SOURCES, SINKS, AND POPULATION REGULATION

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Many animal and plant species can regularly be found in a variety of habitats within a local geographical region. Even so, ecologists often study population growth and regulation with little or no attention paid to the differences in birth and death rates that occur in different habitats. This paper is concerned with the impact of habitat-specific demographic rates on population growth and regulation. I argue that, for many populations, a large fraction of the individuals may regularly occur in "sink" habitats, where within-habitat reproduction is insufficient to balance local mortality; nevertheless, populations may persist in such habitats, being locally maintained by continued immigration from more-productive "source" areas nearby. If this is commonly the case for natural populations, I maintain that some basic ecological notions concerning niche size, population regulation, and community structure must be reconsidered.

Several authors (Lidicker 1975; Van Horne 1983) have discussed the need to distinguish between source and sink habitats in field studies of population regulation; however, most theoretical treatments (Gadgil 1971; Levin 1976; McMurtie 1978; Vance 1984) of the dynamics of single-species populations in spatially subdivided habitats have not explicitly addressed the maintenance of populations in habitats where reproduction fails to keep pace with local mortality. Holt (1985) considered the dynamics of a food-limited predator that occupied both a source habitat containing prey and a sink habitat with no prey. He demonstrated that passive dispersal from the source can maintain a population in the sink and that the joint sink and source populations can exceed what could be maintained in the source alone. Furthermore, he showed that "time-lagged" dispersal back into the source from the sink can stabilize an otherwise unstable predator-prey interaction. Holt argued, however, that passive dispersal between source and sink habitats in a temporally constant environment is usually selectively disadvantageous, implying that sink populations will be transient in evolutionary time.

In this paper, I consider the consequences of active dispersal (i.e., habitat selection based on differences in habitat quality) on the dynamics of single-species populations in spatially heterogeneous environments. I argue that active dispersal from source habitats can maintain large sink populations and that such dispersal may be evolutionarily stable.

BIDE MODELS

One approach to modeling spatially heterogeneous populations is to employ *BIDE* models (Cohen 1969, 1971), which simultaneously consider birth (B), immigration (I), death (D), and emigration (E). Normally, in *BIDE* models, the parameters are considered random variables but not spatially heterogeneous. In this paper, I make the opposite assumptions, namely, that rates of birth, death, immigration, and emigration are deterministic but may differ between habitats.

First, consider a spatially distributed population with m subpopulations, each occupying a discrete habitat or "compartment." If b_j and d_j are, respectively, the number of births and the number of deaths occurring over the course of a year in compartment j, then the total number of births and deaths during that year in all compartments is given, respectively, by

$$B = \sum_{j=1}^{m} b_j \quad \text{and} \quad D = \sum_{j=1}^{m} d_j, \tag{1}$$

since every birth and every death takes place in some compartment.

Now, let i_{jk} be the number of individuals immigrating from compartment k *into* compartment j. Each immigrant into j must come from one of the other $m - 1$ compartments or come into j from outside the m compartments that constitute the ensemble of interest. That is, immigration into compartment j is given by

$$i_j = \sum_{k=1}^{m} i_{jk} + i_{j0} = \sum_{k=0}^{m} i_{jk},$$

where i_{j0} represents immigration from outside the ensemble into compartment j and i_{jj} is zero.

Similarly, if e_{jk} represents the number of emigrants from j into k, then

$$e_j = \sum_{k=1}^{m} e_{jk} + e_{j0} = \sum_{k=0}^{m} e_{jk}.$$

Note that $e_{kj} = i_{jk}$ for all j, $k \neq 0$. Finally, to complete the definitions of the *BIDE* parameters, let

$$I = \sum_{j=1}^{m} i_{j0} \quad \text{and} \quad E = \sum_{k=1}^{m} e_{k0}.$$

The ensemble of all compartments is said to be in dynamic equilibrium in ecological time when the number of individuals (n_j) in each and every compartment does not change from year to year. This occurs only if the number of births plus the number of immigrants exactly equals the number of deaths plus the number of emigrants for every compartment. That is,

$$b_j + i_j - d_j - e_j = (bide)_j = 0, \tag{2}$$

for every j, and $BIDE = 0$. Source and sink compartments can now be defined in terms of the *BIDE* parameters. A source compartment (or habitat) is one for which

$$b_j > d_j \quad \text{and} \quad e_j > i_j \tag{3}$$

"WINTER"

End of "WINTER"

$n' = P_A n + P_J \beta n$

DISPERSAL

n

$n + \beta n$

ANNUAL CENSUS

End of "SUMMER"
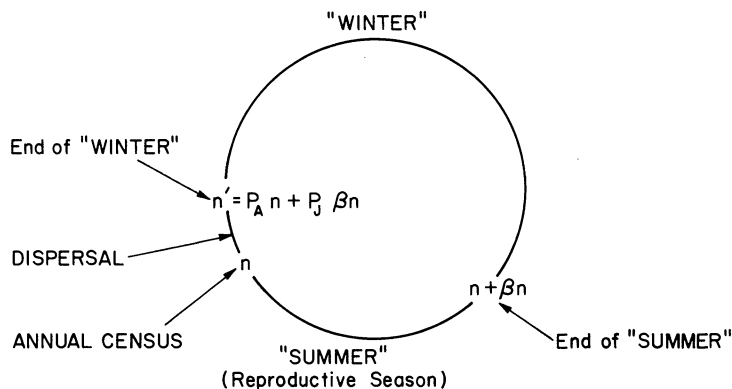
"SUMMER"
(Reproductive Season)

FIG. 1.—An annual census is taken in each habitat or "compartment" in the spring at the initiation of the breeding season (summer). Each individual breeding in the habitat produces β juveniles that are alive at the end of the breeding season. There is no adult mortality during the breeding season; adults survive the nonbreeding (winter) season with probability P_A and juveniles survive with probability P_J.

when $(bide)_j = 0$. A sink compartment (or habitat) is one for which

$$b_j < d_j \quad \text{and} \quad e_j < i_j \tag{4}$$

when $(bide)_j = 0$.

The above definitions apply strictly for equilibrium populations only. A more general definition of a source is a compartment that, over a large period of time (e.g., several generations), shows no net change in population size but, nonetheless, is a net exporter of individuals. Similarly, a sink is a net importer of individuals.

HABITAT-SPECIFIC DEMOGRAPHICS

To see how the *BIDE* parameters relate to habitat-specific survival probabilities and per capita birthrates, consider a simple annual cycle for a population in a seasonal environment (see fig. 1). An annual census is taken in the spring at the initiation of the breeding season. Each individual breeding in habitat 1 produces (on the average) β_1 juveniles that are alive at the end of the breeding season. There is no adult mortality during the breeding season; adults survive the nonbreeding (winter) season with probability P_A and juveniles survive with probability P_J. Thus, the expected number of individuals alive at the end of the winter and just before spring dispersal is given by

$$n_1(t + 1) = P_A n_1(t) + P_J \beta_1 n_1(t) = \lambda_1 n_1.$$

If there were only one compartment (habitat), λ_1 for a small population would be the finite rate of increase for the population. In a multi-compartment model, the λ_j's indicate which compartments are sources and which are sinks. For a simple example, consider two habitats that do not differ in either adult or juvenile survival probabilities but that do differ in per capita reproductive success. If

habitat 1 is a source and habitat 2 a sink, then by definition,

$$\lambda_1 = P_A + P_J\beta_1 > 1 \tag{5a}$$

and

$$\lambda_2 = P_A + P_J\beta_2 < 1. \tag{5b}$$

The finite rate of increase for a multi-compartment model depends on the fraction of the population in each habitat. This, in turn, depends on how individuals distribute themselves among available habitats at the time of dispersal, before the onset of breeding (fig. 1).

Before considering how habitat dispersal between source and sink habitats influences population regulation, I briefly discuss population regulation in a source habitat in the absence of a sink habitat. To do this, I must specify the nature of density dependence in the source habitat. For the model discussed below, the critical feature of density dependence is that some individuals in the source habitat do predictably better than others in terms of fitness. Simple assumptions reflecting this feature are that the number of breeding sites is limited and that some individuals obtain breeding sites and others do not. A more general, and more realistic, model of the distribution of habitat quality is discussed briefly in the next section.

I assume that there are only $\hat{n}$ breeding sites available in the source habitat. If the total population size is N and no other breeding sites are available, $N - \hat{n}$ individuals either stay in the source habitat as nonbreeding "floaters" or migrate to nearby sink habitats. In either case, they fail to reproduce but survive with the same probability (P_A) as do breeding individuals. (The qualitative features of the model are unchanged by the assumption that nonbreeding individuals survive with higher or lower probability than breeders.) Since the average reproductive success of an individual securing a breeding site is β_1, the average reproductive success for the entire population is given by

$$\beta(N) = \begin{cases} \beta_1 & \text{if } N \leq \hat{n}, \\ (\hat{n}/N)\beta_1 & \text{if } N > \hat{n}. \end{cases} \tag{6}$$

Thus, according to the definition of a source habitat (eq. 5a), the population increases when rare and continues to grow at the rate $\lambda_1 = P_A + P_J\beta_1$ until all breeding sites are occupied. The population will be regulated when

$$\lambda(N) = P_A + (\hat{n}/N)P_J\beta_1 = 1$$

or

$$N^* = \hat{n}P_J\beta_1/(1 - P_A). \tag{7}$$

Again, from the definition of a source, $P_J\beta_1/(1 - P_A)$ is greater than one; thus, the equilibrium population density (N^*) exceeds the number of breeding sites ($\hat{n}$), implying the existence of a nonbreeding surplus.

Assume that, adjacent to the source habitat, is a large sink habitat, where breeding sites are abundant but of poor quality. According to the definition of a

sink (eq. 5b), $\beta_2 < (1 - P_A)/P_J$; thus, the sink population declines and eventually disappears altogether in the absence of immigration from the source. Individuals unable to find a breeding site in the source emigrate to the sink because a poor-quality breeding site is better than none at all. If the source is saturated and there are sufficient breeding sites in the sink, the entire nonbreeding surplus from the source emigrates, yielding an increase in the growth rate of the total population:

$$\lambda(N) = (n_1/N)\lambda_1 + (n_2/N)\lambda_2$$
$$= (\hat{n}/N)\lambda_1 + \lambda_2(N - \hat{n})/N \qquad (8)$$
$$= \lambda_2 + (\hat{n}/N)P_J(\beta_1 - \beta_2).$$

The total population equilibrates when $\lambda(N) = 1$; and, according to equation (8),

$$N^* = P_J\hat{n}(\beta_1 - \beta_2)/(1 - P_A - P_J\beta_2). \qquad (9)$$

A relatively simple way to determine the equilibrium populations that will inhabit the source and sink habitats under this model is to note that, since the annual census is taken after the emigration of the reproductive surplus, $\hat{n}$ individuals remain in the source and $\hat{n}(\lambda_1 - 1)$ immigrate. Therefore, in terms of the *BIDE* model, $i_{21} = \hat{n}(P_A + P_J\beta_1 - 1)$. The local reproduction and survival in the sink is supplemented by this immigration, so that

$$n_2(t + 1) = (P_A + P_J\beta_2)n_2(t) + i_{21} = \lambda_2 n_2(t) + \hat{n}(\lambda_1 - 1).$$

At equilibrium, $n_2^* = i_{21}/(1 - \lambda_2)$, or

$$n_2^* = \hat{n}(\lambda_1 - 1)/(1 - \lambda_2). \qquad (10)$$

Notice that $\lambda_1 - 1$ is the per capita reproductive surplus in the source and $1 - \lambda_2$ is the per capita reproductive deficit in the sink.

If there are many habitats, the total population reaches an equilibrium when the total surplus in all source habitats equals the total deficit in all sink habitats. That is,

$$\sum_{j=1}^{m_1} e_j = \sum_{j=1}^{m_1} n_j^*(\lambda_j - 1) = \sum_{k=1}^{m_2} n_k^*(1 - \lambda_k) = \sum_{k=1}^{m_2} i_k,$$

where there are m_1 source habitats and m_2 sink habitats.

ECOLOGICAL AND EVOLUTIONARY STABILITY

In the preceding analysis, I calculated the equilibrium population sizes in source and sink habitats without addressing the stability of this equilibrium. A local-stability analysis involves finding the slope (b) of $\lambda(N)$ evaluated at the equilibrium population size N^*. If $-bN$ is less than one, the equilibrium is locally stable and approached monotonically (Maynard Smith 1968). The rate of increase for the combined source-sink population is given by equation (8). Differentiating, one obtains

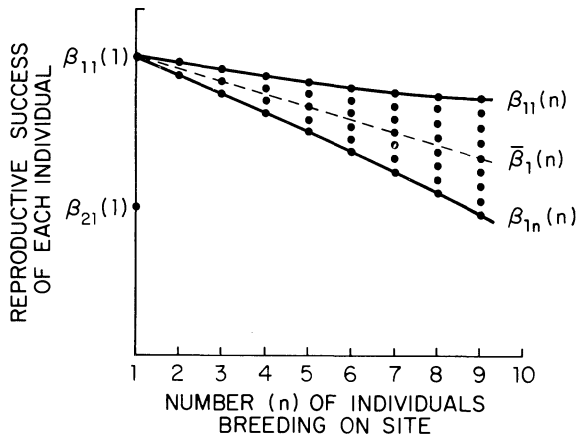$$d\lambda(N)/dN = -\hat{n}P_J(\beta_1 - \beta_2)/N^2.$$

Fig. 2.—The reproductive success of each individual breeding in a particular habitat depends on the number of other individuals in that habitat. $\beta_{1j}(n)$, the expected reproductive success of the individual occupying the jth-best breeding site in habitat 1 when there are a total of n individuals breeding there; $\bar{\beta}_1(n)$, the average reproductive success in the habitat.

Noting the equilibrium population size given in equation (9), the value of $-bN$ is easily seen to be $1 - P_A - P_J\beta_2$ or $1 - \lambda_2$. Since habitat 2 is a sink, λ_2 is less than 1, and, therefore, $-bN$ is also less than one. As for the case of a source habitat with no sink, β_2 equals zero and $-bN$ equals $1 - P_A$. Thus, with or without a sink habitat, the equilibrium population size is locally stable. For the simple cases analyzed above, there is only one nonzero equilibrium, and this equilibrium is approached monotonically from any positive initial population size.

A different question of stability concerns the evolutionary stability of the dispersal rule that determines the proportion of individuals in each habitat. Holt (1985) argued that passive dispersal between a source and a sink is evolutionarily unstable. Two essential differences between the current model and that of Holt are passive versus active dispersal and unequal versus equal fitnesses within a habitat. In my model, individuals choose to leave the source whenever their expected reproductive success is higher in the sink. This never happens in Holt's model because all individuals in the source have equal fitness and the mean fitness in the source never drops to less than one. Since the mean fitness in the sink is always less than one, it always pays for individuals not to immigrate and the evolutionarily stable strategy is no dispersal.

In my model, when the local population in the source exceeds the number of breeding sites available, it pays all surplus individuals to emigrate because they can achieve a higher fitness by doing so. The habitat-selection rule built into the model is a special case of the more general rule "never occupy a poorer breeding site when a better one is still available." Assuming no habitat-specific differences in survival probability, this is the evolutionarily stable habitat-selection rule because no individual can do better by changing habitats (see Pulliam and Caraco 1984; Pulliam 1989).

A more general application of an evolutionarily stable habitat rule that also results in stable occupancy of sink habitats is illustrated in figure 2. In this figure,

$\beta_{11}(n)$ is the expected breeding success of the individual using the best breeding site in habitat 1, and $\beta_{1n}(n)$ is the expected success of the individual using the poorest site occupied when there are n individuals in habitat 1 (the source). Assuming that individuals never occupy a poorer site when a better one is still available, habitat 2 (the sink) will not be occupied as long as $\beta_{1N}(N) > \beta_{21}(1)$. That is to say, the sink habitat will not be occupied as long as all N members of the population can enjoy greater reproductive success in the source. However, if $\beta_{21}(1)$ exceeds $\beta_{1N}(N)$ before the average reproductive success in the source reaches one, the sink will be occupied and the habitat distribution will be evolutionarily stable. Of course, the relative numbers of individuals in the source and sink habitats depend on details of how reproductive success changes with crowding in each habitat. If good breeding sites in the source are rare and poor sites in the sink are relatively common, a large population may occur in the sink.

IMPLICATIONS

Sink habitats may support very large populations despite the obvious fact that the sink population would eventually disappear without continued immigration. Consider the simple situation in which each year i individuals are released into a habitat where local reproduction is incapable of keeping up with local mortality. The equilibrium population maintained in this sink habitat would be $i/(1 - \lambda)$. Thus, if no individuals survived the winter ($\lambda = 0$), only the i recently released individuals would be censused each year. If adults survived winter with probability ½, $2i$ individuals would be censused each year. If, in addition, each adult produced an average of 0.4 juveniles that survived to the following spring, the equilibrium population would be 10 times i, even though the population could not be maintained without an annual subsidy.

In some circumstances, only a small fraction of the population may be breeding in a source habitat. Figure 3 shows the fraction of the equilibrium population in source habitat based on the assumptions of the model developed above and calculated according to equation (10). Clearly, if the reproductive surplus of the source is large and the reproductive deficit of the sink is small, a great majority of the population may occur in the sink habitat. For example, with a per capita source surplus of 1.0 and a sink deficit of 0.1, less than 10% of the population occurs in habitats where reproductive success is sufficient to balance annual mortality.

The concept of niche.—Joseph Grinnell is often credited with introducing the niche concept into ecology. James et al. defined the Grinnellian niche as "the range of values of environmental factors that are necessary and sufficient to allow a species to carry out its life history"; under normal conditions, "the species is expected to occupy a geographic region that is directly congruent with the distribution of its niche" (1984, p. 18). Though James et al. suggested that a species with limited dispersal may not occur in some areas where its niche is found, they clearly implied that the species will not occur where its niche is absent. A sink habitat is by definition an area where factors are not sufficient for a species to carry out its life history, but as discussed above, some species may be more
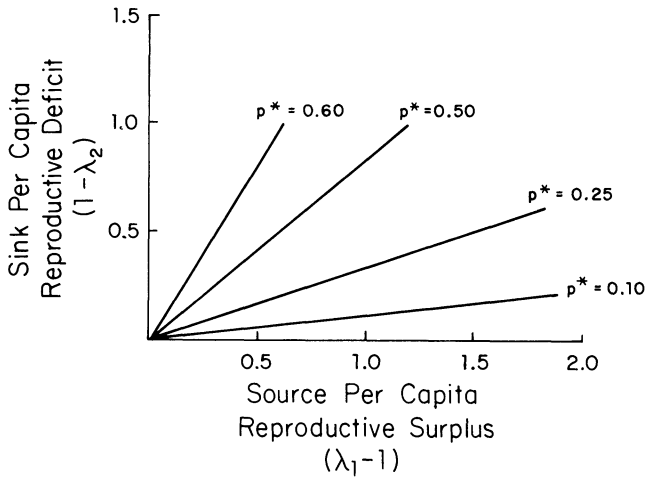
Fig. 3.—The equilibrium proportion ($p*$) of the population in the source habitat depends on both the per capita surplus in the source and the per capita deficit in the sink. A large proportion of the population may occur in the sink habitat if the source surplus is large and the sink deficit is small.

common in sink habitats than in the source habitats on which sink populations depend.

Hutchinson's (1958) particularly influential formulation of the niche concept differentiated between the fundamental niche and the realized niche. Hutchinson argued that the realized niche of most species would be smaller than the fundamental niche as a result of interspecific competition. I have argued in this paper that reproductive surpluses from productive sources may immigrate into and maintain populations in population sinks. If this is commonly true in nature, many species occur where conditions are not sufficient to maintain a population without continued immigration. Thus, in such cases, it can be said that the fundamental niche is smaller than the realized niche.

Species conservation.—Given that a species may commonly occur and successfully breed in sink habitats, an investigator could easily be misled about the habitat requirements of a species. Furthermore, autecological studies of populations in sink habitats may yield little information on the factors regulating population size if population size in the sink is determined largely by the size and proximity of sources.

Population-management decisions based on studies in sink habitats could lead to undesirable results. For example, 90% of a population might occur in one habitat. On the basis of the relative abundance and breeding status of individuals in this habitat, one might conclude that destruction of a nearby alternative habitat would have relatively little impact on the population. However, if the former habitat were a sink and the alternative a source, destruction of a relatively small habitat could lead to local population extinction.

Community structure.—What is a sink habitat for one species may be a source for other species. Thus, a "community" may be a mixture of populations, some of

which are self-maintaining and some of which are not. Attempts to understand phenomena such as the local coexistence of species should, therefore, begin with a determination of the extent to which the persistence of populations depends on continued immigration.

Many attempts to understand community structure have focused on resource partitioning and the local diversity of food types. The diversity and relative abundance of the organisms in any particular habitat may depend as much on the regional diversity of habitats as on the diversity of resources locally available. In extreme cases, the local assemblage of species may be an artifact of the type and proximity of neighboring habitats and have little to do with the resources and conditions at a study site. This is not to imply that local studies of the mechanisms of population regulation and species coexistence are unnecessary, but rather that they need to be done in concert with "landscape" studies of the availability of habitat types on a regional basis.

My goal is to draw attention to some of the implications of habitat-specific demographic rates. In many ways, they may be ecologically more important than the age-specific demographic rates that have received so much attention in the ecological and evolutionary literature.

SUMMARY

Animal and plant populations often occupy a variety of local areas and may experience different local birth and death rates in different areas. When this occurs, reproductive surpluses from productive source habitats may maintain populations in sink habitats, where local reproductive success fails to keep pace with local mortality. For animals with active habitat selection, an equilibrium with both source and sink habitats occupied can be both ecologically and evolutionarily stable. If the surplus population of the source is large and the per capita deficit in the sink is small, only a small fraction of the total population will occur in areas where local reproduction is sufficient to compensate for local mortality. In this sense, the realized niche may be larger than the fundamental niche. Consequently, the particular species assemblage occupying any local study site may consist of a mixture of source and sink populations and may be as much or more influenced by the type and proximity of other habitats as by the resources and other conditions at the site.

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