TWO GENERAL METAPOPULATION MODELS AND THE CORE-SATELLITE SPECIES HYPOTHESIS

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Abstract.—This article describes two general metapopulation models with spatial variation in the sizes of habitat patches. The first model is a simple, nonstructured model that includes the mainland-island and Levins models as two limiting cases. The second model is a structured model explicitly including the size distribution of habitat patches, the size distribution of local populations, and migration among local populations. The models may have up to four equilibria, including two stable, positive equilibria. We discuss the core-satellite species hypothesis in light of these models. This hypothesis predicts that the distribution of patch-occupancy frequencies is bimodal in many species assemblages. We extend the original concept by demonstrating that the bimodal distribution of patch-occupancy frequencies can be generated by structurally more complex and more realistic metapopulation models than the original one; that the bimodal distribution is predicted by deterministic models, with no or infrequent switches of species between the core and the satellite state; and that metapopulation extinctions of rare species may be compensated by migration from outside the metapopulation (from a mainland), or metapopulation extinction may be prevented by low extinction probabilities of local populations in large or high-quality habitat patches. In every case the bimodal core-satellite distribution is due to the rescue effect, that is, the increasing migration rate and hence the decreasing probability of local extinction with an increasing fraction of patches occupied. We discuss how the metapopulation dynamic mechanisms described in this article may generate the bimodal core-satellite distribution in different kinds of communities.

Andrewartha and Birch (1954, p. 657), among others, pioneered the view that "a natural population occupying any considerable area will be made up of a number of . . . local populations." Levins (1970) coined the term *metapopulation* for an assemblage of local populations connected by migration. Metapopulation dynamics is currently receiving increasing attention in population ecology (Hanski 1985; Hastings 1990; Gilpin and Hanski 1991) and conservation biology (Quinn and Hastings 1987; Gilpin 1988).

Theoretical analyses of metapopulations have used two models, based on different assumptions about the structure of the environment. The mainland-island model assumes a large and invulnerable source population on the "mainland," from which individuals migrate to smaller habitat patches ("islands") with more transient populations (fig. 1). In this model, there may or may not be migration among the island populations; the former case is often referred to as stepping-stone dispersal or migration. The equilibrium theory of island biogeography (MacArthur and Wilson 1967) is a multispecies version of the mainland-island model.
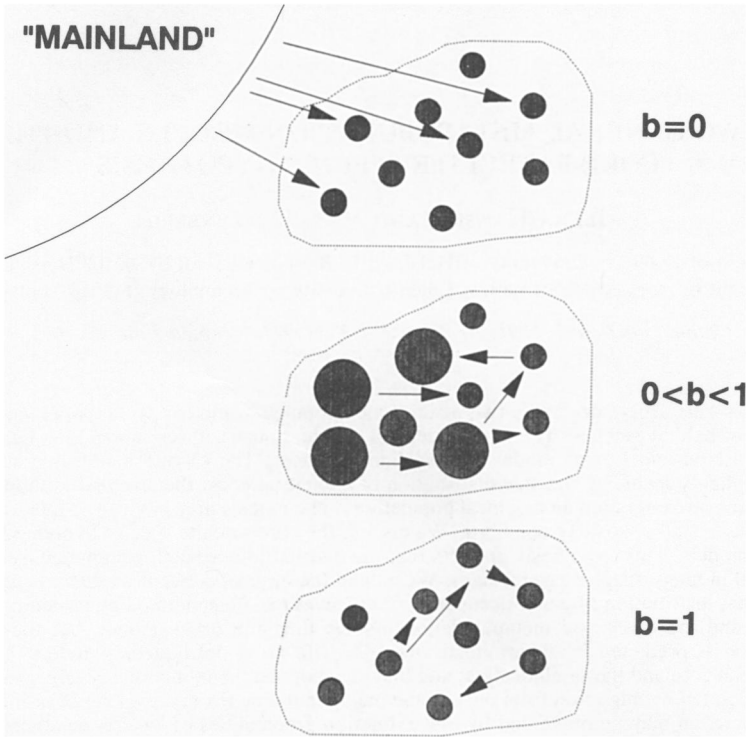
FIG. 1.—Distribution of patch sizes in the simple model when $b = 0$ (the mainland-island model), $0 < b < 1$ (spatial variation in patch sizes), and $b = 1$ (the Levins model). The *dashed line* delimits the system of patches inhabited by the metapopulation and included in the calculation of P, the fraction of patches occupied. *Arrows* give examples of individuals moving from one patch to another.

In contrast, Levins's (1969, 1970) metapopulation model assumes a set of equally large habitat patches, or islands, with local populations frequently going extinct and the vacated patches being recolonized from the currently occupied set of patches; there is no mainland in this model (fig. 1). The Levins model has been extended in various ways to describe single-species (Hanski 1985, 1991; Hastings and Wolin 1989; Gyllenberg and Hanski 1992), competitive (Horn and MacArthur 1972; Slatkin 1974; Hanski 1983; Hanski and Ranta 1983), and predator-prey metapopulation dynamics (Vandermeer 1973; Hastings 1977; Zeigler 1977; Sabelis et al. 1991).

Although the two models are occasionally contrasted as alternatives, a more useful perspective is to consider them as the two extremes of a continuum, defined by increasing the size range of habitat patches (fig. 1). Most species in nature occur in environments that are intermediate between the two extremes: there is significant spatial variation in habitat patch sizes, even if there is no true mainland, where the local population never goes extinct (Harrison 1991). Therefore, it is important to develop concepts and models that bridge the gap between the mainland-island and Levins models.

The purpose of this article is twofold. We shall first describe and analyze two general metapopulation models that allow for spatial variation in habitat patch size. The first one is a simple, phenomenological model that has the models of MacArthur and Wilson (1967) and Levins (1969) as two limiting cases (see Gotelli 1991 for a comparison of these and two other simple metapopulation models). The second model is a structured metapopulation model that takes into account spatial variation in patch size and the effect of migration on local dynamics in a more mechanistic manner than the simple model. The structured model contains, as special cases, our structured model (Gyllenberg and Hanski 1992) for identical patches and a mainland-island type model. We shall then use these models to reconsider the core-satellite species hypothesis (Hanski 1982a), which predicts that many species assemblages show a bimodal distribution of patch-occupancy frequencies; that is, at any given time most species are present in either most patches or only a small fraction of patches. Several authors have attempted to test the model (see especially Hanski 1982c; Gotelli and Simberloff 1987; Gaston and Lawton 1989; Collins and Glenn 1990, 1991). Our message in this article is that there are alternative metapopulation dynamic mechanisms that may create the bimodal core-satellite distribution and that different mechanisms may operate in different kinds of species assemblages.

A PHENOMENOLOGICAL MODEL WITH SPATIAL VARIATION IN PATCH SIZE

Consider a species that inhabits a system of habitat patches with different sizes. Let P denote the fraction of occupied patches. Assuming realistically that the average size of local populations increases with patch size and that the extinction probability decreases with increasing average population size (Schoener and Spiller 1987; Hanski 1991 and references therein), the pattern of patch occupancy at any one time is nonrandom, the incidence of the species (Diamond 1975) increasing with patch size (references to many metapopulation examples are cited in Hanski 1991). In this case, the rate of extinction per occupied patch decreases with decreasing P, as the species becomes confined to the patches with the lowest extinction probabilities when P decreases. The rate of colonization per unoccupied patch is an increasing function of P, because new populations are established by individuals moving from the occupied patches to currently empty ones. However, the greater the spatial variation in patch sizes, the faster the rate of colonization per unoccupied patch approaches its maximum value with increasing P, because, with increasing spatial variation in patch sizes, an increasing fraction of migrants originates from a few large populations. The following model of P incorporates the above assumptions about the colonization and extinction rates:

$$dP/dt = m[(1 + a)P/(a + P)](1 - P) - e[a/(1 + a) + P/(a + P)]P, \quad (1)$$

where m and e are the colonization and extinction parameters, respectively, and a is a parameter describing the range of patch sizes. With increasing value of a the frequency of larger patches decreases, and hence the colonization rate per unoccupied patch decreases. Setting $a = 0$ yields

$$dP/dt = m(1 - P) - eP, \quad (2)$$

which is the mainland-island model: all unoccupied patches (fraction $1 - P$) have the same probability of being colonized by migrants originating from the mainland (note that the mainland population is not included in P; fig. 1), and all local populations have the same extinction probability. Setting $a = \infty$ yields the Levins model,

$$dP/dt = mP(1 - P) - eP, \tag{3}$$

in which colonization occurs from the currently extant set of local populations. In the Levins model, all local populations are equally large, and hence the colonization rate per unoccupied patch is a linearly increasing function of P. The extinction term is the same in both models. With intermediate values of a, the extinction rate is lower than in either extreme given by equations (2) and (3), because with intermediate values of a the frequency of larger patches (included in P) is greater (fig. 1).

The implications of the general model are more transparent if we substitute $b = a/(1 + a)$ and rearrange the terms in equation (1):

$$dP/dt = \{P/[b + (1 - b)P]\}\{m(1 - P) - e[b^2 + (1 - b^2)P]\}. \tag{4}$$

The model has two equilibria, 0 and $(m/e - b^2)/(1 + m/e - b^2)$. Setting $b = 0$ and $b = 1$ yields the nontrivial equilibria of the mainland-island and Levins models, respectively, $m/(m + e)$ and $1 - e/m$.

THE RESCUE EFFECT

The above model assumes that local dynamics occur on a much faster time scale than metapopulation dynamics (all patches are either empty or fully occupied) and that migration has no effect on local dynamics apart from the colonization events. These assumptions, which are unrealistic for most metapopulations in nature, can be relaxed in structured metapopulation models (Gyllenberg and Hanski 1992), and we shall use this approach in the next section. One likely consequence of assuming that local and metapopulation time scales are not very different and that migration affects local dynamics is a positive relationship between P and the average size of local populations (Hanski 1985, 1991; Gyllenberg and Hanski 1992). A positive relationship between P and average population size has been frequently observed in multispecies assemblages (Hanski 1982a; Brown 1984; Hanski et al. 1993), but our point is that it can also be expected in single-species dynamics. Increasing average population size typically decreases extinction probability (Hanski 1991 and references therein). Given a positive relationship between P and average population size, we would therefore expect a negative relationship between P and the probability of local extinction. This relationship has been observed for multispecies assemblages (fig. 2) (Hanski 1982a), but once again we suggest that it also occurs in single-species dynamics.

We call the decreasing rate of extinction of local populations with increasing P the "rescue effect." The rescue effect is generated by two processes: the decreasing risk of local extinction with increasing immigration rate, as originally envisioned and demonstrated by Brown and Kodric-Brown (1977), and the in-
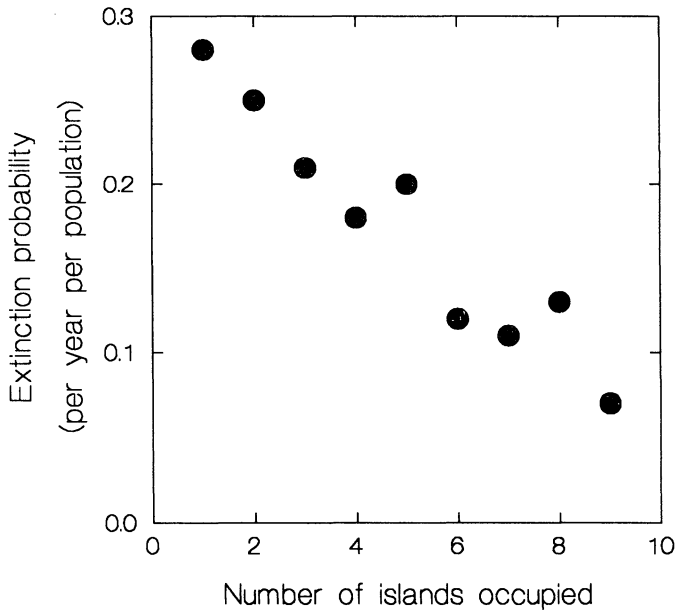
Fig. 2.—Probability of local extinction against the number of extant populations (*P*) in mangrove island insects (data from Simberloff 1976). Each dot gives the average for many species. All habitat patches were roughly the same size.

creasing immigration rate per patch with increasing *P*. In the scalar model of equation (4), the rescue effect may be incorporated, albeit in a nonmechanistic manner, by multiplying the extinction term with a decreasing function of *P*. We have used the exponential function for that purpose (Hanski 1991). Dividing further both sides of equation (4) by *e* (scaling time with the extinction rate) yields the final model,

$$dP/dt = \{P/(b + (1 - b)P)\}\{m(1 - P) - [b^2 + (1 - b^2)P]Pe^{-cP}\}, \tag{5}$$

where *c* describes the strength of the rescue effect (no rescue if $c = 0$) and where *m* sets the relative colonization rate (relative to extinction rate).

EQUILIBRIA AND THEIR STABILITY

The model (eq. [5]) has three parameters that describe the species' relative colonization rate (*m*), the degree of spatial variation in patch sizes (*b*), and the strength of the rescue effect (*c*), respectively. In the following section we shall examine how the stability of the model equilibria is affected by the three parameters. The salient results are summarized in figures 3 and 4, which give the bifurcation diagrams for four particular cases, with much and little spatial variation in patch sizes and with strong and weak rescue effects, respectively.

Apart from the trivial equilibrium, which corresponds to metapopulation extinction, the model may have one, two, or three other equilibria. It can be shown
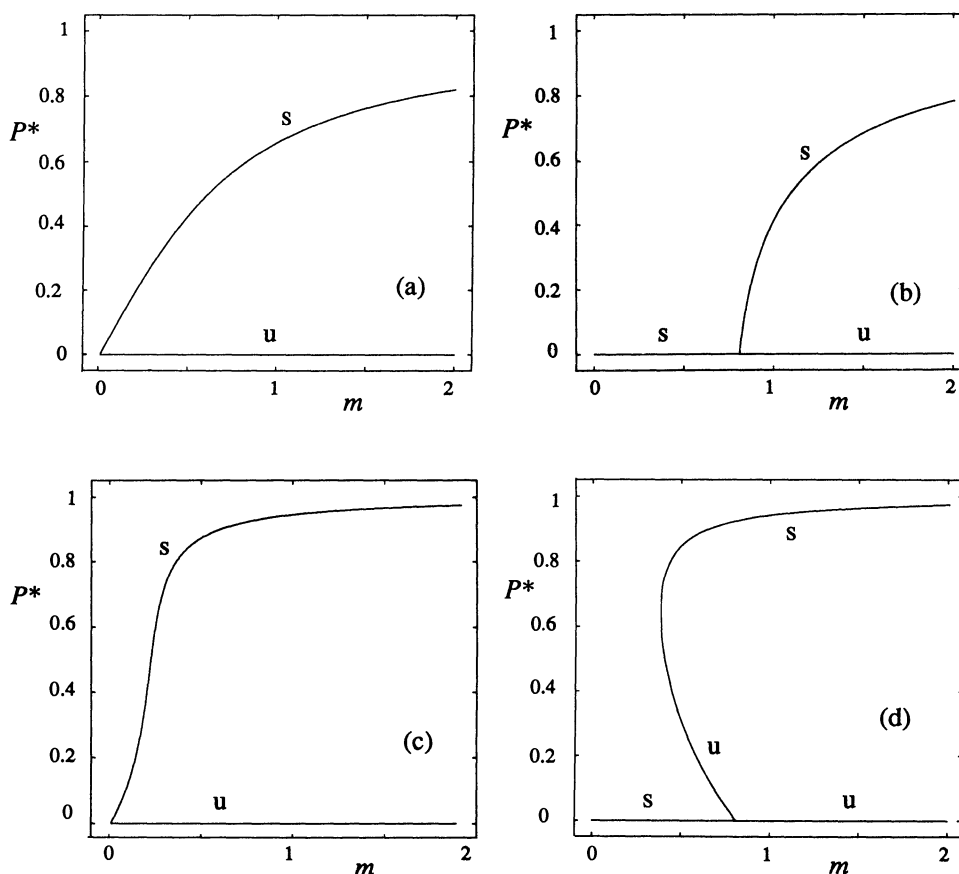
Fig. 3.—Equilibria of the simple model, eq. (5), for four combinations of parameters: *a*, *b* = 0.1 (much spatial variation in patch sizes), *c* = 1.0 (weak rescue effect); *b*, *b* = 0.9 (little spatial variation in patch sizes), *c* = 1.0; *c*, *b* = 0.1, *c* = 3.0 (strong rescue effect); and *d*, *b* = 0.9, *c* = 3.0. These bifurcation diagrams give the equilibrium fraction of patches occupied (*P**) as a function of colonization rate (*m*). Branches marked with the letter *s* correspond to stable equilibria and branches marked with *u* correspond to unstable equilibria. Note that there are alternative stable equilibria for a limited range of *m* values in *d*.

that, of the positive equilibria, the one with the largest value of *P* is stable (figs. 3 and 4) (see also Hanski 1985; Hastings 1991; Gyllenberg and Hanski 1992). Equation (5) has therefore no, one, or two stable, positive equilibria, depending on the values of the parameters *b*, *c*, and *m*.

The key consequence of increasing the importance of larger patches (decreasing *b*) is to allow metapopulation survival with smaller values of *m* (fig 3): rare species with small *P* survive in the largest patches, where local populations tend to be large and hence have small extinction probabilities. Alternatively, instead of varying the size of habitat patches, one could vary their quality, rare species being confined to the best-quality patches. In any case, the rescue effect enhances
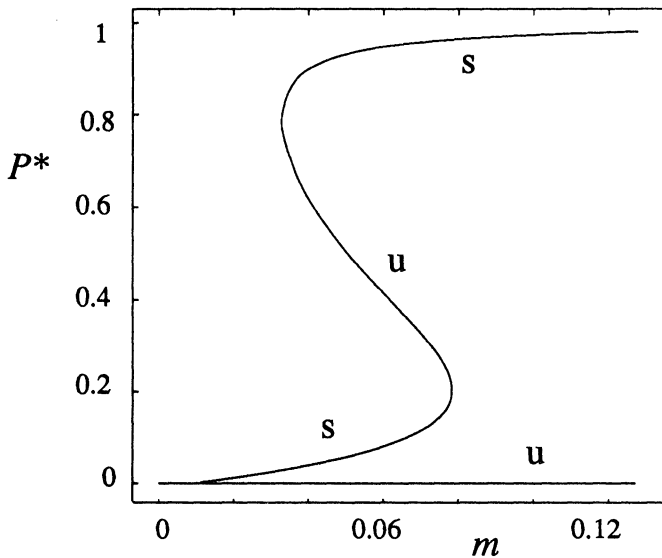
Fig. 4.—As fig. 3, but for much spatial variation in patch sizes ($b = 0.1$) and a very strong rescue effect ($c = 6.0$). Compare with fig. 3c with weaker rescue effect (note the different scale on the horizontal axis).

the survival of local populations when P is large and may create alternative equilibria (figs. 3 and 4). Assuming realistically that the distribution of species' relative colonization rates (m) is unimodal in an assemblage of species, the rescue effect may transform this unimodal distribution to a bimodal distribution of P values, because most m values generate either a small or a large value of P. (If all species have very small or large values of m, the corresponding P values may naturally be all small or large, but in no case should the P distribution peak at an intermediate value.) Figure 5 gives a numerical example in which all species have a small value of P without the rescue effect, but with increasing rescue effect the distribution of P values becomes bimodal.

In the following section we analyze a more detailed metapopulation model, in which spatial variation in patch sizes and the dynamics of local populations are explicitly taken into account. Our purpose is to generalize the previous results with a structurally more realistic model. The final section on the core-satellite species hypothesis is, however, comprehensible on the basis of the previous nonstructured model.

A STRUCTURED METAPOPULATION MODEL

Let y denote the size (carrying capacity) of a patch, and let $n(y)$ be the patch size distribution. We assume that n is normalized, that is,

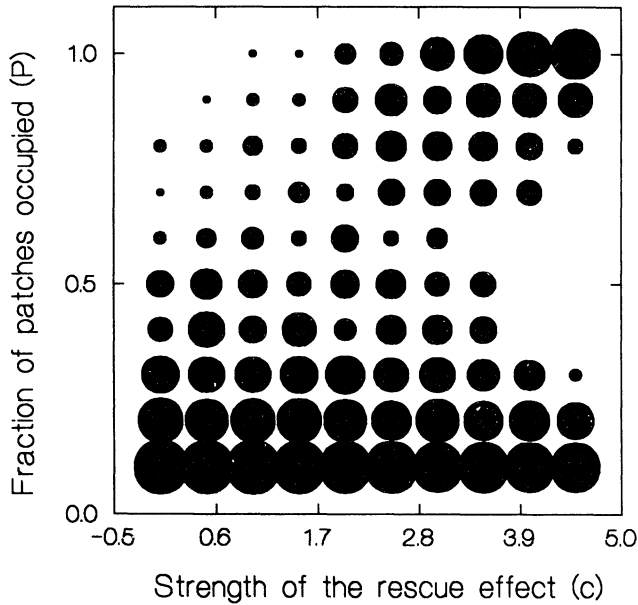$$\int_1^\infty n(y)dy = 1. \tag{6}$$

FIG. 5.—Effect of the rescue effect on the distribution of P values in the simple model, eq. (5). This example assumes large differences in habitat patch sizes ($b = 0.1$). For each value of c (the rescue effect), P values were generated for an assemblage of 300 species with m distributed lognormally (average $= -1.0$, SD $= 0.5$). Other unimodal distributions could be used instead without changing the conclusions qualitatively. The size of the black dot is proportional to the logarithm of the number of species with a P value given on the vertical axis.

For convenience the minimum patch size is taken to be equal to one. The normalized size distribution of empty patches at time t is denoted by $e(t,y)$. An occupied patch is characterized by its size y and the size x of its local population. The normalized (x,y) distribution of occupied patches at time t is denoted by $p(t,x,y)$. Observe that

$$\int_1^\infty p(t,x,y)dx + e(t,y) = n(y) \qquad (7)$$

for all t. The number $P(t) := \int_1^\infty \int_1^\infty p(t,x,y)dxdy$ is the fraction of occupied patches at time t.

Let $g(x,y)$ denote the growth rate, due to births and deaths only, of a local population inhabiting a patch of carrying capacity y. By the interpretation of carrying capacity we assume that $g(x,y) > 0$ for $x < y$ and $g(x,y) < 0$ for $x > y$. The most commonly used expression for g is the logistic function

$$g(x,y) = rx\left(1 - \frac{x}{y}\right). \qquad (8)$$

In addition to births and deaths local dynamics are affected by migration. Let $\gamma(x,y)$ denote the emigration rate. If emigration is density-independent, we have

$$\gamma(x,y) = kx \qquad (9)$$

for some constant k. Emigration may also be density-dependent; for instance, it may be proportional to density:

$$\gamma(x,y) = kx\frac{x}{y} \tag{10}$$

for some constant k.

Let $D(t)$ be the number of migrants per patch at time t and let α be the rate at which migrants arrive at a patch. This means that per unit of time $\alpha D(t)$ migrants arrive at some patch. The probability of arriving at a certain patch may depend on its carrying capacity. To model this we introduce the nonnegative function $\psi(y)$ with the following interpretation. Per unit of time, $\alpha\psi(y)D(t)$ migrants arrive at a patch of size y. Since the size distribution of patches is $n(y)$ we must assume

$$\int_1^\infty \psi(y)n(y)dy = 1. \tag{11}$$

Migrants have a greater probability of landing at a patch with a greater value of $\psi(y)$. It is often reasonable to assume that ψ is an increasing function of patch size y. If $\psi(y)$ is exactly equal to one, then migrants choose their new patch at random, independently of patch size.

The dynamics of a local population inhabiting a patch of carrying capacity y are thus described by the ordinary differential equation

$$\frac{dx}{dt} = g(x,y) - \gamma(x,y) + \alpha\psi(y)D(t). \tag{12}$$

Let $\mu(x,y)$ be the extinction rate of a local population of size x inhabiting a patch of size y. The patch balance equation is given by the partial differential equation

$$\frac{\partial}{\partial t}p(t,x,y) + \frac{\partial}{\partial x}\{[g(x,y) - \gamma(x,y) + \alpha\psi(y)D(t)]p(t,x,y)\}$$
$$= -\mu(x,y)p(t,x,y). \tag{13}$$

Colonization of empty patches is described by a boundary condition supplementing equation (13). Let $\beta(y)$ be the rate (per migrant per patch and empty patch) of successful colonization. Then we have

$$[g(1,y) - \gamma(1,y) + \alpha\psi(y)D(t)]p(t,1,y) = \beta(y)D(t)[n(y) - \int_1^\infty p(t,x,y)dx], \tag{14}$$

since by equation (7) $e(t,y) = n(y) - \int_1^\infty p(t,x,y)dx$. The balance equation for migrants is given by

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + \int_1^\infty \int_1^\infty \gamma(x,y)p(t,x,y)dxdy, \tag{15}$$

where ν is the death rate of migrants.

Equations (13)–(15) equipped with appropriate initial conditions constitute our model. A rigorous derivation of these equations depends on a limiting procedure, which we explain in detail elsewhere (Gyllenberg and Hanski 1992) and which justifies, mathematically, the presence of empty patches in spite of a continuous flow of migrants among the patches. Biologically, several mechanisms may keep

the rate of colonization of empty patches low in spite of much migration, including various local Allee effects (e.g., low probability of mating at low density), conspecific attraction (Ray et al. 1991), and nonrandom migration among local populations. Although our deterministic models do not include these factors explicitly, it is not unreasonable to interpret low values of the colonization parameter β as reflecting such real-life complications.

Suppose now that all patches are identical, that is, have the same carrying capacity y_0. Then $n(y) = \delta(y - y_0)$, the Dirac measure concentrated at y_0, and $\psi(y_0) = 1$. The solution $p(t,x,y)$ is of the form $\bar{p}(t,x)\delta(y - y_0)$, where the local population size distribution $\bar{p}(t,x)$ satisfies our other equations (Gyllenberg and Hanski 1992). Thus the model (eqq. [13]–[15]) contains the system of identical patches as a special case.

The structured model of identical patches contains the Levins model as a special case. To see this, assume that the colonization, emigration, and extinction rates β, γ, and μ are all constants; that is, all patches are equal and the rates are independent of local population sizes. Integrating equation (13) with respect to patch size y and local population size x and taking into account the boundary condition (14), one finds that the fraction

$$P(t) := \int_1^\infty \int_1^\infty p(t,x,y)\,dy\,dx \tag{16}$$

of occupied patches satisfies the ordinary differential equation

$$\frac{d}{dt}P(t) = \beta D(t)[1 - P(t)] - \mu P(t), \tag{17}$$

and the balance equation (15) for migrants becomes

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + \gamma P(t). \tag{18}$$

Assume now, as is tacitly done in the derivation of the original Levins model, that local dynamics are much faster than the dynamics at the metapopulation level; that is, the rates α, ν, and γ are much greater than the rates β and μ. The number of migrants per patch will then be in a quasi-steady state given by

$$D(t) = \frac{\gamma}{\alpha + \nu}P(t). \tag{19}$$

A change in P is immediately reflected in a change in D according to equation (19). Substituting equation (19) into equation (17), one obtains the Levins model (eq. [3]), with $m = \beta\gamma/(\alpha + \nu)$ and $e = \mu$.

In the subsequent analysis of the model (eqq. [13]–[15]) we assume that the patch-size distribution is not continuous but that there are only two types of patches, small and large ones. We call the small patches "islands" and denote their carrying capacity by y_1. The carrying capacity of the large patches is denoted by y_2. The patch-size distribution is then given by

$$n(y) = q\delta(y - y_1) + (1 - q)\delta(y - y_2), \tag{20}$$

where $q \in (0,1)$ is the fraction of small patches (islands).

The structured model (eqq. [13]–[15]) can also describe, as an extreme case, a mainland-island constellation. To see this, assume that the patch-size distribution n is given by equation (20), where y_2 is much greater than y_1. The large patches together represent the mainland. We further assume that $\mu(x,y_2) = 0$—that is, the population on the mainland does not go extinct—and that $\psi(y_2) = 0$, which means that there is no migration from the islands to the mainland.

The solution $p(t,x,y)$ is now of the form

$$p(t,x,y) = q\bar{p}_1(t,x)\delta(y - y_1) + (1 - q)\bar{p}_2(t,x)\delta(y - y_2),$$

where $\bar{p}_1(t,x)$ and $\bar{p}_2(t,x)$ are the population-size distributions on islands (small patches) and the mainland (large patches), respectively. We assume that the mainland is initially inhabited; that is, none of the large patches is empty. Therefore, for the component describing the large patches, the right-hand side of equation (14) is exactly zero, and the populations of the large patches all grow to $\bar{x}(y_2)$, which is the root of the equation

$$g(\bar{x},y_2) - \gamma(\bar{x},y_2) = 0. \tag{21}$$

Since the component of equations (13) and (14) describing the change in $\bar{p}_2(t,x)$ is independent of D (recall that $\psi[y_2] = 0$), we may assume that the equilibrium $x(y_2)$ of the large patch populations has already been reached and that we have a constant mainland population of size $(1 - q)\bar{x}(y_2)$. The equation for D now becomes

$$\frac{d}{dt}D(t) = -(\alpha + \nu)D(t) + \Gamma + q\int_1^\infty \gamma(x,y_1)\bar{p}_1(t,x)dx, \tag{22}$$

where $\Gamma = (1 - q)\gamma[\bar{x}(y_2),y_2]$ is the constant rate of emigration from the mainland. We shall refer to this variant of the model as the structured mainland-island model. If $\gamma(x,y_1) = 0$, there is no migration among the islands and we have a pure mainland-island model, whereas, if $\gamma(x,y_1) \neq 0$, there is migration among the islands. If one assumes that local dynamics take place on a much faster time scale than metapopulation dynamics and that there is no migration among islands, equations (13) and (14) can be replaced by equation (17) and equation (22) by

$$D(t) = \frac{\Gamma}{\alpha + \nu}. \tag{23}$$

Substitution of equation (23) into equation (17) yields the original mainland-island model (eq. [2]) of MacArthur and Wilson (1967), with $m = \beta\Gamma/(\alpha + \nu)$ and $e = \mu$.

The general metapopulation model (eqq. [13]–[15]) contains a variety of intermediate cases between a pure mainland-island model and the case of identical patches.

An equilibrium solution or steady state is a time-independent solution

$$p(t,x,y) = p^*(x,y)$$

and

$$D(t) = D^* \tag{24}$$

for all t.

We show in the Appendix that a necessary and sufficient condition for D^* to be a nontrivial equilibrium level of migrants per patch is that it satisfies the
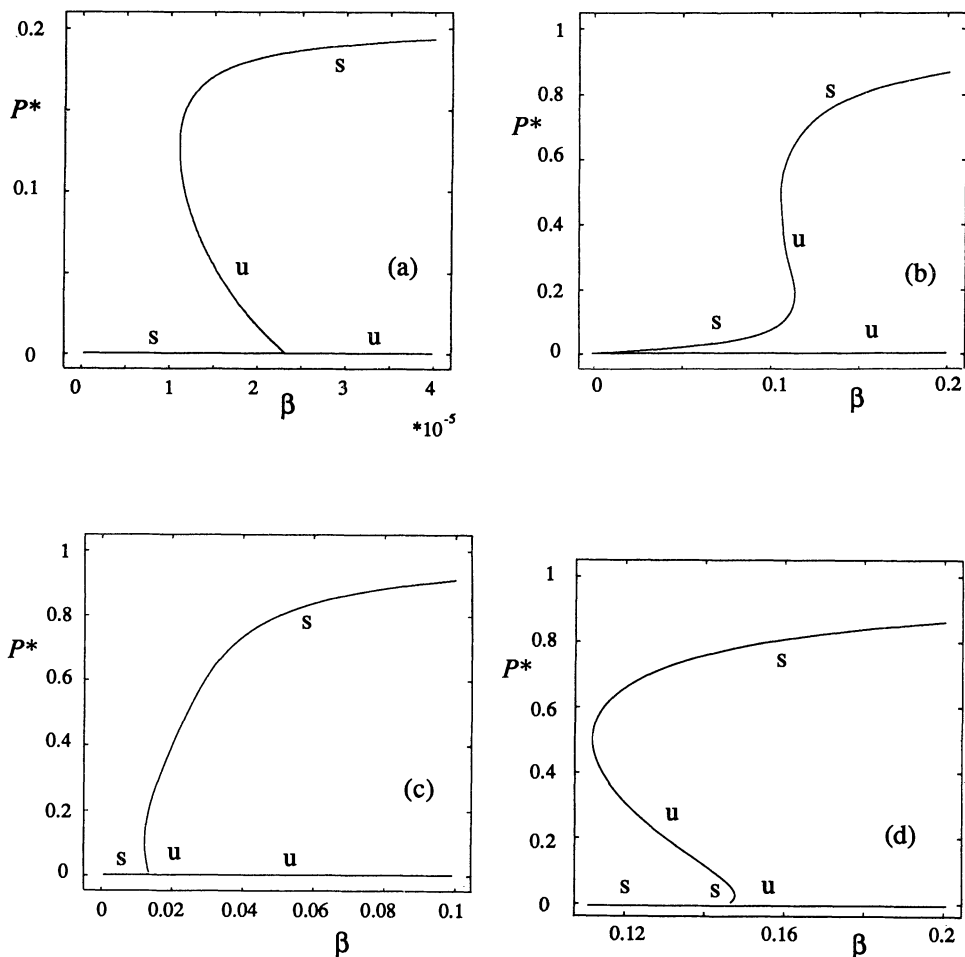
FIG. 6.—Equilibria of the structured model, eqq. (13)–(14), for four combinations of parameters: *a*, $q = 0.8$ (80% of the patches are small), $y_2 = 100$ (large patches are 10 times greater than small patches); *b*, $q = 0.996$ (99.6% of the patches are small), $y_2 = 100$; *c*, $q = 0.8$, $y_2 = 40$ (large patches are 4 times greater than small patches); and *d*, $q = 0.996$, $y_2 = 40$. The other parameters have the following values: $y_1 = 10$, $\nu = 0.1$, $\alpha = 1$, $k = 0.6$, $r = 1$, and $\mu(x) = e^{-0.23x}$. Note the different scales on the horizontal axis. These bifurcation diagrams give the equilibrium fraction of patches occupied (P^*) as a function of the colonization rate (β). Branches marked with the letter *s* correspond to stable equilibria, and branches marked with *u* correspond to unstable equilibria. Note that in each case there are alternative stable equilibria for a limited range of β values. In *a*, the upper branch (stable equilibria) approaches monotonically the asymptote $P^* = 1$ as β tends to infinity. In *b* the lower stable branch bifurcates from the trivial equilibrium ($P^* = 0$) at $\beta = 0.001$.

transcendental equation

$$R(D^*) := \frac{1}{\alpha + \nu} \int_1^\infty \frac{\beta(y)\,n(y)}{1 + \beta(y)D^*l(y,D^*)} E(y,D^*)dy = 1 \,, \qquad (25)$$

where $l(y,D)$ is the expected lifetime of and $E(y,D)$ is the expected number of migrants produced by a local population inhabiting a patch of carrying capacity y, when there are D migrants per patch. It is further shown that, for each equilibrium value D^*, the corresponding equilibrium proportion P^* of occupied patches is given by

$$P^* = \int_1^\infty \frac{\beta(y)D^*l(y,D^*)n(y)}{1 + \beta(y)D^*l(y,D^*)}\,dy \,. \qquad (26)$$

If the dynamics at the level of local populations are fast compared with the dynamics at the metapopulation level, we can make the approximation that the population of a newly colonized patch instantaneously grows to its equilibrium size $x = \tilde{x}(y,D)$, obtained by putting $dx/dt = 0$ in equation (12) and solving for x (see Gyllenberg and Hanski 1992). We also assume that the extinction rate μ is a function of local population size x only. With this approximation we have

$$l(y,D) = 1/\mu[\tilde{x}(y,D)] \qquad (27)$$

and

$$E(y,D) = \gamma[\tilde{x}(y,D)]/\mu[\tilde{x}(y,D)] \,. \qquad (28)$$

Assuming equations (27) and (28), logistic growth (eq. [8]), and density-independent emigration (eq. [9]), we investigated two special cases of the model:

1. The structured model (eqq. [13]–[15]) with patch-size distribution of the form in equation (20). We assumed that the extinction rate μ decreases rapidly with increasing population size, that migrants choose their new patch at random ($\psi[y] \equiv 1$), and that colonization is independent of patch size ($\beta[y]$ constant).
2. The structured mainland-island model.

The main difference between case 1 and case 2 is that in case 1 there is migration among all patches, including migration from the small to the large ones, whereas in case 2 there is only migration from the mainland to the islands and, if $\gamma > 0$, among islands.

Figures 6–9 summarize the key results in the form of bifurcation diagrams. Figures 6 and 7 are for case 1 and use the colonization rate β and the size ratio y_2/y_1 of large to small patches, respectively, as bifurcation parameters. Figures 8 and 9 are for case 2, with the migration rate Γ from the mainland to islands and the emigration rate k varying as shown in the figures.

An increase in the fraction of large patches $(1 - q)$, which support local populations with a low extinction probability, allows metapopulation persistence with a lower value of the colonization parameter β (fig. 6). In figure 6a migration among the large populations creates two alternative equilibria. With increasing colonization rate a monotonically increasing fraction of small patches becomes occupied, but emigration from large patches dominates the migration process. In figure 6b
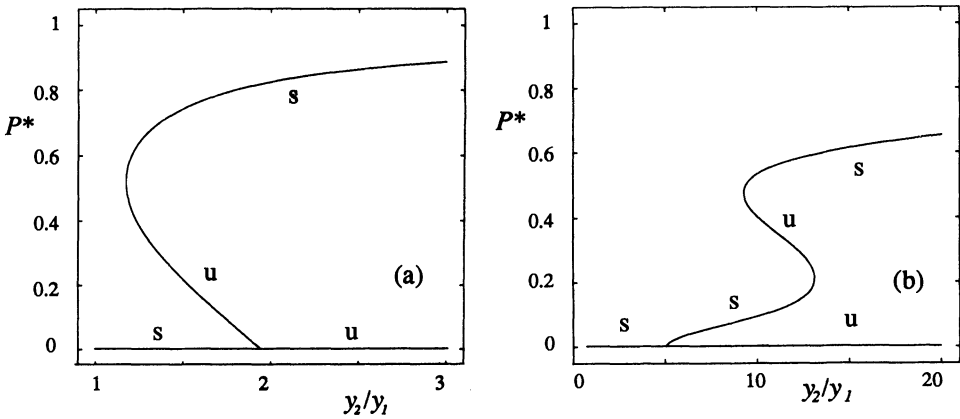
FIG. 7.—As fig. 6 but the fraction of occupied patches at equilibrium (P^*) is now plotted against the size ratio of large to small patches (y_2/y_1). In a, the fraction of small patches is smaller ($q = 0.8$) than in b ($q = 0.996$). The other parameters have the following values: $\nu = 0.1$, $\alpha = 1$, $\beta = 0.106$, $k = 0.6$, $r = 1$, $y_1 = 10$, and $\mu(x) = e^{-0.23x}$.
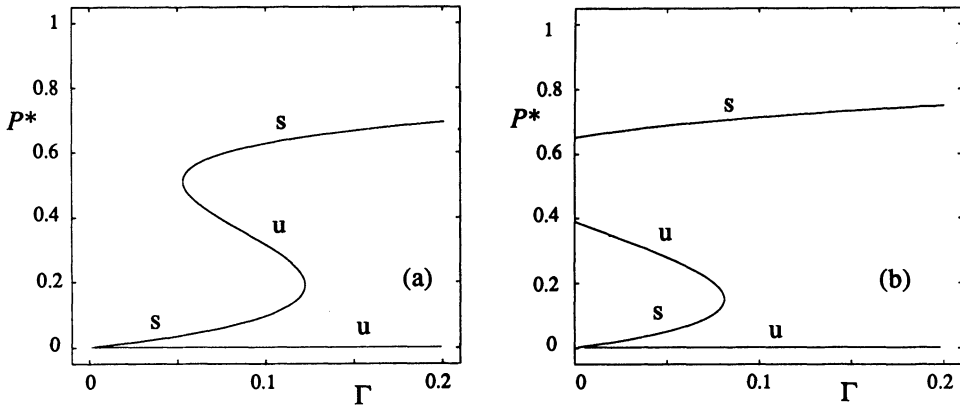

FIG. 8.—Bifurcation diagrams for the structured mainland-island model with migration among the island populations. In a, $\beta = 0.1$, and in b, $\beta = 0.11$. The other parameter values are as follows: $\alpha = 1$, $k = 0.6$, $r = 1$, $\mu(x) = e^{-0.23x}$, $\nu = 0.05$, and $y_1 = 10$. For other explanations see fig. 6.

the fraction of large patches is very small; there is no rescue effect among the large patches, but there is a rescue effect in the entire system of small and large patches; that is, migration among the small patches also contributes to the rescue. In this case there are two alternative stable, nontrivial equilibria. Figure 6c and d gives analogous results for a smaller ratio of y_2/y_1.

Figure 7 demonstrates how the size ratio of large to small patches influences the dynamics of the metapopulation. The parameters were chosen in such a way
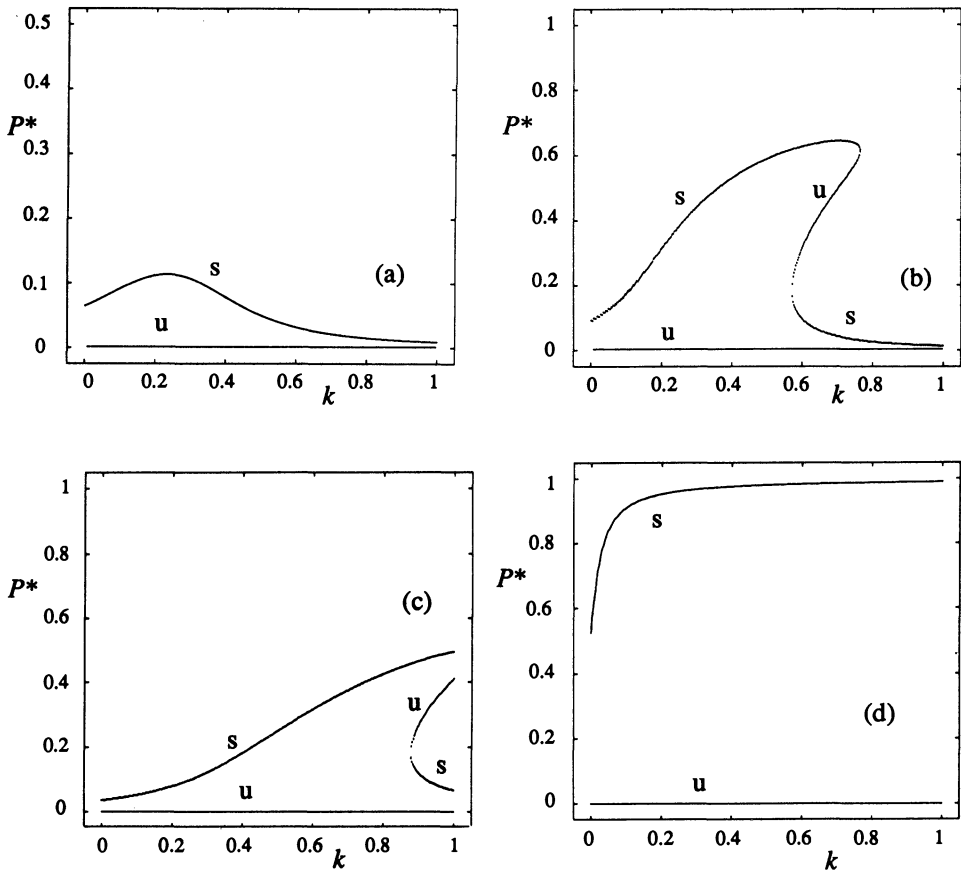
FIG. 9.—Bifurcation diagrams for the structured mainland-island model with migration among the island populations. The following parameter values are the same in all four cases: $\alpha = 1$, $r = 1$, and $\Gamma = 0.1$. In a and b extinction of local populations is density-dependent: $\mu(x) = e^{-0.23x}$; in c and d extinction is density-independent (μ = constant). In a mortality during migration is high ($\nu = 0.5$) and colonization rate is low ($\beta = 0.1$). In b mortality during migration is low ($\nu = 0.05$) and colonization rate is low ($\beta = 0.1$). In c and d there is no mortality during migration ($\nu = 0$) and colonization rate is high ($\beta = 1$). In c, $\mu = 2.7$, and in d, $\mu = 0.1$. For other explanations see fig. 6.

that metapopulation persistence is not possible if all patches are the same size. As the size of the large patches increases, the survival probability of their populations also increases, and a stable, nontrivial equilibrium appears (fig. 7). The bifurcation pattern depends on the fraction of large patches. In figure 7b the fraction of large patches is very small (0.4%), the rescue effect is negligible even for quite large values of y_2/y_1, and the trivial solution (metapopulation extinction) remains the only equilibrium. For even larger y_2 the extinction probability in the large patches becomes finally so small that a stable equilibrium emerges, with a small fraction of patches occupied, most of which are large ones. The rescue effect now becomes stronger with an increasing fraction of small patches occu-

pied, and for a range of y_2 values there are alternative stable, nontrivial equilibria. When the fraction of large patches is greater (20% in fig. 7a), the situation is different. A critical increase in y_2 immediately rescues many small populations, and there are no alternative stable, nontrivial equilibria (fig. 7a).

The result in figure 8 indicates how increasing migration rate from the mainland increases the fraction P^* of islands occupied. In figure 8a the colonization rate β is so small that without migration from the mainland ($\Gamma = 0$) the entire meta-population of islands would go extinct. Figure 8b gives an example in which β is so large that the metapopulation of islands can persist even without migration from the mainland. If $\Gamma = 0$, the trivial equilibrium is stable, but, for positive values of Γ, the trivial solution is unstable, and the metapopulation of islands will not go extinct. Observe that once again there is a possibility for alternative stable equilibria.

One might expect that increasing migration among local populations would always increase the fraction of patches occupied. Figure 9 shows that this is not so. An increase in the emigration rate k has two opposing consequences. On the one hand, it increases the number of migrants and hence strengthens the rescue effect. On the other hand, a very heavy emigration will make local populations smaller and hence more vulnerable to extinction. As shown in figure 9, the relations among k, β, the mortality ν during migration, and extinction μ of local populations determine which effect is stronger. Note that if there is no migration among islands ($k = 0$), we have a pure mainland-island model with a unique nontrivial equilibrium $D^* = \Gamma/(\alpha + \nu)$. Thus migration among islands is a necessary condition for alternative equilibria. Alternative stable nontrivial equilibria may occur even if the extinction rate is density-independent ($\mu = $ constant) and there is no mortality during migration ($\nu = 0$) (see fig. 9d).

COMPARISON OF THE SIMPLE AND STRUCTURED MODELS

Both the simple model (eq. [5]) and the structured model (eqq. [13]–[15]) generalize the Levins model (eq. [3]) and the mainland-island model (eq. [2]) to situations in which there is spatial variation in patch sizes. The simple model is similar in spirit to the Levins model and the mainland-island model in ignoring local dynamics and in focusing on the fraction of occupied patches, P. The model is nonmechanistic, but it captures the key consequences of spatial variation in patch sizes on the dynamics of P.

The structured model is very different. It is based on a detailed mechanistic description of the dynamics of local populations incorporating growth, emigration, and immigration. The dynamics of migrants are modeled separately. The colonization and extinction rates are not modeled, unlike in the simple model, as functions of the fraction of occupied patches. Instead, colonization depends on the number of migrants, and extinction is a function of the size of the local population and the patch's carrying capacity.

The difference between the two models is apparent in the way the rescue effect enters the model. In the simple model, the rescue effect was introduced in a purely ad hoc fashion by postulating that the extinction rate decreases exponen-

tially with an increasing fraction of occupied patches P. In the structured model the rescue effect is not assumed but is a consequence of the model dynamics. Local extinction is assumed to be a decreasing function of population size. An increase in the fraction of occupied patches will lead, on the average, to an increase in the number of migrants, which in turn increases immigration; hence, local populations become larger and experience a lower risk of extinction. Thus the structured model serves as a mechanistic explanation of the rescue effect.

As a matter of fact, the explicit assumption of the simple model that extinction is a decreasing function of P need not be valid in real metapopulations under all circumstances. To see this, assume that a fraction P of the patches are occupied by large local populations. The extinction rate per occupied patch is then almost zero. If, on the other hand, a fraction P' of the patches are occupied but all local populations are small, then the extinction rate per patch may be quite large even if $P' > P$.

Another limitation of the simple model is that the parameter b cannot be precisely interpreted. It describes spatial variation in patch sizes but includes both the fraction of the large patches and the size ratio of large to small patches. In the structured model, these two quantities are modeled separately, with q and y_2/y_1, respectively. Nonetheless, in both models increasing spatial variation in patch sizes by increasing the importance of large patches allows metapopulation persistence with a lower rate of colonization: the metapopulation persists because of low extinction rate in the large patches. Similarly, in both models increasing the importance of immigration in local dynamics (strengthening the rescue effect) generates the possibility of alternative, stable equilibria. In both models alternative stable equilibria are generated by the rescue effect, that is, the increasing immigration rate per patch and hence the decreasing probability of local extinction, with increasing fraction of patches occupied. The simple model exhibits the same key qualitative behavior as the more realistic structured model. We therefore conclude that the unstructured model (eq. [5]), though it is not a formal approximation of the structured model (eqq. [13]–[15]), may nonetheless be used as a convenient phenomenological model of metapopulations with spatial variation in patch sizes.

THE CORE-SATELLITE SPECIES HYPOTHESIS

Many assemblages of plants and animals show a bimodal distribution of site occupancy frequencies, denoted by P in our models. In other words, the majority of species occur, at any one time, either in all or most sites suitable for the species or only in a few sites. Figure 10 gives four examples. We refer to such bimodal distributions of P values in species assemblages as core-satellite (species) distributions (Hanski 1982a). An earlier article (Hanski 1982a) described a simple metapopulation dynamic model, which predicted the core-satellite distribution for a range of parameter values. Generalizing this work, we refer to any metapopulation dynamic explanation of core-satellite distributions as the core-satellite (species) hypothesis. Below, with the help of the models analyzed in this article, we discuss the related metapopulation dynamic mechanisms that may yield the
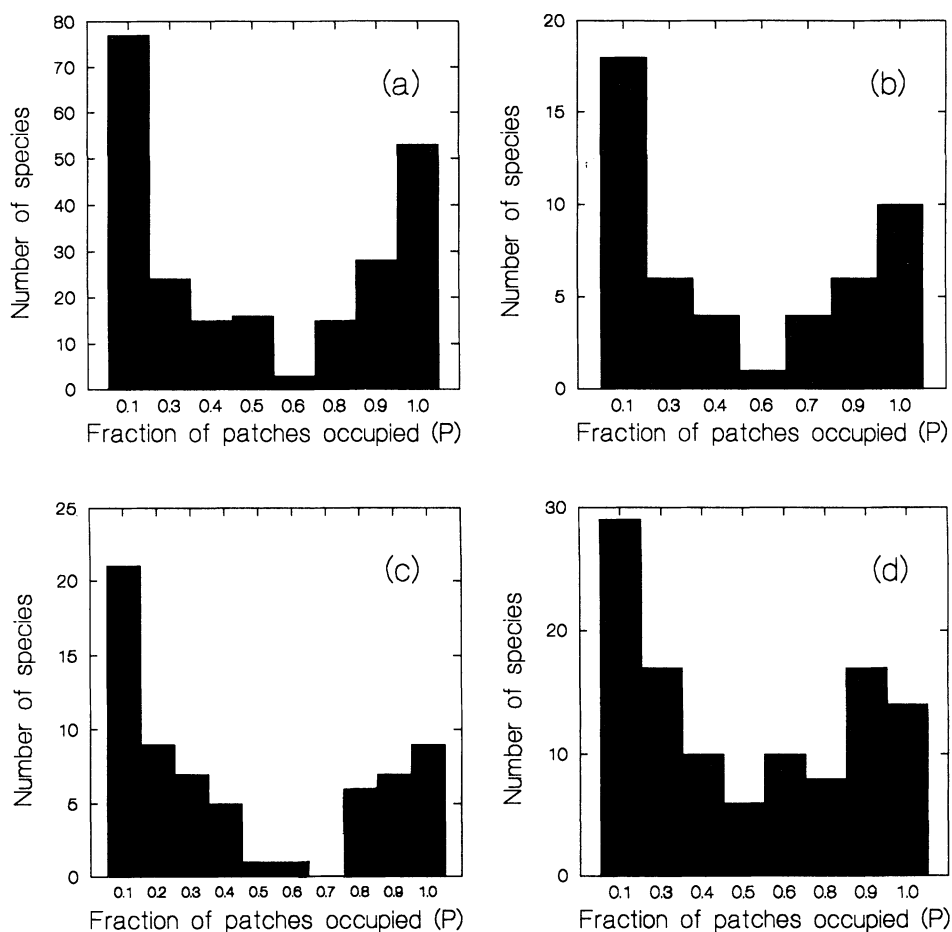
Fig. 10.—Examples of bimodal core-satellite distributions of P values: a, anthropochorous plants inhabiting small villages surrounded by forest (Linkola 1917; see also Hanski 1982b); b, British butterflies (data from Pollard et al. 1986; see analysis in Hanski et al. 1993); c, intestinal helminths in three species of grebes (pooled data for *Aechmophorus occidentalis*, *Podiceps griseigena*, and *Podiceps nigricollis*; Stock 1985; see also Stock and Holmes 1988); and d, cynipine gall wasps on oaks (pooled data for *Quercus lobata, Quercus chrysolepis, Quercus douglasii*, and *Quercus agrifolia*; Cornell 1985).

core-satellite distribution. But, before doing that, let us briefly review the two alternative hypotheses that have been suggested in the literature for core-satellite distributions.

Raunkiaer (1934) and Williams (1950) suggested that bimodality is an artifact of sampling, as P is constrained to be equal to or less than unity. They also pointed out that the shape of the distribution of P values depends on the spatial scale of sampling. Their argument is based on the assumptions that individuals are randomly distributed in space and that the mean abundances of the different species are lognormally distributed. Sampling and the spatial scale are indeed

important considerations when one attempts to explain the distribution of species' frequencies in, for example, quadrat samples taken from a homogeneous vegetation (Hanski 1982b), but it is more difficult to see the relevance of the sampling hypothesis in the case of genuine metapopulations consisting of local populations with relatively independent dynamics. Nonetheless, when dealing with natural populations with often complex and unknown spatial structure, it is clearly important to be alert to artifacts of sampling and spatial scale. We assume in the following that problems of sampling can be avoided, as is the case in models.

Brown (1984) suggested that bimodality results from some species being generalists and therefore present in most habitat patches, while others are specialists and are therefore confined to a small number of patches (the other patches are unsuitable for them). However, the core-satellite species hypothesis attempts to explain the distribution of species that may occupy the same set of habitat patches, and habitat specialization is therefore not a directly relevant issue. Furthermore, even if one were to examine the distribution of species in two or more kinds of patches, it is not obvious why interspecific differences of the type conceived by Brown (1984) should necessarily yield a bimodal distribution of P values.

The third explanation of the core-satellite distributions, metapopulation dynamics, was first suggested in two earlier articles (Hanski 1982a, 1982b) that demonstrated how bimodality may result from stochastic metapopulation dynamics. The rest of this article is restricted to metapopulation dynamic explanations of bimodal distributions of P values. We shall first review the original core-satellite species hypothesis (Hanski 1982a) and then describe the implications of the present models for bimodal distributions of P values.

To obtain the original core-satellite species model, equation (3) was modified by assuming that, because of a strong rescue effect, the extinction rate per occupied patch decreases linearly to zero with increasing fraction of patches occupied (Hanski 1982a). With this assumption, equation (3) simplifies to the logistic model, $dP/dt = m'P(1 - P)$, where $m' = m - e$. This model has a stable equilibrium point at $P = 0$ for negative m' and at $P = 1$ for positive m'. Assuming now that m' is a random variable with variance much greater than the mean value, it can be shown that the expected distribution of P values in the long course of time is bimodal, P being most of the time close to one or close to zero. This result implies that, in an assemblage of species occupying the same set of habitat patches, most species are either common (P close to one) or rare (P close to zero) at any one point in time (Hanski 1982a). For some parameter values all species may be rare, or common, but in no case should the majority of species have an intermediate value of P, assuming that all patches are suitable for colonization by all species.

There are two apparent difficulties with the original core-satellite species hypothesis. First, the model assumes migration from outside the metapopulation to compensate for metapopulation extinctions of rare species (Hanski 1982b). This may be an unreasonable assumption, because regionally rare species are often rare also in the neighboring regions, and hence no or only a few individuals may be expected to migrate between the regions (Brown 1984). But in other cases a

metapopulation may be located next to a mainland, a large expanse of suitable habitat with a large and practically invulnerable population, from which a continuous flow of migrants may reach the metapopulation and prevent metapopulation extinction. Another criticism of the original model is that species often are not observed to switch from the core (P close to 1) to the satellite state (P close to 0), and vice versa, as predicted by the model (Lawton and May 1983; Gaston and Lawton 1989). However, such switches may not be uncommon in mainland-island systems with migration among the islands (to generate the rescue effect). It has been observed in several mainland-island systems that colonization and/or extinction events on islands are very much correlated (Harrison 1991; Peltonen and Hanski 1991; Solbreck 1991), which is another way of saying that there is much temporal variation in the respective rates.

To summarize, the original core-satellite species model was based on a strong rescue effect, it was constructed as a multispecies extension of a stochastic single-species model, and it required migration from outside the metapopulation to compensate for the otherwise inevitable metapopulation extinctions of rare species. We shall now turn to the implications of the present models, which are structurally more complex but also more realistic than the original model.

There are two main differences between the original model and the present ones, though both differences are more apparent than real. First, the original concept was based on a stochastic model, as described above, whereas the present ones are deterministic models. However, the original model $dP/dt = m'P$ $(1 - P)$ generates deterministically a clear-cut dichotomy between core ($P^* = 1$) and satellite species (P^* close to zero) in an assemblage of species, with some species having positive and some negative values of m', and assuming that there is migration from outside the metapopulation to prevent extinctions of the satellite species. Second, in the original model the deterministic equilibrium fraction of occupied patches, P^*, may attain only two values, zero and one, and at a critical value of m' (at zero) P^* jumps abruptly from the lower equilibrium point to the upper one. In contrast, in the models analyzed in this article, P^* may attain any value between zero and one, if there is only one stable equilibrium, or P^* may have values from zero to one but excluding a range of intermediate values, if there are alternative stable equilibria. In the former case, and when the rescue effect is strong, there is a narrow range of parameter values within which P^* increases rapidly, corresponding to the jump from zero to one in the original model. Therefore, in an assemblage of species, the distribution of P values is likely to be bimodal, because most parameter values lead to either a low or a high value of P. Only if all species have a very low or a very high value of the critical parameter(s) can there be no bimodality, and all species have a small or a large value of P. If there are alternative stable equilibria, as in many of the examples in figures 3–9, the tendency toward bimodality is even stronger, as some intermediate P^* values, corresponding to unstable positive equilibria, repel rather than attract P. Now bimodality may also occur in an assemblage of identical species, as in the original model, if different species happen to be at different equilibria. In this case, a perturbation may push species from one equilibrium to another and produce core-satellite switching.

The original model required migration from outside the metapopulation (from a mainland) to prevent metapopulation extinctions. The present models demonstrate an obvious alternative: if local extinction probability is sufficiently low in some patches, because they are large or have superior habitat quality, that may be enough to prevent metapopulation extinctions of rare species, and no outside migration is necessarily needed.

The common feature of all these mechanisms is a strong rescue effect, under which most parameter values will generate either a small or a large value of P, and hence a bimodal distribution of P values in a species assemblage in which both kinds of species are represented. While drawing attention to this critical function of the rescue effect, we also remind the reader of the exact meaning of the term *rescue effect* as used in this article (see the section on the rescue effect). Very often, this term is used in a narrow sense to describe how immigration decreases the probability of local extinction (as in Brown and Kodric-Brown 1977). In the mainland-island model without migration among the islands, there is this kind of rescue, due to migration from the mainland to the islands, but no possibility for alternative equilibria, because immigration rate per patch does not depend on P. Our rescue effect has two components: decreasing extinction rate with increasing immigration rate and increasing immigration rate with increasing value of P. Both components are required for the more complex dynamic repercussions described in this article.

What are the situations in the real world in which we might expect the bimodal core-satellite distribution? First of all, as we have discussed, bimodality is fundamentally due to a strong rescue effect: if there is no rescue effect, there should be no bimodality, at least not for the metapopulation dynamic reasons discussed in this article. Second, to have a bimodal distribution of P values in an assemblage of species, there must be appropriate temporal or interspecific variation in parameter values, as we have discussed above. This is not a very restrictive requirement, however, because only unusual variation in parameter values would produce a unimodal distribution of P values with a peak between zero and one. Finally, there must be a mechanism that enhances metapopulation survival of rare (satellite) species. If the habitat patches are the same size and quality, this mechanism can be migration from outside the metapopulation, as in mainland-island situations. Alternatively, metapopulation extinction of rare species can be prevented or greatly slowed down by spatial variation in patch sizes or qualities, with the extinction probability being sufficiently low in some patches.

Possible examples of the first situation are provided by many assemblages of macroparasites, with host individuals functioning as habitat patches. In this case all patches are roughly the same size, and additionally all patches (host individuals) have a strictly finite lifetime. Many intestinal helminth communities show a tendency toward a bimodal distribution of incidence (fig. 10) (see also Bush and Holmes 1986*b*; Stock and Holmes 1988; Esch et al. 1990). There are no well-documented cases of core-satellite switching, but note that such switches do not need to be common if bimodality is not a result of alternative equilibria. Metapopulation extinction of rare species may be prevented by migration from other, sympatric host species. It is especially noteworthy and consistent with this

suggestion that among macroparasites specialist species tend to have a higher incidence (larger P) than generalists (Bush and Holmes 1986a, 1986b), contrary to the pattern in many free-living animals and plants (Brown 1984; Hanski et al. 1993). Apparently only those specialist parasites that have a large probability of permanently staying as core species have viable metapopulations. Constantly large P may be achieved in parasites via high transmission rate (large m and β in our models).

Contrary to parasites, most free-living animals and plants, for instance the ones included in figure 10, inhabit systems of habitat patches with much spatial variation in patch sizes (Harrison 1991), which should greatly decrease the risk of metapopulation extinction. Strong rescue effects may generate the bimodal core-satellite distribution also in these cases. The key prediction of all these models is that bimodal P distributions are associated with a strong rescue effect.

APPENDIX

EQUILIBRIUM FRACTION OF PATCHES OCCUPIED

In this Appendix we derive the equilibrium condition (25) and the expression (26) for the equilibrium fraction of patches occupied. We employ the notation introduced in the main text.

We first show that at equilibrium all local populations are smaller than a bound $\bar{x}$ that depends on the carrying capacity and the number of migrants per patch. To see this, observe that, since a local population will decrease if $x > \bar{x}$, where $\bar{x} = \bar{x}(y,D)$ is the root of the equation

$$g(\bar{x},y) - \gamma(\bar{x},y) + \alpha\psi(y)D = 0,\qquad\qquad (A1)$$

and since there is no source term in equations (13) and (14) in the region $x > \bar{x}(y,D^*)$, it is clear that

$$p^*(x,y) = 0 \text{ for } x > \bar{x}(y,D^*).\qquad\qquad (A2)$$

The equilibrium distribution of empty patches is denoted by $e^*(y)$. From equations (7) and (A2) we have

$$e^*(y) = n(y) - \int_1^{\bar{x}(y,D^*)} p^*(x,y)dx.\qquad\qquad (A3)$$

Putting $\partial p^*/\partial t = 0$, $dD^*/dt = 0$ in the equations (13)–(15), one obtains

$$p^*(x,y) = \beta(y)D^*e^*(y)\phi(x,y,D^*),\qquad\qquad (A4)$$

where

$$\phi(x,y,D) = \frac{1}{g(x,y) - \gamma(x,y) + \alpha\psi(y)D}\exp\left(-\int_1^x \frac{\mu(\xi,y)d\xi}{g(\xi,y) - \gamma(\xi,y) + \alpha\psi(y)D}\right)\quad (A5)$$

and

$$D^* = \frac{1}{\alpha + \nu} \int_1^\infty \int_1^{\bar{x}(y,D^*)} \gamma(x,y)p^*(x,y)dxdy .$$ (A6)

Substituting equation (A4) into equation (A3) and solving for $e^*(y)$, one obtains

$$e^*(y) = \frac{n(y)}{1 + \beta(y)D^*l(y,D^*)},$$ (A7)

where

$$l(y,D) = \int_1^{\bar{x}(y,D)} \phi(x,y,D)dx$$ (A8)

is the expected lifetime of a local population inhabiting a patch of size y when the number of migrants per patch is held fixed at D. Substitution of equation (A7) into equation (A4) and substitution of the so-obtained expression for $p^*(x,y)$ into equation (A6) yields

$$1 = \frac{1}{\alpha + \nu} \int_1^\infty \frac{\beta(y)n(y)}{1 + \beta(y)D^*l(y,D^*)} E(y,D^*)dy ,$$ (A9)

where

$$E(y,D^*) = \int_1^{\bar{x}(y,D)} \gamma(x,y)\phi(x,y,D)dx$$ (A10)

is the expected number of migrants produced by a local population inhabiting a patch of size y during its lifetime when the number of migrants per patch is held fixed at D. As a matter of fact, instead of equation (A9) one obtains the same equation where both sides are multiplied by D^*, but, since we are interested in nontrivial equilibria (i.e., equilibria with $D^* \neq 0$), we were allowed to divide by D^*. Equation (A9) is a necessary and sufficient condition for a nontrivial equilibrium. Once D^* has been solved from equation (A9), the distribution $e^*(y)$ of empty patches is obtained from equation (A7) and finally the distribution $p^*(x,y)$ of occupied patches from equation (A4). Integrating the expression (A4) with respect to x and y and using equations (A3) and (A5), one obtains the expression

$$P^* = \int_1^\infty \frac{\beta(y)D^*l(y,D^*)n(y)}{1 + \beta(y)D^*l(y,D^*)} dy$$ (A11)

for the proportion P^* of occupied patches at equilibrium.

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