CONGESTION MODELS OF COMPETITION

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July 1995

Abstract

A model of habitat use, or more generally of resource use in a coarse-grained environment, is presented. Competitors are assumed to respond to the combined competitive pressure of conspecifics and heterospecifics by an ideal free distribution among (micro-)habitats—"ideal" in the sense that individuals are choosing only habitats where the negative effects of congestion are minimal and "free" in the sense that no direct interference and no travel costs are involved. It is shown that an ideal free habitat distribution generically has the following graph-theoretic property: when competitors and habitats are represented by vertices and each competitor is connected with each of the habitats in which it occurs, the resulting (undirected) graph contains no cycles. This property has many implications. The fraction of (micro-)habitats occupied by an average competitor should vary inversely with the number of competing species. Pairwise overlap between competitors should be limited to a maximum of one habitat. Ideal free distribution of predators may promote stability of two-trophic level communities. The chances that incipient species will be able to complete their speciation process during secondary contact are enhanced if their habitat distribution is ideal free.

Much of the evidence supporting the view that interspecific competition is important in shaping animal communities is concerned with the patterns of distribution of actual or potential competitors among habitats or microhabitats or with the ways the habitat distribution and the abundance of species are changed in the presence of competitors (e.g., Lack 1971; Schoener 1974; Diamond 1978, 1986; Cody 1985, p. 36; Diamond and Case 1986).

1

One possible outcome of an interspecific competitive interaction that is potentially important in determining the habitat distribution of competitors is competitive exclusion (Hardin 1960). Competitive exclusion is often observed in the laboratory: almost without exception, where two species compete for identical food in a closed and homogeneous habitat (laboratory universe), one species displaces the other completely within relatively few generations (DeBach 1966). Interspecific competition may, however, affect communities without necessarily leading to local extinctions. The presence of competitors may have an influence on the optimal use of a patchy environment (MacArthur and Pianka 1966) and may therefore affect habitat selection (Rosenzweig 1991). Habitat selection may be limited in time or involve only one stage in the ontogenesis of the species concerned (Werner 1986). The resulting habitat distribution may vary seasonally or from year to year, reflecting regular or stochastic variations in resource levels and other environmental fluctuations as well as population changes.

A theory of habitat distribution and regulation of numbers (population size) of bird communities in a seasonal environment was developed by Fretwell and Lucas (1970) and Fretwell (1972). A key concept in this theory is the ideal free distribution (IFD) of competitors (Milinsky and Parker 1991; Kacelnik et al. 1992). Where resources are limited, the suitability of a habitat patch decreases with increasing competitor density. Congestion may also catalyze the spread of disease or increase the risk of predation. Hence, the optimal habitat selection of an "ideal" individual depends on the habitat distribution of its conspecifics as well as on the habitat distribution of other competitors. The IFD assumes that individuals are free to enter any habitat patch on an equal basis with residents. This assumption may not hold true where despotic or territorial behavior is involved. The distribution may still be considered free if the territorial behavior does not affect population density and only serves to space out the animals present (see Lack 1954), but not if the number of territory holders is strictly constrained by, say, the number of available nesting sites. An IFD may apply to any coarse-grained environment (MacArthur and Pianka 1966), where each resource type is associated with a distinct habitat or microhabitat and competitors cannot simultaneously search for two types of resources. The only restriction on the size of habitat patches is put by the "free" assumption, which implies that travel costs are negligible.

Rosenzweig (1981, 1985, 1991) used a graphical model for exploring the habitat selection of two species in the whole two-dimensional space of population sizes. If habitat selection is cost-free and animals choose habitats where their density-dependent fitness is highest, then in different

regions in this space the two competitors should occupy different sets of habitats. The stationary, or equilibrium, population sizes correspond to the intersection point of the zero isoclines of the two species. The shape of these isoclines is affected by density-dependent habitat selection and, unlike in the case of models based on Lotka-Volterra-type equations with constant competition coefficients (MacArthur and Levins 1967; MacArthur 1969, 1972), is generally not linear.

The graphical approach of Rosenzweig (1981, 1985, 1991; see also Morris 1988) applies only to situations in which there are just two competing species or just two habitats. The more general case of an arbitrary number of competitors and of habitats requires a different approach. In the present article I present a new analytical approach to the study of IFD, which applies to any number of competitors and habitats. It reveals new ways in which the IFD of competitors may affect community structure.

My model, which is described in detail in section A, makes two assumptions. The first, the optimality assumption, is that individuals of each species occupy only those habitats that provide the greatest contribution to expected individual fitness. The second, the congestion assumption, is that every habitat becomes less suitable as the total density of the competitors in it increases. The congestion assumption implies that competitors do not partition resources in habitats: they utilize the same resources, in exactly the same proportions. The optimality assumption says that the distribution of competitors among habitats is an IFD. In particular, source-sink situations, where some individuals in the source habitat do predictably better than others in terms of fitness (Pulliam 1988), are excluded. No specific assumptions are made concerning behavioral mechanisms underlying habitat selection, kinds of resources that the competitors utilize, or ways by which congestion affects fitness. Neither a particular causal relation between the last two factors nor a particular functional one (e.g., a linear relation or inverse proportionality) is assumed. In particular, the model does not involve the concepts of competition coefficients and carrying capacities. Correspondingly, the predictions of the model do not involve such numerical quantities as competitor density, resource levels, or intake rates (cf. Kacelnik et al. 1992). Rather, the predictions, described in sections B and C, are concerned with patterns of habitat distribution and with quantitative and qualitative relations between species diversity and niche width and between habitat diversity and species overlap. The phrase "interspecific competition of close competitors in a coarse-grained environment" will be reserved for situations in which the above two assumptions are met. It is acknowledged that these assumptions may correspond only to a special, rather extreme case of interspecific competition.

3

Any other case would require at least some modification of the assumptions. It is shown in section D, however, that the results deduced from the above assumptions also hold true in certain previous models of interspecific competitive interactions (e.g., Parker and Sutherland 1986) where the differential impact of competitors on resources is allowed to vary across habitats.

What this basic model does not tell us is whether, in a stable environment, coexistence of several close competitors in the same habitat is a potentially durable condition or, alternatively, can only be a transient state eventually giving way to the habitat segregation brought about by competitive exclusion. Persistence of habitat distributions and stability of populations can be studied only when the model is embedded in a wider population dynamics model where the positive connection between habitat suitability and population growth is explicitly considered. This is done in section E, where stationary equilibria are studied, and in section F, where their local stability is examined. The potential importance of the partial habitat separation that results from competition and habitat selection in the process of animal speciation is discussed in section G.

A. THE MODEL

There are s species and h habitats. The population size of species i is n^i. An individual of species i spends on the average p_j^i of its time in habitat j. It is not specified whether individuals actually move between habitats or whether a fixed part of the population always stays in habitat j. In either case the (average) total density in j is $n_j = \sum_i p_j^i n^i$. Since $\sum_i p_j^i = 1$, the sum $\sum_j n_j$ is equal to $\sum_i n^i$. The populations are assumed to be large enough for n^i to be seen as a continuous, rather than a discrete, parameter and for a single individual not to have an appreciable effect on the density. The case where the number of individuals is small and each individual potentially has a significant effect on others is analyzed elsewhere (Milchtaich 1996).

The suitability of habitat j for species i, which is the average contribution to the fitness of an individual of species i that is attributable to its occurrence in j, is denoted S_j^i. Since by the congestion assumption suitability is negatively affected by congestion, S_j^i is a strictly decreasing continuous function of n_j, denoted $S_j^i(n_j)$. The suitability function is determined by such attributes as the size of the habitat patch (which affects the rate by which the suitability of the habitat declines with n_j), its productivity, and the efficiency with which the competitor in question uses the particular habitat.

4

The optimality assumption, the assumption that individuals of species i occur in habitat j only if the suitability of this habitat is maximal, is written analytically as

$$p_j^i > 0 \quad \text{implies} \quad S_j^i = \max_k S_k^i. \tag{1}$$

It is shown in Appendix A that there always exists at least one optimal habitat distribution. The corresponding habitat densities n_1 through n_h, called optimal densities, are always unique for a given set of population sizes n^1 through n^s (appendix B). Furthermore, the optimal densities are determined as a continuous and nondecreasing function by the population sizes.

Species that differ, say, in size may contribute differently to the congestion. So n^i can more generally be interpreted not as the number of individuals of species i but as the "equivalent number": two species contribute equally to the congestion in habitat j if their equivalent numbers there are equal. The current model does not, however, cover the case where the differential impact of competitors is not uniform across habitats: some competitors affect the congestion more strongly in one habitat, others in other habitats. This case is discussed in section D.

In a single biological species, groups of individuals that differ, for example, in age, sex, reproductive status, physical condition (McNamara and Houston 1990) or competitive ability (Parker and Sutherland 1986) may have different suitability functions. However, as long as population dynamics is not involved, such infraspecific competitor types may be treated on equal footing with real species.

B. AVERAGE GENERALISM AND HABITAT OVERLAP

Consider a particular optimal distribution of s species among h habitats. Let h^i be the number of habitats where species i occurs. The equality of the suitability of these h^i habitats is expressed by a set of $h^i - 1$ equations of the form $S_j^i(n_j) = S_k^i(n_k)$ (where j and k are two habitats in which species i is found). In all, there are $\sum_i (h^i - 1)$ such equations, in at most h unknowns, namely, the optimal densities n_1 through n_h. No more than $h - 1$ of these h unknowns are independent, for the quality $\sum_j n_j = \sum_i n^i$ holds. Heuristically, the number of equations cannot exceed the number of independent unknowns. Thus,

$$\sum_i \left(h^i - 1 \right) \leq h - 1. \tag{2}$$

It follows from this equation that when the number of competing species is large, all but at most $h - 1$ species must be specialists (cf. Peleg et al. 1992).

Define the degree of generalism of species i as follows: the degree of generalism is zero if i is a specialist, occurring in one habitat only, and unity if i is a full generalist, occurring in all h habitats. Between these two extremes it varies linearly with the number of habitats in which species i occurs. The degree of generalism is thus $(h^i - 1)/(h - 1)$. The average generalism, denoted Gen, is $(1/s) \sum_i (h^i - 1)/(h - 1)$. Equation (2) may be rewritten as

$$Gen \leq \frac{1}{s}. \tag{3}$$

Equation (3) expresses a relation between average habitat range and the number of competitors. While a priori Gen may take any value from zero to one, optimality considerations constrain this figure to be no greater than $1/s$. When the number of competing species increases, fractional habitat ranges may have to decrease; conversely, where the number of competitors is small, ecological release may take place. In a sense, the maximal average niche width thus reflects the intensity of interspecific competition. Note, however, that the parameter involved is the number of types of competitors, not the total number of competing individuals. This result depends critically, of course, on the assumption that congestion affects habitat distribution at any level that is likely to be attained, not only when some critical level is exceeded. It is consistent with the observation that on islands, where the number of bird species is often significantly smaller than on the neighboring mainland, birds tend to occupy a larger variety of habitats and microhabitats, in comparison with birds on the mainland (MacArthur and Wilson 1967; Lack 1969, 1971; MacArthur 1972).

MacArthur and Pianka (1966) argued that in a patchy environment an optimal forager faced with competition should respond by changing its patch utilization but not its diet. This is the "compression hypothesis" (MacArthur and Wilson 1967). The value of a particular dietary item does not depend on the presence or absence of competitors, and thus the range of food taken in patches should not be affected by competition. But, in order to avoid patches that are heavily foraged by competitors, the space searched for food should shrink as more species invade. Occasionally, however, the competitors may reduce the food in a species' own favored feeding location. In such situations, the effect would be to increase the species' range of foraging places (MacArthur 1972, p. 64). The model of MacArthur and Pianka (1966) differs from the present model primarily in

that the variety of habitats visited by an individual is assumed to be a factor affecting its success. In this model, a forager travels between suitable habitat patches, crossing unsuitable patches in its way. Not all the patches in the itinerary are equally suitable, but the inclusion of the less productive ones reduces the time spent in traveling and thus increases the total number of food items consumed per unit of time. When competitors reduce food density in one kind of patch, it may no longer pay to include these patches of scarce food in the itinerary. Therefore, the selection of feeding places should normally be restricted by competitors. Equation (3) may be considered a quantitative expression for the contraction of feeding habitats predicted by MacArthur and Pianka (1966). It should, however, be remembered that the underlying models are quite different.

If competitors occupy mutually disjoint habitat ranges, then equation (3) is clearly satisfied: in this case an average competitor necessarily occupies no more than $1/s$ of the habitats. Similarly, if each competitor occupies an interval in a spectrum of resources or habitats—such as a range of foraging heights in a tree—and if the average overlap between neighboring species is a constant fraction of the average interval length, then the proportion of resources used by an average competitor is inversely proportional to the number of competing species; the coefficient of proportionality depends on the pairwise overlap between neighboring competitors (MacArthur 1972, p. 171). This relation is formally similar to equation (3), but its biological justification depends on the concept of a limiting similarity between competitors: a maximal degree of overlap between the utilization curves of neighboring competitors that would permit the persistence of a sandwiched species (MacArthur and Levins 1967) or guarantee the stability of the whole set of species against environmental fluctuation (May 1974). In contrast, the present derivation of equation (3) is based on optimality considerations in a model where competitors can adjust their habitat selection (and hence their utilization curves) and persistence and stability do not (yet) play a role. This equation and its qualitative implications are therefore relevant and may be tested, even in cases where competition is not year-round but takes place in one season only.

To see what degree of habitat overlap is consistent with equations (2) or (3), let s_j denote the number of species in habitat j and let $(s_j - 1)/(s - 1)$ be called the overlap in habitat j. If only occupied habitats are considered, the overlap in habitat j varies between zero (only one species occurs in j—no overlap there) and unity (all species occur in habitat j). The average overlap, denoted Ovr, is $(1/h) \sum_j (s_j - 1)/(s - 1)$. It follows from the identity $\sum_i h^i = \sum_j s_j$ (where both sides express the number of subpopula-

7

tions, or groups of animals of a particular species that occupy a particular habitat) that equations (2) and (3) are both mathematically equivalent to each of the following inequalities:

$$\sum_j \left(s_j - 1\right) \leq (s - 1) \qquad (4)$$

and

$$Ovr \leq \frac{1}{h}. \qquad (5)$$

Thus, with a constant number of species, an increase in the number of habitats may result in a smaller number of species occupying an average habitat. In the limit, when a continuum of habitats is approached, almost all occupied habitats should be occupied by only one species. A testable corollary of this result is that, as a general rule, spatial segregation of close animal competitors should be more complete along a habitat gradient than in an environment where habitats are few and distinct.

Eric Pianka proposed the "niche overlap hypothesis," which asserts that maximal tolerable niche overlap should vary inversely with the intensity of competition. He showed (Pianka 1974, 1975) that the mean overlap between pairs of species of desert lizards is strongly negatively correlated (though overall overlap is positively correlated) with the number of lizard species in the community. Mean pairwise overlap in trophic, spatial, and temporal niche dimensions were incorporated. This raises the question of whether or not existence of an upper limit to the permissible degree of pairwise overlap, as distinct from overall and average (per habitat) overlap, is predicted by the present model. An affirmative answer to this question is provided by the following graph-theoretic characterization of permissible habitat distributions.

C. THE HABITAT DISTRIBUTION GRAPH

Equations (3) and (5) can be analyzed further with the aid of the habitat distribution graph. This is a bipartite (two-sided) graph having one vertex corresponding to each of the s species and one vertex corresponding to each of the h habitats. A particular habitat distribution is represented qualitatively by joining each species to each of the habitats in which it occurs (Figure 1). Unlike food web graphs (Cohen 1978), this graph is by definition undirected.

It may be assumed that the habitat distribution graph is connected. (If not, a single connected component, representing a detached group of species and habitats, should be considered.) A well-known result in graph
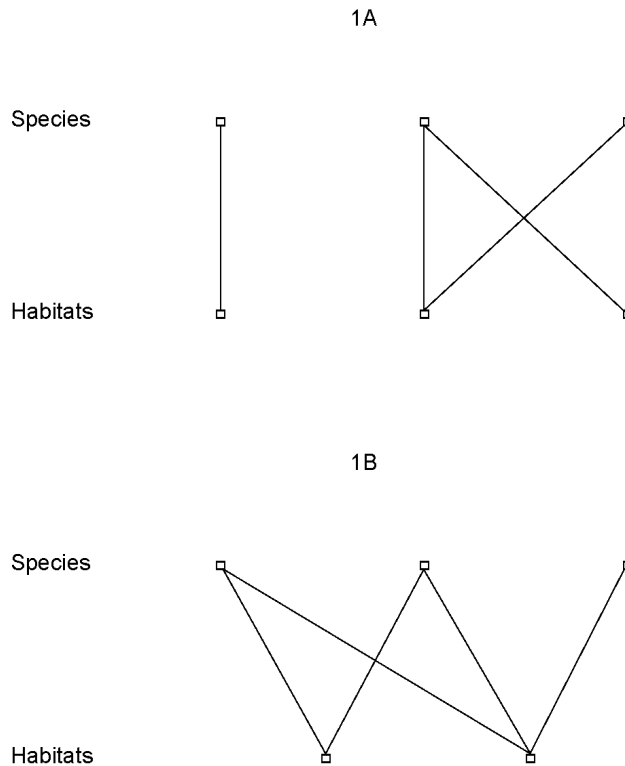
Figure 1: Habitat distribution graphs. The edges connect species with the habitats in which they occur. *A*, Acyclic graph. This graph is not connected. It has two connected components. Each connected component is a tree. *B*, Graph possessing a four-cycle. This graph is connected.

theory (see Berge 1962) is that the number of vertices of a connected graph is either smaller than or equal to the number of edges plus one. An equality implies that the graph is a tree. (A tree is a connected graph without cycles; it is not possible to walk along the edges of a tree in a closed path, started and terminated by the same vertex, without crossing any other vertex more than once and without walking along any edge more than once.) There are $s + h$ vertices in the habitat distribution graph; h^i edges are incident with the vertex corresponding to species i, and the total number of edges is thus $\sum_i h^i$. Hence, $s + h \leq \sum_i h^i + 1$, or $h - 1 \leq \sum_i \left(h^i - 1 \right)$, must hold. Since equation (2) asserts the converse of this inequality, an equality, $s + h = \sum_i h^i + 1$ (as well as equalities in each of the equivalent equations (2)–(5)), holds. The graph is therefore a tree and, thus, acyclic. We will

say that the habitat distribution represented by the graph is acyclic. It is possible to substitute a formal analysis for the heuristic arguments given in section B (based on counting equations and unknowns) and to establish rigorously that, for any given ordered set of population sizes, a unique, acyclic optimal habitat distribution indeed corresponds to a generic ordered set of suitability functions (Milchtaich 2000).

The result, that an optimal habitat distribution should be cyclic, has the following corollary, concerning the maximum permissible degree of pairwise overlap: no two competitors should occur together in more than one habitat. Indeed, joining two species to two common habitats results in a (forbidden) four-cycle (Figure 1B). This result may help to explain the spatial niche shifts observed in the overlap zone of partly allopatric closely related bird species (Diamond 1986; see also section G).

Since two species are predicted to overlap in no more than one habitat, the species combination in any habitat in which there is more than one species must be unique. Since each such combination of (two or more) species makes a positive contribution to the left-hand side of equation (4), the number of species combinations is constrained by that equation to be less than the number of species. The number should be even smaller if large combinations occur.

One of the empirical assembly rules found by Diamond (1975) for the bird communities of New Guinea and its satellite islands is that only certain combinations of related species exist in any of these islands. Although superficially similar, the above theoretical result is probably more relevant to the assembly rules for habitat communities within islands, close enough to each other so that physical barriers to dispersal are negligible (Diamond 1975, p. 417).

D. HABITAT-DEPENDENT DIFFERENTIAL COMPETITIVE WEIGHTS

Parker and Sutherland (1986) considered a model where there is a continuous arrival of food or mates into habitat patches. Each competitor has a certain competitive weight in each patch, and the individual's share of the gain in a patch is equal to its competitive weight there divided by the total competitive weight of all the individuals in the patch. The model of Parker and Sutherland (1986) differs from my model in two respects. First, the species-specific contribution of individual competitors to the congestion (as quantified by the total competitive weight) varies across patches. Second, the payoffs are inversely proportional to the parameter that quantifies congestion; other functional relations are excluded. In spite of these differences, it turns out that all of the results derived in the last two sec-

10

tions (i.e., equations (2)–(5) and their graph-theoretic implications) also hold, in the generic case, for the model of Parker and Sutherland. This follows from the fact that in this model, too, an optimal distribution is generically acyclic (and unique). This result, which is proved in appendix C, extends a previous, more particular, result of Peleg et al. (1992). Heuristically, it is not difficult to see how this result follows from the arguments given in sections B and C. By assumption, the gain of a competitor in a patch is inversely proportional to the congestion parameter there (the total competitive weight). Thus, the relative gains of a competitor in any two habitat patches remain the same when the congestion parameters are all multiplied by an arbitrary common positive factor; only the proportions among the h congestion parameters matter. These proportions can be expressed by a set of $h - 1$ variables. As shown in section B, this fact leads to equation (2), from which the rest of the results in sections B and C are deduced.

Parker and Sutherland (1986) showed that if there are only two patch types and two competitor types, and if competitive weights for the two types of competitors do not alter in the same proportion when individuals are switched between patches (in the present terminology, this is the generic case), then there is always a unique evolutionarily stable strategy (ESS) distribution. At the ESS (i.e., at the IFD), at least one of the patches is not occupied by both types of competitors; only one of the two species can be a generalist. This result follows as a special case from our result in section C, that competitors should not occur together in more than one habitat. It also follows from equation (3), which in the present special case reads $Gen \leq 1/2$.

Since the two models give similar results, it is natural to ask to what extent these results also hold for their greatest common denominator: a model where, as in the model of Parker and Sutherland (1986), the contribution of individual competitors to the congestion parameter (the variable n_j that determines the suitability of habitat j) is both patch and species specific and where, as in my model, the suitability functions are arbitrary continuous and strictly decreasing functions of n_j. The above heuristic argument is not valid for this more general model: all of the h congestion parameters matter, not just the $h - 1$ proportions among them. Therefore, the term -1 must be deleted from the right hand side of equations (2) and (4), and equations (3) and (5) must be correspondingly modified. These modifications do not, however, affect the qualitative implications of these equations, with one exception: the habitat distribution graph may contain, in each of its connected components, a single cycle. In particular, two species may occur in two common habitats, but not in three.

E. STATIONARY EQUILIBRIA

Under an ideal free distribution of competitors, all habitats in which species i occurs are equally suitable for that species. The common suitability of these habitats, S^i, is equal to $\max_j S^i_j$, where j ranges over all habitats. The S^i measures the contribution that habitat selection makes to the expected fitness of an individual of species i. However, since habitats may be occupied in only one season or may provide only one class of resources (breeding sites and feeding sites are examples), expected reproductive success or survival may be affected by intraspecific controlling factors additional to those which are associated with habitat selection. Thus, not only suitability of habitats S^i but also population size n^i may be a factor affecting the growth or decline of species i.

The population size of species i is stationary when the (annual) per capita increase rate Φ^i of species i vanishes. We assume that Φ^i is a continuous function of S^i and n^i. Since S^i itself depends on n^1 through n^s, the increase rate of species i is determined by the population sizes of all the competitors. The population sizes that correspond to a zero increase rate, $\Phi^i = 0$, constitute the zero isocline of species i. An intersection point of the s zero isoclines represents a set of stationary population sizes. Such an equilibrium point is said to be saturated (Hofbauer and Sigmund 1988) if it corresponds to an uninvadable species assembly. (This suggests that the zero isocline of species i is best defined as the set of points where either $n^i > 0$ and $\Phi^i = 0$ or $n^i = 0$ and $\Phi^i \leq 0$; see appendix A.) It is shown in appendix A that if population sizes cannot exceed some finite upper limit, then at least one saturated equilibrium exists. The corresponding habitat densities are called stationary densities. Two special functional forms of Φ^i are now considered.

If each Φ^i actually depends only on S^i and vanishes for a unique critical value S^i_{crt}, then the stationary densities are unique. In this special case species should generally occupy non-overlapping habitats. The reason for this is that species i and k may both occur in habitat j only in the unlikely case where S^i_{crt} is attained by $S^i_j(n_j)$ and S^k_{crt} is attained by $S^k_j(n_j)$ for the same stationary density n_j. More likely, only one species will occur in j, that species whose critical value is attained at the highest value of n_j. This, in fact, is the standard argument for competitive exclusion (Hardin 1960). Furthermore, since the identity of the single occupant of each habitat and its stationary density there are uniquely determined, the total stationary population size of each species is unique, too.

If the per capita increase rate Φ^i of every competitor i increases with habitat suitability S^i (holding n^i constant) and decreases with population

size n^i (holding S^i constant), then the equilibrium condition $\Phi^i(n^i, S^i) = 0$ can be solved for n^i, which can be expressed as a continuously increasing function of S^i. It is shown in appendix B that in this case (as in the case where Φ^i depends only on S^i) the stationary habitat densities—and therefore also habitat suitabilities and stationary population sizes—which correspond to a saturated equilibrium are unique. Stationary densities can only increase when new competitors are introduced into the community, and habitat suitabilities and stationary population sizes can correspondingly only decrease. Thus, none of the previously present species may benefit from the introduction. In this respect, the present model differs from competition models based on Lotka-Volterra equations where competition coefficients are constants. In those models, it may be possible that a species benefits from the introduction of a new competitor. As shown by Levine (1976) and Lawlor (1979), this is possible since the introduction may induce changes in the population of a third species, changes that may indirectly help the species in question and outweigh the direct detrimental effects of the introduction. Conversely, when one population is removed or is otherwise artificially held at a lower population size, the stationary density in every habitat either decreases or remains the same. Therefore, the other competitors can only benefit from such a manipulation, and their populations may increase. However, since there is no density increase in any habitat, the sum of the population sizes after the manipulation does not exceed the sum before the manipulation; there is no density overcompensation (MacArthur et al. 1972; Wright 1980) in ecological time.

Fretwell (1972, p. 5) expressed stability of a bird population by an equality between the density-dependent increase in the breeding season and the density-dependent mortality in the winter. He hypothesized (p. 132) that breeding success is influenced by the total breeding density of all bird species that build similar nests, possibly because this affects predation rate. If suitability is identified with average breeding success, measured as the ratio between population size before and after the breeding season (incorporating breeder mortality), then IFD of breeders implies that average breeding success S^i is the same in all the breeding habitats used by species i, provided that these habitats are close enough for the birds to move freely from one to another. The population size thus increases from n^i at the beginning of the breeding season to $n^i S^i$ at its end. Density-dependent winter mortality d^i (a function of $n^i S^i$) in the common winter habitat of the species reduces this figure to $n^i S^i \cdot (1 - d^i)$ at the beginning of the next breeding season. The population size of species i is stationary if and only if the net annual per capita increase rate $\Phi^i(n^i, S^i) = S^i \cdot (1 - d^i(n^i S^i)) - 1$ vanishes. (To account for the observed lower breeding success of those

13

field sparrows *Spizella pusilla* that also breed in the winter habitat, Fretwell actually hypothesized that winter mortality is differential: a higher winter survival rate for those birds compensates for their lower breeding success. The possibility of a differential winter mortality is not considered in the present discussion.)

In this example, both density-dependent winter mortality $d^i(n^i S^i)$ and breeding success S^i are (respectively, intra- and interspecific) controlling factors that affect the population size of species i. The net annual per capita increase rate of the species cannot be expressed as a function of S^i alone. This would be the case only if winter mortality d^i were density-independent; the equilibrium condition in such a case would be $S^i = 1/\left(1 - d^i\right)$ (which equals S^i_{crt}). If (fractional) winter mortality is negatively density dependent but the absolute number of birds surviving the winter is nevertheless an increasing function of the population size at the beginning of winter (this is the case if the latter function is increasing and concave downward), then $\Phi^i(n^i, S^i)$ decreases with n^i and increases with S^i. The results of the previous paragraphs show that in this case, as well as in the case of density-independent winter mortality, the stationary habitat densities are unique.

F. STABILITY

It is more difficult to study the dynamics of the present model than to study its statics. The two equilibrium conditions, optimal habitat distribution (section B) and stationary populations (section E), could be investigated one after the other. The dynamics, on the other hand, potentially involve simultaneously changing habitat distribution and population sizes. Another complication with nonequilibrium analysis is that suitability of habitats, which, for example, reflects prey abundance within them, may depend, not only on the current density of consumers but also on history. Local stability of a community depends, however, only on population dynamics in a vicinity of an equilibrium point. Therefore, if the equilibrium habitat selection of competitors is genetically fixed (see next section), or is otherwise slow to change in comparison with the time it takes the perturbed community to return to equilibrium, then for the purpose of stability analysis it can be assumed that competitors do not occupy habitats that they did not occupy at the equilibrium and that their populations are therefore not directly affected by the abundance of prey in those habitats. The dynamics of consumer and prey populations may still depend in intricate ways on the interplay between population changes and habitat selection adjustments. However, at least in the case that is presently de-

scribed, the exact form and magnitude of the nonequilibrium intraspecific and consumer-prey interactions do not matter: if at equilibrium suitability of habitats is density dependent and habitat selection by consumers is optimal, then the equilibrium is (locally) stable.

The community under consideration is one in which the only relevant resource in every habitat is a single self-regulated prey population. It is immaterial whether these populations belong to the same or to different species; we assume that the second possibility holds. Intraspecific controlling factors tend to decrease the size of each prey population when it exceeds its equilibrium, or stationary, size and to increase it when it falls below equilibrium size, everything else being equal. In addition to being self-regulated, the prey populations are negatively affected by predation. The competing predator species are also assumed to be self-regulated, and they are positively affected by the prey populations on which they depend. (These two controlling factors correspond respectively to n^i and S^i). One predator species does not directly interact with another but affects it only via its effect on the prey populations. The different prey populations are assumed to be physically confined to their respective habitats and, hence, not to interact directly with one another.

The stability of this two-trophic-level community is a consequence of the sign, or qualitative, stability of its community matrix (May 1973, p. 70). The stability of the community matrix follows from the assumed optimality of the equilibrium habitat (and hence prey) selection by predators. As shown in section C, an optimal habitat distribution is generically acyclic. It is proved in appendix D that acyclic distribution of competitors and self-regulation of predator and prey populations together guarantee sign stability of the community matrix. In fact, the second condition, self-regulation of all the populations involved, is not absolutely necessary. If it is possible to choose for every predator one of its prey population in such a way that different predators are assigned different prey populations, then the second condition can be replaced by the weaker condition that every prey population be self-regulated and that predators do not exhibit a destabilizing positive feedback in their intraspecific interactions. For example, when the competing predators are not self-regulated but are regulated only by the abundance of their prey (which determines the suitability of habitats), self-regulation of the prey populations should be sufficient for community stability. The reason is that, as shown in section E, in such a case there should normally be no overlap in habitat (and hence prey) selection.

Lawlor and Maynard Smith (1976) addressed the question, How might the stability of a community of several coevolved species differ from the

15

stability of a community of randomly chosen species? They considered a model in which the patch selection of two consumer species in a coarse-grained environment with two resources, each found in a distinct patch type, is an "evolutionary variable." The optimality of patch selection is brought about by coevolution. An evolutionarily stable strategy for species i, in the presence of its competitor, is to consume only the resource or resources j that provide the highest expected intake rate, weighted by the value w_j of a unit of the resource. The intake rate is equal to the instantaneous number of resource items R_j times the probability β_j^i that consumer i will find and capture a resource item j per unit of time spent searching in the relevant resource patch. In the terminology of the present article, $S_j^i = \beta_j^i w_j R_j$ is the suitability of resource patch j for species i. An individual of species i spends on the average p_j^i of its time in j. The dynamics of the ith consumer population size n^i and of the jth resource are given by

$$\frac{1}{n^i}\frac{dn^i}{dt} = \sum_j p_j^i \beta_j^i w_j R_j - T^i, \qquad i = 1, 2, \tag{6a}$$

and

$$\frac{1}{R_j}\frac{dR_j}{dt} = \phi_j(R_j) - \sum_i p_j^i \beta_j^i n^i, \qquad j = 1, 2, \tag{6b}$$

where T^i is the threshold food requirement for consumer i to maintain itself and ϕ_j is the renewal rate of resource j, which is a strictly decreasing function of R_j. The per item consumption rate of j, $n_j = \sum_i p_j^i \beta_j^i n^i$, may be identified with the congestion parameter in resource patch j. At equilibrium ($dR_j/dt = 0$) n_j determines R_j (which equals $\phi_j^{-1}(n_j)$). Thus, at equilibrium, S_j^i is density dependent. The optimality assumption implies that S_j^i should have a common, maximal value S^i in all the patches j visited by consumer species i. The equilibrium condition for consumer i (derived from equation (6a)) is therefore $0 = S^i - T^i$. This condition does not involve n^i (i.e., the consumers are not self-regulated) and therefore, as indicated in section E, the stationary patch distributions of the consumers should normally be nonoverlapping. In the present two-patch case this says that the two consumers should coevolve to become specialists. This was the conclusion that Lawlor and Maynard Smith (1976) reached.

Since in this model the resources are self-regulated (ϕ_j is decreasing) and the consumers are not, by the above general results the coevolved community is locally stable. Lawlor and Maynard Smith (1976) examined

16

the stability of the community to small perturbations by means of a numerical investigation of the eigenvalues of the community matrix, which is the Jacobian matrix of the system of four differential equations (6) calculated at equilibrium. They found that the system is locally stable with or without coevolution; changes in p_j^i's have negligible effects on the real part of the dominant eigenvalue. Their conclusion was that the coevolved divergence of the consumers do not lead to a significantly greater Lyapunov stability of the community. This was considered to be a special case of the general point derived by May (1971) for a similar but somewhat more general two-predator, two-prey model: stability at one trophic level (the lower one in this case) tends to go along with stability of the entire community. It turns out, however, that this result depends critically on the assumption that the value of a resource item is the same for the two consumers.

Mathematically, the stability of the system of equations (6) depends on the fact that the Jacobian determinant of this system is always nonnegative. A negative determinant would imply instability, for the matrix would then admit a positive eigenvalue. (May (1971) explicitly assumes that the Jacobian determinant is positive.) If species 1, say, were more efficient (i.e., spent less energy) than species 2 in capturing and consuming resource item j, then the value of j would not be the same for the two species: w_j^1 would be greater than w_j^2. In such a case the Jacobian determinant would not necessarily be nonnegative. Suppose, for example, that species 1 is twice as quick as species 2 in finding and capturing resource 1 ($\beta_1^1 = 2\beta_1^2$) and also twice as efficient in capturing and consuming it ($w_1^1 = 2w_1^2$) and that the reverse relations hold for resource 2 ($\beta_2^2 = 2\beta_2^1$ and $w_2^2 = 2w_2^1$). Suppose also that each species spends between two to four times more time searching for the resource to which it is least adapted than it spends searching for the resource to which it is better adapted ($2 < p_2^1/p_1^1 < 4$ and $2 < p_1^2/p_2^2 < 4$). Then the Jacobian determinant is negative, and therefore the corresponding equilibrium is locally unstable.

It is intuitively clear (and not too difficult to prove) that although it can sometimes be optimal for a species, in the absence of its competitor, to spend most of its time searching for the resource to which it is least adapted, such a strategy can never be optimal simultaneously for both competitors. Two coevolved competitors would therefore not exhibit such a behavior. The last example, which goes only a short way beyond the original model of Lawlor and Maynard Smith, thus demonstrates that nonoptimality of patch selection may result in community instability, and therefore, in general, a coevolved community is indeed more stable, in the sense of local stability, than a community of randomly chosen species.

G. HABITAT SELECTION AND SPECIATION

Consider two (sub)species, derived from one ancestral species, which re-establish contact after a period in which they have been geographically isolated. Being phylogenetically close and morphologically similar, the two forms are probably similar in the kinds of resources that they can potentially utilize. In a coarse-grained environment they are therefore affected by common parameters of congestion. But, because of their origin in different geographical areas, the two (sub)species are likely to differ in their adaptations to different types of habitats, in their tolerance of different climatic conditions, and so forth. In the terminology of the present model, their suitability functions may be different. If these differences are small, then allopatric populations of the two forms may still be found in broadly similar habitats. But it is suggested by the present model that even small differences should result in largely nonoverlapping habitat distributions of sympatric populations and thus in niche shifts in at least one of the populations. Ecological shifts are indeed characteristic of such zones of secondary contact (Mayr 1963, p. 493). Different authors have, however, expressed different opinions regarding their origin.

David Lack postulated that two closely related species of birds "could persist in the same area only if they differ sufficiently in ecology for one not to eliminate the other through competition. Their ecological differences might be small when they first meet, but since those individuals with such differences will tend to survive better than those which lack them, they will be intensified by natural selection until the two species no longer compete effectively for essential resources. This explained the otherwise puzzling point that, though closely related species of birds arise only through geographical isolation, they often occupy separate habitats" (Lack 1971, p.6). Lack's (1944) view was that habitat segregation probably results from natural selection operating over a long period. In contrast, Grant (1972), considering the reverse phenomenon of ecological release, remarked that in none of the cases cited by him has the role of selection been demonstrated: all the cases can be interpreted as purely phenotypic responses to the absence of competitor species. Diamond (1986, p. 109) hypothesized that when two closely related species with similar diets and foraging techniques first come into contact, the resulting spatial segregation is likely to be phenotypic, based on reversible choices of habitat made during the lifetime of each individual, and brought about "probably by exaggeration of slight differences in allopatry that cannot be detected with confidence." Diamond based his argument on the demonstration that spatial segregation, the most common mode of ecological segregation among

18

sympatric New Guinea montane bird species, usually develops, or at least becomes more marked, during early stages of sympatry and on the theory of habitat selection developed by Rosenzweig (1981). It follows as a corollary from this hypothesis that largely nonoverlapping habitat distributions may develop in sympatry well before coevolution—involving the modification of genetically determined attributes—had time to take place. The habitat distributions may, however, be reinforced by subsequent differential evolution of behavioral, physiological and morphological adaptations to lives in the different habitats. Diamond (1986) supported the hypothesis that coevolution in sympatry produces genetic fixation of the (initially phenotypic) habitat selection by the demonstration of an evolutionary loss of niche elasticity in New Guinea montane avifauna: the more advanced the inferred stage of speciation is, the less likely is the spatial niche of one bird species to expand in absence of the related taxon.

Phenotypic habitat segregation may help incipient species complete their speciation process in sympatry by reducing interbreeding where the ranges of these taxa overlap. If the (sub)species involved have not yet acquired an effective reproductive isolation, hybridization between them may be limited if they differ in their habitat preferences (Mayr 1942). It is suggested by the present model that such differences, though having their roots in allopatric speciation, may be fully expressed only in sympatry, where the optimal habitat use of each species depends on that of the other species. This is congruous with the partly allopatric model of animal speciation (Grant and Grant 1983): speciation is initiated through morphological divergence in isolation and completed when the two populations come together; the differences between the previously separated populations are enhanced during secondary contact. It would be interesting to check whether there are consistent differences between large taxonomic groups in the prevalence of niche shifts and the frequency of hybridization in areas of secondary contact that are correlated with the degree to which habitat selection is possible for these organisms.

APPENDIX A

EXISTENCE OF AN OPTIMAL HABITAT DISTRIBUTION AND STATIONARY POPULATIONS

The habitat distribution of s species among h habitats is described by an $s \times h$ matrix $\mathbf{N} = (n_j^i)$ whose nonnegative elements n_j^i are equal to $n^i p_j^i$, the number of individuals of species i times the fraction of the population that occurs in habitat j. The elements in the ith row of $\mathbf{N}$ sum up to the population size n^i of species i. The elements in the jth column sum up to the density n_j in habitat j. Clearly, $\sum_j n_j = \sum_i n^i$. The distribution is said to be optimal if, for every i and j,

$$n_j^i > 0 \quad \text{implies} \quad S_j^i(n_j) = \max_k S_k^i(n_k), \tag{A1}$$

where $S_j^i(n_j)$ is the continuously decreasing suitability function of species i in habitat j. We show that an optimal distribution exists for every given s-tuple of population sizes $(n^i) = (n^1, n^2, \ldots, n^s)$.

Consider the ith row $\mathbf{N}^i$ of $\mathbf{N}$; $\mathbf{N}^i$ is an element of the simplex Δ^i defined by the equation $\sum_j n_j^i = n^i$. The optimality condition (equation (A1)) requires $\mathbf{N}^i$ to lie in the subsimplex $M^i(\mathbf{N})$ spanned by those j's where $S_j^i(n_j)$ is maximal; the distribution of i is optimal if and only if $\mathbf{N}^i \in M^i(\mathbf{N})$. The distribution of all s species is optimal if and only if

$$\mathbf{N} \in \prod_{i=1}^{s} M^i(\mathbf{N}). \tag{A2}$$

Because of the assumed continuity of the suitability functions, the correspondence $\mathbf{N} \mapsto \prod_i M^i(\mathbf{N})$, defined on $\prod_i \Delta^i$, is closed. Kakutani's fixed-point theorem (see, e.g., Border 1985) hence guarantees the existence of a matrix $\mathbf{N}$ for which equation (A2) holds. Thus there exists at least one optimal distribution.

It is shown in appendix B that the optimal habitat densities $(n_j) = (n_1, n_2, \ldots, n_h)$, corresponding to (n^i) via some optimal distribution, are unique and that the mapping $(n^i) \mapsto (n_j)$ is continuous. Denoting $\max_j S_j^i(n_j)$ by S^i, the composed mapping $(n^i) \mapsto (n_j) \mapsto (S^i)$ is therefore continuous, too.

The per capita increase rate $\Phi^i(n^i, S^i)$ of population i is assumed to be a continuous function of n^i and S^i. The population is stationary when $\Phi^i = 0$. A set of stationary populations constitute a saturated equilibrium (Hofbauer and Sigmund 1988) if none of the remaining species, those for

which $n^i = 0$, can invade; for every species i in this complementary set, $\Phi^i \leq 0$. We now show that such a saturated equilibrium always exists.

The first step is to express the two different conditions for the two sets of species by the single equation $\Psi^i = 0$, where Ψ^i is the maximum between Φ^i and $-n^i$. This equation asserts that either $n^i > 0$ and $\Phi^i = 0$ or $n^i = 0$ and $\Phi^i \leq 0$. The value of Ψ^i depends continuously on n^i and S^i. As discussed in a previous paragraph, the latter is itself a continuous function of the population sizes of all the competitors. Therefore, Ψ^i, too, can be expressed as a continuous function of the population sizes, denoted $\Psi^i(n^1, n^2, \ldots, n^s)$. Geometrically, the set of points where $\Psi^i = 0$ constitutes the zero isocline of species i. Next we make the assumption that, regardless of the sizes of the other populations, population i cannot exceed some upper limit $n^i_{\max}$; beyond that limit the population increase rate either vanishes or becomes negative. Thus, for all i, it is always the case that $\Psi^i(n^1, n^2, \ldots, n^{i-1}, n^i_{\max}, n^{i+1}, \ldots, n^s) \leq 0$. As Ψ^i is, by definition, nonnegative when $n^i = 0$ and, by assumption, nonpositive when $n^i = n^i_{\max}$, there is no point on the faces of the box $\prod_{i=1}^s [0, n^i_{\max}]$ where the vector field $(\Psi^1, \Psi^2, \ldots, \Psi^s)$ points outward. It follows that there exists at least one point $(n^1, n^2, \ldots, n^s)$ in the box where this continuous vector field vanishes (see Border 1985, p. 80). This point corresponds to a saturated equilibrium. Geometrically, it is an intersection point of the s zero isoclines $\Psi^i(n^1, n^2, \ldots n^s) = 0$, $i = 1, 2, \ldots, s$.

The optimal habitat densities that correspond to the stationary populations of a saturated equilibrium are called stationary densities.

APPENDIX B

UNIQUENESS OF OPTIMAL DENSITIES AND STATIONARY DENSITIES

Let $(\bar{n}^i_j)$ and $(\tilde{n}^i_j)$ be two optimal distributions. The corresponding optimal densities are $(\bar{n}_j)$ and $(\tilde{n}_j)$, respectively, and the population sizes are $(\bar{n}^i)$ and $(\tilde{n}^i)$, respectively. We show that if $(\bar{n}^i) = (\tilde{n}^i)$ then $(\bar{n}_j) = (\tilde{n}_j)$—optimal densities are unique. In fact, we prove a stronger result:

$$\sum_j \left| \bar{n}_j - \tilde{n}_j \right| \leq \sum_i \left| \bar{n}^i - \tilde{n}^i \right|. \tag{B1}$$

Denoting $\max_j S^i_j(\bar{n}_j)$ by $\bar{S}^i$ and $\max_j S^i_j(\tilde{n}_j)$ by $\tilde{S}^i$, we first show that

$$\sum_{\substack{j \\ \bar{n}_j > \tilde{n}_j}} \left(\bar{n}_j - \tilde{n}_j \right) \leq \sum_{\substack{i \\ \tilde{S}^i > \bar{S}^i}} \left(\bar{n}^i - \tilde{n}^i \right). \tag{B2a}$$

21

Consider the difference between the two sides of (B2a):

$$\sum_{\substack{i \\ \tilde{S}^i > \bar{S}^i}} \left(\bar{n}^i - \tilde{n}^i\right) - \sum_{\substack{j \\ \bar{n}_j > \tilde{n}_j}} \left(\bar{n}_j - \tilde{n}_j\right) = \sum_{\tilde{S}^i > \bar{S}^i} \sum_j \left(\bar{n}^i_j - \tilde{n}^i_j\right) - \sum_{\bar{n}_j > \tilde{n}_j} \sum_i \left(\bar{n}^i_j - \tilde{n}^i_j\right)$$

$$= \sum_{\tilde{S}^i > \bar{S}^i} \sum_{\bar{n}_j \leq \tilde{n}_j} \left(\bar{n}^i_j - \tilde{n}^i_j\right) - \sum_{\bar{n}_j > \tilde{n}_j} \sum_{\tilde{S}^i \leq \bar{S}^i} \left(\bar{n}^i_j - \tilde{n}^i_j\right)$$

$$\geq - \sum_{\tilde{S}^i > \bar{S}^i} \sum_{\bar{n}_j \leq \tilde{n}_j} \tilde{n}^i_j - \sum_{\bar{n}_j > \tilde{n}_j} \sum_{\tilde{S}^i \leq \bar{S}^i} \bar{n}^i_j.$$

The last two sums actually vanish, for if $\bar{n}_j > \tilde{n}_j$ and $\tilde{S}^i \leq \bar{S}^i$, then since $S^i_j(n_j)$ is strictly increasing, $S^i_j(\bar{n}_j) < S^i_j(\tilde{n}_j) \leq \tilde{S}^i \leq \bar{S}^i$. Since $\bar{n}^i_j$ satisfies (A1), it must be zero. Similarly, $\tilde{S}^i > \bar{S}^i$ and $\bar{n}_j \leq \tilde{n}_j$ together imply $\tilde{S}^i > \bar{S}^i \geq S^i_j(\bar{n}_j) \geq S^i_j(\tilde{n}_j)$, and therefore $\tilde{n}^i_j = 0$. Now, to complete the proof of (B1), we switch between $(\bar{n}^i_j)$ and $(\tilde{n}^i_j)$. Equation (B2a) becomes

$$\sum_{\substack{j \\ \tilde{n}_j > \bar{n}_j}} \left(\tilde{n}_j - \bar{n}_j\right) \leq \sum_{\substack{i \\ \bar{S}^i > \tilde{S}^i}} \left(\tilde{n}^i - \bar{n}^i\right). \tag{B2b}$$

The sum of equations (B2a) and (B2b) implies equation (B1).

It follows from equation (B1) that the function that maps population sizes into optimal densities is continuous, even Lipschitz continuous. It follows from equation (B2a) that this function is nondecreasing: If $\tilde{n}^i \geq \bar{n}^i$ for all i, then the right-hand side of equation (B2a) is nonpositive, and therefore the left-hand side must vanish, or $\tilde{n}_j \geq \bar{n}_j$ for all j. Furthermore, in such a case, (B2b) reads $\sum_j \left(\tilde{n}_j - \bar{n}_j\right) \leq \sum_{\bar{S}^i > \tilde{S}^i} \left(\tilde{n}^i - \bar{n}^i\right)$. But $\sum_j \left(\tilde{n}_j - \bar{n}_j\right)$ is equal to $\sum_i \left(\tilde{n}^i - \bar{n}^i\right)$, and all the terms in the latter sum are, by assumption, nonnegative. Hence, $\bar{S}^i > \tilde{S}^i$ must hold for every species i for which $\tilde{n}^i - \bar{n}^i > 0$. Thus, a species whose population strictly increases occupies habitats where the suitability is strictly lower than the suitability in the habitats that were occupied by the species before its population increased.

With one further assumption concerning stationary populations, the uniqueness of stationary densities (the optimal densities that correspond to a saturated equilibrium) can also be deduced from the above equations. The assumption, which is discussed in section E, is that for every species i the stationary population size n^i is an increasing, or at least a nondecreasing, function of S^i. If $\bar{n}^i$ and $\tilde{n}^i$ are two stationary population sizes that correspond respectively to $\bar{S}^i$ and $\tilde{S}^i$, then $\tilde{S}^i > \bar{S}^i$ implies that $\tilde{n}^i \geq \bar{n}^i$. The sum on the right-hand side of equation (B2a) is therefore nonpositive. Hence, the left-hand side must vanish. For a similar reason, the

22

left-hand side of equation (B2b) must vanish. Thus, $\bar{n}_j = \tilde{n}_j$ holds for all j—stationary densities are unique.

The effect of the introduction of a new competitor or, conversely, the removal of a competitor on the stationary population sizes of the other species can be studied in a similar way. Let $(\bar{n}_j^i)$ and $(\tilde{n}_j^i)$, respectively, be the habitat distribution before and after the introduction of species i_0. Further, $\tilde{n}^{i_0}$ is the stationary population size which the introduced species reaches; $\bar{n}^{i_0}$ is zero. Thus, $\bar{n}^{i_0} - \tilde{n}^{i_0}$ is nonpositive. Assuming that the condition spelled out in the last paragraph holds for all $i \neq i_0$, all the terms on the right-hand side of equation (B2a) are nonpositive, and therefore, the left-hand side must vanish. Thus, following the introduction of the new competitor, the density in all habitats either increases or remains the same; $\tilde{n}_j \geq \bar{n}_j$ holds for all j. Hence (by the monotonicity of the suitability functions), none of the other species benefits from the introduction; $\tilde{S}^i \leq \bar{S}^i$ holds for all i. Reversing the course of events, let $\tilde{n}^{i_0}$ be the original population size of species i_0, which is removed from the community, or its population size is otherwise artificially lowered and held at a new level $\bar{n}^{i_0}$. Let $(\bar{n}_j^i)$ be the new habitat distribution that is established after the manipulation. It was just shown that $\tilde{n}_j \geq \bar{n}_j$ holds for all j. Thus, there is no density increase in any habitat, and therefore there is no density overcompensation.

APPENDIX C

A MODEL OF HABITAT-DEPENDENT DIFFERENTIAL COMPETITIVE WEIGHTS

In the continuous-input model of Parker and Sutherland (1986) there are s competitor types and h habitat patches where the competitors search for food or for mates. The number of individuals of competitor type i searching in habitat patch j is n_j^i. The payoff S_j^i of competitor type i in habitat patch j is β_j^i/n_j. The competitive weight, β_j^i, is a positive constant that expresses the effect of congestion in habitat patch j on competitor type i. The congestion parameter, n_j, is in Parker and Sutherland's model the total competitive weight in patch j, $\sum_i \beta_j^i n_j^i$, divided by the resource input rate into j. But, in what follows, it need only be assumed that n_j is some continuous and strictly increasing nonnegative function of n_j^1 through n_j^s. (Therefore, if S_j^i is proportional not to the reciprocal of n_j as assumed here but to some other continuous, strictly decreasing, and positive patch-specific

function ϕ_j of n_j [i.e., if $S_j^i = \beta_j^i \phi_j(n_j)$], then S_j^i can be made inversely proportional to the congestion parameter simply by calling $1/\phi_j(n_j)$, rather than n_j, the congestion parameter.)

For each competitor i, $\sum_j n_j^i$ is equal to the population size n^i. But $\sum_i n_j^i$ is generally different from the congestion parameter n_j. In this, the present model differs from the model introduced in section A. The proof of the existence of an optimal distribution (appendix A) depends only on the continuity of n_j as a function of n_j^1 through n_j^s. Hence, the same proof works for the present model as well. The uniqueness of the optimal distribution is discussed below. We first show that a generic optimal distribution is acyclic.

A particular patch distribution of competitors is described qualitatively by the habitat distribution graph defined in section C. It is an (undirected) bipartite graph with s vertices (competitors) on one side and h vertices (patches) on the other side. Competitor i and patch j are connected if and only if i occurs in j. For a generic matrix of competitive weights $\mathbf{B} = (\beta_j^i)$ we show that if the patch distribution is optimal, then the graph is acyclic. A cycle in a bipartite graph consists of $2k$ ($k \geq 2$) distinct vertices, $j_1, i_1, j_2, i_2, \ldots, j_k, i_k$, and $2k$ distinct edges. The first edge connects patch j_1 and competitor i_1, the second edge connects competitor i_1 and patch j_2, and so forth. The last edge connects competitor i_k and patch j_1.

LEMMA (Peleg et al. 1992). If a patch distribution is optimal and its graph has a $2k$-cycle, then the following (nontrivial) equality holds:

$$\beta_{j_1}^{i_1} \beta_{j_2}^{i_2} \cdots \beta_{j_k}^{i_k} = \beta_{j_2}^{i_1} \beta_{j_3}^{i_2} \cdots \beta_{j_k}^{i_{k-1}} \beta_{j_1}^{i_k}. \tag{C1}$$

Proof. Since competitor i_m occurs in both patch j_m and patch j_{m+1} ($m = 1, 2, \ldots, k$; $j_{k+1} = j_1$), both patches must yield maximal payoffs. Hence, $\beta_{j_m}^{i_m}/n_{j_m} = \beta_{j_{m+1}}^{i_m}/n_{j_{m+1}}$ must hold. Multiplying and canceling out identical factors, these k equalities yield equation (C1). This equality is nontrivial, in the sense that it is not an identity: the two sets of entries of $\mathbf{B}$, those on the right-hand side of equation (C1) and those on the left-hand side, are different (actually disjoint). This completes the proof of the lemma.

The matrix $\mathbf{B}$ corresponds to a point in the $s \times h$ dimensional positive orthant. For a particular k and $2k$ particular indices $j_1, i_1, j_2, i_2, \ldots, j_k, i_k$, the points where (the nontrivial) equation (C1) holds lie on a manifold of dimension $s \times h - 1$, having Lebesgue measure zero. Hence, in the measure-theoretic sense, almost every $\mathbf{B}$ does not admit any nontrivial equality of the form in equation (C1). For such a generic $\mathbf{B}$, an optimal patch distribution always corresponds to an acyclic graph.

Under the same genericity condition that implies that an optimal patch distribution is acyclic, the distribution is also unique: for any given s-tuple (n_j^i) of population sizes, only one distribution of competitors among patches is consistent with the optimality assumption (equation (A1)). We now prove this result.

Suppose the contrary, that there exist two optimal patch distributions, $(\bar{n}_j^i)$ and $(\tilde{n}_j^i)$, such that

$$\bar{n}_{j_1}^i > \tilde{n}_{j_1}^i \quad \text{holds for some } i \tag{C2a}$$

and some j_1. For every i, both $\sum_j \bar{n}_j^i$ and $\sum_j \tilde{n}_j^i$ are equal to the the given population size of competitor i. Hence, equation (C2a) implies that

$$\bar{n}_{j_2}^i < \tilde{n}_{j_2}^i \quad \text{holds for some } i \tag{C2b}$$

and some $j_2 \neq j_1$ and that there exists some i_1 for which both the inequality in (C2a) and the inequality in (C2b) hold. Since $\bar{n}_{j_1}^{i_1}$ (and $\tilde{n}_{j_2}^{i_1}$) is strictly greater than zero, the assumed optimality of the first (respectively, second) distribution implies that patch j_1 (respectively, j_2) is optimal for competitor i_1. Hence, in particular,

$$\beta_{j_1}^{i_1}/\bar{n}_{j_1} \geq \beta_{j_2}^{i_1}/\bar{n}_{j_2} \tag{C3a}$$

and

$$\beta_{j_1}^{i_1}/\tilde{n}_{j_1} \leq \beta_{j_2}^{i_1}/\tilde{n}_{j_2}. \tag{C3b}$$

Dividing equation (C3a) by (C3b) yields

$$\tilde{n}_{j_1}/\bar{n}_{j_1} \geq \tilde{n}_{j_2}/\bar{n}_{j_2}. \tag{C4}$$

It is impossible that $\bar{n}_{j_1}^i \geq \tilde{n}_{j_1}^i$ and $\bar{n}_{j_2}^i \leq \tilde{n}_{j_2}^i$ hold for all i. The reason is that, by assumption, n_{j_1} is a strictly increasing function of $n_{j_1}^1$ through $n_{j_1}^s$, and therefore the first set of inequalities, with strict inequality for some i (equation (C2a)), implies that the value of this congestion parameter is greater for the first distribution $(\bar{n}_j^i)$ than it is for the second distribution $(\tilde{n}_j^i)$, that is, $\bar{n}_{j_1} > \tilde{n}_{j_1}$. Similarly, the second set of inequalities (together with equation (C2b)) implies that $\bar{n}_{j_2} < \tilde{n}_{j_2}$. But these two inequalities together contradict (C4). Hence, it must be that

$$\bar{n}_{j_1}^i < \tilde{n}_{j_1}^i \quad \text{holds for some } i \tag{C5a}$$

or

$$\bar{n}_{j_2}^i > \tilde{n}_{j_2}^i \quad \text{holds for some } i. \tag{C5b}$$

25

There is no loss of generality in assuming that equation (C5b) holds. The reason is that equation (C5a) can be transformed into equation (C5b) by reindexing: swooping j_1 with j_2 and $(\bar{n}_j^i)$ (the first distribution) with $(\tilde{n}_j^i)$ (the second distribution). It is immediate to check that this transformation does not affect equation (C2) (whose two parts are transformed into one another), (C3) (the same as with equation (C2)), or (C4). The formal similarity between equation (C2a), which asserts that

$$\bar{n}_{j_1}^i > \tilde{n}_{j_1}^i \quad \text{holds for some } i, \tag{C6a}$$

and equation (C5b) allows us to conclude at once that the analog of equation (C2b) holds:

$$\bar{n}_{j_3}^i < \tilde{n}_{j_3}^i \quad \text{holds for some } i$$

and some $j_3 \neq j_2$, and there exists some i_2 for which both the inequality in (C5b) and the inequality in (C6b) hold. Hence,

$$\beta_{j_2}^{i_2}/\bar{n}_{j_2} \geq \beta_{j_3}^{i_2}/\bar{n}_{j_3} \tag{C7a}$$

and

$$\beta_{j_2}^{i_2}/\tilde{n}_{j_2} \leq \beta_{j_3}^{i_2}/\tilde{n}_{j_3}, \tag{C7b}$$

and therefore $\tilde{n}_{j_2}/\bar{n}_{j_2} \geq \tilde{n}_{j_3}/\bar{n}_{j_3}$. Together with equation (C4) the last inequality yields

$$\tilde{n}_{j_1}/\bar{n}_{j_1} \geq \tilde{n}_{j_2}/\bar{n}_{j_2} \geq \tilde{n}_{j_3}/\bar{n}_{j_3}.$$

Since the inequalities in (C2b) and (C5b) cannot both hold for the same i, it must be that $i_2 \neq i_1$.

The arguments that lead from equations (C2) and (C4) to equations (C6) and (C8) can now be applied to equations (C6) and (C8). Continuing in this manner k times, a chain of inequalities,

$$\tilde{n}_{j_1}/\bar{n}_{j_1} \geq \tilde{n}_{j_2}/\bar{n}_{j_2} \geq \cdots \geq \tilde{n}_{j_{k+1}}/\bar{n}_{j_{k+1}}, \tag{C9}$$

of an arbitrary length k is generated; $j_m \neq j_{m+1}$ for $m = 1, 2, \ldots, k$. These inequalities cannot all be strict inequalities, for there are only h distinct values that the index j_m can take. If, for example, $j_1, j_2, \ldots, j_k$ are distinct but $j_{k+1} = j_1$ ($k \geq 2$), then all k inequalities in (C9) must, in fact, be equalities. The first of these equalities implies equalities in (C3), the second implies equalities in (C7), and so forth. Thus, $\beta_{j_1}^{i_1}/\bar{n}_{j_1} \geq \beta_{j_2}^{i_1}/\bar{n}_{j_2}, \beta_{j_2}^{i_2}/\bar{n}_{j_1} \geq \beta_{j_3}^{i_2}/\bar{n}_{j_3}, \ldots, \beta_{j_k}^{i_k}/\bar{n}_{j_1} \geq \beta_{j_1}^{i_k}/\bar{n}_{j_1}$, where $i_m \neq i_{m+1}$ for $m = 1, 2, \ldots, k-1$. These equalities imply equation (C1), which is a nontrivial equality: except perhaps for $\beta_{j_1}^{i_1}$ and $\beta_{j_1}^{i_k}$ (which may have the same indices), no entry of **B** appears in this equality more than once. As explained above, a matrix **B** for which such a nontrivial equality holds is nongeneric.

APPENDIX D

STABILITY OF A TWO-TROPHIC-LEVEL COMMUNITY

The linearized population dynamics of a two-trophic-level community in the neighborhood of an equilibrium point is

$$\frac{dx^k(t)}{dt} = \sum_l a_{kl} x^l(t), \qquad (D1)$$

where $x^k(t)$ is the (initially small) difference between the size of population k at time t and its equilibrium size and $\mathbf{A} = (a_{kl})$ is the community (or interaction) matrix (May 1973). The matrix is made of four blocks:

$$\mathbf{A} = \begin{bmatrix} \mathbf{A}_{11} & \mathbf{A}_{12} \\ \mathbf{A}_{21} & \mathbf{A}_{22} \end{bmatrix}.$$

The two square matrices $\mathbf{A}_{11}$ and $\mathbf{A}_{22}$ describe, respectively, the effect of s predators upon predators and the effect of h prey populations upon prey populations. It is assumed that no direct interaction between different populations on the same trophic level takes place and, thus, that these matrices are diagonal. It is also assumed that no population exhibits a destabilizing positive feedback in its intraspecific interactions and, thus, that all diagonal elements of $\mathbf{A}$ are either negative (the population is self-regulated) or zero (no self-regulation). The $s \times h$ matrix $\mathbf{A}_{12}$ describes the effect of prey populations upon their predators; entry j in row i is positive if predator i consumes prey population j, and zero otherwise. The matrix $\mathbf{A}_{21}$ describes the reverse effect of predators upon their prey; it has the opposite sign pattern to that of $\mathbf{A}_{12}$ transposed (entry i in row j is negative if entry j in row i of $\mathbf{A}_{12}$ is positive, and zero otherwise). It follows that for every off-diagonal ($k \neq l$) element a_{kl} of $\mathbf{A}$, $a_{kl}a_{lk} \leq 0$.

A cycle of $\mathbf{A}$ of length r (Maybee and Quirk 1969) is a product of the form $a_{l_1 l_2} a_{l_2 l_3} \cdots a_{l_r l_1}$, where $l_1, l_2, \ldots, l_r$ are r distinct indices. A nonzero cycle of length greater than two corresponds to a cycle in the habitat distribution graph, which in the present case is just an undirected version of the food web graph: l_1, one of the prey populations, say, is consumed by predator l_2, which also consumes prey population l_3, and so forth; predator l_r consumes both prey population l_{r-1} and prey population l_1. If, as we now assume, the graph is acyclic (see section C), then $\mathbf{A}$ has no nonzero cycles of length greater than two. As explained above, all cycles of $\mathbf{A}$ of length two are nonpositive.

If all predator and prey populations are self-regulated, then all the diagonal elements of $\mathbf{A}$ are negative. In this case, the indicated signs of the

cycles of **A** of length two and of length greater than two (nonpositive and zero, respectively) are necessary and sufficient conditions for sign, or qualitative, stability of **A**: by virtue of its sign pattern, and regardless of the magnitude of the matrix elements, all eigenvalues of **A** have a negative real part (Quirk and Ruppert 1965; Hofbauer and Sigmund 1988). Zero (no deviation from equilibrium population sizes) is therefore a stable solution of the system of linear differential equations (D1); the equilibrium under consideration is stable.

Self-regulation of all the populations involved is not, however, a necessary condition for sign stability. It is sufficient for sign stability that the prey populations be self-regulated and that every s' predators together consume at least s' prey populations (for $s' = 2, 3, \ldots, s$). (The second part of this condition is satisfied if and only if it is possible to choose for every predator one of its prey population in such a way that different predators are assigned different prey populations.) If this condition is satisfied, then there is a nonzero term in the expansion of the determinant of A. This term has the form $\pm \left(a_{k_1 l_1} a_{l_1 k_1} \cdots a_{k_s l_s} a_{l_s k_s} \right) \left(a_{l_{s+1} l_{s+1}} \cdots a_{l_h l_h} \right)$, where $k_1, k_2, \ldots, k_s$ are the s predators, $l_1, l_2, \ldots, l_h$ are the h prey populations, and, for $m = 1, 2, \ldots, s$, l_m is consumed by k_m. The existence of such a nonzero term, together with the above conditions concerning the signs of the cycles of **A**, are necessary and sufficient conditions for sign stability of a matrix with nonpositive diagonal elements that fails the "color test" for the arrangement of its negative diagonal elements (Jefferies 1974). The community matrix does not pass the color test: it is not possible to color the vertices of the habitat distribution graph black and white in such a way that all self-regulated species (and hence in particular all prey population) are colored black, at least one species is colored white, and every vertex colored white is connected by an edge to at least one other vertex colored white. This matrix is therefore sign stable.

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