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REVIEW

How to disarm an evolutionary trap

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Abstract

Evolutionary traps occur when rapid environmental change leads animals to prefer resources (e.g., food, mates, habitats) that reduce their fitness. Traps can lead to rapid population declines, extirpation, and species extinction, yet they have received little attention within the context of wildlife conservation efforts. We first demonstrate that traps are affecting a taxonomically diverse range of animals including key pollinators and important human food species and commonly impact threatened and endangered species. We then provide a conceptual framework for wildlife scientists and practitioners that outlines: (1) the detectable symptoms of evolutionary traps which require further investigation if a trap is affecting the target of existing conservation management; (2) management options for eliminating traps or mitigating their demographic impacts; (3) case studies illustrating how practitioners have applied these mitigations in specific cases; and (4) a structure for considering how these management options should be integrated into existing decision-making frameworks. Management to eliminate evolutionary traps is a new challenge for conservationist scientists requiring a deeper understanding of the sensory-cognitive world experienced by nonhuman animals. To do so, it will be essential to diagnose the behavioral mechanisms causing traps and then identify solutions to restore adaptive behavior in target populations.

KEYWORDS

conservation behavior, conservation biology, ecological trap, environmental cue, interdisciplinary science, maladaptation, wildlife management

1 | EVOLUTIONARY TRAPS AS A CONSERVATION THREAT

Human-induced global environmental change is capable of creating a diverse array of ecologically novel conditions to which animals have not evolved (Sih et al. Sih, Ferrari, & Harris, 2011). In making decisions, organisms commonly rely upon environmental cues to assess the current or future state of their environment. Rapid environmental change can cause a mismatch between the environmental cues animals use to guide their behavior, and the conditions and fitness rewards they are typically associated with (reviewed in Candolin & Wong, 2012). As a result, animals may be unable to accurately assess the fitness value of habitats, mates, food items, or other resources that can influence their survival or reproductive success. In the most severe cases known as evolutionary traps, the most fitness-negative behavioral options become associated with environmental cues that animals historically associate with the highest fitness rewards, and animals can actually prefer behaviors that lead to the lowest fitness outcomes (Schlapfer et al. Schlaepfer, Runge, & Sherman, 2002; Robertson, Rehage, & Sih, 2013). Evolutionary traps are a maladaptive behavioral phenomenon that results from rapid ecological change to which animal populations have had insufficient time to adapt.

Male Giant Jewel Beetles (*Julodimorpha bakewelli*), for example, use the size, color (red-brown), and texture (bumpy) of potential mates as cues to their suitability (Gwynne & Rentz, 1983). This already rare species faced an evolutionary trap in that the bumpy tubercles around the base of discarded brown, short-profiled beer bottles (a.k.a. "stubbies") simulated the shape and color of an aggregation of female beetles, causing males to mob beer bottles which they perceived to be large, fecund females, while ignoring the solitary and fertile available females nearby (Gwynne & Rentz, 1983). Subsequent changes in the bottle design by the manufacturer eliminated the tubercles, releasing males to return to mating with females and thus successfully eliminating this trap.

The conservation importance of evolutionary traps has not been empirically assessed, although traps are commonly recognized as a threat to the persistence of populations of affected species. This conclusion is based almost entirely on the outcomes of demographic and eco-evolutionary simulations that conclude that wildlife populations caught in evolutionary traps can decline very rapidly (Delibes, Gaona, & Ferreras, 2001; Donovan & Thompson, 2001; Fletcher, Orrock, & Robertson, 2012; Kokko & Sutherland, 2001); experience Allee effects at low densities that accelerate population declines (Delibes et al., 2001) and experience elevated probability of population (Fletcher et al., 2012; Kokko & Sutherland, 2001) and metapopulation (Hale, Treml, & Swearer, 2015) extirpation. And because evolutionary traps seem to be associated with a diverse range of behaviors (Robertson et al., 2013), and are found across major taxonomic groups (Hale et al. Hale & Swearer, 2016, Robertson et al., 2013, Figure 1A), we should be concerned about their potential to have significant and wide-ranging impacts on biodiversity at a global scale.

Species caught in an evolutionary trap in at least a portion of their range include charismatic megafauna (African wild dogs, *Lycaon pictus*: van der Meer, Fritz, Blinston, & Rasmussen, 2014; Rasmussen, Gusset, Courchamp, & Macdonald, 2008, leopards, *Panthera pardus*: Balme, Slotow, & Hunter, 2010; Burton, Sam, Balangtaa, & Brashares, 2012, hawksbill sea turtles, *Eretmochelys imbricata*: Leighton, Horrocks, Krueger, Beggs, & Kramer, 2008), and microfauna [monarch butterfly], *Danaus plexippus*: Faldyn, Hunter, & Elderd, 2018), animals of economic importance that humans rely upon for food (tuna, *Scombridae* spp.: Hallier & Gaertner, 2008; Jaquemet, Potier, & Ménard, 2011, coho salmon, *Oncorhynchus kisutch*: Jeffres & Moyle, 2012), as well as the most important pollinators of human food crops (European honey bees, *Apis mellifera*: Kessler et al., 2015; Rundlöf et al., 2015, Table 1). Indeed, an evolutionary trap is known to have caused the extirpation of a population of Edith's checkerspot butterfly (*Euphydryas editha*, Singer & Parmesan, 2018) and one of the two remaining populations of the endangered Be'er Sheva fringe-fingered lizard (*Acanthodactylus beershebensis)* placing that species the precipice of extinction (Hawlena et al., 2010).

Empirical information on the demographics of evolutionary traps is typically limited to short-term estimates of the fitness costs of traps to affected animals (but see Singer & Parmesan, 2018). For this reason, it has been difficult to partition the relative contribution of traps to population declines and endangerment in affected species. We compared measures of endangerment in several major taxonomic groups (birds, mammals, amphibians, and reptiles) to the frequency of endangerment in species experiencing evolutionary traps. We found that half (50%) of the species known to be experiencing an evolutionary trap are endangered at the global scale, and rates of endangerment in trapped species exceed those of any of the vertebrate taxonomic groups from which they come (IUCN, 2018, Figure 1B). Whether evolutionary traps are drivers of endangerment in these species, or scientists are simply detecting evolutionary traps as a byproduct of their unrelated research focus on rare species, it is clear that evolutionary traps are commonly experienced by rare and endangered species and therefore should be a key consideration in efforts to stabilize populations and prevent extinctions.

Studies of evolutionary traps have almost exclusively been published in scientific journals focusing on ecology, evolution, and behavior, leading to a relatively broad awareness about the causes and consequences of evolutionary traps among scientists in these fields. In contrast, evolutionary traps are rarely recognized by wildlife conservation practitioners as a significant conservation threat that should be integrated into conservation planning and management. The fact that so many species of conservation concern are experiencing traps indicates that there is an existing need amongst conservation practitioners to understand how to better identify evolutionary traps, to mitigate their impact, and to eliminate them where possible. Yet, what little guidance has been published on the topic has been overly general with respect to conservation approaches (e.g., Robertson et al., 2013) or has focused on specific case studies or ecosystems (e.g., Hale et al. 2015). Here, we aim to: (1) provide wildlife conservation practitioners with a practical guide for how and when investigate the possibility that a population is stuck in an evolutionary trap; (2) use empirical examples to create a toolkit of options to eliminate evolutionary traps or minimize their demographic impacts; (3) show how conservation practitioners have responded to threats represented by traps, and (4) integrate these options within a management context that considers a diversity of management options within a framework of logistical and economic trade-offs.

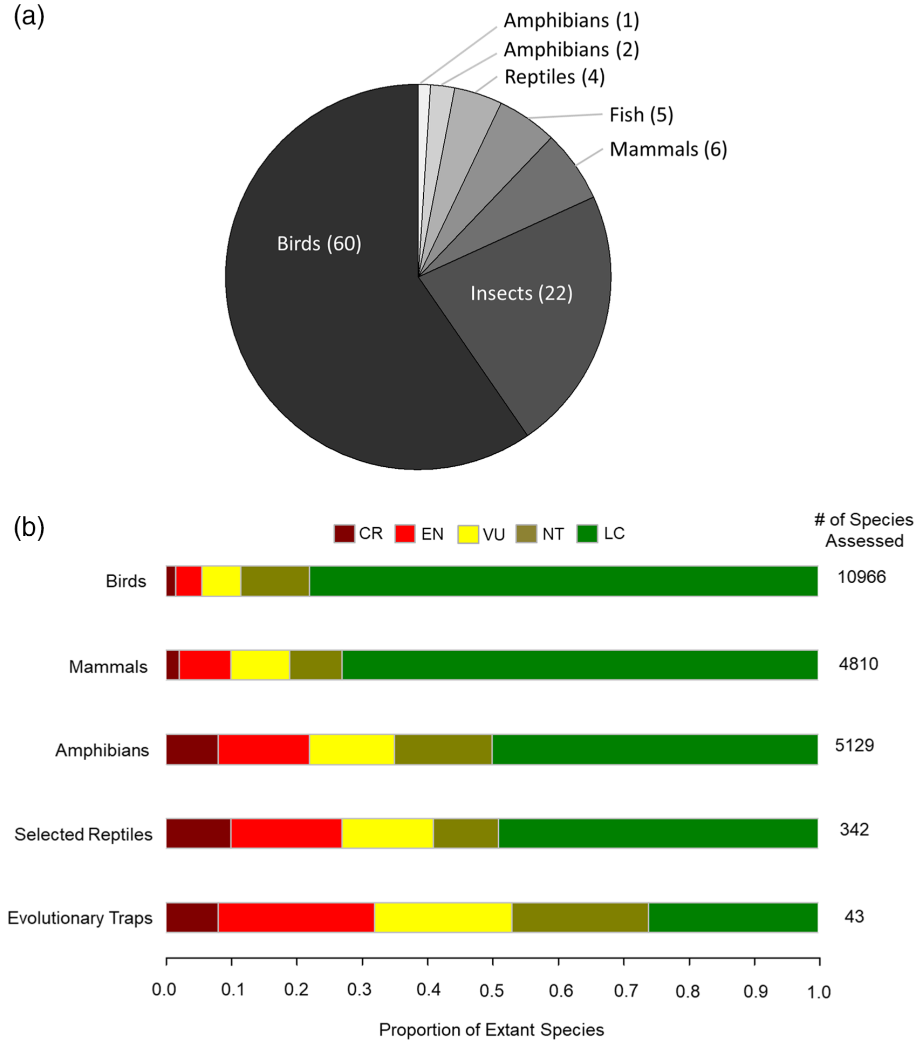

FIGURE 1 Conservation status of evolutionarily trapped species. We searched for published articles by using the terms ecological trap or evolutionary trap in web of science and by locating all articles cited by or citing three core conceptual and review papers on the subject of evolutionary traps (Robertson et al., 2013; Robertson & Hutto, 2006; Schlaepfer et al., 2002). Of the 594 papers we identified, 43 were conducted on species whose conservation status was assessed by IUCN and 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 resource or behavioral option and (2) they included a measure of the effect of the behavioral options on a reasonable measure of fitness (survival or reproduction, Robertson et al., 2013). Species for which available data was insufficient to assess their conservation status (IUCN category: "data deficient") are excluded from each category. These papers demonstrated the existence of evolutionary traps affecting a total of 100 species that we clustered into six higher taxonomic categories. Part (A) indicates the fraction of species caught in ecological trap that fall in major taxonomic categories. Part (B) shows the proportion of extant species in the IUCN Red List of Threatened Species Version 2017-3 assessed for birds, mammals, amphibians, selected reptiles, and animals of any taxonomic group known to be caught in an evolutionary trap, assessed in each conservation category. Groups are ordered according to increasing fractions of species in each that are considered threatened (CR, EN, or VU). Estimates of percentage threatened species for each group are: birds 12%; mammals: 20%; amphibians: 41%; selected reptiles (marine turtles, sea snakes, chameleons, crocodiles and alligators): 35%, and evolutionary traps: 53%. The numbers to the right of each bar represent the total number of extant species assessed for each group. Conservation status abbreviations are: CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; and LC, least concern

2 | DIAGNOSING THE SYMPTOMS AND STRENGTH OF AN EVOLUTIONARY TRAP

To demonstrate that an evolutionary trap is occurring, one must show that individuals exhibit preference for a behavior associated with a resource (e.g., food, mate, habitat, nesting site) or situation (e.g., social context) relative to other available behavioral options, but that animals executing the preferred behavior exhibit lower survival and/or reproductive success than those that are associated with other options (Robertson et al., 2013; Schlaepfer

TABLE 1 Strategic approaches to eliminating traps or mitigating their demographic impacts. Empirical examples are used to illustrate relevant management strategies representative of broader conceptual approaches

Example of evolutionary trap	Management strategy	Category of approach
Novel type of planted vegetation provides perches for predators of an endangered lizard in its preferred habitat (Hawlena, Saltz, Abramsky, & Bouskila, 2010).	Remove/prevent planting perch trees.	Improve performance in trap
Songbirds find dense (Mänd, Leivits, Leivits, & Rodenhouse, 2009) or large (Demeyrier, Lambrechts, Perret, & Grégoire, 2016) nest boxes most attractive but they lead to reduced productivity.	Use intermediate-sized nest boxes and adjust placement of nest boxes to reduce population density.	Improve performance in trap
Industrial noise pollution does not deter settlement but induces stress and reduces fecundity in songbirds (Kleist, Guralnick, Cruz, Lowry, & Francis, 2018).	Regulate natural gas treatment facilities to require noise suppression in facility design.	Improve performance in trap
African wild dogs (*Lycaon pictus*) and leopards experience high fitness near park borders and buffer zones but experience higher mortality from human hunters (Balme et al., 2010; van der Meer et al., 2014)	Development of management approaches that control human activities on both sides of administrative borders are needed.	Increase performance in trap
Salmon oviposit below dams where restoration has improved suitability for oviposition, but late-season water flow is restricted, reducing water quality and increasing offspring mortality (Jeffres & Moyle, 2012).	Require flow management regulations that maintain water quality suitable for juvenile survival during late summer; improve gravel beds only below dams were dam flows can be managed.	Improve performance in trap; reduce attractiveness of trap
Poaching of Andean bear (*Tremarctos ornatus*) in high-quality habitat creates an ecological trap in both protected and unprotected high-quality habitats (Sánchez-Mercado et al., 2014).	Reduce habitat connectivity between hunted preserves; focus poaching enforcement on highest quality habitat in and outside of reserves.	Improve performance in trap; reduce access to trap
Red-necked grebes (*Podiceps grisgena*) are attracted to food supply at commercial fish ponds, but even-aged fish are too large to feed young leading to reproductive failure (Kloskowski, 2012).	Use avian exclusion devices such as netting over ponds.	Reduce access to trap
Timber and logging residues are stored in extraction sites where they attract ovipositing endangered bark beetles. Offspring are killed in sawmills (Hedin, Isacsson, Jonsell, & Komonen, 2008).	Removing logs and residue to central storage hubs and away from prospecting adults will increase reproductive success by 5.2–23.1% (Victorsson & Jonsell, 2013).	Reduce access to trap
Adult sea turtles avoid lamp-lit beaches in egg laying, whereas hatchlings are disoriented and attracted by lamplight to migrate away from the ocean where they are killed by human	Replacement of street, residential and area lighting with long-wave lighting, use of shades and devices that force light downward, along with reduction of	Reduce trap attractiveness

(Continues)

TABLE 1 (Continued)

Example of evolutionary trap	Management strategy	Category of approach
activity or predators, or die of exhaustion, dehydration (Witherington, Martin, & Trindell, 2014).	lamp use along beaches and during nesting season.	
Migratory songbirds are attracted to heavily lighted urban areas where they are more likely to be killed by collisions with buildings (McLaren et al., 2018).	Reduce overnight lighting of tall buildings during the migratory period (reviewed in Loss, Will, Loss, & Marra, 2014).	Reduce trap attractiveness
Aquatic insects attracted to lay eggs on solar panels because they polarize reflected light and appear to be natural water bodies (Horváth et al., 2010).	Addition of non-polarized white gridding eliminates attraction (Horváth et al., 2010); anti-reflective coatings reduce ability of panels to polarize light (Száz et al., 2016)	Reduce trap attractiveness
Aquatic insects are attracted away from rivers to by bridge street lighting. Roadways polarize this light, attracting insects to oviposit on asphalt (Száz et al., 2015).	Lamps placed at the base of the bridge keep insects near the water where they successfully oviposit (Egri et al., 2017).	Increase attractiveness of trap alternatives
Post-fire specialist insectivorous birds are attracted to thinned forest due to abundant insects, retained standing dead trees emergent to the canopy height (Robertson & Hutto, 2007).	Employ harvest guidelines to remove the tallest, most emergent snags that attract males, and the smallest snags preferred as foraging perches by females; avoid retention of tall spruce-fir trees in favor of tree species not used as nesting sites (Robertson et al. Robertson, 2012)	Reduce trap attractiveness; increase attractiveness of alternatives

et al., 2002). A lack of behavioral preference between two options that differ in their fitness payoffs is considered an "equal-preference" evolutionary trap, compared to a "severe" evolutionary trap described above (Robertson & Hutto, 2006).

Evolutionary traps can be difficult to detect because humans are commonly unaware of the environmental cues animals use to make particular decisions and how they might change over time. Those cues may even be undetectable by human sensory systems and/or the equipment deployed by biologists. To study evolutionary traps, we must first develop a map of a species' Umwelt (Von Uexküll, 1909), the envelope of the perceptual world it experiences, and link that to human-induced changes in the landscape it experiences (Van Dyke Van Dyck, 2012). Nevertheless, evolutionary traps leave traces; they can be detected by wildlife conservation practitioners via their indirect effects on the distribution, behavior, and abundance of affected animals.

One of the most common symptoms of an evolutionary trap should be a decline in abundance of animals. The speed and severity of this decline will be shaped by the relative fitness cost of the trap, the fraction of the population experiencing the trap conditions, how common the evolutionary trap is in time and space relative to alternative behavioral options, and the ability and speed of the population to learn or evolve adaptive behavior (Donovan & Thompson, 2001; Fletcher et al., 2012; Kokko & Sutherland, 2001; Schlaepfer, Sherman, Blossey, & Runge, 2005). Declines will result from processes occurring to animals associated with the evolutionary trap (e.g., those settling in an altered habitat, or focusing on a particular food supply), but may not be spatially associated with the trap because individuals may be attracted away from higher-quality, but less attractive habitat elsewhere, masking local mortality. This should be especially true for mobile species and where the attractiveness of the trap is high relative to other available options (Fletcher et al., 2012; Kokko & Sutherland, 2001).

Declines will be accompanied by behavioral changes. The exact nature of these behaviors will depend on the type and severity of the trap, the social and dominance structure of the species and its natural history, and the mechanism and type of human activity triggering the trap, but should include one or more of the following (following Robertson & Hutto, 2006). First, traps that trigger maladaptive habitat selection (i.e., "ecological traps") and placement of eggs and/or young may be visible through unusual shifts in abundance away from previously favored habitat types or egg laying or

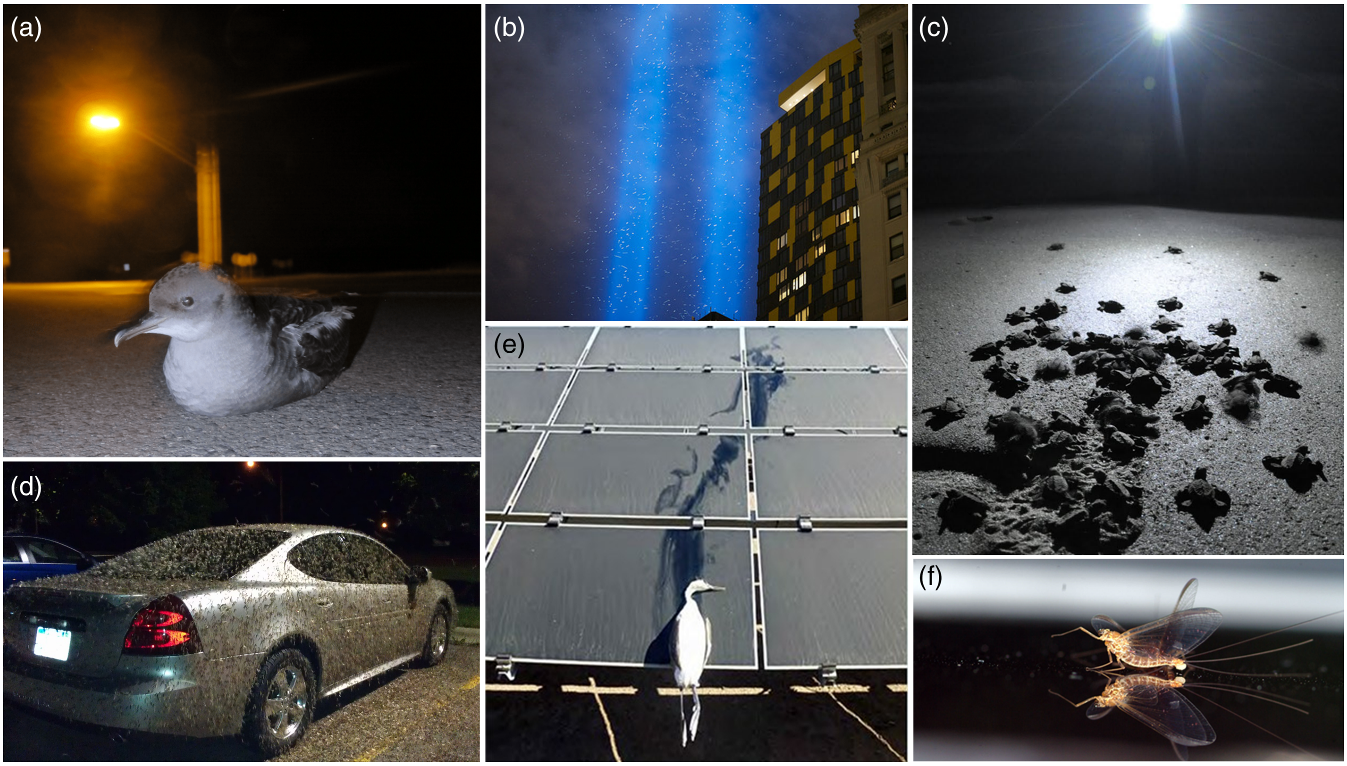

FIGURE 2 Light pollution driven evolutionary traps threatening wildlife populations. (A) At least 18 species of burrow-nesting petrels (e.g., short-tailed shearwater, *Puffinus tenuirostris*, above) are attracted to artificial lights where they become disorientated and are forced to land where they can experience mass-mortality events (Rodríguez et al., 2017, photograph: A. Rodriguez). (B) High-intensity urban lighting, such as the 911 memorial lighting, attracts migrant birds from the surrounding landscape where they experience high mortality via disorientation, exhaustion, and collision with man-made structures (Van Doren et al., 2017; photograph: Flickr user Jason Napolitano). (C) Sea turtle nestlings congregating around a lamp (photograph: D. Witherington). (D) Mayflies (*Ephemeroptera* spp.) attracted to away from water bodies to unpolarized, broad-spectrum lights, but are subsequently attracted to asphalt and car surfaces under bright polarized lamplight and therefore appear to them as supernormally attractive water bodies. The population- and ecosystem-scale impacts of light pollution on aquatic insects are unknown (photograph: R. Allen). (E) Mortality at utility-scale solar installations is estimated to kill 140,000 birds per year in the United States (Walston Jr., Rollins, LaGory, Smith, & Meyers, 2016). Attraction to photovoltaic facilities, especially by waterfowl such as the western grebe (*Aechmophorus occidentalis*, above, photograph: US fish and wildlife service) is likely caused by migrating birds perceiving light-polarizing solar panels as natural waterbodies which they attempt to land on (Horváth et al., 2010). (F) Aquatic insects (e.g., *Ephemeroptera*, photograph: G. Horváth) are also attracted to the polarized light signature of photovoltaic panels, upon which they readily lay eggs

rearing sites, respectively (e.g., Leighton et al., 2008; Rodríguez et al., 2017, Figure 2). Second, the introduction of exotic species is a leading cause of evolutionary traps (Robertson et al., 2013) and are often caused by, and observable through, failure to avoid novel predators, pathogens or disease vectors (Brown & Rohani, 2012; Carthey & Blumstein, 2018; Dixson, Munday, & Jones, 2010). Third, "navigational traps" will be visible through atypical movement patterns between habitats and portions of the range, typically through abnormally strong avoidance or attraction to human-altered habitats (e.g., Keefer, Peery, & High, 2009; McLaren et al., 2018), structures (e.g., Malik et al., 2010, Szaz et al. Száz et al., 2016), or sources of activity (e.g., Tuxbury & Salmon, 2005), possibly even via failure to detect dangerous man-made objects (e.g., Grief et al. Greif, Zsebők, Schmieder, & Siemers, 2017, Figure 2). Environmental change may also trigger organisms to pursue maladaptive developmental pathways (Van Dyck, Bonte, Puls, Gotthard, & Maes, 2015). For example, photoperiod induces diapause in insects, but temperature can modify rates of development in ways that make insects invest in risky developmental strategies (Bale & Hayward, 2010). Trends in the timing of key life history events like migration (e.g., Both, Bouwhuis, Lessells, & Visser, 2006) or diapause (Van Dyck et al., 2015) or shifts in investments in focal life-history strategies (e.g., offspring sex ratio in reptiles with temperature-dependent sex determination: reviewed in Mitchell & Janzen, 2010) that accompany population declines should be investigated as potential evolutionary traps.

By definition, trap-driven elevated mortality among adults or young will be associated with novel habitats, nest sites, or movement patterns and may be more or less visible given the size, life-history, and habitat-associations of the focal taxa. Because individuals should be competing most strongly for the highly attractive traps resources, densities of individuals may be highest around evolutionary traps (e.g., Hollander, Van Dyck, San Martin, & Titeux, 2011; Semeniuk & Rothley, 2008). In species where sexual, age, or condition-dependent social hierarchies exist, older and dominant individuals should be concentrated (often at low density) around evolutionary trap resources/conditions, whereas young or otherwise subordinate individuals should be relegated to higher-quality habitats/resources where they may exist at higher densities (e.g., Hollander et al., 2011; Sherley et al., 2017; Weldon & Haddad, 2005). Association with novel man-made objects (bottles: Gwynne & Rentz, 1983; fish aggregating devices: Hallier & Gaertner, 2008), human food supplies or crops (wood product piles: Hedin et al., 2008; fish farms: Kloskowski, 2012), or even humans themselves (poachers: Sánchez-Mercado et al., 2014) should be looked upon with suspicion if traps are a potential explanation for declines (Figure 2). A failure to respond to changes likely to impact survival can also be symptomatic of a trap (e.g., climate change: Santangeli et al., 2018; noise pollution: Kleist et al., 2018).

Behaviors symptomatic of an evolutionary trap, though, are not necessarily diagnostic of one. Rather, such behaviors could indicate that environmental change is happening and that animals have a limited degree of adaptive plasticity (Ghalambor, McKay, Carroll, & Reznick, 2007). Animals are often able to rapidly modify their behavior through phenotypic plasticity to cope with change (e.g., Maldonado-Chaparro, Martin, Armitage, Oli, & Blumstein, 2015) or rapidly evolve to meet demands of new conditions (Suárez-Rodríguez, López-Rull, & Garcia, 2013) in ways that partially or completely ameliorate the impacts of that change on their survival or reproductive success. Nevertheless, confirming that a trap exists is a crucial prerequisite for devising options to manage them (Figure 3, top center). Methods to confirm the existence of an evolutionary trap (reviewed in Robertson & Hutto, 2006, Robertson et al., 2013) focus on approaches capable of demonstrating behavioral preference and essentially require demonstrating that preferred resources, mates, or other choice scenarios lead to reduced fitness than alternative and available options. Where animals

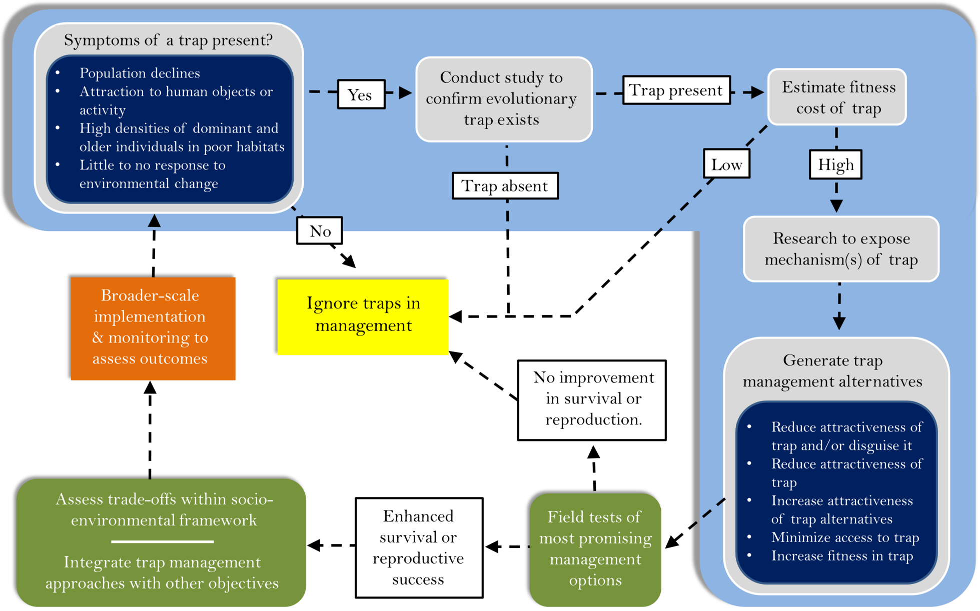

FIGURE 3 A conceptual approach for integrating the management of evolutionary traps into existing conservation practice. Beginning at the top left, animal conservation practitioners first suspect an evolutionary trap based on observable behavioral and demographic symptoms. Gathering evidence to confirm the existence of a trap follows the identification of initial symptoms, in turn followed by a need for practitioners to assess the likely impact of the trap on population growth rates. Trap-based management alternatives are developed and integrated with existing conservation plans, then assessed for their feasibility and impacts to non-target species. Management plans that are implemented are monitored and assessed for their efficacy within an adaptive management framework. The blue-shaded background encompassing the top and right portions of the diagram distinguish regions of this decision-making framework unique to the management of evolutionary traps and distinguish them from elements of management (highly compressed) that are more standardized components of modern conservation planning and implementation (green circles). The central yellow-square represents the end point of the process of management to eliminate a trap and where the trap has either been eliminated, demographically mitigated as much as possible, or ignored due to its lack of demographic importance or because existing approaches have been exhausted without effect

are attracted to an evolutionary trap (e.g., an attractive but poor-quality habitat), but there are no other available options, an evolutionary trap does not, by definition, exist and animals are simply making the best of a bad situation. However, this does not obviate the need for management to improve the fitness-value of the habitat or other resource, to provide higher fitness options, or to relocate the animals to areas with more suitable habitats, for example.

Assessment of the strength, or fitness cost, of a trap is important because when the relative preference for a trap is strong ("severe" traps), theory (Delibes et al., 2001; Fletcher et al., 2012) and empirical data (Hale et al. Hale & Swearer, 2016, Robertson et al. 2017) demonstrate larger deleterious demographic consequences than when animals are unable to tell the difference between high and low-quality resources ("equal-preference" traps, Robertson & Hutto, 2006). Elimination of equal-preference traps will, then, have a reduced effect in reversing population decline, especially when traps act in concert with other impacts (e.g., Martinez-Abrain et al. Martínez-Abraín, Viedma, Bartolomé, Gómez, & Oro, 2007, Martínez-Abraín et al., 2013). Identifying the relative demographic benefits of alternative management scenarios that focus on traditionally recognized demographically important causes of decline may ignore the evolutionary trap altogether. Before doing so, it is essential to estimate the fitness consequence of a trap by quantifying its effect in reducing survival or reproductive success (Figure 3, top right).

If an evolutionary trap is empirically confirmed and deemed a significant threat to population persistence, the next step in management is to determine why (Figure 2, right). Follow-up studies that investigate the mechanistic basis of traps are critical because knowledge of the cues guiding maladaptive behavior and their relationship with preferences are essential to generate alternative management options to eliminate the trap or mitigate its impacts (Robertson, 2012; Robertson & Chalfoun, 2016). Indeed, atypical or novel behaviors with no apparent fitness benefit are often the way traps are discovered in the first place (e.g., Figure 2). Collectively, the general mechanisms by which traps are formed (Robertson et al., 2013; Schlaepfer et al., 2002), and empirical examples of these provide a framework by which such studies can be designed to identify the now maladaptive behavioral mechanism. Once the behavioral mechanism underlying a trap is identified, it should be possible to develop management options to disarm the trap.

3 | DISARMING EVOLUTIONARY TRAPS: FROM MECHANISMS TO MANAGEMENT

Because evolutionary traps are the outcome of behavioral responses to changing environmental cues and the fitness outcomes of responding to those cues, traps are both a behavioral and demographic phenomenon. Thus, management can focus on targeting actions that reduce attraction to fitness-reducing options (i.e., by modifying preferences), and/or by focusing on actions that enhance survival or reproductive success (i.e., by increasing performance).

Wildlife management to improve the survival and/or reproductive performance of focal taxa has a long history in conservation. Where evolutionary traps exist, management interventions could focus on reducing the fitness cost of the trap, and therefore, temporarily or permanently re-aligning preference with performance (Table 1). For example, Sherley et al. (2017) found that juvenile endangered African penguins (*Spheniscus demersus*) migrate to feed off the coast of Namibia and western South Africa that have cold surface water and high chlorophyll levels normally associated with abundant sardine and anchovy populations. However, overfishing has severely decreased prey fish populations in these areas, leaving the penguins caught in an evolutionary trap that contribute to long-term population declines. The south African population of this species has been declining at an annual rate of 5.6% since 1978 (Birdlife International, 2018), but limited experimental fishing closures improved chick survival and condition, increasing penguin population growth rates by as much as 1% per year (Sherley et al., 2018). This case study highlights the potential for these such interventions to reduce the cost of rigid preferences that drive ecological traps for other declining species (e.g., Cape Gannet, *Morus capensis*: Grémillet et al., 2008: Ganges River dolphins, *Platanista gangetica gangetica*: Khanal et al., 2016).

A second application of conventional wildlife management relevant to evolutionary traps is to limit physical access to them and thus minimize trap encounter rate (Figure 2). Ecological traps (cases of maladaptive habitat preference), for example, will commonly exist as islands of falsely attractive habitat within a mosaic of higher-quality, but less attractive habitat. Increasing habitat connectivity between attractive patches is a common conservation tool to increase habitat availability and quality for mobile species (reviewed in Crooks & Sanjayan, 2006). Yet, if traps are found on the landscape, actively lowering the connectivity between high-quality patches and traps will reduce the encounter rate of attractive sink habitat (e.g., Sánchez-Mercado et al., 2014, Penteriani et al., 2018, see Table 1 for examples).

It is the alignment of attractive environmental cues with poor-quality resources that make evolutionary traps unique among eco-evolutionary phenomena. Yet, it is through the management of the distribution, form, and composition of these environmental cues that provides a unique and powerful tool for their elimination. To eliminate traps, managers should focus on the resource, object or scenario where individuals aggregate, or on resources animals appear to preferentially and inappropriately exploit relative to behavioral alternatives.

The most obvious approach to reducing the attractiveness of a trap is to eliminate or manipulate the environmental cues animals use to assess the quality of the habitat, resource, or situation. This has been the approach of wildlife managers to mitigating what was the earliest evolutionary trap seen as a conservation threat: the attraction of endangered hatchling green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles away from moonlight skyglow and its ocean surface reflection (which guides them to the ocean) and toward brighter lighting of human structures (which guides them away from the from it and increases mortality, Witherington, 1992, reviewed in Witherington et al., 2014, Figure 3). Nocturnal lighting also deters pregnant females from approaching suitable laying beaches (Witherington, 1992) by deceiving them into perceiving a valuable habitat as a poor one (a.k.a., an "undervalued resource," Gilroy and Sullivan Gilroy & Sutherland, 2007). Because conservation actions beginning in early 2000's by the Florida Fish and Wildlife Conservation Commission have included replacement of existing lighting with longer-wavelength lamps that turtles cannot see, as well as the adoption of nocturnal lighting designs and management schemes that keep light directed downward and close to its source (Witherington et al., 2014). In response, over 83 coastal municipalities have adopted their light management recommendations, Florida power and light has refitted over 1,000 street lights in sensitive areas, and public education campaigns have been enacted to encourage private landowners to cooperate and build public support for broader-scale efforts (Witherington et al., 2014). These and other conservation efforts have resulted in a 100-fold increase in nest counts of green sea turtles, exponentially increasing nest counts in loggerhead sea turtles and positive population trends for these and hawksbill sea turtles (*Eretmochelys imbricate*, Witherington et al., 2014). A similar, but larger-scale approach will be necessary to ameliorate the large-scale attraction of migratory birds to bright urban areas (McLaren et al., 2018) where they collide with buildings at such high levels that it is reducing populations continentally (Loss et al., 2014, Figure 2B). Enhancing the attractiveness of alternatives to evolutionary traps can re-align preference and performance (Table 1).

Adding repulsive cues to a falsely attractive habitat, food supply, or other resource, even while leaving the existing evolutionary trap and its associated cue complex alone, can eliminate some traps. For example, Horváth et al. (2010) found that solar panels were strong sources of polarized light pollution that triggered aquatic insects to preferentially lay eggs upon them, but that the addition of a non-polarizing grid within the matrix of the black solar-active area almost entirely "disguised" this attractive cue to three families of insects, effectively eliminating the evolutionary trap. The addition of energy efficient anti-reflective coatings to solar panels has a similar, but weaker effect (Száz et al., 2015). Other approaches to reducing the attractiveness of traps include manipulating their spatial context (i.e., spatial contagion, Resetarits & Binckley, 2009), the introduction of chemicals or other stimuli that disrupt the ability of animals to detect attractive cues (Lürling & Scheffer, 2007), exploiting behavioral biases (e.g., loss aversion: Silberberg et al., 2008), and the introduction of cues evolved to guide behaviors in other contexts, but which can be used to re-align preference and performance in the behavioral context that is being undermined by an evolutionary trap (Robertson et al. 2017).

Decisions about how and whether to manage for evolutionary traps are embedded within the context of financial and logistical limitations on wildlife management agencies, prioritizing trap management within a broader conservation context (Figure 3). Where conservation practitioners have noticed the symptoms of evolutionary traps, they should follow up with research capable of gathering the additional evidence necessary to demonstrate that an evolutionary trap is in operation, but also to estimate its relative fitness cost and attractiveness to alternative options. Traps estimated to have weak impacts on fitness or to cause minimal reduction in population growth rates may be deprioritized relative to other drivers of endangerment (Figure 3, top right). The next step in eliminating an evolutionary trap is to develop a library of management alternatives based on the sort of sensory-cognitive framework and discussion we have develop herein. This step is crucial because subsequent steps in the management process will reveal some options to be infeasible and may require additional research to expose the underlying behavioral mechanism causing the trap if it is not already known.

Trap-based management alternatives must then be field tested and monitored for their efficacy (Figure 3, bottom), and successful options integrated with existing approaches or those demanded by other conservation threats acting in concert with evolutionary traps. And because conservation solutions typically exist within a network of socio-environmental interactions whose dynamics can facilitate or undermine conservation actions (Cook, Mascia, Schwartz, Possingham, & Fuller, 2013), these must be considered at this point within the context of modern conservation practice. Adaptive management approaches to implementing trials of management alternatives are, then, evaluated for their efficacy in eliminating traps or reducing their demographic impacts (Walters, 1986, Figure 3, left). Monitoring may not only involve measures of survival or reproductive success, but behavioral data capable of assessing the efficacy of management to reduce the attractiveness of fitness-poor resources.

Collectively, we advocate an approach to the management of evolutionary traps that works to assess the conservation efficacy of managing any evolutionary traps that are present. Management options are identified and then considered within the context of a complex socio-environmental framework that assesses social, cultural, economic, and environmental drivers causing evolutionary traps, assessing each as potential targets for conservation action and trap mitigation, that then prioritizes options to match political realities and minimize trade-offs with other conservation priorities (Bennett et al., 2017).

The U.S. State of Florida's successful approach to management of light pollution to eliminate evolutionary traps for nesting sea-turtles epitomizes the approach to managing evolutionary traps we advocate, although it faces challenges in its efficacy (Witherington et al., 2014). It relies upon local ordinances that differ in their efficacy and can suffer from regulatory loopholes that impede implementation and its public-outreach and educational programs face challenges in convincing property owners to manage their light usage and management.

4 | CONSERVATION CONTEXT AND CAVEATS

Traps will persist despite the best efforts of conservation practitioners due to variation in the efficacy of conservation efforts in time and space and because individuals vary in their genetically determined and learned preferences for resources. The latter will mean that not all animals in a population will be trapped in the first place, but also that management practices will never be perfectly effective; a challenge to all trap-based remediation efforts. The relative importance of learning and evolution in facilitating “escape” from traps is unclear and is poorly documented (but see Keeler et al Keeler & Chew, 2008, Singer & Parmesan, 2018), but variation in these factors, too, may reduce the efficacy conservation management. The top conservation priority, then, should be to minimize the demographic impacts of traps by weakening preference, improving performance, eliminating the frequency of traps on a landscape or the probability of encountering them, which might also buy time for learning or evolution to occur (Fletcher et al., 2012). Maximizing the trade-offs among management alternatives in their efficacy in meeting conservation goals will likely be the most challenging aspect of designing a conservation plan to eliminate an evolutionary trap and also in adaptively responding to information about its efficacy (Figure 3).

We encourage managers to cast evolutionary trap mitigation in the context of active adaptive management, because it is through carefully designed management-related experiments and monitoring their outcomes that we will most rapidly learn the most about the efficacy of interventions to manage traps (Lyons, Runge, Laskowski, & Kendall, 2008; Walters, 1986; Walters & Holling, 1990). Trap mitigation, because of its powerful demographic consequences, will likely be an important management tool in stabilizing population trends, but comparative effectiveness evaluation (Smith, Dicks, Mitchell, & Sutherland, 2014) of trap management versus other management options is also necessary to properly allocate limited conservation funds.

5 | CONCLUSIONS

Although a robust ability to predict the appearance of evolutionary traps may reside in the future, current knowledge of the mechanisms that create traps and shape their demographic consequences are sufficient to suggest new ways to manage wildlife populations affected by them. Given the rarity of research seeking evidence for evolutionary traps, existing cases of traps and their conservation impacts likely underestimate their conservation impact relative to other sources of population decline. Certainly, recognition of the existence of traps can provide new options for slowing down population declines and ensure that individual and genetic variation is maximized for evolution to act on in the face of climate change or other global extinction drivers (Schlaepfer et al., 2005). Some evolutionary traps appear to broadly affect large groups of ecologically and/or taxonomically similar organisms (e.g., aquatic insects and polarized light pollution, Robertson et al., 2018), whereas others are highly species- and location-specific (e.g., Hawlena et al., 2010). For these reasons, developing management strategies for eliminating traps will challenging.

The effective development and implementation of management plans to eliminate evolutionary traps will likely require interdisciplinary teams of sensory scientists, ecologists, evolutionary biologists, and taxonomic specialists for strategy development, but also wildlife managers and land administrators to help assess the feasibility of alternative management options and how they can be integrated with other conservation objectives. These new behaviorally based management approaches will need to be combined with more traditional approaches with the goal of stabilizing populations until species can transition to new selective environment (Schlaeper et al. Schlaepfer et al., 2005). Attempting to understand the sensory-cognitive world experienced by nonhuman organisms will be one of the more novel challenges for conservation practitioners. There is a critical need for empirical data on population-dynamics resulting from traps, their eco-evolutionary interactions with other causes of population decline to help inform and prioritize evolutionary trap management options. Deeper understanding of the sensory-cognitive mechanisms that are undermined in the creation of evolutionary traps will be useful in developing a wealth of new management approaches for species of conservation concern caught in evolutionary traps, and for designing ways to intentionally create evolutionary traps that target "nuisance" species and hasten their decline and control their distribution (Barrett, Stanton, & Benson-Amram, 2019; Robertson et al. 2017).

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ETHICAL STATEMENT

This work did not require the collection of empirical data outside of the synthesis of existing published studies and therefore required no special permits outside of basic ethical guidelines for the production of science.

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