



The Demographic Significance of 'Sink' Populations

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ABSTRACT

Rates of reproduction and mortality undoubtedly vary across the ranges of most species. Local demographic 'sources', where reproduction exceeds mortality, may subsidize non-sustaining 'sink' subpopulations, where local reproduction fails to compensate for mortality. We examine model metapopulations of sources and sinks, connected by intrinsic dispersal of juveniles and density-dependent dispersal of adults or juveniles. Results show that a large but finite proportion of the metapopulation might reside in non-sustaining subpopulations. Although these demographic sinks are unable to persist independently, they may contribute significantly to metapopulation size and longevity. Our analysis leads to several recommendations for the conservation of natural populations: (1) demographically productive subpopulations need to be identified and protected; (2) conservation of buffer habitats and marginal subpopulations should be a part of comprehensive conservation plans; and (3) the long-term status of even seemingly secure metapopulations should be carefully monitored.

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INTRODUCTION

Populations in nature typically inhabit a range of qualitatively different habitats, some of which undoubtedly are incapable of supporting isolated self-sustaining demes (e.g. Thompson & Nolan, 1973; King & Mewaldt, 1985; Opdam, 1988; Pulliam, 1988) view such habitat heterogeneity as an important element of population dynamics. Habitat fragmentation by humans has further warranted this view. Whitcomb *et al.* (1981) and Temple and Carey (1989), for example, considered the metapopulation dynamics of birds in fragmented forest landscapes. They concluded that certain populations in severely dissected landscapes are doomed to local extinction without persistent immigration from other 'source' areas. Brown and Kodric-Brown (1977) had earlier coined the term 'rescue effect' to describe the influence of self-sustaining populations on non-sustaining populations.

Pulliam (1988) introduced a simple model of metapopulation dynamics with profound implications for conservation biology and ecology. Like several previous authors (Levins, 1970; Boorman & Levitt, 1973; Buechner, 1987), Pulliam recognized 'source' and 'sink' subpopulations connected by density-dependent immigration. His model implies that a large proportion of individuals within a metapopulation might occupy demographically unstable sink habitats. In this case, field observations of habitat suitability and other ecological variables may be dangerously misleading.

The importance of reproductively successful source populations is obvious; without them, the metapopulation as a whole cannot persist. Here we explore a rather different element of metapopulation dynamics: the contribution of sink populations to metapopulation size and stability. Under what circumstances, if any, do sink populations improve the long-term stability and size of a metapopulation? Under what conditions are they a detriment? Such questions have direct relevance to ecology and conservation biology, particularly if, indeed, a significant fraction of today's animal and plant populations occur in non-sustaining habitats.

THE MODEL

We begin with a deterministic model of a population which breeds at discrete (e.g. annual) time intervals (Fig. 1). The overall population (the metapopulation) is divided into m subpopulations, at least one of which (a source) maintains a positive balance between births and deaths. Associated with the source is a variable number of sink subpopulations, where deaths outnumber births. The number of individuals in any subpopulation in

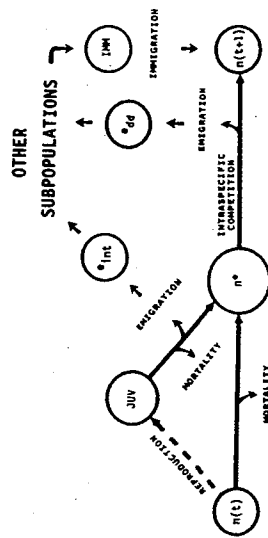


Fig. 1. Summary of the metapopulation model described in the text. Diagram follows demographic events during a single time unit or 'generation', where $n(t)$ is the starting population size and $n(t+1)$ is the ending population size. Emigration has two components: e_{im} = intrinsic dispersal of juveniles (eqn (2) in text), whose relative magnitude is independent of population size; e_{ad} = density-dependent dispersal of adults and juveniles (square bracketed term in eqn (3)), which occurs only when the population size exceeds the environmental carrying capacity. n^* is the post-breeding population size before density-dependent dispersal takes place. Shortly after the dispersal phase, emigrants from all sites are combined into a pool of immigrants (IMM), divided evenly among available populations.

habitat i consists of survivors from the previous time interval (ADULTS), non-emigrating juveniles (JUV), and immigrants from other subpopulations (IMM):

$$\begin{aligned} n_i(t+1) &= (\text{ADULTS}) + (\text{JUV}) + (\text{IMM}) \\ &= n_i(t)P_{Ai} + B_i\beta_i P_{Ji}(1 - \delta_i) + \sum_{j \neq i} e_{ji}/(m-1) \end{aligned} \quad (1)$$

where

$n_i(t)$ is the population of habitat i at time t ;

P_{Ai} is the average probability of adult survival to the next breeding season in habitat i ;

B_i is the number of individuals which can breed in habitat i and is given by

$$B_i = \begin{cases} n_i(t) & \text{if } n_i(t) < \hat{n}_i \\ \hat{n}_i & \text{if } n_i(t) \geq \hat{n}_i \end{cases}$$

where $\hat{n}_i$ is the number of available breeding opportunities in habitat i ;

β_i is the average reproductive success for habitat i ;

P_{Ji} is the average probability of juvenile survival to the next breeding season in habitat i ;

δ_i is the intrinsic probability of juvenile leaving habitat i (density-independent juvenile dispersal probability).

e_i is the number of emigrants from subpopulation i during one time interval and is given by

$$e_i = B_i \beta_i P_i \delta_i \quad (2)$$

when the annual production plus survivors does not exceed the number of breeding opportunities, or

$$e_i = B_i \beta_i P_i \delta_i + [(n_i(t)P_{A_i} + B_i \beta_i P_{J_i}(1 - \delta_i) - \hat{n}_i)] \quad (3)$$

when the annual production of non-emigrating offspring plus adult survivors exceeds the number of breeding opportunities.

The first term (eqn (2)) represents intrinsic or 'passive' emigration (Holt, 1985), while the additional term in eqn (3) (in square brackets) represents density-dependent or 'active' emigration (Pulliam, 1988). We assume that during a given generation (e.g. year) emigration precedes immigration and reproduction precedes both immigration and emigration. We also assume that non-dispersing juveniles (from eqn (2)) actively compete for the next year's breeding opportunities. This assumption can be relaxed by introducing more complex age structure and reproductive delays. However, in order to emphasize general metapopulation dynamics we restrict our analysis to a two-stage population. Like Pulliam (1988), we also assume that all juveniles or survivors from the previous year emigrate if they are unable to secure a breeding opportunity and if a secondary site is available. We also assume no mortality during the emigration/immigration process. Relaxation of these assumptions can be accomplished by incorporating additional terms to the model's equations, but doing so adds no critical substance to our general conclusions.

Another useful variable, λ_i , describes the balance between births and deaths in any subpopulation:

$$\lambda_i = P_{A_i} + P_{J_i} \beta_i$$

Subpopulations with a positive λ_i are defined as source populations whereas subpopulations with a negative λ_i are considered sink populations.

This model extends the treatment of Pulliam (1988) to include intrinsic dispersal of juveniles, immigration into source (as well as sink) populations, and limits ($\hat{n}_i$) to the population size of all subpopulations (including sink). Like previous treatments, we assume that emigrants from a population have an equal probability of immigrating into any of the other populations (source or sink).

METHODS

In addition to mathematical analysis, we use hypothetical but realistic data to simulate the behavior of this model. Analytical results show a wide range of outcomes depending on values assigned to the parameters in the model. The simulations here are limited to a rather narrow range of biologically realistic circumstances and should not be viewed as comprehensive. Initial values of adult survivorship, juvenile survivorship, birth rate, and carrying capacity are similar to those reported for temperature breeding passerines (Temple & Carey, 1989). Variations reflecting more reproductively conservative (K -selected) or reproductively prolific (r -selected) species are discussed where appropriate.

Simulations were carried out on a microcomputer with a program written in TURBO-PASCAL. Our cases are restricted to a single source population with 0-10 identical sink populations. Of course, metapopulations in nature are far more complex, but these simple examples are employed to illustrate some fundamental characteristics of metapopulation dynamics.

RESULTS

Intrinsic dispersal ($\delta = 0$)

Starting with any small source population (e.g. $n_i = 100$), the metapopulation model eventually generates a stable equilibrium. In the case of a single population with a positive net reproductive rate ($\lambda > 1.0$) this equilibrium (Fig. 2(A)) is equivalent to the number of breeding opportunities plus a non-breeding population of 'floaters' which, we assume, remains in the same area. From Pulliam (1988) we know that a solitary source population will come to an equilibrium population of $\hat{n}P_{J_i}\beta_i/(1 - P_{J_i})$. In the presence of an accessible sink habitat, we assume for the sake of simplicity that all non-breeding individuals emigrate. If adult survivorship is as high or higher than in the source habitat, then the metapopulation will attain a larger size than that of the solitary source, in some cases considerably larger (Fig. 2(B)).

Additional sink habitats may increase the equilibrium metapopulation size, but only to a limit. At some point new sink populations merely divide a fixed number of extra-source individuals into smaller units (Fig. 3). A similar effect occurs with increase in the number of breeding opportunities in the sink habitats (Fig. 4); metapopulation size increases until a threshold is reached, beyond which further increases in breeding opportunities have no influence on metapopulation size.

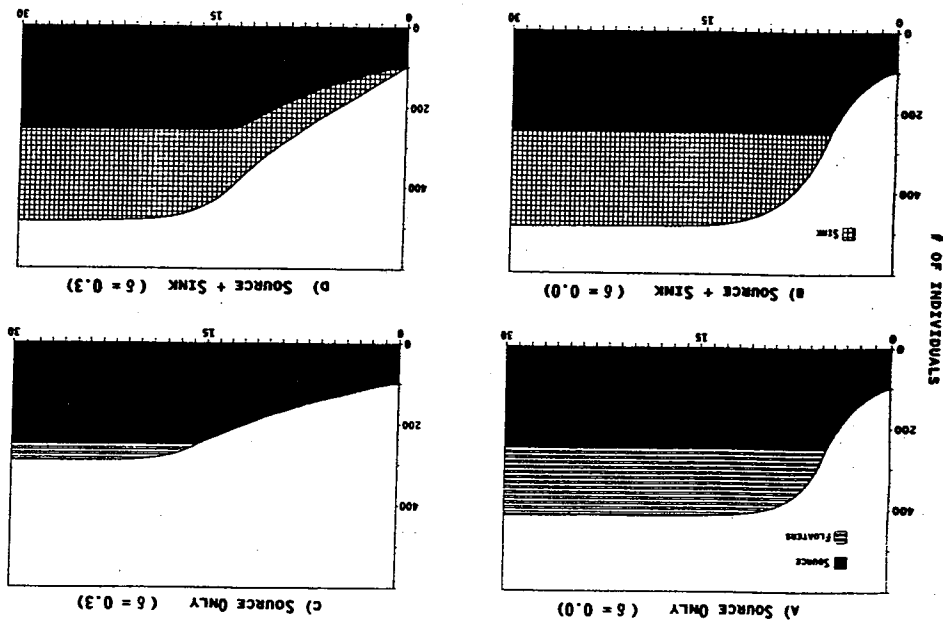


Fig. 2. Equilibrium dynamics of populations with (B and D) and without (A and C) an accompanying sink population. In all cases, adult survivorship (P_A) = 0.62, juvenile survivorship (P_J) = 0.31, source birth rate (λ) = 2.03, and sink birth rate (λ) = 0.90. Net reproductive rate (R_0) is 1.25 for source, 0.75 for sink. Simulations begin with a population of 100 in the source habitat and (in B and D) an unoccupied sink habitat. Rate of intrinsic dispersal (δ) is described in text. In the absence of an available sink habitat (A and C) surplus individuals (i.e. individuals which exceed environmental carrying capacity) remain in the source habitat as non-breeding juveniles.

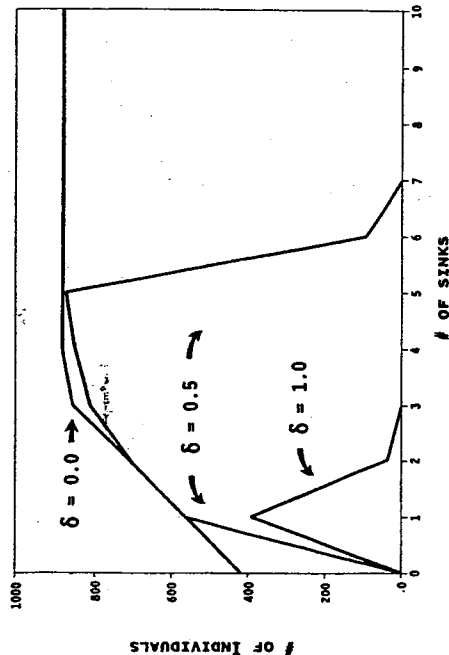


Fig. 3. Effects of increasing the number of sink habitats for three source populations differing in the rate of intrinsic dispersal (δ). Vertical axis (# of individuals) indicates the metapopulation size after 500 generations. P_A , P_J , λ (source), λ (sinks) and starting population sizes are the same as in Fig. 2. Per capita birth rate is 2.03 ($\lambda = 1.25$) for the source population and 0.90 ($\lambda = 0.90$) for all sink populations.

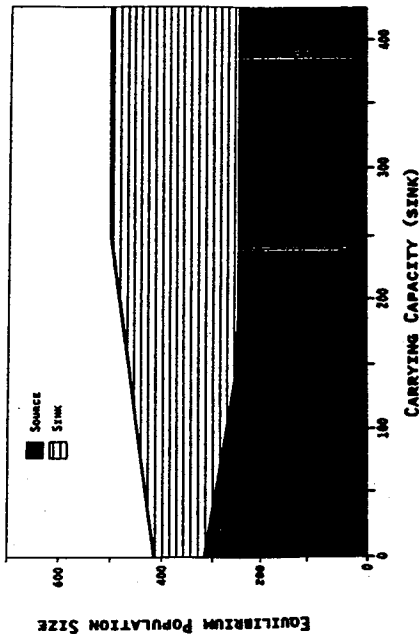


Fig. 4. Effects of increasing the carrying capacity (K) of a single sink habitat on the equilibrium size of a simple source/sink metapopulation. Characteristics of the source and sink except K (sink) are identical to the metapopulation described in Fig. 2(B).

More generally, suppose that we have a source (habitat 1)-sink (habitat 2) pair. In this situation, eqn (1) becomes

$$\begin{aligned}n_1(t+1) &= n_1(t)P_{A_1} + B_1P_{J_1}\beta_1 - e_1 + e_2 \\n_2(t+1) &= n_2(t)P_{A_2} + B_2P_{J_2}\beta_2 - e_2 + e_1\end{aligned}$$

Equilibrium populations are found by determining the fixed points to the model's equations. That is, by solving the system $n_1(t+1) = n_1(t)$, $n_2(t+1) = n_2(t)$ for equilibrium source and sink populations and then adding these values, we obtain the metapopulation equilibrium. In turn, these equilibrium populations are seen to be globally stable by invoking stability conditions in May *et al.* (1974). Here we have that the equilibrium metapopulation size increases monotonically from

$$\frac{\lambda_1\hat{n}_1 + P_{A_2}\hat{n}_1(P_{J_1}\beta_1 - 1)}{1 - P_{A_1}P_{A_2}} \quad \text{to} \quad \frac{\hat{n}_1(\lambda_1 - \lambda_2)}{1 - \lambda_2}$$

as $\hat{n}_2$ increases from 0 to $\hat{n}_1(\lambda_1 - 1)/(1 - \lambda_2)$. Further increase in sink habitat breeding opportunities has no effect on the equilibrium population size. A sink with unlimited breeding opportunities, for example, can support no more individuals than can a sink with the threshold number of opportunities. The maximum metapopulation size at equilibrium is given by $\hat{n}_1(\lambda_1 - \lambda_2)/(1 - \lambda_2)$ for a single source population (habitat 1) and a single sink population with unlimited breeding opportunities (habitat 2). Notice that the equilibrium size of a source/sink metapopulation will exceed the size of an isolated source population if adult survivorship in the sink habitat exceeds adult survivorship in the source habitat, even in the case that $\hat{n}_2 = 0$.

Also, increase in sink quality (λ_2) has the predictable effect of increasing overall metapopulation size (Fig. 5). The contribution of sinks continues to increase (with increase in sink quality) until the sinks, by definition, become source populations.

Non-zero intrinsic dispersal ($\delta > 0$)

The examples above assume no intrinsic juvenile dispersal ($\delta = 0$) among subpopulations. Relaxing this assumption leads to a rich variety of outcomes. Recall that intrinsic dispersal permits colonization of sink habitats even when source populations are lower than carrying capacity (Fig. 2(D)). Likewise, migration of individuals from the sink into the source habitat may occur even when the quality of the sink is very low or the carrying capacity high.

Below a critical level of δ , intrinsic dispersal may affect the distribution of

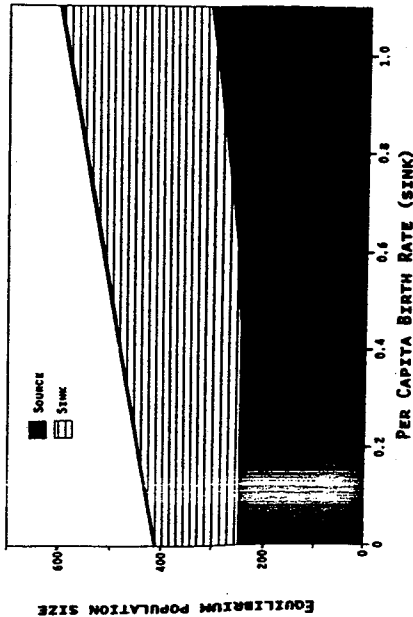


Fig. 5. Effects of increasing the net reproduction rate (λ) or 'quality' of a single sink habitat on the equilibrium size of a simple source/sink metapopulation. Characteristics of the source and sink except β (per capita birth rate) are identical to the metapopulation described in Fig. 2(B).

individuals among sources and sinks but not the overall metapopulation size. Levels of intrinsic dispersal may lead to an increase, a decrease, or no change in overall metapopulation size depending on complex relationships among demographic parameters and the dispersal parameter.

Again consider the case where we have a single source population (habitat 1) and a single sink population (habitat 2), as other cases are similar. If we assume that $\delta_1 = \delta_2 = \delta$ and $\hat{n}_2 \geq \hat{n}_1(\lambda_1 - 1)/(1 - \lambda_2)$ then the critical value of δ is found to be $\delta_c = (\lambda_1 - 1)/P_{J_1}\beta_1$. δ represents the value of the juvenile dispersal parameter which would separate the onset of density-dependent dispersal if the source population were equal to its maximum number of breeding opportunities. Notice that δ is not a function of δ and its value is between 0 and 1. Another important value of the dispersal parameter δ will be denoted by δ_e . The value of δ_e is the value of δ for which the origin of the (n_1, n_2) plane changes stability from repelling to attracting in our model's equations. It can be shown that

$$\delta_e = \frac{(\lambda_1 - 1)(\lambda_2 - 1)}{P_{J_1}\beta_1(\lambda_2 - 1) + P_{J_2}\beta_2(\lambda_1 - 1)}$$

The value of δ_e is always greater than or equal to δ but δ_e may be greater than 1. If δ_e is greater than one it has no biological significance. In the case that δ_e is less than or equal to one, then δ_e is an important threshold value for juvenile dispersal. If δ lies above this critical threshold, then extinction of

both source and sink subpopulations is inevitable. That is, no matter what the initial population configuration as t increases $n_1(t) \rightarrow 0$ and $n_2(t) \rightarrow 0$. Intrinsic dispersal tendencies, presumably under genetic control, are unlikely to change rapidly in nature, especially in the vicinity of the fatal threshold. However, notice that the threshold level (δ_c) is a function of the demographic variables (P_A, P_J, β) which can be modified within a single generation by environmental factors. A reduction in the critical dispersal threshold through habitat deterioration, hunting, or other novel environmental perturbation may lead to a sudden collapse of the metapopulation. Metapopulations with an initially low dispersal threshold or a high level of intrinsic dispersal are particularly vulnerable to such environmental changes.

Sink populations augment metapopulation size and may even prevent extinction when intrinsic dispersal is non-zero. Consider the case where a fraction of juveniles emigrates from a single, isolated source population (Fig. 2(C)). Because there exists (by definition) no habitat where these emigrants can survive and reproduce, they are effectively lost to the population. Presence of an accessible sink habitat (Fig. 2(D)), on the other hand, provides a 'refuge' where these individuals and their descendants may persist, albeit under circumstances that could not sustain an isolated population.

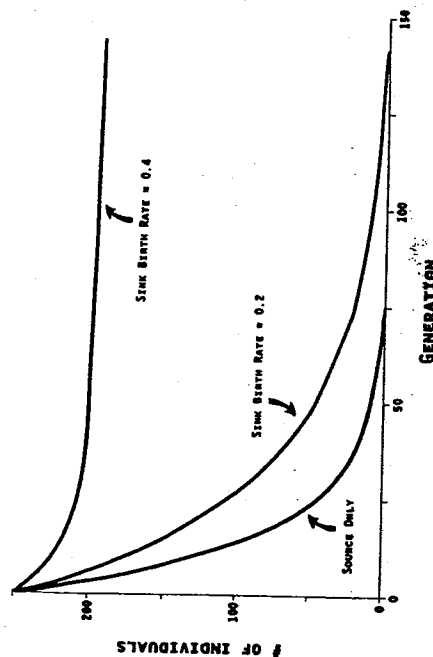


Fig. 6. Persistence time (in generations) of non-viable source/sink metapopulations differing in the net reproductive rate (λ) of sink habitats. Characteristics of source and sink are identical to populations described in Fig. 2 except for sink birth rates (β) and intrinsic dispersal rate ($\delta = 0.5$). The source alone and source/sink pairs persist indefinitely when δ is low, but in this case (when $\delta = 0.5$) the metapopulations eventually decline to extinction.

If the net reproductive rate of a source population is low (i.e. λ is not much greater than 1), intrinsic juvenile dispersal, which might have evolved under more favorable conditions, may subtract enough individuals to cause the population's eventual demise (Fig. 3). Presence of one or more sink populations may delay this extinction or prevent it altogether. The higher the quality (λ) of sink(s) the longer such a metapopulation will survive (Fig. 6). In the case illustrated here, a sink of moderate quality leads to survival of a metapopulation for thousands of generations; in the absence of such a sink, the solitary source population expires after only 74 generations. The most effective source-sink combinations consist of one or more source units with a limited number of sink populations (Fig. 3). In such cases, emigrants from the sinks are more likely to return to the source population(s). If more sink habitats are added, a larger fraction of these migrants are exchanged with other sinks, where reproduction or survival is suboptimal.

LIFE HISTORY EFFECTS

Variations in life history characteristics (P_A, P_J , or β) independent of net reproductive rate (λ) may have important effects on metapopulation dynamics if intrinsic dispersal and density-dependent dispersal are affected unequally. Thus, if there is no intrinsic dispersal ($\delta = 0$), an 'r-selected' species (e.g. $P_A = P_J = 0.31$, $P_J = P_A = 0.00075$, $\beta_1 = 1253$, $\beta_2 = 587$) will have the same equilibrium metapopulation configuration as a 'K-selected' species (e.g. Fig. 2(B)) with the same net productive rate (λ). Compensatory variations in P_J and β (with P_A constant) also fail to affect equilibrium population sizes because, in our model, these two variables affect dispersal in the same ways.

Compensatory variations involving P_A and either P_J or β , on the other hand, may lead to significant changes in metapopulation sizes when $\delta_j > 0$. The nature of these effects is again a complex function of demographic variables and habitat conditions in different subpopulations. Simulations using a wide range of life history characteristics ($P_A, P_J, \beta_1 = 0.005 \rightarrow 0.9$, $\beta_2 = \delta_2 = 0 \rightarrow 0.9$, $\lambda_1 - \lambda_2 = 0.1 \rightarrow 1.0$, $\bar{n}_1 - \bar{n}_2 = 0 \rightarrow 4500$) show that relative decreases in adult survivorship (i.e. decreasing P_A , while keeping λ constant) invariably lead to either no change or to a decrease in metapopulation size at equilibrium. When the number of breeding opportunities in the sink habitat is large, decreases in P_A also lead to a decrease in the critical dispersal threshold, δ_c . Biologically, higher levels of adult survivorship enhance the opportunities of immigrants to re-emigrate into sites where breeding opportunities are available.

Just as sink habitats tend to be especially important for metapopulations

with non-zero intrinsic dispersal, their importance also increases as P_A declines. That is, sink habitats appear to be most critical for metapopulations of 'r-selected' species with high rates of juvenile dispersal and low adult survivorship.

STOCHASTIC VARIATION

Stochastic variation (e.g. 'environmental noise') can be introduced to our model easily by converting the fixed demographic parameters to random variates within a specified range or distribution. Such a modification may have several important consequences. First, as pursued by others (e.g. Goodman, 1987; Quinn & Hastings, 1987), a stochastic model invites the possibility that an otherwise persistent metapopulation might go extinct through random fluctuation. This is particularly likely when the equilibrium population or starting population is low.

Here we compare the magnitude of variation among qualitatively different subpopulations. If reproductive rates (β_i) or probabilities of juvenile survival (P_{ji}) are converted to random variables with similar relative ranges (e.g. $\pm 10\%$) in all habitats, population size will tend to vary more in the sink habitat(s) than in the source habitat(s) (Fig. 7). This phenomenon seems to hold over wide ranges of our model's parameters and fits an intuitive expectation that sink populations, which ultimately depend on overproduction in the source habitat, should be more sensitive to stochastic variation in reproductive variables. A similar effect seems to hold for variation in P_A .

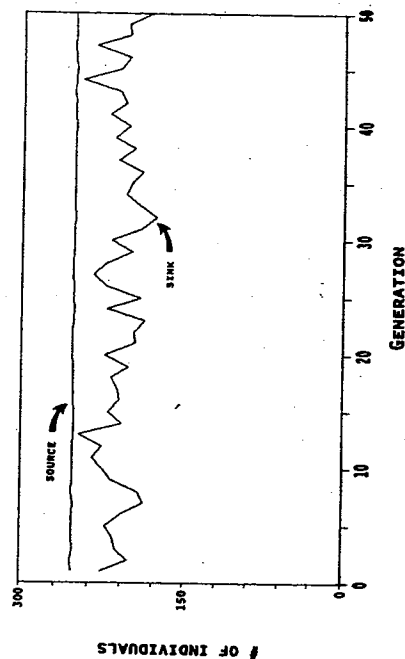


Fig. 7. Stochastic variation of the source/sink pair described in Fig. 2(B) when birth rates (β_i) vary randomly within 10% of mean values ($\beta_1 = 2.03$, $\beta_2 = 0.42$).

If the nature of environmental variation (e.g. annual climatic changes) is roughly comparable throughout the metapopulation, unequal fluctuations in populations present a potentially powerful tool for differentiating source and sink habitats. As pointed out by others (van Horne, 1983), population density is not a reliable indicator of habitat quality. If conditions described in our simulations prevail, population *variability* might be a much better indicator of habitat quality. In general, source habitats will tend to be occupied by more stable populations than will sink habitats. Application of this generalization might be difficult for long-lived species but nevertheless our model argues for continuous, site-specific monitoring of target species.

DISCUSSION

The dynamics of metapopulations can be exceedingly complex. Our model ignores several important characteristics of natural systems (see below) yet the range of outcomes still includes threshold effects, multiple stable points, and bidirectional relationships between variables. These complications preclude simple, comprehensive statements about metapopulation dynamics. Nevertheless, we have demonstrated characteristics of metapopulations that are evident over significant and realistic ranges of key variables. These generalizations might prove to be most useful for managers of conservation lands.

Our results show that sink habitats can benefit metapopulations in several ways. Under a wide range of circumstances, reproductively inferior subpopulations can promote (1) larger overall metapopulation size; (2) larger size of source subpopulations; and (3) extended survival of declining metapopulations.

In addition to these benefits, non-viable populations may help avert the stochastic extinction of small metapopulations (Goodman, 1987) and they almost certainly contribute to a more diverse gene pool (Lande & Barrowclough, 1987). In practical terms, secondary habitats may have significant conservation value even though they are incapable of supporting viable populations by themselves.

By the same token, sites occupied by breeding individuals of a given species are not necessarily suitable for that species in the long term. Field observations might lead to the misleading conclusion that these local populations are secure (van Horne, 1983). In order to guide effective conservation planning, inventories of sensitive species must identify not only where individuals occur, but also where local reproduction exceeds local mortality. In other words, conservationists need to locate and protect source populations before secondary habitats can serve a useful role. Our analysis

shows that temporal variability in numbers might help distinguish viable from non-viable subpopulations.

The strength of these conclusions rests on the validity of our model's assumptions. Most fundamentally, application of our metapopulation model requires that a species' net reproductive rate varies significantly within its range. Careful demographic studies suggest that non-viable 'sink' populations are widespread if not common elements of nature. King and Mewaldt (1987), for example, concluded that isolated montane populations of white-crowned sparrows (*Zonotrichia albicollis*) are unable to persist without periodic immigration. Thompson and Nolan (1973), Probst and Hayes (1987), and Temple and Carey (1988) reached similar conclusions for birds of fragmented forests in the eastern United States. Gill (1978) documented a high degree of reproductive variability in salamander (*Notophthalmus viridescens viridescens*) populations of the Shenandoah Mountains in West Virginia and an even more pronounced effect was reported by Whitham (1989) for aphids on genetically different host plants. Finally, Janzen (1986) observed that populations of sphingid moths in Costa Rica's Santa Rosa National Park are maintained by source populations outside of the park.

The analysis presented here makes additional, less realistic assumptions, including (1) no mortality during immigration and emigration; (2) equal distribution of emigrants among available sites; (3) identical demographic characteristics among sink populations; and (4) geographically invariant adult and juvenile survivorship. We also have considered metapopulations consisting of a single source and a small number of sink subpopulations. Relaxing these restrictions, in most cases, does not affect the qualitative conclusions described above.

Note that source and sink populations do not need to be discrete, isolated units. The range of virtually all species incorporates landscape irregularities such as intermixed habitat types or environmental gradients. Human activities, including conservation measures, may further accentuate these irregularities (Schonewald-Cox & Bayless, 1986). Reproduction and survival can be expected to vary significantly among these qualitatively different areas. As long as some of the occupied areas are incapable of supporting persistent populations and as long as individuals are interchanged regularly between the subpopulations, the conditions of our model are satisfied. Given the natural heterogeneity of landscapes and the tendency of human activities to cause further fragmentation of animal and plant populations, the potential applications of this model are extensive.

Movement of individuals between source and sink habitats is particularly relevant to the concerns about habitat fragmentation (Robbins, 1979, and others). The benefits of sink habitats will not exist if immigrants and

emigrants are not successfully exchanged among subpopulations. In this paper we have assumed 100% placement of migrants. What happens if a fraction of emigrants perish before reaching another site? What happens if certain sites are perceived by migrants as more attractive than others? Our model can be adjusted to accommodate incomplete or non-uniform placement of immigrants and emigrants by modifying eqns (2) and (3). In general, the influence of sink habitats declines as they become more isolated from source populations or as they become less isolated from one another.

Other scientists (e.g. Buechner, 1987) have pointed out that secondary areas may be detrimental to metapopulations by draining individuals away from productive habitats. This would be the case in our model if intrinsic rates of emigration (δ) from source populations are affected by the presence or absence of sink habitats. We have assumed that intrinsic emigration is independent of external circumstances; in the absence of sink habitats, juvenile emigrants are simply lost from the metapopulation. Density-dependent emigration, on the other hand, is influenced by the presence or absence of sink habitats; in the absence of sinks, excess individuals remain in the source habitat as non-breeding 'floaters'. When the population is below its carrying capacity, intrinsic dispersal is the only mechanism for movement between subpopulations.

In conclusion, we maintain that effective conservation of natural populations must recognize the spatial heterogeneity of reproduction and survival. Managers must identify and protect sites where annual reproduction exceeds annual mortality. These source areas may support a finite assemblage of non-viable sink populations, which themselves may contribute significantly to metapopulation size and survival. Because a large fraction of a species' population might reside and reproduce in sink habitats, their management should be a key element of long-term conservation plans. Finally, the ability of secondary habitats to extend the survival time of doomed populations leads to a rather sobering possibility that many of today's animal and plant species might consist of non-viable metapopulations, in the midst of slow but inexorable decline toward extinction.

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