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Effects of an Attractive Sink Leading into Maladaptive Habitat Selection

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ABSTRACT: Habitat sinks can attract dispersing animals if high mortality or breeding failure are difficult to detect (e.g., when due to human hunting or pollution). Using a simple deterministic model, we explore the dynamics of such source-sink systems considering three scenarios: an avoided sink, no habitat preference, and an attractive sink. In the second two scenarios, there is a threshold proportion of sink habitat above which the whole population decreases to extinction, but this extinction threshold varies with habitat preference and the relative qualities of the two habitat types. Hence, it would be necessary to know the habitat preferences of any species in a source-sink system to interpret data on population increases and declines. In the attractive sink scenario, small changes in the proportion of sink habitat may have disproportionate effects on the population persistence. Also, small changes in growth rates at the source and the sink severely affect the threshold and the time of extinction. For some combinations of demographic parameters and proportion of habitat sink, the decline affects the source first; thus, during some time, it will be hidden to population monitoring at the sink, where numbers can even increase. The extinction threshold is also very sensitive to the initial population sizes relative to carrying capacity. Attractive sinks represent a novel aspect of source-sink dynamics with important conservation and management implications.

Keywords: attractive sink, source-sink metapopulation, extinction, conservation, management.

q1 Populations are generally spatially structured. For a given species living in a heterogeneous environment, changes in habitat quality will likely lead to local demographic differences (MacArthur 1972). Good-quality patches will tend to yield a demographic surplus (births exceeding mortality), while bad-quality patches will likely yield a demographic deficit (births below mortality). Since Pulliam (1988), the former patches are labeled as sources ("source habitats," "source patches," or "source local populations" in metapopulation terminology; Harrison and Taylor 1997), while the latter are labeled as "sinks." By definition, this kind of sink cannot persist deterministically without immigration from sources, and the population dynamics for the whole system are balanced through dispersal (Holt 1985).

Sinks are frequently associated with substandard habitats where resources are scarce and, consequently, survival is possible, but reproduction, although feasible, is generally poor (Danielson 1992). In some extreme cases, habitats are so poor that they allow for survival but not for reproduction (e.g., Smith 1968). Adaptive habitat selection would allow animals to recognize and, if possible, avoid these suboptimal habitats (Rosenzweig 1981). In these conditions, only two basic ecological mechanisms are recognized as capable of generating source-sink dynamics in heterogeneous environments (Holt 1993; Dias 1996). These are intraspecific density-dependent interference competition for good habitat (i.e., sinks are occupied because individuals in source habitats force subdominant individuals into sinks) and passive density-independent dispersal (i.e., sinks are occupied because some individuals leave source habitats regardless of resource availability, e.g., due to the influence of physical forces such as wind or water currents).

However, although rarely considered under the perspective of source-sink theory (but see Davis and Howe 1992), there is also the possibility of ecological sinks resulting from high mortality or breeding failure in otherwise good habitats, where resources are abundant and reproduction could be high (Gaona et al. 1998). These kinds of sink are frequently reported in the literature associated with human activities (e.g., Knight et al. 1988; Woodroffe and Ginsberg 1998; Martin and Szuter 1999; Revilla et al. 2001). In these cases, the actual anthropogenically caused poor-habitat conditions may be difficult to detect by individual animals, as the causes of mortality or reduced

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breeding would be different from those in their evolutionary history. Hence, maladaptive behaviors may be expected because most of these attractive sinks probably will be perceived by animals as sources (or, at least, as good habitats allowing a high reproductive success) and therefore could be considered "deceptive sources."

Previously, several authors have modeled source-sink systems, relaxing the assumption of an optimal-habitat selection by dispersers. In some of these cases, it was assumed that dispersing individuals were unable to distinguish habitat quality and moved at random (Doak 1995); in other cases, it was assumed that dispersers sampled few habitats, remaining in the first empty place they could find (Pulliam and Danielson 1991). However, to our knowledge, the population dynamic effects of an attractive sink have not been explored until now, in spite of the potentially important conservation and management implications of these sink habitats.

The aim of this article is to analyze the behavior of a structured population system, including a source and a sink, to compare the responses of the whole population to different amounts of sink habitat under three scenarios: q2 in scenario 1, individuals avoid sink habitat (the classical "attractive source" scenario); in scenario 2, individuals are not able to discriminate between sink and source habitat ("no habitat preference" scenario); and in scenario 3, individuals prefer sink habitat ("attractive sink" scenario), fooled by the apparently high breeding potential and low mortality there.

In considering scenario 3 (i.e., attractive sink), we pose several additional questions: How do different proportions of source and sink habitat influence the growth of the whole population? What is the influence of the initial size of source and sink subpopulations on the dynamics of the combined source and sink population? How can small changes in mortality at the sink influence population growth? Can the risk of extinction of the whole population be estimated by monitoring numbers just at the sink?

The Model

We have built a simple deterministic model with two habitat patches (a source and a sink) in a limited and constant total area. This area determines the whole-population carrying capacity (CC) so that $CC_{source} + CC_{sink}$ is constant. Both patches are linked by migration, with no cost and with no effect on reproduction and survival. Also, there is no dilution effect (Pulliam and Danielson 1991; Danielson 1992), and individuals are always able to find empty places in their preferred habitat, which is immediately recognized. By definition, reproduction exceeds mortality at the source, while the opposite occurs at the sink. Birth and mortality rates are density independent, although carrying capacity determines a maximum number of breeding individuals.

We considered two age classes: young (<1 time unit old) and adult (≥1 time unit old). Sequential phases in the model follow (table 1): First, once the initial parameter q3 values for each patch (population size, birth and survival rates, and carrying capacity) are read, the model applies survival values and calculates the number of reproductive vacancies created in each habitat. Second, vacancies are replenished with young survivors, which first occupy the empty places in the preferred patch; the model gives priority to the young born in the preferred habitat; all young unable to find an empty place in the source or the sink die. Third, the reproductive rates are applied to the new adult class.

Each scenario was incorporated in the model in the following way (see table 1): scenario 1, "avoided sink"—young migrate from the source to the sink only when the source is saturated; conversely, young migrate from the sink if there is an empty place in the source; scenario 2, "no habitat preference"—young migrate in proportion to the availability of empty places in each habitat; scenario 3, "attractive sink"—young migrate from the sink to the source only when the sink is saturated; young migrate from the source if there is some empty place at the sink.

Overall transient population finite growth rate, λ_{total}, was estimated as the geometric mean of the rate of change in the number of adults per time unit for the simulation period before the population became stabilized in a constant level. For each scenario, we analyzed the effects over λ_{total} of different percentages of source and sink habitats and of different values of local demographic parameters. Simulations lasted 100 time steps.

The scenarios were evaluated for larger and smaller initial demographic differences between source and sink. For this, we used an arbitrary value for the reproductive rate of 1.5 and survival probabilities yielding finite growth rates, in absence of density dependence and immigration/emigration, of 1.05 and 1.1 in the source (λ_{source}) and ranging between 0.8 and 0.95 in the sink (λ_{sink}). The arbitrary value assigned to the reproductive rate does not affect the results, as only the growth rates in the source and the sink have influence on them. Whole carrying capacity was made equal to 100. Again, this convenience does not affect the results, as only the relative proportion of source and sink is relevant.

Results

For any level of demographic difference between source and sink habitats, the response of λ_{total} to the percentage of sink habitat is notably different depending on the pref-

Table 1: Summary of simulation algorithms used in the model

Habitat preference ("avoided sink" and "attractive sink")	"No habitat preference"
Survival: $A^a(t) = A^a(t-1) \times s^a$ $\mathrm{NA}^a(t) = Y^a(t-1) \times s^a$ $A^b(t) = A^b(t-1) \times s^b$ $\mathrm{NA}^b(t) = Y^b(t-1) \times s^b$	
Occupation of reproductive vacancies in the preferred habitat (population *a*) at time *t*: $V^a = \mathrm{CC}^a - A^a$ $\mathrm{NA}^a_a = \min(V^a, \mathrm{NA}^a)$ $A^a = A^a + \mathrm{NA}^a_a$ $\mathrm{NA}^a = \mathrm{NA}^a - \mathrm{NA}^a_a$ $V^a = V^a - \mathrm{NA}^a_a$ $\mathrm{NA}^a_b = \min(V^a, \mathrm{NA}^b)$ $A^a = A^a + \mathrm{NA}^a_b$ $\mathrm{NA}^b = \mathrm{NA}^b - \mathrm{NA}^a_b$	Occupation of reproductive vacancies in populations *a* and *b* (migration in proportion to the availability of vacancies in each population) at time *t*: $V^b = \mathrm{CC}^b - A^b$ $\mathrm{NA} = \mathrm{NA}^a + \mathrm{NA}^b$ $\mathrm{NA}^a = \mathrm{NA} \times V^a/(V^a + V^b)$
Occupation of reproductive vacancies in the nonpreferred habitat (population *b*) at time *t*: $V^b = \mathrm{CC}^b - A^b$ $\mathrm{NA}^b_b = \min(V^b, \mathrm{NA}^b)$ $A^b = A^b + \mathrm{NA}^b_b$ $V^b = V^b - \mathrm{NA}^b_b$ $\mathrm{NA}^b_a = \min(V^b, \mathrm{NA}^a)$ $A^b = A^b + \mathrm{NA}^b_a$	Occupation of reproductive vacancies in the nonpreferred habitat (population *b*) at time *t*: $\mathrm{NA}^b = \mathrm{NA} \times V^b/(V^a + V^b)$ $A^a = A^a + \min(V^a, \mathrm{NA}^a)$ $A^b = A^b + \min(V^b, \mathrm{NA}^b)$
Reproduction: $Y^a(t) = A^a(t) \times r^a$ $Y^b(t) = A^b(t) \times r^b$	

Note: The algorithms for "avoided sink" and "attractive sink" scenarios (habitat preference) are the same; in both cases, population *a* occupies the preferred habitat: the source in the "avoided sink" scenario and the sink in the "attractive sink" scenario. For the "no habitat preference" scenario, population *a* is the source and the population *b* is the sink. Survival and reproduction have the same formulation in all scenarios. For numerical values of the parameters, see the text. Definitions of symbols used for parameters and variables in the model: A^i, number of adults in population *i*; CC^i, carrying capacity of population *i* (CC is constant overall); NA^i, number of new adults (surviving young) in population *i*; NA^i_j, number of new adults from the population *j* that occupy reproductive vacancies in the population *i*; r^i, reproductive rate in population *i*; s^i, survival rate in population *i*; *t*, time; V^i, number of reproductive vacancies in population *i*; Y^i, number of young in population *i*.

erence scenario. Beginning with a saturated population (i.e., both the source and the sink are at carrying capacity and the population cannot grow), there is a threshold proportion of sink habitat above which the whole population tends to decrease ($\lambda_{\mathrm{total}} < 1$) in all three scenarios (fig. 1). However, the change in this transient growth rate, with increasing sink habitat, is smooth when the source is preferred, linear when there is no preference, and nonlinear and with very sharp decline when the sink is preferred (fig. 1). Differences between the attractive sink scenario and the others are larger close to the threshold. Hence, small changes in the amount of sink habitat near the threshold will have disproportionate short-term effects on the populations persistence in this scenario.

Changes in the growth rates in source and sink affect both the time and the threshold to extinction for scenarios 2 and 3 (with attractive sources, extinction will not occur without 100% sink habitat). Keeping $\lambda_{\mathrm{source}}$ constant, a decrease in λ_{sink} results in a noticeable decrease in λ_{total} and a reduction in the percentage of sink habitat that represents the extinction threshold. For instance, for initial populations at carrying capacity, $\lambda_{\mathrm{source}} = 1.1$, and in an attractive sink, a decrease of λ_{sink} from 0.9 to 0.7 results in the extinction threshold changing from 50% to 25% of sink habitat (fig. 2).

When the proportion of sink habitat is above the threshold, the fate of the whole population varies dramatically between the three scenarios. With an avoided sink, the

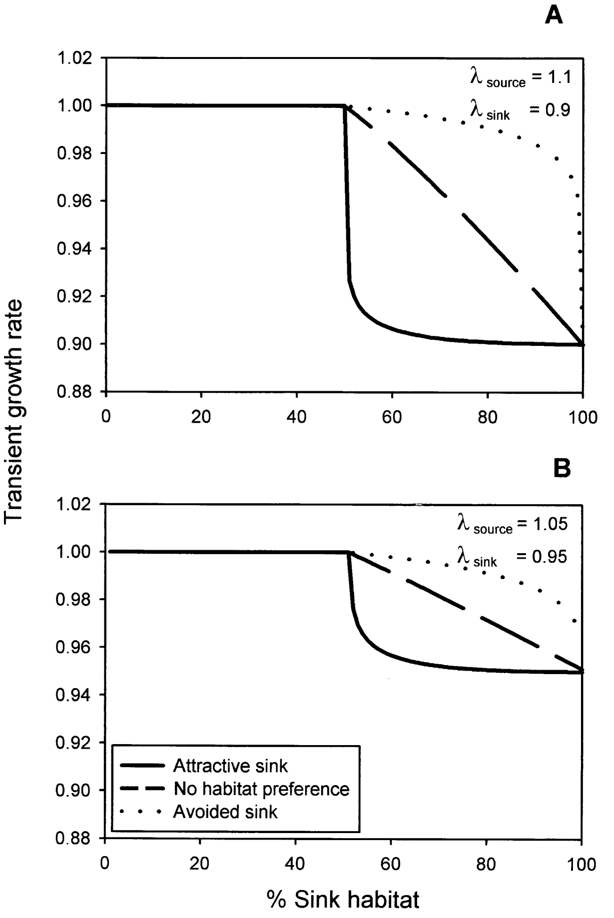

Figure 1: Response of the transient overall growth rate to changes in the proportion of sink habitat. There is a threshold value of sink habitat above which the whole population tends to decrease in the three simulated scenarios (attractive sink, no habitat preference, and avoided sink). Two situations of larger (*A*) and smaller (*B*) initial demographic differences between source and sink are shown.

whole population tends to decrease and becomes stabilized above the sources carrying capacity (fig. 3*A*). The amount of sink population maintained by the source's surplus (and therefore the stabilization level of the whole population) depends on the proportion of sink and the relative demographic differences of the source and the sink (fig. 3*A*, 3*B*). When there is no habitat preference, the whole population decreases relatively slowly, leading in the long term to the extinction of both sink and source populations (fig. 3*C*, 3*D*). Similarly, this is also the fate when the sink is attractive (fig. 3*E*), but in this case, the decline may not be simultaneous in the source and the sink. As the sink continuously absorbs the source's production, the decline affects the source first, and it does not affect the sink for a time (fig. 3*F*). This is specially clear for combinations of demographic parameters and proportion of habitat sink near the threshold. In this situation, population numbers in the sink can even increase for a time when initial values are under the carrying capacity (fig. 4).

The threshold of sink habitat determining the extinction of the entire population (in scenarios 2 and 3) depends on the initial occupation of both habitats, moving toward lower values when they are unsaturated. In particular, the threshold is very sensitive to the level of initial occupation of the source (fig. 5). For instance, changing the initial source population from 100% to 25% of its carrying capacity moves the extinction threshold from 50% to 23% of sink habitat (fig. 4*B*). The model simulations were also run considering the possibility of a surviving surplus of nonbreeding adults, but the results do not change significantly.

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Discussion

Both attractive sinks and no-preference sinks imply the inability of individual organisms to recognize and evaluate mortality risks or potential breeding failures. There is no rule to generalize when attractive sinks can occur, as there are many kinds of organisms and many potential causes of mortality or unsuccessful reproduction. For instance, some animals could learn to avoid hunters, but they probably will have more problems learning to avoid pesticides or poison, whose effects are frequently delayed or result from bioaccumulation (Newton 1998).

To our knowledge, the dynamics of a population, including an attractive sink, have not been explored. We

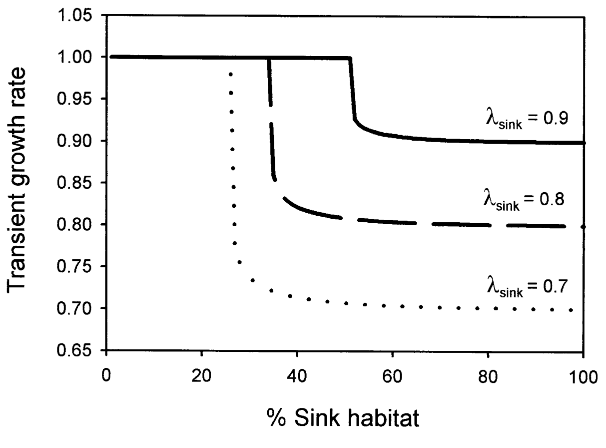

Figure 2: Effects on the transient overall growth rate and the extinction threshold of changes in the demographic parameters at the sink for the attractive sink scenario, with $\lambda_{source} = 1.1$ and the initial population at carrying capacity. A reduction of λ_{sink} from 0.9 to 0.8 and 0.7 result in noticeable decreases in the transient overall growth rate and the proportion of sink habitat that represents the extinction threshold.

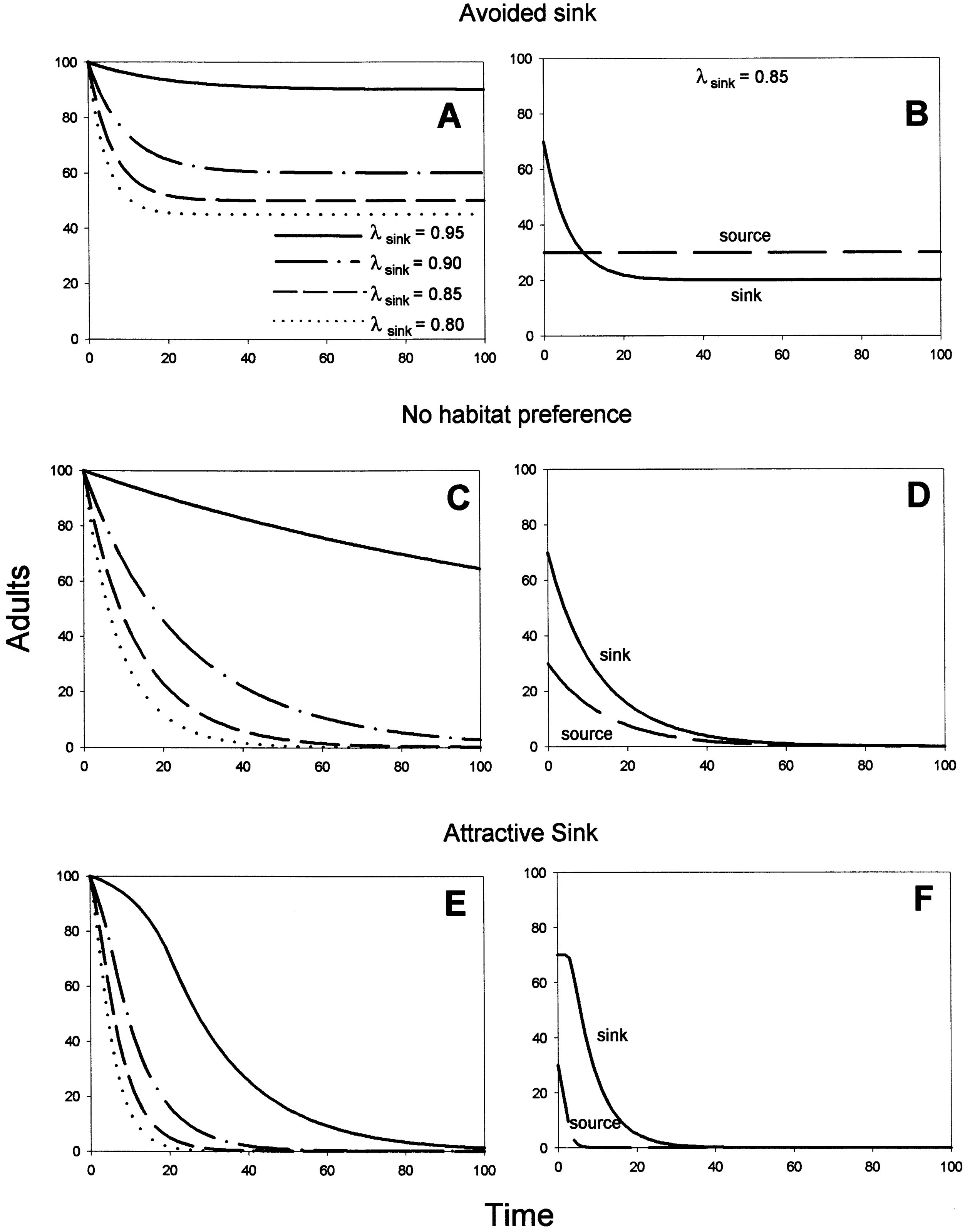

Figure 3: Adult population changes over time for the three scenarios and several levels of initial growth rate at the sink (λ_{sink}). For all figures, $\lambda_{source} = 1.1$, and the initial population is at carrying capacity, distributed in 30% at the source and 70% in the sink (above the extinction threshold). *A*, *C*, *E*, Overall adult population (source + sink) for λ_{sink} equal to 0.95, 0.9, 0.85, and 0.8. *B*, *D*, *F*, Adult population (separately in the source and the sink) in the particular case of $\lambda_{sink} = 0.85$.

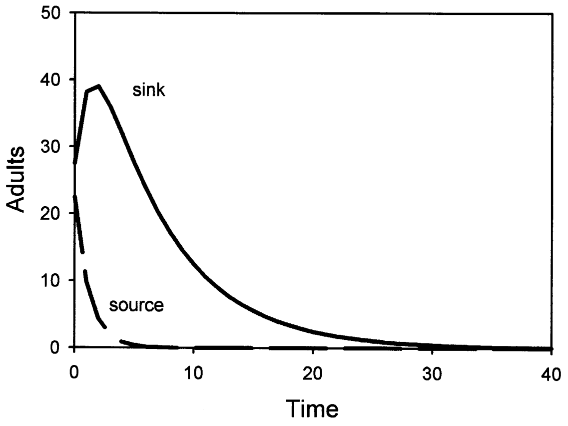

Figure 4: Temporal changes of sink and source populations (numbers of adults) under the attractive sink scenario for a combination of demographic parameters and proportion of sink habitat close to the threshold ($\lambda_{source} = 1.1$, $\lambda_{sink} = 0.9$, and 52% of sink habitat) and initial populations at 50% of their carrying capacity. As the sink absorbs the production from the source, during a time, the negative trend of the whole population would be hidden to censuses carried out at the sink where numbers can even increase.

think the main cause for this lack of investigation has to do with the conceptual framework within which source-sink studies traditionally have been completed. Although source-sink models are commonly applied to conservation problems (Harrison and Taylor 1997; Hoopes and Harrison 1998), their roots derive from evolutionary ecology theory (e.g., see discussions about the "paradoxes" of the ecological niche and carrying capacity in source-sink systems; Dias 1996), where human-caused mortality or reduced recruitment usually are not considered.

From an evolutionary perspective, a population dominated by phenotypes attracted to sinks should disappear or change toward another population dominated by phenotypes that select the source properly (niche conservatism; Holt 1995) or by phenotypes with improved fitness at the sink (source-sink inversion; Dias 1996). In ecological time, however, attractive sinks resulting from high human-caused mortality (or reduced birth rate) are probably very common. Overkilling is usually considered one of the main causes of extinction (Diamond 1989) and a common factor driving the decline of otherwise healthy populations (Caughley 1994). It is reasonable to think that people usually harvest in the target species favorite habitats (although sometimes animals might be more abundant in bad habitats; Van Horne 1983). Whenever prey originally occupying substandard habitats migrate to replace the harvested conspecifics, the favorite habitat can be acting not just as a mortality sink but as an attractive sink in the sense here proposed.

Attractive sinks do not necessarily arise from human activities alone. If sinks are described as habitats where a species is unable to replace itself without immigration, it should make no difference whether the cause was resource scarcity, heavy competition, or strong predation. For instance, Kruuk (1995) has proved that European otters (*Lutra lutra*) repeatedly remove fish from rocky patches where q5 "vacancies are filled up almost as soon as they arise" (otters hunt during the day and fish move at night; then, they are unaware of the mortality risk in the attractive patch). These patches are "natural," although very local, attractive sinks for fish. Also, some British rivers with high densities of the recently introduced American mink (*Mustela vison*) could be attractive sinks for coots (*Fulica atra*), whose populations should be replenished by birds from nearby mink-free populations (Ferreras and Macdonald 1999). In the same sense, Gates and Gysel (1978) called field-forest q6

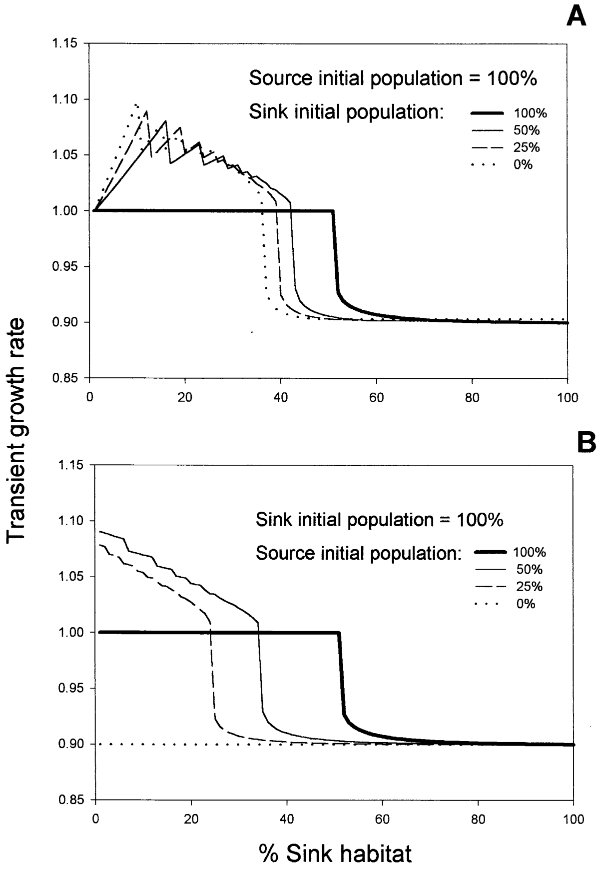

Figure 5: Effects on the proportion of sink habitat on transient growth rate, for different levels of initial occupation of the sink (*A*) and the source (*B*) patches. All results are for the attractive sink scenario. The lower the initial occupation of each of the habitats, the lower the proportion of sink defining the threshold (the point at which transient growth rate = 1), other parameters kept constant.

ecotones characterized by high mortality but attractive for birds "ecological traps."

To analyze the effects of an attractive sink, we have used a very simple model, but population dynamics and real landscapes are complex (Wiens 1997). Indeed, some of our results are conditioned by the characteristics of the model. For instance, to include absolute habitat preference and density dependence as a ceiling results in the existence of a definite threshold point where the population begins to decline. Different density-dependence functions and partial habitat preferences could yield smoother changes in the transient population growth rate. Some other features of populations in the real world, such as differential movement rates, migration costs, demographic and environmental stochasticities, and others, were not considered. More sophisticated models adapted to particular situations could introduce these refinements, but we think that in order to explore the qualitative effects of an attractive sink our simpler model is preferable.

The impact of an attractive sink can be stressed by drawing comparisons with the effects of more usual scenarios, such as preference for the source or lack of habitat preference. In all three cases, there is a threshold amount of sink habitat above which the whole population decreases. With amounts of sink habitat below such a threshold, even populations with an attractive sink can be stable or growing. Therefore, harvesting resulting in attractive sinks could still be compatible with population persistence.

The results of the scenario corresponding to an avoided sink are well known (Pulliam 1988). The source is extinction resistant but the sink is not. Thus, reserves must be established in sources since preserving only sink habitats will probably lead to population extinction (Dias 1996). Also, sources must be preserved to allow the existence of some subpopulations inhabiting sinks (Wootton and Bell 1992).

Our "no habitat preference" scenario is rather similar to the model proposed by Doak (1995) for animals that disperse at random with relative movement between source and sink, determined by relative densities since these individuals evaluate habitat quality inefficiently and have high mobility. Also, results coincide: the habitat threshold is an extinction threshold, above which the decrease of the transient population growth rate is linear and gradual yet continuous, leading the population to extinction in the long term. However, in this case, the relatively slow decreases in population size are more likely to be recognized by managers soon enough to modify the population parameters (e.g., reducing hunting or fishing quotas) or the proportion of sink habitat (e.g., increasing the number and surface of reserves) in order to avoid extinction (e.g., Allison et al. 1998).

More novel results arise from the attractive sink scenario. In this case, unlike in the other scenarios, a small increase in the proportion of sink or a small decrease in survival can lead the population to extinction in the short term. Moreover, the extinction threshold is highly dependent on initial population levels and growth rates in the source and the sink. In practice, all this makes it difficult to recognize the limits between sustainable and unsustainable amounts of mortality (or breeding failure) in the wild, as well as threshold of sink habitat determining sustainability. The extreme sensitivity of some modeled real populations to very small changes in mortality rates (e.g., tigers, *Panthera tigris*, in Nepal [Kenney et al. 1994]; bears, *Ursus arctos*, in Spain [Wiegand et al. 1998]) suggests that, in some cases, individuals are being killed in their favorite habitats, which could be attractive sinks.

The high influence of initial population sizes on the probability of early extinction is an outcome of stochastic density-independent population growth (Ludwig 1996). For initially small population sizes, there is an early phase when a fraction of the starting populations become extinct by stochastic reasons (Lande and Orzack 1988; Lande 1993). In our deterministic model, the influence of initial population sizes seems to be related to the point in which the process of "drainage" from the source by the attractive sink begins (the smaller the initial population in the source, the lower the extinction threshold of sink habitat).

The delayed and sharp response of an attractive sink population to conditions leading to extinction (figs. 3*F*, 4) can have important conservation and management consequences. For instance, animal censuses in some refuges or reserves that function as attractive sinks (e.g., marshes with a high content of lead pellets, producing poisoning of waterfowl; Pain 1991) could lead to misinterpretations, as the apparently stable or growing sink population could be identified as a source and the declining source as a sink. Also, some exploitation in spatially structured populations could be wrongly estimated as sustainable because a decline is not observed in the harvested patches (McCullough 1996). In both examples, sink populations could be temporarily sustained by the sources, before resulting in a rapid collapse of the whole system. Effects on the sink will become evident only when the source is exhausted, probably too late for successfully recovering the population.

The comparison of our three scenarios indicates that dynamics of a source-sink population are dramatically dependent on the habitat preference of the target species. Even a detailed knowledge of the proportions of sink and source habitat and the demographic parameters on each of them may be inadequate to predict the population trends, as it will be necessary to take into account individual decisions with respect to the available habitats (Lima and Zollner 1996). Moreover, if habitat preferences are unknown, it is not possible to obtain reliable conclusions about population trends from censuses carried out at the source or the sink or even decide whether the source or sink subpopulation was better to track. Given the difficulty of measuring habitat preferences for many species (Doak 1995), cautious criteria must be applied when managing populations of animals that could be misperceiving sink-habitat quality.

Attractive sinks for animal populations are at least as old as mankind and have been more or less indirectly approached in different contexts of conservation (e.g., refuge theory, predator-prey metapopulations) and management biology (e.g., game sinks, harvesting in structured populations) but not integrated into source-sink theory. Using this theory as a framework to analyze all of these situations can bridge gaps between conservation biology and wildlife management (Caughley and Gunn 1996) and between compositionalist and functionalist approaches to conservation biology (Callicott et al. 1999). Admitting the possibility of attractive sinks and their potential influence on the dynamics of structured populations will help to manage exploited and pest species and to conserve endangered ones.

Acknowledgments

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