When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations

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Abstract: *The concept of the ecological trap, a low-quality habitat that animals prefer over other available habitats of higher quality, has appeared in the ecological literature irregularly for over 30 years, but the topic has received relatively little attention, and evidence for traps remains largely anecdotal. Recently, however, the ecological trap concept has been the subject of a flurry of theoretical activity that is likely to raise its profile substantially, particularly in conservation biology. Ecological trap theory suggests that, under most circumstances, the presence of a trap in a landscape will drive a local population to extinction. A number of empirical studies, almost all of birds, suggest the existence of traps and demonstrate the difficulties of recognizing them in the field. Evidence for ecological traps has primarily been found in habitats modified by human activities, either directly (e.g., through the mowing of grassland birds' nests) or indirectly (e.g., via human-mediated invasion of exotic species), but some studies suggest that traps may occur even in relatively pristine areas. Taken together, these theoretical and empirical results suggest that traps may be relatively common in rapidly changing landscapes. It is therefore important for conservation biologists to be able to identify traps and differentiate them from sinks. Commonly employed approaches for population modeling, which tend to assume a source-sink framework and do not consider habitat selection explicitly, may introduce faulty assumptions that mask the effects of ecological traps and lead to overly optimistic predictions about population persistence. Given the potentially dire consequences of ecological traps and the accumulating evidence for their existence, greater attention from the community of conservation biologists is warranted. In particular, it is important for conservation biologists and managers to incorporate into conservation planning an explicit understanding of the relationship between habitat selection and habitat quality.*

Key Words: ecological trap, habitat quality, habitat selection, population dynamics, source-sink system

Cuando Animales Buenos Aman a Hábitats Malos: Trampas Ecológicas y la Conservación de Poblaciones Animales

Resumen: *El concepto de la trampa ecológica, hábitat de baja calidad que los animales prefieren por encima de otros hábitats disponibles, ha aparecido irregularmente en la literatura ecológica por más de 30 años, pero el tema ha recibido relativamente poca atención, y la evidencia sobre trampas es principalmente anecdótica. Sin embargo, el concepto de trampa ecológica recientemente ha sido sujeto de una agitada actividad teórica que probablemente eleve su perfil sustancialmente, particularmente en biología de la conservación. La teoría de la trampa ecológica sugiere que, bajo la mayoría de las circunstancias, la presencia de una trampa en un paisaje conducirá a una población local a la extinción. Numerosos estudios empíricos, casi todos de aves, sugieren la existencia de trampas y demuestran las dificultades para reconocerlas en el campo. La evidencia de trampas ecológicas ha sido encontrada principalmente en hábitats modificados por actividades humanas, ya sea directa (e.g. por siega de nidos de aves de pastizales) o indirectamente (e.g. por vía de invasiones de especies exóticas provocadas por humanos), pero algunos estudios sugieren que las trampas pueden ocurrir en áreas relativamente prístinas. En conjunto, estos resultados teóricos y empíricos sugieren que las trampas*

son relativamente comunes en paisajes con cambios rápidos. Por lo tanto, es importante que los biólogos de la conservación puedan identificar trampas y diferenciarlas de vertederos. Los métodos utilizados comúnmente para modelar poblaciones, que tienden a asumir un marco de fuente-vertedero y no consideran la selección hábitat explícitamente, pueden introducir suposiciones erróneas que enmascaran los efectos de las trampas ecológicas y conducen a predicciones demasiado optimistas acerca de la persistencia de la población. Dadas las consecuencias potencialmente desastrosas de las trampas ecológicas y la acumulación de evidencia de su existencia, se requiere una mayor atención por parte de la comunidad de biólogos de la conservación. Particularmente, es importante que los biólogos y los gestores de la conservación incorporen en la planificación de la conservación un entendimiento explícito de la relación entre selección de hábitat y calidad de hábitat.

Palabras Clave: calidad del hábitat, dinámica de poblaciones, fuente-vertedero, selección de hábitat, trampa ecológica

Introduction

It has been over three decades since the concept of the ecological trap—a low-quality habitat that organisms prefer over superior habitats—was first described (Dwernychuk & Boag 1972), but only recently has it received theoretical treatment. Unlike other areas of population biology, such as metapopulation biology and source-sink theory, in which the development of theory preceded the application of concepts to specific systems, the ecological trap concept has, for the last three decades, been applied piecemeal to a variety of case studies in the absence of any overarching theoretical framework. This lack has not gone unnoticed, and ecological traps have recently been the subject of a flurry of attention (Delibes et al. 2001; Donovan & Thompson 2001; Kokko & Sutherland 2001; Kristan 2003), which deserves broad consideration from the community of conservation scientists.

The term "ecological trap" has been used to describe several different, interrelated phenomena, but recently researchers have converged on a definition that links ecological traps to the more familiar source-sink theory. An ecological trap is a habitat "low in quality for reproduction and survival [that] cannot sustain a population, yet . . . is preferred over other available, high-quality habitats" (Donovan & Thompson 2001). Thus, a trap is simply a sink habitat that is preferred rather than avoided (Fig. 1), or an "attractive sink" (Delibes et al. 2001).

In their simplest form, source-sink systems involve two habitats, one of high quality (source) in which the population growth rate is positive, and one of low quality (sink) in which population growth is negative (Pulliam 1988). Animals settle in the superior habitat until it fills up, and the remaining individuals are forced to settle in the inferior habitat. This leads to a relatively stable population that conforms to a logistic pattern of population growth, with high population growth rates at low densities, when all animals can settle in the source habitat. A source-sink system therefore tends toward a stable population size unless an animal's ability to find source habitat is limited and there is very little source habitat in the landscape (Pulliam & Danielson 1991). The assumption of some form of op-

Habitat quality

Figure 1. Representation of the relationship between sources, sinks, and traps, illustrating the four possible combinations of habitat selection and habitat quality in a landscape containing one habitat of high quality in which the population growth rate is positive ($\lambda > 1$) and one of low quality in which population growth is negative ($\lambda < 1$). All high-quality habitats, whether selected or avoided, are considered sources. Sinks occur when low-quality habitat is avoided, and traps occur when low-quality habitat is selected.

timal habitat selection is therefore central to source-sink models. An animal's ability to assess the available patches accurately and to settle in the best patches ensures that the highest-quality source patches are occupied first.

In an ecological trap, on the other hand, animals make errors in habitat assessment as a result of some mismatch between the environmental cues they use to select habitats and actual habitat quality (Donovan & Thompson 2001; Kokko & Sutherland 2001; Schlaepfer et al. 2002; Kristan 2003). These errors cause them to choose inferior habitat preferentially over what is actually superior habitat. In the presence of an ecological trap, populations tend toward extinction as animals abandon superior habitats to settle in poorer ones. Landscapes that, when viewed in a source-sink framework, would be expected to support a stable population may instead lead to population extinction if the sinks are actually traps (Donovan

& Thompson 2001; Kokko & Sutherland 2001). Because ecological traps and source-sink systems have such different implications for a population's long-term survival, it is essential for managers and conservation biologists to be aware of the consequences of ecological traps and to understand how they might be distinguished from sinks.

Unfortunately, many of the population models routinely used in conservation biology point us away from an explicit consideration of ecological traps. Some population-modeling software packages (e.g., Alex, Patch) enforce a source-sink framework (Possingham & Davies 1995; Schumaker 1998), equating habitat preference and habitat quality. This reflects a more general shortcoming in ecological modeling, in which optimality is often assumed but rarely demonstrated. Even those models that do not assume source-sink dynamics (e.g., RAMAS, Vortex) cannot effectively model an ecological trap because habitat selection is not explicitly considered (Akcakaya 1994; Miller & Lacy 2003). By using these models to predict the population-level consequences of rapid environmental change, researchers and managers may unwittingly be making incorrect assumptions about habitat selection that could lead to overly optimistic predictions about species persistence.

Ecological traps may present a serious threat to conservation, and the ecological trap concept has, over time, been applied to a wide range of biological systems. Agricultural fields (Best 1986), airports (Kershner & Bollinger 1996), linear habitat corridors (Henein & Merriam 1990, but see Little et al. 2002), artificial wetlands (Tilton 1995), urban areas (Boal & Mannan 1999), the entire prairie pothole region (Rotella & Ratti 1992), and, most commonly, habitat edges (Gates & Gysel 1978; Chasko & Gates 1982; Ratti & Reese 1988; Marini et al. 1995; Pasitschniak-Arts & Messier 1995; Pösyä et al. 1997; Suarez et al. 1997; Flaspohler et al. 2001*b*) have all been suggested as ecological traps for various vertebrate taxa. Although traps have often been suggested, however, it remains unclear how often they actually occur.

The fundamental concept of the ecological trap and its evolutionary underpinnings have been summarized well by Schlaepfer et al. (2002), but the strength of the evidence for ecological traps and the question of where and when they are most likely to occur have not yet been addressed. In this review, I (1) briefly summarize recent advances in ecological trap theory, (2) assess the strength of the empirical evidence for the existence of traps, and (3) discuss the circumstances under which traps are likely to occur and the implications of ecological trap theory for biological conservation.

Ecological Trap Theory

The four recently published models of ecological traps all share a common conceptual framework that owes much

to source-sink theory. Unlike source-sink models, however, ecological trap models treat habitat attractiveness and habitat quality as separate issues. Habitat attractiveness can be parameterized so that animals are attracted to superior habitats (creating a source-sink system) or inferior ones (causing an ecological trap). Habitat selection follows a form of either the ideal despotic model (Fretwell & Lucas 1970) or the ideal preemptive model (Pulliam & Danielson 1991), but animals settle in the most attractive available habitat patch, regardless of whether it is the "best" in terms of population growth rates and population persistence.

The models share a number of simplifying assumptions. None is spatially explicit. Animals are assumed to have immediate and complete knowledge of habitat attractiveness (but not habitat quality), and there is no cost to moving among patches. None of the models incorporate age structure or "floaters"—nonreproductive, nonterritorial adults. Three are based on generalized life-history traits of some group of terrestrial vertebrates, either birds (Donovan & Thompson 2001; Kokko & Sutherland 2001) or mammals (Delibes et al. 2001), whereas the fourth models a highly generalized animal (Kristan 2003). Three (Delibes et al. 2001; Donovan & Thompson 2001; Kokko & Sutherland 2001) use discrete-time simulations to model a landscape containing two habitats of differing qualities, one in which population growth is positive and one in which it is negative. The fourth (Kristan 2003) models a landscape containing a continuum of habitats spanning a range of quality and attractiveness and operates in continuous time.

Taken together, ecological trap models yield the following conclusions. (1) Ecological traps usually lead to population extinction. (2) Initial population size is important in determining the fate of a "trapped" population. When population size is low, traps lead to rapid extinction because no animals will use the less-preferred (higher quality) habitat. When population size is larger and the preferred (lower quality) habitat is fully occupied, some individuals will occupy the less preferred habitat, where they will be more successful. Stochastic declines in population size caused by cyclical population crashes, environmental variability, or other causes—events from which a population would normally recover—may push populations below this population size threshold, placing them on a trajectory toward extinction. (3) There is a threshold proportion of trap habitat in the landscape above which populations experience deterministic extinction. The level of this threshold depends on the quality of habitat in the trap: the poorer the habitat, the less is needed. (4) Negative effects on either reproduction or adult mortality can lead to ecological traps. (5) Source-sink and ecological trap dynamics are at opposite ends of a continuum based on the relationships among habitat quality, habitat selection, and habitat availability. This broader framework encompasses scenarios in which no

habitat is preferred but habitat quality differs (e.g., Doak 1995; DiMauro & Hunter 2002), as well as complex hierarchies of habitat quality and preference in which there is not necessarily a one-to-one match between the two.

Evidence for the Existence of Ecological Traps

Few studies have shown clear evidence of ecological traps. It is unclear whether this is because ecological traps are rare or because researchers simply have not been looking for them. It is not uncommon for authors to report findings that are consistent with the presence of a trap but to ignore the ecological trap concept when discussing the implications of their results (e.g., Johnson & Temple 1986; Crabtree et al. 1989; Vickery et al. 1992; Donovan et al. 1995*a*, 1995*b*). The low profile of the ecological trap concept, coupled with the ascendance of source-sink theory in spatial ecology, may influence investigators and dissuade them from interpreting their results in an ecological trap framework. On the other hand, many studies have shown a positive relationship between habitat quality and habitat selection (Kellner et al. 1992), suggesting that traps may be relatively unusual.

To determine the level of empirical support for the ecological trap concept, I searched the literature for studies showing evidence of a negative relationship between habitat selection and habitat quality. Because of the difficulty in estimating overall population growth rates, I included studies that could not demonstrate negative population growth in the trap if they showed evidence of maladaptive habitat selection, the mechanism by which traps are created. I therefore limited my search to studies that considered at least two habitat types between which animals could move freely and that reported data on habitat selection and some component of habitat quality, for each habitat type. The use of these criteria excluded a number of studies that have been cited elsewhere as examples of ecological traps. For instance, studies demonstrating the use of a low-quality habitat without evidence that it was preferred over other habitats were not included (e.g., Kriska et al. 1998).

This search yielded 13 studies, all but one on birds (Table 1). This avian bias suggests that the ecological trap concept has not received much attention outside of the ornithological circles in which it was originally formulated. Of these 13 papers, 10 (Dwernychuk & Boag 1972; Gates & Gysel 1978; Chasko & Gates 1982; Kershner & Bollinger 1996; Purcell & Verner 1998; Boal & Mannan 1999; Schmidt & Whelan 1999; Misenhelter & Rotenberry 2000; Flaspohler et al. 2001*b*; Ries & Fagan 2003) discuss ecological traps explicitly, whereas 3 (Johnson & Temple 1986; Crabtree et al. 1989; Vickery et al. 1992) present similar data but do not consider that an ecological trap might explain their results.

Perhaps the best-documented trap is the case of Cooper's Hawks (*Accipiter cooperii*) nesting in the city of Tucson, Arizona (Boal 1997; Boal & Mannan 1999). The hawks occur at much higher densities in the city than in exurban areas. Nesting begins earlier in the city, and clutches are larger than in outlying areas. The trap is sprung after the eggs hatch: nestling mortality is much higher in the city (>50%) than in exurban areas (<5%). The primary cause of mortality is trichomoniasis, a disease carried by pigeons and doves, which make up 84% of the diet of urban hawks. Based on demographic analysis, the urban population should experience significant declines (Boal 1997), but it appears to be stable or increasing, suggesting that birds are immigrating from outside the city. This analysis, taken together with the observation that birds nest earlier and at greater densities in the city, suggests that birds are being drawn into the city to nest, perhaps in response to plentiful prey and nest sites. Although the authors lack direct evidence of animals' movements from higher-quality exurban sites, they make a strong case for the selection of the trap (the key to differentiating an ecological trap form a source-sink scenario) and provide reasonable hypothesized mechanisms driving the trap.

No other study purporting to demonstrate an ecological trap is as thorough, but several others are suggestive. Purcell and Verner (1998) found that California Towhees (*Pipilo crissalis*) show large differences in productivity and abundance between grazed and ungrazed sites in a pine-oak woodland. They were >40% more abundant in the ungrazed site, but birds in the grazed site fledged, on average, over 4.5 times more offspring. This is an unusual example in that the site most heavily affected by human activities (i.e., grazing) was the superior habitat and the more "pristine" habitat served as the trap.

Crabtree et al. (1989) found that Gadwall (*Anas strepera*) appear to select nest sites with high canopy cover, despite the fact that sites with lower canopy cover have thicker understory, shielding them from nest predators, particularly striped skunks (*Mephitis mephitis*). Nest predation is higher in preferred habitats, leading to significantly higher rates of nest failure. Several studies of habitat edges as ecological traps (Gates & Gysel 1978; Chasko & Gates 1982; Johnson & Temple 1986; Flaspohler et al. 2001*b*; Ries & Fagan 2003) suggest that, although animals settle disproportionately at edges, predation on eggs and young at edges is higher. This pattern has been documented in birds (Gates & Gysel 1978; Chasko & Gates 1982; Johnson & Temple 1986; Flaspohler et al. 2001*b*) and insects (Ries & Fagan 2003).

Results of two studies demonstrate the potential for within-habitat heterogeneity to create ecological traps. In Illinois the exotic shrubs *Lonicera mackii* (Rubr.) and *Rhamnus cathartica* L. appear to serve as ecological traps for nesting birds (Schmidt & Whelan 1999). Over the course of 6 years, American Robins (*Turdus migratorius*) increased their use of these species for nesting, even

Table 1. Studies reporting results consistent with the existence of ecological traps.

Citation	Focal species	Findings
Boal 1997; Boal & Mannan 1999	Cooper's Hawk	Urban area (Tucson) had high density of hawks; population steady or increasing, but nestling mortality much higher in urban areas due to high trichomoniasis infection rate.
Chasko & Gates 1982	forest passerines—several species	At study site with gradual forest-powerline right-of-way edge, nest predation higher at edge than interior; nest density also somewhat higher near edge.
Crabtree et al. 1989	Gadwall	Of three habitats studied, Gadwalls nested disproportionately in the habitat in which nest mortality was highest, especially early in the season.
Dwernychuk & Boag 1972	ducks—several species	Ducks nested in higher densities on islands with gulls than on islands without them. Gulls protected nests from egg predation but killed virtually all young.
Flaspohler et al. 2001*b*	Hermit Thrush (*Catharus guttatus*), Ovenbird (*Seiurus aurocapillus*)	For these two ground-nesting species, nest density was higher near forest-clearcut edge but nest success was lower. For canopy-nesting species, edges did not serve as traps.
Gates & Gysel 1978	forest passerines—several species	Nest density was higher at a field-forest edge than in forest interior, but nest success and clutch size were both lower.
Johnson & Temple 1986, 1990	grassland passerines—several species	Nest success for all species was lower near edge than in habitat interior and highest in recently burned plots. Some species more abundant at edge.
Kershner & Bollinger 1996	Eastern Meadowlark (*Sturnella magna*)	Nest densities at airports generally higher and reproductive success lower than in other habitats.
Misenhelter & Rotenberry 2000	Sage Sparrow	Multivariate analysis found that Sage Sparrows were more likely to nest in vegetation associated with poor nesting success.
Purcell & Verner 1998	California Towhee	Towhees occurred at higher densities and experienced lower reproductive success in an ungrazed oak-pine woodland than in a similar grazed woodland.
Ries & Fagan 2003	*Stagmomantis limbata* (a mantid)	Egg-case density and predation rate were higher near riparian habitat edges than away from them.
Schmidt & Whelan 1999	American Robin	Robins increased their proportional use of exotic shrubs for nesting over the course of the study, even though nests in these shrubs experienced higher predation rates.
Vickery et al. 1992	Savannah Sparrow (*Passerculus sandwichensis*)	Nest success highest in habitat in which birds were least abundant, lowest in habitat with highest abundance.

though nest success in these exotic plants is lower than it is for birds nesting in nearby native species. Similarly, Sage Sparrows (*Amphispiza belli*) nesting in California coastal sage-scrub appear to select nesting territories in sites where nest failure is highest (Misenhelter & Rotenberry 2000).

None of these studies presents an unassailable case for the existence of ecological traps, because none has been conducted over a long enough time period to document population declines in source habitats or in the overall population, as predicted by ecological trap theory (declines in the trap habitat would not be expected until the source was largely depleted). Due to incomplete fitness measures, indirect and sometimes problematic measures of habitat selection (such as those based on density estimates), and other gaps in the data, all studies suggesting the existence of ecological traps are open to other interpretations.

All empirical ecological trap studies conducted to date have used some measure of the relative densities of animals in two or more habitats as their primary measure of habitat selection, but higher animal densities may, for a variety of reasons, not indicate that a habitat is actually being selected (Kellner et al. 1992; Vickery et al. 1992). All these studies also used a measure of reproductive output as their sole surrogate for habitat quality. Other components of habitat quality may counterbalance negative effects on reproduction, however. Low reproduction may be offset by higher adult survival rates (Schiers et al. 2000; Mayhew 2001). Low nest success may be counterbalanced by higher clutch sizes (Flaspohler et al. 2001*a*) or lower rates of blowfly (*Protocalliphora* sp.) parasitism (Germaine & Germaine 2002), leading to similar rates of young production. What appears to be maladaptive habitat selection may, therefore, in some cases turn out to be the result of unmeasured fitness tradeoffs.

Temporal variation in habitat quality may not be captured by relatively short-term studies such as those summarized here. For instance, many diseases, such as avian trichomoniasis, experience periodic outbreaks (Cole 1999). If the trichomoniasis infection rate in Tucson pigeons and doves were to decline, the city might be transformed from a trap to a source for Cooper's Hawks because other aspects of habitat quality are higher in the city than in surrounding areas (Estes & Mannan 2003). Additionally, density-dependent effects may produce a pattern of low fitness at high densities, with low population growth rates at high densities and high rates at low densities (Watkinson & Sutherland 1995).

Despite these difficulties, and despite the fact that few studies have been designed to address this issue directly, the cumulative evidence suggests that ecological traps may be operative in many highly altered landscapes. More definitive empirical tests are now needed that provide rigorous demographic comparisons of suspected trap habitats and address the question of whether previously unmeasured variables compensate for apparent traps (e.g., Flaspohler et al. 2001*a*). Experimental systems in which habitat attractiveness and quality can be manipulated (e.g., Gundersen et al. 2001) may provide additional insight, and such inquiries are likely to be stimulated by recent advances in trap theory.

Ecological Traps and Conservation

Ecological traps have obvious management implications: any situation that attracts organisms to inferior habitat can lead to rapid population declines and rapid local extinction. Any attempt to conserve animal populations, particularly in changing landscapes, may be severely complicated by the presence of ecological traps. Given their potential importance, four central questions emerge for conservation biologists and managers. (1) Where are ecological traps most likely to occur? (2) What species are most likely to be vulnerable to traps? (3) How do we identify an ecological trap? (4) How do we incorporate the ecological trap concept into conservation planning?

Where Are Traps Most Likely to Occur?

A striking feature of the ecological trap literature is that, although the number of studies is relatively small, it appears that traps can be created by a remarkably diverse array of processes and in a broad array of habitat types. They may be caused by human activities, either directly, as in the destruction of nests by mowing (Kershner & Bollinger 1996), or indirectly, as in the case of increased densities of Brown-headed Cowbird (*Molothrus ater*) nest parasites in agricultural landscapes (Johnson & Temple 1986). Areas that appear relatively pristine compared with the surrounding landscape may also contain traps (Purcell &

Table 2. Characteristics of landscapes and organisms that increase vulnerability of animal populations to ecological traps.

Characteristics
Landscape
high ratio of trap to source habitat
rapid pace of landscape change
high rate of exotic species invasion
Organism
slow rate of evolution
low capacity for learning
low within-population variation in habitat-selection traits
no behavioral adaptations to change
low level of knowledge about landscape
reliance on indirect habitat-selection cues
low population size
cyclical population fluctuations

Verner 1998; Misenhelter & Rotenberry 2000), and traps may even occur in situations where human influence is apparently not important (Dwernychuk & Boag 1972). Traps may occur at a variety of scales, from the landscape (e.g., a large urban area and its surroundings) to within-patch gradients (e.g., edge effects) to small-scale site selection (e.g., selection of nest sites).

This diversity of mechanisms suggests that there is unlikely to be an easy prescription for identifying situations in which traps will or will not occur. The few ecological trap studies that have been published provide little guidance, and the theoretical studies do not address the question of where traps are most likely to occur, except in the most general terms. Both the empirical and theoretical studies, however, suggest some initial guidelines regarding the circumstances most likely to generate ecological traps. Because traps are caused by an interaction between habitat quality and habitat selection, potential causative factors can be broken down into two general categories (Table 2): (1) landscape characteristics and (2) organism (or population) characteristics (discussed in the next section). Several of the factors listed in Table 2 (proportion of trap habitat in the landscape, initial population size, frequency and severity of stochastic population declines) are dealt with in the ecological trap models discussed above. Here, I outline some additional causative factors that have been suggested.

Most researchers documenting ecological traps have found them in areas that have undergone rapid anthropogenic alteration, suggesting that the rate of landscape change may be central to the creation of traps (Schlaepfer et al. 2002; Kristan 2003). Some ecological trap models also suggest the importance of the rate of landscape change in the creation of traps (Kokko & Sutherland 2001). Given what we know about ecological traps, this conclusion makes sense: the less time organisms have to adapt to a changing environment—through either adaptation or learning—the more likely they are to make habitat-selection mistakes. The impacts of specific types

of change, however, are much more difficult to predict. Radical changes in habitat (e.g., habitat type conversion associated with crop agriculture or urbanization) cause major shifts in habitat quality, but they are likely to be easier for animals to detect, whereas subtle changes (e.g., the invasion of an exotic species) may have less impact on habitat quality but could be much harder to detect. The studies reviewed here suggest that traps can be caused by habitat changes both radical (Kershner & Bollinger 1996; Boal & Mannan 1999) and subtle (Schmidt & Whelan 1999; Misenhelter & Rotenberry 2000).

Invasive exotic species present a particular challenge, regardless of the mechanism by which they change habitat quality because, by definition, native species have had no evolutionary experience with them. Exotics can also interact with and exacerbate the effects of other forms of landscape change. For instance, in areas recently colonized by Brown-headed Cowbirds, this open-habitat species' propensity for parasitizing nests of birds near field-forest edges can transform edges, which are attractive to many songbird species, into traps (Johnson & Temple 1986).

Which Species Are Most Vulnerable to Traps?

The most important characteristic governing an organism's vulnerability to ecological traps is its ability to adapt, either behaviorally or evolutionarily, to changes in the relative quality of available habitats. Ecological traps can be seen as a case of evolutionary lag (Robinson & Morse 2000) in which animals have not yet evolved the mechanisms to respond properly to a changed environment. In this view, traps are inherently transitory phenomena because populations will either adapt to the trap through learning or evolution, outlast it (i.e., whatever is causing the trap will go away before the population becomes extinct), or become extinct. Little is know about the ability of animals to evolve new habitat preferences or adapt to changed environmental conditions, or about the speed at which they do so, so it is unclear how often or for which species it is reasonable to consider the possibility of "trapped" populations evolving new habitat preferences before a trap drives them to extinction.

It does seem clear, however, that the relationship between the rate of learning (or evolutionary change) and the rate of population decline brought on by the trap will determine the severity of the trap's impact on the population. When the demographic effects of the trap are relatively mild (i.e., causing a slow population decline) and habitat preferences can change rapidly (perhaps in animals with a high capacity for learning or in short-lived animals with high reproductive output), the trap will pose relatively little danger of population extinction. Where there is meaningful preexisting variation in habitat selection within a population upon which selection can

act, a trap will be unlikely to persist. For instance, many insect taxa show considerable intraspecific variability in host-plant preference, and some insects are capable of evolving new host-plant preferences in a relatively short amount of time (Singer et al. 1993). Species will be most vulnerable to ecological traps when learning or adaptation is slow and where variation in habitat preferences is low. High levels of gene flow between habitats, resulting in an inability of some subpopulations to adapt to local conditions (Hendry et al. 2001), will likely also contribute to the maintenance of a trap, particularly when the trap habitat is relatively rare (Garcia-Ramos & Kirkpatrick 1997).

If a species can respond successfully to changes in habitat quality through the use of previously evolved behaviors, it is unlikely to be vulnerable to an ecological trap. Systems of philopatry in birds provide an example of behavioral plasticity that may have evolved as a mechanism for responding to a changeable environment. Individuals of many migratory bird species are more likely to return to breeding sites where they have experienced success (i.e., where their nests were not depredated) than to those where they have been unsuccessful (Schmidt 2001). Switching to a superior habitat after a failed breeding attempt will substantially mitigate the effects of an ecological trap, but only if species can differentiate, directly or indirectly, among habitats of differing quality. If, for instance, a bird with a failed nest near a habitat edge returns to a different breeding location but still uses the same cues to select a breeding site, it is likely to settle in an equally unsuitable site near the edge. In this case, the species' evolved mechanisms for dealing with habitat change are of little use in avoiding the ecological trap. Natal philopatry, in which offspring return to the habitat in which they are born, provides a highly efficient mechanism for trap avoidance (Kokko & Sutherland 2001). Because the trap habitat is less productive than source habitat, more animals will return to the source with each generation until most are breeding there.

Another important factor affecting animals' vulnerability to ecological traps is the amount of information they possess when making habitat-selection decisions. Migratory birds, for instance, must select a breeding habitat within days or even hours of arriving on their breeding grounds. Because they have a limited amount of time in which to choose their breeding location and must do so based on cues available in the spring, they must use indirect indicators, such as information on vegetation structure, to assess what will be the best habitat 2 months later (Orians & Wittenberger 1991). One might expect species that have to make habitat selection decisions on such fragmentary information to be more vulnerable to ecological traps than species that have more time to assess habitat quality or that can assess the relevant variables more directly.

Identifying an Ecological Trap

To establish that a particular area of habitat is functioning as a trap, one needs to know that the habitat is of low quality relative to those around it and that it is preferred by the species in question. This is often accomplished by measuring some surrogate for habitat selection—usually animal abundance—and a surrogate for habitat quality—usually some measure of reproduction—in two or more habitats. A pattern of higher abundance and lower reproductive output in one habitat suggests the presence of a trap.

To demonstrate unequivocally that an apparent trap is truly a trap, researchers must demonstrate that the trap, like a sink, does not produce enough individuals to replace those lost to the population, and that animals actually prefer that habitat to others. Population growth rates can be estimated from long-term mark-recapture data or other intensive monitoring techniques, whereas habitat selection can be measured by documenting a flow of marked individuals from one habitat into another. Other types of data, such as information on animal settling order or the distribution of older versus younger animals, may also serve as indicators of animals' preference for different habitats. Although highly desirable, such data are notoriously difficult to obtain, and, in many cases, conservation planning will have to move forward with less-definitive evidence. In declining populations, a habitat may be identified as a trap if, despite appearing inferior to surrounding habitats, it maintains its population while populations in other, apparently superior habitats decline. In such cases, the continued presence of high animal densities, despite poor reproductive success, is assumed to result from the movement of animals into the trap habitat.

A further complicating factor in the diagnosis of ecological traps is the potential for density-dependent processes (e.g., competition for resources) to cause habitat quality to decline when population densities are high, presenting investigators with a habitat that appears to be a trap (i.e., densities are high and habitat quality is low) but is not when densities are low. It may be difficult to determine the role that density-dependent processes play in determining habitat quality without waiting for the population in a given habitat to decline to a low level, at which point, if the habitat is indeed a trap, the population may be nearing extinction.

Incorporating Ecological Traps into Management and Planning

The ecological trap concept alters in important ways our understanding of the population dynamics of animals in mosaic landscapes composed of habitat patches that vary in quality. Ecological trap theory demonstrates that, even in cases where habitat preference and habitat quality can be accurately determined, the conservation of high-

quality habitats may not be sufficient to ensure that a species will thrive. In fact, the creation of even modest amounts of poor habitat can pose a significant danger to population persistence if the species in question selects it preferentially. This contrasts with source-sink theory, which suggests that, unless poor habitat is extremely abundant relative to good habitat, the presence of poor habitat in the landscape is neutral or beneficial. In the case of the Cooper's Hawk in southern Arizona, managers operating in a source-sink framework would likely focus on preserving increased amounts of habitat in exurban areas, a strategy that could ultimately fail if a large, urban trap were drawing birds away.

Ecological traps present a substantial management challenge. An extreme implication of ecological trap theory is that animals would be better off if trap habitats were destroyed. In practice, managers are unlikely to be certain of the location, size, and implications of a suspected trap, and it is unlikely that a habitat would serve as a trap for all species of management concern. Therefore, habitat destruction will rarely, if ever, be a feasible or desirable response. Managers, then, must find ways to mitigate the effects of ecological traps. Mitigation efforts can focus either on increasing the quality of the trap habitat or decreasing the trap's attractiveness. For example, if grassland birds nest preferentially in airfields due to the presence of abundant perches (e.g., fences, light poles) but experience low reproduction as a result of their nests being mowed, managers could decrease the population-level impacts of this trap by adjusting mowing schedules during nesting or decrease the habitat's attractiveness by eliminating perches or actively driving birds away.

Ecological traps also have implications for the management of harvested populations. Because maximum hunting pressure often occurs in animals' favored habitats, because that is where they generally occur at highest density, hunting can transform high-quality habitats into traps by increasing adult mortality (Delibes et al. 2001). Such traps may be masked by immigration from adjacent, less-preferred areas, maintaining high densities in preferred habitats even as the population as a whole declines. This suggests that population monitoring of harvested species should occur in all occupied habitats, not only those favored by the species in question.

Incorporating the ecological trap concept into conservation planning requires explicit consideration of habitat selection when predicting animal population dynamics, whether through population growth estimates or more involved demographic modeling. Currently available modeling software is, for the most part, not capable of modeling ecological traps. To allow effective modeling of traps, models must permit habitat attractiveness and quality to be parameterized separately, and they must allow explicit modeling of habitat selection, in which habitats are filled according to their attractiveness and animals search for the most attractive, but not necessarily the

best, available habitat. Efforts to alter one such model (PATCH) to achieve this are already under way (N. Schumaker, personal communication). More generally, we must recognize that source-sink dynamics and ecological traps represent two ends of a continuum defined by all possible permutations of the relationship between habitat selection and habitat quality (Kristan 2003). Source-sink dynamics represent the case of pure optimality, and ecological traps represent its opposite. To predict more accurately the responses of animal populations to complex, changing landscapes, we must begin to identify where species of management concern fall along this continuum.

It is, as yet, unclear how important the consideration of ecological traps will be in long-term conservation efforts. On the one hand, we must be cautious in applying this new body of theory to real-world situations. Models can be seductive, and, in too many cases, ecologists try to fit their system or problem into an available theoretical framework (Harrison 1994). We must guard against becoming overly enthusiastic in embracing the newly minted theory of ecological traps. There is, however, a growing body of evidence supporting the ecological trap concept, and we now have access to several models that provide firm theoretical foundations for exploring the potential influence of traps on real conservation issues. Because the implications of ecological traps for population persistence are so dire and because, as a result of human activities, rapid changes in landscape structure and habitat quality are now commonplace, we cannot afford to ignore the possibility of ecological traps or fail to take them into account in the study, management, and conservation of animal populations.

Acknowledgments

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