolution of sexual ornamentation (also known as sensory traps; box 1), further supporting that this strategy is a realistic one for creating evolutionary traps in sexual and nonsexual behavioral contexts alike. In the design of evolutionary traps, the best candidates for out-of-context cues will be those that rarely or never occur in the behavioral context in which the trap is being set.

Cue weighting and redundancy in setting traps

It is not uncommon for organisms to have evolved the use of multiple cues to guide a single behavior. Cues might be weighed equally or multiplicatively in triggering focal behaviors, or they could act in a redundant fashion such that their actions are only affected by changes in multiple cues (Munoz and Blumstein 2012). For example, male giant jewel beetles (*Julodimorpha bakewelli*) appear to use the size, color, and texture of potential mates as cues to their suitability and seem to prefer to mate with brown beer bottles primarily because of their relatively large size compared with that of female beetles (Gwynne and Rentz 1984). However, texture and size alone are not sufficient to attract males, because males find green beer

bottles unattractive, suggesting that although supernormally strong versions of individual cues can increase preference, these cues are weighed in a redundant 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 in their behavioral decision-making, and what shapes behavioral reaction norms take (e.g., unimodal versus threshold response of behavior to increasing cue strength) is essential to understanding why traps occur and to devising strategies for dismantling them. Mapping these reaction norms can be done through field- or lab-based experimentation (Ghalambor et al. 2007) and will provide conservation interventionists and wildlife managers with information useful in selecting cues and cue combinations that will be most effective in creating highly attractive evolutionary traps. From a practical point of view, setting an evolutionary trap via the deployment of multiple cues to influence a single behavior (e.g., Khan et al. 2008) is more likely to increase the relative attractiveness of an evolutionary trap. Manipulating single cues that influence multiple behaviors (e.g., Cruz et al. 2009) can provide an element of redundancy if one effort is likely to fail.

Preventing escape

Preference for dangerous resources or behaviors, or the inability to distinguish between high- and low-fitness options, is what distinguishes evolutionary traps from adaptive behavior (figure 2a). Computer simulations show that traps can cause source–sink population dynamics that can result in rapid declines (Donovan and Thompson 2001, Kokko and Sutherland 2001). When traps are present, older, more experienced, or fecund individuals might outcompete younger or less competitive individuals for the worst-quality resources (e.g., habitats; Weldon and Haddad 2005), creating high densities of organisms associated with traps and further reducing populations through density dependence (Kokko and Sutherland 2001, Mänd et al. 2009). Both simple two-population (Donovan and Thompson 2001, Kokko and Sutherland 2001, Fletcher et al. 2012) and metapopulation models (Hale et al. 2015) of evolutionary traps agree that preference for poor-quality resources (severe traps) leads to population collapse much more rapidly than when traps are not present or when individuals are unable to distinguish between high- and low-quality resources (equal-preference trap), suggesting that severe traps will be highly effective tools in crashing and controlling animal populations.

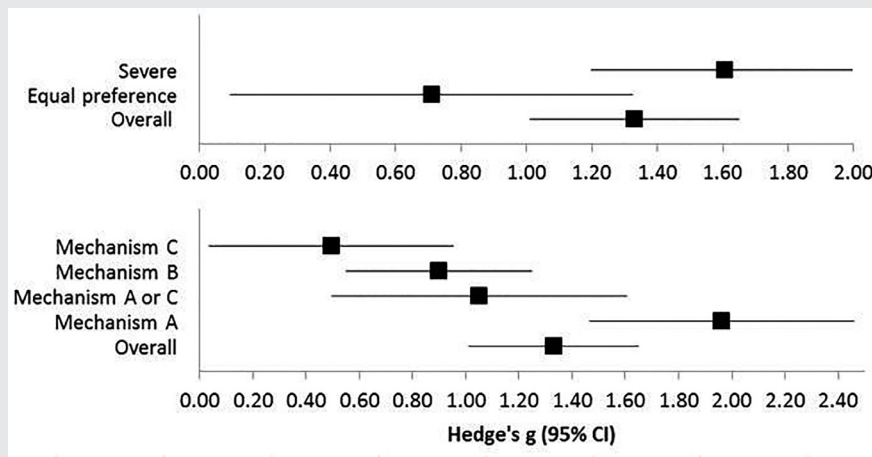
The hypothesis that a greater mismatch between perceived and real fitness value of a resource will result in greater fitness penalties remains untested, but it is a fundamental assumption of evolutionary trap theory. Our own meta-analysis of the fitness consequences of unintentionally created evolutionary traps indicates that animals caught in severe traps experience more negative-fitness consequences than those caught in equal-preference traps (box 2). Our results illustrate for the first time that the relative preference for an evolutionary trap is a critical determinant of fitness outcome across taxa and ecological contexts. They also support the

previously untested hypothesis that stronger preferences for a relatively poor habitat, food, or other resource do translate into worse fitness outcomes that should lead to more rapid population declines. Moreover, our meta-analysis shows that mechanism A, in which cues are manipulated to make a resource relatively more attractive, appears to lead to the most negative fitness outcomes, probably because traps formed this way are more likely to be severe (Robertson et al. 2013). This result suggests that the addition and/or alteration of cue sets alone may be the most effective method for reducing populations of target species via evolutionary traps.

Strong negative selection associated with trap resources will favor learned behavior or evolutionary responses that allow individuals to avoid them. For example, the North American butterfly (*Pieris oleracea*) was first seen to have a maladaptive habitat preference for exotic invasive garlic mustard (*Alliaria petiolata*) by the late 1970s, but larval performance on those exotic hosts improved in areas where garlic mustard was more abundant than native host plants (Keeler and Chew 2008). In another example, it took 70 years for red-legged frogs (*Rana aurora*) to evolve avoidance of a non-native competitor (bullfrog, *Rana catesbeiana*) that reduced their larval performance (Kiesecker and Blaustein 1997, Kiesecker et al. 2001). Consequently, traps targeting the control of animal species need to be designed and deployed in ways that hinder the ability of organisms to escape them via learning or natural selection or that reinforce the evolution of maladaptive behaviors (Massaro et al. 2013). For example, one could design a trap focused on a single behavior but triggered by multiple environmental cues, which could increase the strength of the behavioral response or preference while preventing adaptive responses to any one cue (Huijbers et al. 2012). Alternating the use of particular cues in time and/or across space could also be used to slow or halt directional selection and learning (Thompson et al. 2002). Where possible, targeting behavioral or life-history traits tightly linked to survival or reproduction may be especially profitable. These traits tend to have the least amount of genetic variation (Stearns and Kawecki 1994) or are canalized such that they will have the most negative fitness and demographic consequences while being the least responsive to selection and learning. Population simulations indicate that designing highly attractive traps that occupy a larger fraction of the species' range most rapidly lead to population extirpation while minimizing the potential for escape via learning or contemporary evolution (Fletcher et al. 2012).

In their feral-goat eradication strategy, Cruz and colleagues (2009) sequentially deployed more conventional herding techniques followed by two types of evolutionary traps: An equal-preference trap (Judas goat) followed by a severe trap (Mata Hari goat). In this way, they took advantage of the efficacy of a traditional, low-tech technique at low animal densities. Traps were deployed in the sequence of increasing severity, paralleling their relative ability to attract and concentrate increasingly rare and spatially dispersed individuals. This approach may be unique in the literature but

Box 2.



Meta-analysis of factors predicting fitness costs of evolutionary traps. The hypothesis that a greater mismatch between perceived and real fitness value of a resource will result in greater fitness penalties remains untested, but it is a fundamental assumption of evolutionary trap theory. We conducted a meta-analysis to examine the strength of the effects of evolutionary traps on two fitness measures, survival and reproduction. We searched for published articles by using the terms ecological trap or evolutionary trap in Web of Science and by locating all articles cited by or citing five core conceptual and review papers on the subject of evolutionary traps (Schlaepfer et al. 2002, Robertson and Hutto 2006, Robertson et al. 2013). Of the 594 papers we identified, 44 included data that clearly demonstrated the existence of a trap by meeting two criteria: (1) they provided evidence for equal or strong preference for a low-quality habitat, and (2) they included a measure of the effect of the trap on a reasonable measure of fitness (survival or reproduction). Of these 44 papers, 27 included data appropriate for meta-analysis (supplemental table S1), which we conducted using Comprehensive Meta-Analysis software (CM Development Team 2014). Five of these 27 papers reported effects for more than one study organism. In these cases, results for different study organisms were considered independent, leading to a total of 32 entries in the meta-analysis.

We used random-effects models to estimate the odds ratio and 95% confidence interval (CI) for traps overall. We also classified papers according to five moderator variables: (1) equal preference versus (2) severe preference (sensu Robertson and Hutto 2006), as well as the mechanism causing the trap, including (3) inflated preference for a poor-quality resource, (4) reduced fitness of a high-quality resource, or (5) a combination of the two (sensu Robertson and Hutto 2006, Robertson et al. 2013). We then calculated Hedge's g (\pm 95% CI) to estimate the strength of the evolutionary trap in each of the studies included in our analysis. The overall Hedge's g for all studies was 1.3 (1.0–1.7; 95% CI). For studies in which organisms showed equal preference for trap and nontrap habitats, the mean Hedge's g was lower than for severe preference, but the 95% CIs overlap. The effect size did vary significantly on the basis of the mechanism underlying the trap, with mechanism A (increased preference for a poor-quality habitat) having a significantly higher effect than the other mechanisms. These results illustrate that across taxa and ecological contexts, stronger maladaptive resource preferences have progressively worse fitness outcomes and that traps created via the addition of attractive environmental cues alone (mechanism A) lead to the greatest reductions in fitness.

suggests that traps may be most effective as tools when they are used selectively in time, such that animals cannot learn to avoid them, and in strength, such that the strongest trap is deployed to coincide with the steps that are most critical in determining success versus failure. Even traps that are so successful that they rapidly extirpate a target population will have to incorporate such considerations when reinvasion of the species from remaining populations is possible.

Maximizing encounters with traps

Besides making poor-quality resources attractive, the efficacy of strategies to deploy traps must depend critically

on the degree to which organisms encounter them. For example, the use of acetaminophen-poisoned neonatal mouse bait placed on the ground to eliminate brown tree snakes (*Boiga irregularis*) on Guam has been effective in reducing snake numbers, but helicopter-based aerial baiting has been used to increase bait encounter rates of snakes spending more time in the vegetation canopy (Clark and Savarie 2012). Highly philopatric organisms are especially susceptible to traps in general (Hale et al. 2015). The efficacy of targeting these less-mobile organisms may depend on the careful identification of existing populations to target or of habitat corridors that connect them. For more

highly mobile organisms that may discover new habitats and occupy them readily, managers may worry less about targeting every population than about ensuring that traps are created within some proximity of every known population such that all animals have access to trap resources. As in source–sink systems in which animals are making adaptive decisions, population (Donovan and Thompson 2001) and metapopulation models (Hale et al. 2015) of evolutionary traps predict that the probability of population extinction increases as the fraction of trap habitats or other resources increases, and populations collapse more rapidly than when animals adaptively select habitats (Kokko and Sutherland 2001, Fletcher et al. 2012). Models suggest that the probability of extirpation is high even at low ratios of trap to nontrap habitat (e.g., 30%; Donovan and Thompson 2001), and one empirical example calculates this fraction to be as high as 70% (Novaro et al. 2005).

One of the great advantages of traps as animal-control tools is that trap resources are preferentially sought out. Thus, maximizing encounter rate may focus more on ensuring target taxa have access to them. Locating evolutionary traps along movement corridors (Hartman and Ross 2014) or at dispersal or invasion hubs is a more spatially efficient method that alone can reduce the range of a target species by up to 40% by capturing individuals that would escape traditional methods (Florance et al. 2011). Maintaining connectivity and dispersal corridors helps facilitate movement from less-attractive but high-quality habitats into evolutionary traps, effectively vacuuming target individuals out of their most productive habitat (e.g., Dexter and Murray 2009), and it can actually result in metapopulation extinction even when traps are created only in a fraction the focal species' introduced range (Dexter and McLeod 2015). Species may have different perceptual ranges or acuity depending on their primary sensory modes (e.g., sight or smell). Therefore, trap deployment strategies aimed at maximizing encounter probability will need to account for the efficacy and location of traps relative to the directionality and sensory acuity of the target species.

Avoiding nontarget effects

A primary concern in setting evolutionary traps is the potential for negative impacts on nontarget species. Indeed, the third most common anthropogenic cause of unintentionally set evolutionary traps are ecological restoration projects (Robertson et al. 2013), in which habitat alterations designed to improve fitness for a set of target species actually triggered an evolutionary trap for nontarget species (Robertson and Hutto 2007, Mänd et al. 2009, Hawlena et al. 2010). The unintentional poisoning of honeybees (*Apis* spp.) with neonicotinoid pesticides (Kessler et al. 2015, Rundlöf et al. 2015) aimed at pest insects represents a similar unintentional trap. Several evolutionary traps have led to severe population declines or population extirpations in affected species (e.g., Be'er Sheva fringe-fingered lizard, *Acanthodactylus beershebensis*, Hawlena et al. 2010; African

wild dog, *Lycaon pictus*, van der Meer et al. 2014; honeybees, *Apis* spp., Kessler et al. 2015, Rundlöf et al. 2015). Poisoned baits that are universally attractive to a broad set of taxa but lethal to a specific subset (e.g., 1080 poison to mammals or KCL “biobullets” to filtering bivalves; Aldridge et al. 2006) can be difficult to design and will only be useful in rare places where target specificity is broad (e.g., exotic mammals on historically mammal-free islands). Poisons may be effective in creating equal-preference traps for taxa without the ability to detect them, but attractive baits could accidentally create evolutionary traps for nontarget species if the sensory–cognitive basis for their attractiveness is not sufficiently specific. Baits might also be placed in locations only accessible to a single species (e.g., buried baits for *Vulpes* spp., Dexter and Murray 2009) or that will only become lethal when accumulated by the target taxon itself (Aldridge et al. 2006). In addition to the direct impacts of a trap on individual species, more indirect nontarget effects such as altered species interactions or trophic relationships are possible, and these might shift the favorability of conditions for a broader array of taxa. However, because traps appear to be most fitness negative when manipulating environmental cues (figure 1, mechanism A), doing so can allow managers to target species-specific behavioral, physiological, genetic, and life-history traits and exploit often species-specific cues (e.g., sex pheromones). As such, there exists strong potential to design traps that have minimal nontarget effects even where ecologically similar or taxonomically related species co-occur.

New approaches indicated by an evolutionary-trap perspective

To date, evolutionary traps used in wildlife control have targeted a diverse array of behavioral contexts, including habitat and/or oviposition site selection, mate or conspecific attraction, and host and prey selection, closely paralleling the range of behaviors affected by unintentionally created traps (reviewed in Robertson et al. 2013). Given that severe traps (figure 1b, mechanisms A and C) are more effective in reducing population growth rates (box 2; Donovan and Thompson 2001, Kokko and Sutherland 2001), the common use of equal-preference traps (e.g., Duerr et al. 2007, Clark et al. 2012) suggests that a primary avenue for improving the efficacy of trap-based approaches is increasing the attractiveness of trap resources and behaviors. Following the unique approach of Cruz and colleagues (2009), application of the Judas technique to other taxa and ecosystems (e.g., control of Asian carp) could be further enhanced by exploiting the cognitive ability of animals to aggregate in locations suitable for capture (Bajer et al. 2011). Genetic sabotage- and gene-drive-based approaches (e.g., the sterile-male technique, the daughterless approach, and the Trojan-female technique) can benefit from the use of novel genetic tools (e.g., CRISPR) to link sabotaged genes to new gene insertions that code for an increased sexual attractiveness of genetically altered individuals over wild types.

Box 3. Traits of evolutionary traps advantageous for informing the design of wildlife control efforts.**Preference for most fitness-negative resources**

- increases the encounter rate of traps in the wild;
- increases captures of individuals existing at naturally low densities or in final stages of eradication when populations are most reduced (Cruz et al. 2009);
- accelerates rates of population decline relative to more traditional removal strategies, even when abundance is high (Delibes et al. 2001, Kokko and Sutherland 2001); and
- creates a behaviorally mediated Allee effect—population growth rates decline as population size declines (Delibes et al. 2001).

Evolutionary trap theory

- indicates new mechanisms of generating traps (e.g., triggering out-of-context behaviors) and emphasizes underexploited approaches (e.g., information disruption) and sensory modalities (e.g., sound);
- suggests the targeting of canalized traits to manipulate, or the use of multiple cues that enhance attraction to poor-quality resources and that help slow or prevent learned and evolutionary responses by target taxa;
- has no taxonomic limitation in its application;
- has high target-species specificity; and
- can be deployed strategically with more traditional approaches.

Traps set as management tools have focused almost entirely on the manipulation of visual and olfactory cues, especially within the context of foraging behavior, but categorically different sensory modalities (e.g., vibration, temperature, and electrical information) have great potential to be used to create evolutionary traps. For example, audio broadcasts of mate advertisement and response calls can be used to attract invasive fish (Mensinger 2010), amphibians (Schwartkopf and Alford 2007), or insects (Mankin et al. 2014) into traps. The literature illustrating the mechanisms by which natural selection has favored the evolution of deceptive communication (e.g., Lafferty and Shaw 2013, Stevens 2016) may also suggest novel or underemphasized approaches for creating evolutionary traps. Our article also highlights a diversity of approaches for creating preference–performance mismatches that, to our knowledge, have not been commonly used in traps aiming to control animal numbers. These include creating undervalued resources, exploiting out-of-context behavioral cues, and using multiple and redundant cues to reinforce and enhance the attractiveness of traps. Disruption of sensory abilities or communications channels can be used to create traps, as can disrupting essential conspecific and heterospecific interactions and coevolved mutualisms in ways that animals either cannot detect or actually prefer. Cognition is increasingly being employed as an explicit consideration in conservation efforts (Greggor et al. 2014) but is little considered in pest control, in which cognitive traits such as associative learning, category learning, and habituation could be undermined to create evolutionary traps (e.g., Dexter and Murray 2009). Cognitive biases such as the bandwagon effect (also known as conspecific attraction), neophobia or neophilia (Greenberg and Mettke-Hofmann 2001), and loss aversion (Silberberg et al. 2008) affect a diversity of taxa and represent as-yet-unexploited behavioral targets for manipulating animals into evolutionary traps.

Conclusions

Scientists and land managers engaged in large-scale animal control efforts have clearly been setting evolutionary traps for quite some time, even before the concept of an evolutionary trap was defined. Aside from the chance of failure to control target-species numbers, the most significant risk in the use of evolutionary traps as tools is unintended impacts on other species and ecosystems. Careful design and strategic deployment of traps in coordination with more traditional pest-control strategies (e.g., hunting or poison baiting) will be critical in preventing such effects, but caution is highly warranted. Approaches to setting traps as animal-control measures have been diverse and uneven, particularly with respect to the use of the principles we have outlined. The use of the evolutionary-trap framework has great potential to inform future efforts by making them more efficient and taxon specific, more effective in population control and eradication, and more resistant to escape via learned and evolutionary responses (box 3). This framework is useful for a broad array of taxa (Robertson et al. 2013 and herein); accommodates the biology of diversity of species, field conditions, and ecosystems; is responsive to the practical limitations of wildlife management efforts (economic and logistic constraints, conflicting management goals); and is able to provide conceptual tools for improving existing and ongoing efforts. Traps have even been successfully adapted to the treatment of human cancer (Rana et al. 2009) and viral infections (Asher et al. 2005). And because multiple behaviors and cues can be manipulated, resources cognitively hidden, and cues and communication signals blocked or interfered with, there are a tremendous number of potential options for creating a trap in any one case. The evolutionary-trap framework for controlling wildlife numbers builds on traditional methods (physical, mechanical, and chemical control), as well as biocontrol and genetic approaches, but focuses that effort within a broad conceptual framework whose goal is maximizing maladaptation and behavioral

preference for it. The effective development and implementation of evolutionary traps in wildlife management will require interdisciplinary teams of sensory scientists, ecologists, evolutionary biologists, and taxonomic specialists for design but also wildlife managers and land administrators to help assess the feasibility of potential traps and deployment strategies and to guide logistics and implementation.

Supplemental material

Supplementary data are available at *BIOSCI* online.

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