

## SOURCES, SINKS, AND HABITAT SELECTION: A LANDSCAPE PERSPECTIVE ON POPULATION DYNAMICS

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*Abstract.*—In the model described, we attempt to link breeding-site selection to population dynamics for situations in which there is more than one distinct type of habitat. The distribution of individuals between habitat types depends on the selective abilities of the species. This distribution, in turn, influences the population dynamics of the species as a whole. We show that the consequences of habitat selection on population dynamics for an ideal free distribution of individuals across habitats is predictably different from what would be predicted if habitat selection were preemptive, that is, if individuals, upon selecting a site, prevented others from sharing the site. If preemptive selection is ideal, average reproductive success declines with increasing density because each individual selects the best site available from those sites not yet occupied. The model allows us to compare the relative contribution of different types of habitats to a species' growth rate and population size. Furthermore, we can also predict how the loss of habitat of a particular type may affect a population. This should make the model useful for environmental management problems as well as for describing the present distribution of a species across a spatially heterogeneous landscape.

Animal and plant species often occur in several distinct habitat types in the same local region and may experience different development rates, life spans, and birth and death rates in these different habitats. As natural and anthropogenic forces change the availability of habitats, the proportion of individuals of a given species in any particular habitat type may be altered. Therefore, population size and growth rate may vary as functions of the relative proportion of different habitat types available. In some species, surplus individuals from highly productive source habitats may immigrate into less productive sink habitats, where within-habitat reproduction fails to keep pace with within-habitat mortality (Pulliam 1988). In such cases, alterations of the availability of source habitat may greatly affect the size of populations in other nearby habitats. In this article, we discuss a class of population models suitable for populations inhabiting changing landscapes in which the availability of source and sink habitats may change with time.

Despite the large volume of information in the literature concerning reproductive rates and survival probabilities, few studies directly compare the demographic rates of the same species in different habitats. Grant (1975) demonstrated experimentally that the meadow vole (*Microtus pennsylvanicus*) has lower adult

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survival and lower reproductive success in woodland than in grassland habitat. Van Horne (1981) found differences in population size, breeding activity, and overwinter survival of the deer mouse (*Peromyscus maniculatus*) in various serial stages of coniferous forests. Bergerud (1988), summarizing data from many sources on caribou (*Rangifer tarandus*), suggested that tundra is source habitat (annual recruitment exceeds annual mortality) and woodland is sink habitat (annual mortality exceeds annual recruitment) for this species.

Site-specific mortality may, in some instances, be more important than site-specific reproduction in controlling population dynamics. Smith (1968) found that tree squirrel territories (*Tamiasciurus* spp.) vary enough in cone and fungus production to affect an individual's chances of surviving through the winter. Some territories contained enough food to ensure survival through the most severe winters, some enough for a winter of average severity, and a few were insufficient for survival until spring under any circumstances.

Habitat-specific effects on a population's growth rate can extend to more than just individual fecundity and survival. Bronson (1979) found that golden-mantled ground squirrels (*Spermophilus lateralis*) at high elevations generally took an extra season to mature and reproduce, had smaller litters, and experienced higher survival rates than those at lower elevations. The slower rate of maturity that occurs in high-elevation habitat may have a greater impact on the population dynamics of these animals than the influence of altitude on litter size and survival. In any event, the population dynamics of these ground squirrels is certain to depend on the elevation at which individuals dig their burrows.

Similar information on habitat-specific demographic rates exists for a number of bird species including great tits (*Parus major*; Kluyver and Tinbergen 1953; Krebs 1971), tawny owls (*Strix aluco*; Southern 1970), red-winged blackbirds (*Agelaius phoeniceus*; Robertson 1972), white-crowned sparrows (*Zonotrichia leucophrys*; Petrinovich and Patterson 1982), and pied flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1985). Nettleship (1972) offered a particularly good example for Atlantic puffins (*Fratercula arctica*), which prefer to breed on steep slopes where nesting success is twice as high as at level ground sites. Usually, such data are not sufficient to determine whether a habitat is a source or a sink, although several avian studies concentrating on a single habitat type have indicated that local recruitment is insufficient to balance local mortality (e.g., Rodenhouse and Best 1983), suggesting that the studies were conducted in a sink habitat.

The population dynamics of species inhabiting complex habitat mosaics involve two components: the distribution of individuals among habitats and habitat-specific demographic rates. For highly mobile species, the distribution of individuals among habitats may be largely determined by habitat selection. Thus, we consider models in which the rules of habitat selection are embedded within a model of population dynamics. As the availability of habitat is altered, mobile animals may redistribute themselves among the remaining habitats, thereby controlling their own reproductive and mortality rates to some extent.

In light of the increasing occurrence of managed natural areas, models that incorporate habitat-selection processes are necessary for predicting the effects of habitat manipulations on natural populations. In the Discussion, we describe the

types of data necessary to test the models that we have developed and apply them to the management of real populations.

#### IDEAL PREEMPTIVE DISTRIBUTION

The most widely discussed model of habitat selection is the ideal free distribution, first proposed by Fretwell and Lucas (1970). This model assumes that habitat suitability declines with increased population density and that individuals choose the habitat with the highest average suitability. As applied to breeding-habitat selection, the model assumes that all individuals in the same habitat have the same reproductive success. Thus, when the initially preferred habitat becomes sufficiently crowded that the average reproductive success there drops below the average in an uncrowded alternative habitat, individuals do best by choosing the uncrowded habitat.

A number of alternatives to the ideal free distribution have been proposed. Most of these alternatives are representative of a class of habitat-selection models that assume an equilibrium distribution of individuals among available habitats such that no individual can achieve higher success by moving to another habitat. Thus, the habitat distribution achieved by a population of animals behaving according to the predictions of such a model corresponds to an evolutionarily stable strategy (Maynard Smith 1976). However, when some individuals achieve higher success than others, as, for example, when there is social dominance, choosing a habitat based on average success does not necessarily maximize individual fitness.

A simple alternative to the ideal free distribution that incorporates individual differences in reproductive success is what we call the *ideal preemptive distribution*. The concept is simply that potential breeding sites differ in terms of expected reproductive success and individuals always choose the best unoccupied site. An occupied site is said to have been preempted because it is no longer available, but its occupation does not influence the expected reproductive success that can be achieved at any other site. Thus, if two habitats each have a variety of potential breeding sites, the model assumes that the first individual to occupy a habitat settles in whichever habitat has the best available breeding site. The alternative habitat is used only when the next-best breeding site occurs in it. Thus, the number of individuals occupying each site depends on the total population size and the distribution of breeding-site quality for each habitat.

According to the ideal free distribution, two habitats are used in such a manner that the average reproductive success,  $\bar{\beta}_i(n)$ , in habitat 1 approximately equals that in habitat 2. Thus, as shown in figure 1A, when there are  $n_1$  individuals in habitat 1, there are approximately  $n_2$  individuals in habitat 2, because these numbers equilibrate the average payoffs for both habitats (i.e.,  $\bar{\beta}_1(n_1) = \bar{\beta}_2(n_2)$ ).

To compare the ideal free model with the ideal preemptive model, we define  $\beta_{in}(n_i)$  as the expected reproductive success of an individual occupying the  $n$ th-best breeding site in habitat  $i$  when there are  $n_i$  individuals breeding in habitat  $i$ . According to the ideal preemptive distribution, the individual using the worst of the occupied breeding sites in habitat 1 has approximately the same reproductive

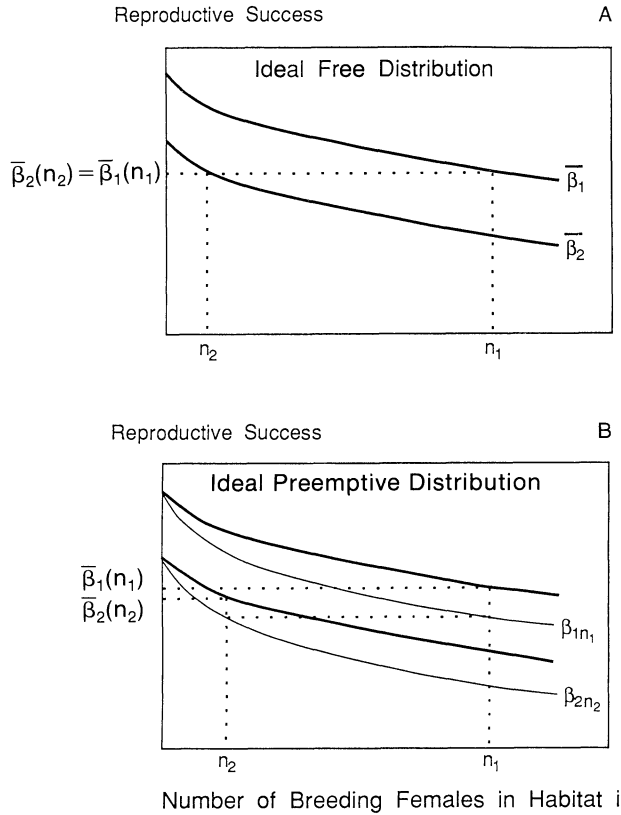


FIG. 1.—Average reproductive success according to two different models. *A*, Ideal free model. The average reproductive success,  $\bar{\beta}_i(n_i)$ , for each habitat is a decreasing function of the number of females in that habitat ( $n_i$ ). If individuals are distributed in accord with the ideal free distribution, the number of individuals in habitat  $i$ ,  $n_i$ , is such that the average reproductive success,  $\bar{\beta}_i(n_i)$ , in each habitat is equal. *B*, Ideal preemptive model. For each habitat, a pair of curves is shown. The upper curve for each habitat is identical to that in view *A*. The lower curve shows the quality of the worst occupied site,  $\beta_m$ , in each habitat as a function of the number of adult females in that habitat. Following the rules of an ideal preemptive distribution, the quality of the worst occupied site in each habitat is equivalent. Hence, when  $n_1$  adults occupy habitat 1, the number occupying habitat 2 is  $n_2$ . Note that this results in a smaller average reproductive success for habitat 2 than for habitat 1.

success as that of the individual in the worst occupied site in habitat 2. Thus,  $\beta_{1n_1}(n_1)$  should be approximately the same as  $\beta_{2n_2}(n_2)$ . As shown in figure 1*B*, this causes the average reproductive success in habitat 2 to be less than the average in habitat 1 (i.e.,  $\bar{\beta}_1(n_1) > \bar{\beta}_2(n_2)$ ). Comparing figures 1*A* and 1*B* shows that if there are  $n_1$  individuals in habitat 1, the number of individuals occupying habitat 2 under the conditions of the ideal free distribution is less than if the animals selected sites according to the rules of the ideal preemptive distribution.

The ideal free distribution and the ideal preemptive distribution are both "ideal" in the sense that individuals are assumed to have the dispersal and cogni-

tive abilities required always to find the best available site. This may be a good assumption for mobile vertebrates in landscapes with highly interdigitated habitats. In this article, we compare the habitat distribution achieved by the ideal preemptive distribution to that achieved by less-than-ideal habitat-selection rules. We also discuss the kinds of data that would be necessary to test the proposed models.

#### WITHIN-HABITAT BREEDING-SITE SELECTION

The calculation of expected reproductive success requires information about both the quality of available breeding sites and the extent to which individuals can find the best available sites. For the purpose of illustration, we assume that the frequency distribution of breeding-site quality conforms to an exponential probability law. The exponential is used simply because it is an easily differentiated function determined by a single parameter, and it gives the desired general frequency distribution with many poor sites and a few very good ones. We wish to emphasize that this distribution is used only for illustration and that the method proposed here can be used for any frequency distribution of breeding-site quality. More important, the method can be applied to data using a measured frequency distribution from nature.

We define breeding-site quality in terms of female reproductive success; more specifically, a breeding site of quality  $x$  corresponds to a site at which  $x$  juvenile females are produced by a female occupying the site. To illustrate the calculation of expected reproductive success, we use the continuous exponential distribution to approximate the discrete process of reproduction. Thus, the probability that  $x$  juvenile females are produced at a randomly chosen site is given by

$$\Pr(\beta = x) = \sigma \exp(-\sigma x), \quad \text{for } x > 0. \quad (1)$$

For a population in which individuals choose breeding sites at random, the mean reproductive success is  $1/\sigma$  and the variance in reproductive success is  $1/\sigma^2$ .

At the opposite extreme from random breeding-site selection, consider the mean success for a population in which only the best of the available sites are used, as assumed by the ideal preemptive distribution. As illustrated in figure 2, in the ideal case, all breeding sites above a minimum quality ( $\beta = a$ ) are used. The proportion of the available sites used is given by

$$p = \int_a^{\infty} \sigma \exp(-\sigma x) dx = \exp(-\sigma a). \quad (2)$$

If there are  $s$  breeding sites available per unit of area in a habitat patch of  $A$  ha, the total number of breeding sites in use is

$$psA = n, \quad (3)$$

where  $n$  is the number of breeding females. Thus, for the case of ideal selection, the minimum-quality breeding site in use can be found by solving for  $a$  using

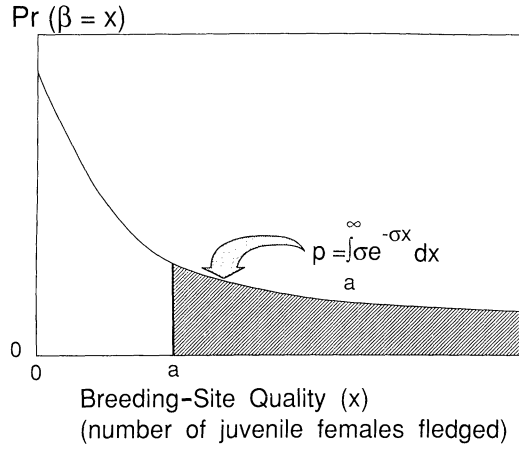


FIG. 2.—Expected reproductive success as a function of breeding-site quality according to the ideal preemptive model. High-quality sites that produce a large number of offspring are relatively rare given an exponential distribution of habitat quality. Under the assumption of ideal preemptive selection of breeding sites, the best sites are filled first. Hence, for a given number of breeding females,  $n$ , the distribution of occupied breeding sites begins with the quality of the  $n$ th-best site available,  $a$  (eq. [4b]). *Shaded area*, the portion of the available habitat that is occupied by a population of size  $n$ . The integral provides the expected birth rate for a population of this size.

equations (2) and (3). That is,

$$sA \exp(-\sigma a) = n, \tag{4a}$$

which yields

$$a = -\ln(n/sA)/\sigma, \quad \text{for } n \leq sA. \tag{4b}$$

Now that the minimum-quality site in use has been found, the mean reproductive success with ideal selection can be calculated as follows:

$$\beta = E(\beta) = \int_a^\infty \sigma x \exp(-\sigma x) dx / \int_a^\infty \sigma \exp(-\sigma x) dx. \tag{5}$$

Figure 3 compares the expected reproductive success for random versus ideal site selection as a function of the number of breeding females,  $n$ . In the case of random selection, mean reproductive success is density-independent until all breeding sites are occupied. When the number of breeding females exceeds the number of breeding sites available, the surplus females have zero reproductive success. Thus, for random breeding-site selection,

$$\bar{\beta} = E(\bar{\beta}) = \begin{cases} 1/\sigma, & \text{if } n \leq sA \\ sA/\sigma n, & \text{if } n > sA. \end{cases} \tag{6a}$$

$$\tag{6b}$$

For the assumption of ideal selection, mean reproductive success is given by equation (5) for  $n \leq sA$ . When there are more breeding females than available

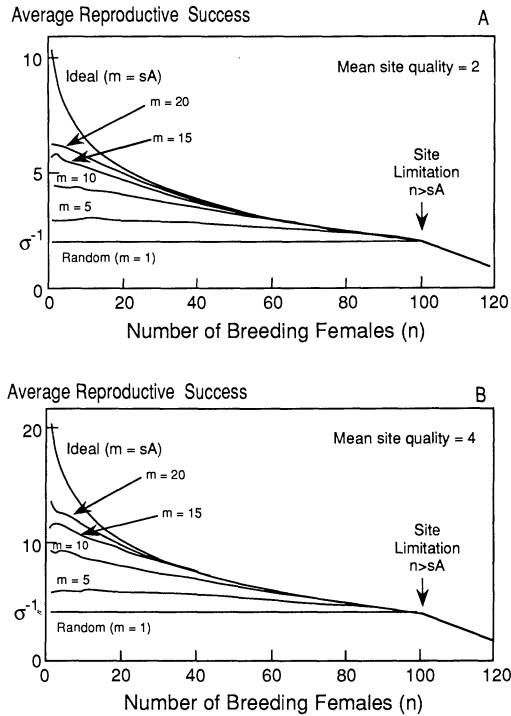


FIG. 3.—Expected reproductive success for random, ideal, and intermediate site selecting abilities as a function of number of breeding females. The average reproductive success of a population is a function of both the population size,  $n$ , and the degree of site selectivity that individuals exhibit. Simulations of intermediate selection abilities ( $1 < m < sA$ ) show that, as  $m$  increases from 1 to  $m = sA$ , the average reproductive success quickly approaches that of ideal selection, especially when the habitat is close to saturation ( $n = sA$ ). This effect is the same whether the mean site quality for the habitat is low (A) or high (B).

sites, those acquiring a breeding site have mean reproductive success equal to that of the average available since all sites are in use. Thus, for ideal selection, as for random selection, mean reproductive success is given by equation (6b) when  $n > sA$ .

Random and ideal breeding-site selection can be related by considering the simple behavioral rule “sample  $m$  unoccupied sites and choose the best found.” For this rule, when  $m = 1$ , site selection is random and when  $m = sA$ , all available sites are sampled; thus, site selection is ideal. Intermediate values of selection ability result in values of expected reproductive success between the expected values for random and ideal site selection. Figure 3 shows that mean reproductive success rapidly approaches the ideal situation as  $m$  increases, especially if the number of animals is close to the number of breeding sites.

#### CHOOSING BETWEEN HABITATS

The concept of ideal selection can easily be extended to a choice between two or more habitats. Equation (4b) gives the reproductive success of the female

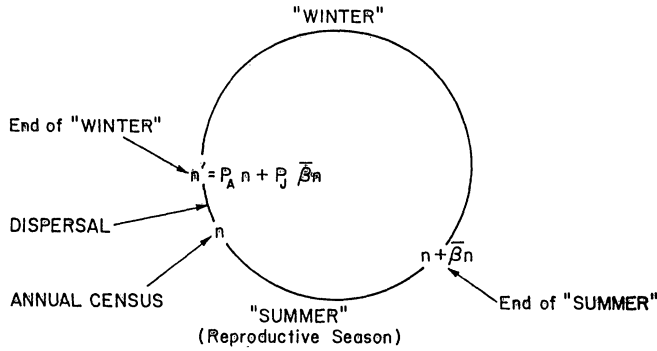


FIG. 4.—Life cycle of simulated species. The life cycle used in our example begins with a dispersal episode during which the selection of a breeding site takes place. After settlement, the population of breeding females is summed. During the summer, reproduction occurs as dictated by the quality of the site selected by each adult. The offspring do not breed until the following breeding season. At the conclusion of the breeding season, offspring and adults experience density-independent mortality until the onset of the next breeding season, when the surviving adults and juveniles repeat the dispersal and site-selection processes.

occupying the poorest breeding site used in a particular habitat. In the ideal case, if there are two habitats in close enough proximity that individuals may sample available breeding sites in both, then the poorest site occupied in one habitat is no worse than the best unoccupied site in the other. Since this is true for each habitat, the poorest sites occupied in both habitats are of approximately equal quality. That is,

$$a_1 = -\ln(n_1/s_1A_1)/\sigma_1 = a_2 = -\ln(n_2/s_2A_2)/\sigma_2,$$

such that

$$\sigma_2 \ln(n_1/s_1A_1) = \sigma_1 \ln(n_2/s_2A_2). \tag{7}$$

After rearranging, we find that

$$n_1/s_1A_1 = (n_2/s_2A_2)^{\sigma_1/\sigma_2}. \tag{8}$$

Since  $n/sA$  is the proportion of breeding sites occupied in a given habitat, equation (8) gives the relationship between the proportion of available sites in use in one habitat in relationship to the proportion in use in the other. Equation (8) also allows for an explicit prediction concerning how the individuals would redistribute themselves following a change in the area of each habitat available.

POPULATION DYNAMICS

As elsewhere (Pulliam 1988), we consider the dynamics of a population exhibiting an annual cycle as illustrated in figure 4. An annual census of population size is taken in the spring just before the start of breeding season. Individuals breeding in habitat  $i$  produce an average of  $\bar{\beta}_i$  juvenile females per breeding site occupied. Adults survive the nonbreeding season with probability  $P_A$ , and juveniles survive with probability  $P_J$ . Any individual having survived at least one



winter is considered an adult and counted in the next spring census. Thus, if there are  $n$  females in a given census, the expected population of females in the following census is given by

$$n' = P_A n + \bar{\beta} P_J n. \quad (9)$$

The finite rate of increase is

$$\lambda = P_A + \bar{\beta} P_J, \quad (10)$$

and the population reaches a stable equilibrium size  $n$ , when  $\lambda = 1.0$ .

As also shown in figure 4, dispersal between habitats is assumed to occur in the spring just before the annual census. Assuming that there are two habitats, let the total population size  $N$  equal  $n_1$  plus  $n_2$ . Thus, if  $N$  is the population size during one census, the population in the next census will be

$$N' = P_A n_1 + \bar{\beta}_1 P_J n_1 + P_A n_2 + \bar{\beta}_2 P_J n_2 = \lambda_1 n_1 + \lambda_2 n_2. \quad (11)$$

Furthermore, since an equilibrium population is defined by  $N' = N$ , a condition for demographic equilibrium is that

$$q\lambda_1 + (1 - q)\lambda_2 = 1.0, \quad (12)$$

where  $q$  is the proportion of  $N$  occupying habitat 1. In the above, we have assumed that habitats differ in expected reproductive success but not in survival probabilities,  $P_A$  and  $P_J$ ; however, habitat-specific differences in both reproductive success and survival probability can easily be represented by differences in  $\lambda_j$ .

#### *Simulation Methods*

Although population dynamics can be directly determined under the rules of random or ideal preemptive selection, the effects of intermediate levels of site selection are difficult to assess. Hence, a simulation model was constructed to determine the effects of different levels of site-sampling ability on the average productivity and population dynamics within a given habitat type as well as for the more global population that encompasses all habitat types. Furthermore, the model also allows us to determine the effect that a given change in the availability of high- and low-quality habitats will have on the global population.

In this model, two habitat types differing only in the average number of young produced per site are created such that the better habitat type has a mean birth rate slightly greater than that required to produce a positive within-habitat growth rate. The poorer habitat type (assuming random selection) has an average quality that is less than the minimum required for a positive population growth. Hence, under the conditions of random habitat selection, the better habitat type (habitat 1) is a source that produces a surplus of individuals available for dispersal elsewhere. The poorer habitat type (habitat 2), on the other hand, is a sink that cannot produce enough young to meet even its own losses.

Following the general life cycle depicted in figure 4, female offspring produced at time  $T$  are assumed to be capable of breeding at time  $T + 1$ . The survival rate for juveniles during this period is assumed to be lower for older animals. Upon

reaching age 1 yr, all animals are assumed to have the higher adult survival rate whether or not they breed.

We describe the site-selection process as follows: initially all sites in each habitat type are empty and therefore available for occupation. Individuals sequentially select a breeding site from the available empty sites. Hence, for each successive individual, there is always one less site empty and available. Each individual is allowed to make  $m$  random selections (without replacement) from the array of empty sites and without regard to the type of habitat. From this set of  $m$  sites, the best site is chosen. If there are more adults than the combined number of sites in the two habitats, the surplus individuals are considered "floaters" (in the sense of Brown 1969). These floaters do not breed and, therefore, are not assigned to either habitat type. They contribute only to the total, or global, population size  $N$ . Floaters and adults from both habitat types experience the same survival rates, and if a floater survives to the next time step, it can breed if a site is available.

The individuals that obtain a site produce as many juvenile females as the quality of the site allows. The total number of juveniles produced in each habitat is, therefore, the sum of the site qualities for the occupied sites. Juveniles from both habitats that survive to the next time step are combined with the surviving floaters and breeding adults to provide the pool of adults that start the next breeding episode.

#### *Simulation Results*

As discussed above, the amount of sampling that an individual performs before selecting a site can have a large effect on the average number of offspring produced. Hence, for  $m > 1$ , the average number of offspring produced can be greater than the average site quality in the habitat under some conditions. As a result of this selection ability, a habitat that is a sink (as described above) may actually produce a surplus, but only when the habitat is not saturated and the residents in the habitat can select the best sites available.

Increasing  $m$  will not increase the average birth rate indefinitely (fig. 3). As the number of sites sampled increases from one to the total number of sites in the environment, the "law of diminishing returns" causes the increase in average birth rate to become progressively less as it converges on the average birth rate that a population of ideal habitat selectors would have. However, since the average birth rates for increasingly greater selective abilities converges so rapidly on that of ideal site selection, the assumption of ideal preemptive selection is probably reasonable for vagile species with moderate dispersal capabilities.

*Effects of habitat loss.*—Because the ability of an individual to select a breeding site can affect the population's productivity, the net result of the loss of a particular type of habitat can, in some instances, highly depend on  $m$ . In figure 5, 90% of the poor-quality habitat is removed after the system reaches equilibrium. Whether  $m$  is small (fig. 5A) or large (fig. 5B), the total population is reduced by only a moderate amount because the high-quality habitat is so productive that it continues to produce enough offspring to saturate both habitats. Notice, however, that the initial population increase is much slower for the less selective population.

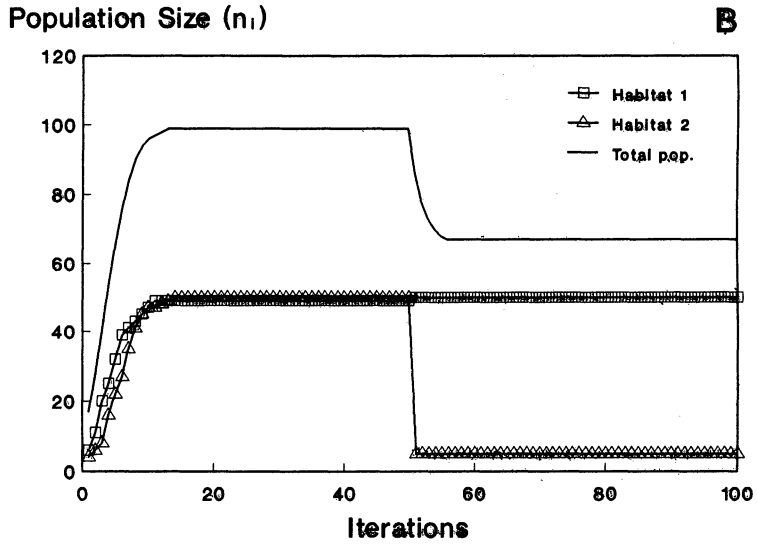
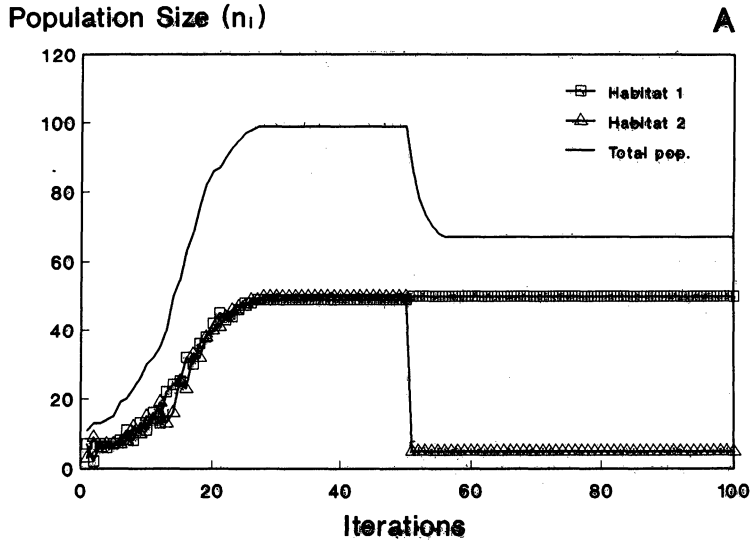


FIG. 5.—Simulated population growth to equilibrium followed by the loss of 90% of the poorer-quality habitat 2. The rate of population growth is slower for small values of  $m$  (A;  $m = 2$ ) than for large values (B;  $m = 20$ ). After 50 breeding seasons, 90% of the poorer-quality sites are removed and the population declines to a new equilibrium. Initially, there are 50 sites each of high-quality habitat ( $\bar{\beta}_1 = 5$ ) and low-quality habitat ( $\bar{\beta}_2 = 3$ ). Overwintering survival is 0.6 for adults and 0.1 for juveniles.

For the same set of conditions, but when high-quality habitat is lost, the effect on the equilibrium population size is, of course, much greater (fig. 6). In this situation, site-selection ability is much more likely to play an important role in determining the outcome. Figure 6 shows that a reduction in high-quality habitat may cause the global population to become extinct when site-selection ability is low (fig. 6A), whereas the same habitat loss, but with greater selection ability, will still allow a viable, albeit much reduced, population to exist (fig. 6B).

These results suggest that the effect of habitat loss, in general, depends on how dilute the high-quality sites become relative to the ability of the breeding individuals to find the best sites available. When high-quality sites are not being consistently used, reducing the amount of poor-quality habitat may actually increase the total population size if the reproduction that occurs in this habitat is more than offset by the higher level of reproduction that occurs in the better habitat type.

In figure 7, population size is shown as a function of the amount of poor-quality habitat. These data represent the number of animals after 25 breeding episodes, averaged over 50 simulations for each amount of poor-quality habitat. High-quality habitat was held constant.

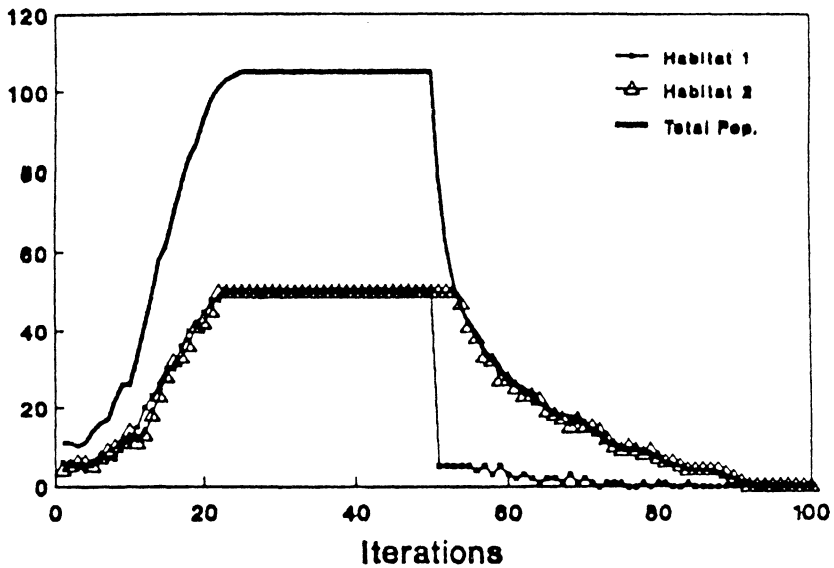
In figure 7A, site-selection ability is very low ( $m = 2$ ). Consequently, higher total population sizes result by decreasing the dilution of the best habitat in the environment. The maximum global population size occurs when there is little or no sink habitat. As increasingly larger amounts of sink habitat are added to the environment, a greater proportion of the breeding adults never find the high-quality habitat sites among the inferior sink habitat sites. These adults end up producing fewer offspring than they might otherwise have produced.

With greater site-selection ability, a more complex relationship exists between population size and habitat dilution. As before, environments with very dilute concentrations of high-quality habitats have relatively low population sizes (fig. 7B, *far right side*). Intermediate dilutions have higher population sizes, but eventually, as the concentration of high-quality habitat becomes great enough that most of the best sites are used, the loss of reproduction in the low-quality habitat becomes relatively more important. When this happens, the total population size begins to decline even though the concentration of high-quality sites is increased (fig. 7B, *far left side*). The dilution of high-quality habitat that produces the maximum global population depends on the ability of the dispersing animal to sample the environment.

We have assumed, for these examples, that the number of sites sampled is fixed within a species and does not vary between individuals or through time. Furthermore, habitat destruction is assumed to have no effect on the amount of sampling by each animal. However, the geometry of the landscape and the pattern of habitat destruction quite likely have a measurable effect on the ability of animals to find the best available sites. If habitat types are reasonably interspersed, removing a portion of one type may increase the distances between successive sites on the animal's dispersal path. Animals that can disperse only a limited distance will, therefore, sample fewer potential breeding sites following a loss of habitat, resulting in a reduction in the value of  $m$ . Reductions in site selectivity

Population Size ( $n_t$ )

A



Population Size ( $n_t$ )

B

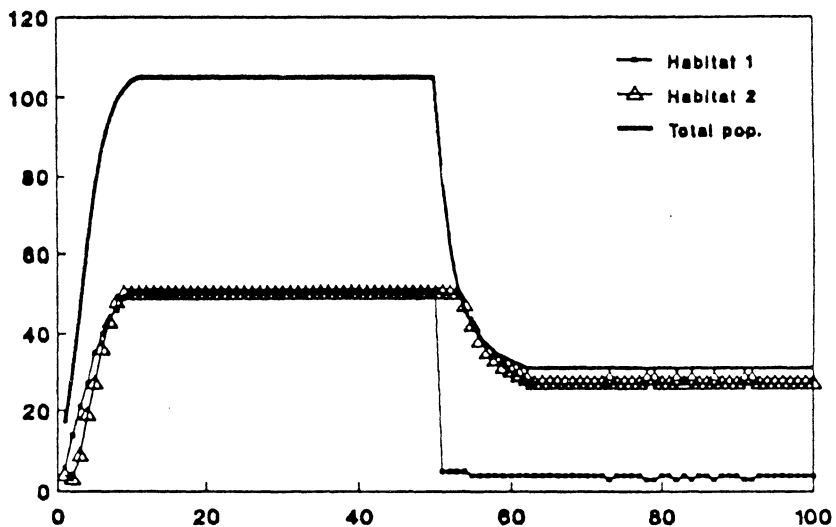


FIG. 6.—Simulated population growth to equilibrium followed by the loss of 90% of the higher-quality habitat 1. After 50 breeding seasons, 90% of the higher-quality sites are removed and the population declines. If individuals have low selection ability ( $A$ ;  $m = 2$ ) the population may become extinct when the best sites are so rare that they are rarely found. Greater selective ability ( $B$ ;  $m = 20$ ) may allow the population to persist in otherwise identical circumstances. Simulation parameter values are the same as in fig. 5.

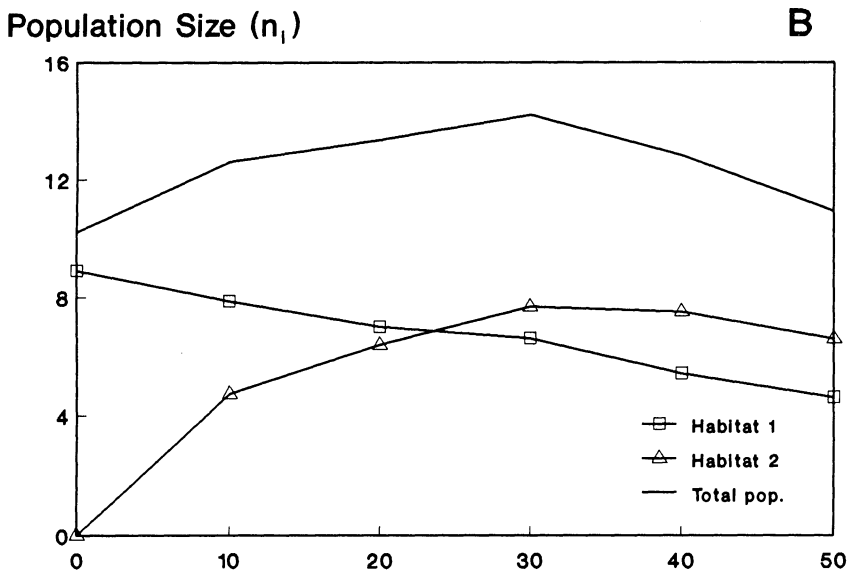
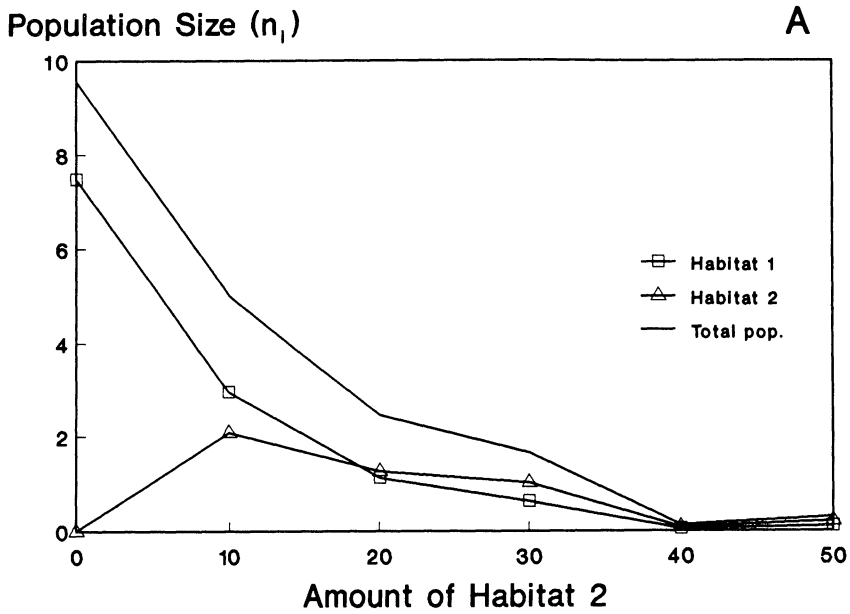


FIG. 7.—Population size as a function of amount of poor-quality habitat. The proportion of the total population that breeds in the higher-quality habitat is a function of the relative amounts of the two habitat types and the selection ability of the species. When poorer-quality habitat is much more abundant than higher-quality habitat and selection ability is low (A;  $m = 2$ ), the total population size may be much smaller than if some of this low-quality habitat is removed. When selection ability is greater (B;  $m = 10$ ), total population size may peak at intermediate proportions of the two habitat types. Each point represents the number of adults after 25 breeding seasons, averaged over 50 simulations. For each simulation there are 10 sites of higher quality ( $\bar{\beta}_1 = 4.5$ ); average reproductive quality for poorer-quality habitat is  $\bar{\beta}_2 = 1$ . Overwintering survival is 0.6 for adults and 0.1 for juveniles.

coupled with habitat loss might be sufficient to cause extinction, whereas the loss of either selectivity or habitat alone would result in only a diminished equilibrium.

#### DISCUSSION

The usefulness of the models proposed in this article depends, in large part, on the extent to which the required parameters can be measured in the field. A model of population dynamics based on the ideal preemptive distribution requires information on the average reproductive success for each habitat and also the frequency distributions of breeding-site quality for each habitat. Numerous studies have attempted to determine correlates of breeding-site success, but we know of only one case in which the frequency distribution of breeding-site quality actually has been suitably measured. Whitham (1980) quantified the relationship between leaf size and the breeding-site position on a leaf and reproductive success of *Pemphigus* aphids in such a way that the frequency distribution of breeding-site quality actually used could be compared to that available in the environment.

The *Pemphigus* aphids studied by Whitham closely approximate the assumptions of the ideal preemptive distribution in two ways. First, the aphids were very selective and, consequently, the breeding success achieved closely approximated the maximum possible, supporting the "ideal" assumption. Second, the occupation of the less preferred breeding sites had little, if any, effect on the breeding success of individuals occupying the more preferred sites, supporting the assumption of preemption. These conditions may be fairly general, at least for highly selective, territorial species.

As discussed in the introduction, a number of authors have quantified average reproductive success for one or more habitats. This is usually done by comparing reproductive success in the same site over a number of years as the total population size fluctuates. Information on density-dependent reproductive success in more than one habitat can be used to predict the pattern of habitat occupancy. According to the ideal preemptive distribution, the occupation of a lower-quality breeding site has no influence on the expected reproductive success of individuals occupying better sites. Thus, assuming the ideal preemptive distribution, we can estimate the quality of the  $n$ th-best breeding site as  $\beta_m(n) = n\bar{\beta}_i(n) - (n - 1)\bar{\beta}_i(n - 1)$ . For example, Klomp (1981) gave the breeding success of great tits (*Parus major*) as  $\bar{\beta}(n) = 8.4 n^{-0.25}$ , where breeding success is measured as the average number of female young fledged. If the assumptions of the ideal preemptive distribution were met, we would expect the breeding success of the individual using the poorest occupied site to be approximately 4.3 for  $n = 5$ , 3.0 for  $n = 20$ , and 2.4 for  $n = 50$ .

If the average reproductive success is calculated for two or more distinct habitat types, we can predict the pattern of habitat occupancy based on which habitat would have the best unoccupied site for any given total population size. This predicted pattern of habitat occupancy could be contrasted to the pattern predicted for random occupancy or to that predicted by the ideal free distribution and, in turn, compared to the observed pattern. Notice that the information required to make such a prediction for the ideal preemptive distribution is the same as that required to make a prediction with the ideal free distribution.

If selection rules approximating the ideal free or the ideal preemptive distributions are in effect, the above mentioned methods will be useful for predicting the pattern of habitat occupation. If, however, the animals of concern use a simpler sampling procedure, such as sampling  $m$  and using the best, predicting habitat occupation patterns will be more difficult. Perhaps the most difficult parameter to quantify empirically is  $m$ . Furthermore, the simple "sample  $m$ " selection rule discussed in this article may not adequately describe the real sampling behavior. Energetic or time constraints may restrict an individual to sampling a given number of sites, whether they be occupied or not. The effect of sampling already-occupied sites would be roughly similar to a smaller value of  $m$  under the original model.

Fortunately, for many animals, the number of sites sampled is probably large enough that the assumption of ideal selection is a reasonable approximation. For instance, even a relatively sedentary species such as the meadow vole is familiar with an area much larger than its home range (Robinson and Falls 1965). Also, for many bird species, females usually have a longer postnatal dispersal episode than males; therefore, female dispersal behavior may approximate ideal selection.

There are some species and environments for which ideal selection is probably not appropriate. For instance, spotted owls (*Strix occidentalis*) have huge home ranges (800–1,700 ha per breeding pair) in old-growth western coniferous forests (Simberloff 1987). Because the territories are so large and dispersal mortality is high, the number of empty breeding sites that can be sampled may be quite small. Although the assumption of ideal selection is probably not justified, neither is it appropriate to assume random selection. This makes the application of the model more difficult, but with the advent of effective radiotelemetric equipment, reasonable estimates of selection ability may be possible for many species.

The type of model developed in this article is potentially useful in management situations. For example, the model points out how the ability to sample habitats will effect population dynamics. When a species with very little selective ability is to be managed, the size and dispersion of the critical habitat that is to be conserved may have very pronounced effects. In fact, it is quite possible that the effect of the spatial configuration of habitat on the species' selective ability could have a more significant impact on the population's dynamics than the total amount of habitat that is preserved. However, because vagile species are little affected by habitat configuration, the total amount of habitat is more likely to be of greater importance to them.

A second aspect of our model is that it allows one to estimate the relative contributions of different habitat types to population size and growth. Hence, in a landscape matrix of different types of habitat, the model will assist in determining how much each habitat type contributes to the total population. This should be useful in managing habitats and in targeting the critical habitats to be preserved. The model also shows that in some circumstances (perhaps rare) not all utilized habitats are necessarily valuable to the species. The preservation of marginal or sink habitat may actually reduce the global population size, even though some individuals may reproduce successfully in this habitat type. We hope that models of this sort make it easier to answer questions dealing with management options such as conserving a large amount of mediocre habitat or a lesser amount



of prime habitat, determining whether managed habitats should be numerous and small or few and large, and determining what ratio of good to poor habitat will have the best chance of maintaining a population of a particular species. By assessing the contribution of each habitat type to a species' abundance, the relative contribution of two or more habitats can be compared in a meaningful manner such that the management of those habitats can be prioritized according to their importance in maintaining a viable population.

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