On the Coexistence of Specialists and Generalists

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Species are often faced with an evolutionary trade-off between performing a few activities well (specialists) and many activities poorly (generalists). This trade-off is a central concern for evolutionary ecologists interested in the coexistence of species and the coexistence of genotypes within species. At least four factors that influence the relative fitness of generalists and specialists have been identified (table 1).

The first factor is the shape of the fitness set. Following Levins (1962, 1968), figure 1 shows fitness associated with two activities, such as resources that require different techniques to capture or habitats that require different behaviors to exploit successfully. Each genotype is represented by a *point,* and the set of genotypes that exist in the population is represented by a *line*. Both fitness sets in figure 1 have a negative slope, which indicates that fitness associated with one activity can be increased only at the expense of fitness associated with the other activity. Generalists are only slightly inferior to the specialists in the convex fitness set (*A*) and are greatly inferior to the specialists in the concave fitness set (*B*). A variety of models conclude that the fitness set must be concave for the advantages of specialization to outweigh the costs (see, e.g., Levins 1962, 1968; MacArthur and Levins 1964, 1967; MacArthur and Pianka 1966; Pulliam 1974; Rosenzweig 1974; Lawlor and Maynard Smith 1976; Wilson and Turelli 1986).

It is important to emphasize that fitness sets do not always have a negative slope. Some activities can be performed well without compromising other activities, which leads to a jack of all trades that is also a master of all. Several authors have properly cautioned that trade-offs between activities must be demonstrated and not assumed (e.g., Bernays and Graham 1988; Futuyma and Moreno 1988). Nevertheless, few would doubt the basic existence of trade-offs or their importance in the evolution of specialization.

The second factor affecting fitness is activity selection. The foregoing models assume that each genotype performs both activities so that fitness is a weighted average of the x- and y-coordinate values. If animals can choose to perform one activity and avoid the other, however, specialists can be favored even when the fitness set is convex because the cost of specializing—inferior performance at the other activity—is seldom experienced (see, e.g., Imanishi 1938, 1941, 1949; Kani 1944; Svardson 1949; MacArthur and Pianka 1966; Charnov 1976).

Activity selection has been modeled in two ways. First, we can assume that a

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TABLE 1

MODELS OF SPECIALIST-GENERALIST COMPETITION

Reference	1	2	3	4
Single-factor models:				
Levins 1962, 1968	x			
MacArthur and Pianka 1966	x			
MacArthur and Levins 1964, 1967	x			
Charnov 1976		x		
Imanishi 1938, 1941, 1949		x		
Kani 1944		x		
Svardson 1949		x		
Cohen 1966, 1968			x	
Lewontin and Cohen 1969			x	
Two-factor models:				
Pulliam 1974	x	x		
Rosenzweig 1974, 1981	x	x		
Bulmer 1974	x		x	
Lawlor and Maynard Smith 1976	x		x	
Lively 1986	x		x	
MacArthur and Levins 1964, 1967	x		x	
May 1974	x		x	
Wilson and Turelli 1986	x		x	
Cooper and Kaplan 1982	x			x
Levins 1962, 1968	x			x
Yoshimura and Clark 1991	x			x
Brew 1982		x	x	
Fretwell and Lucas 1979		x	x	
Holt 1985		x	x	
Morishita 1950, 1952, 1954		x	x	
Templeton and Rothman 1981		x	x	
Castillo-Chavez et al. 1988		x		x
Templeton and Rothman 1981		x		x
Chesson 1982, 1983, 1985			x	x
Chesson and Warner 1981			x	x
Clark and Yoshimura 1993			x	x
Ellner 1985*a*, 1985*b*			x	x
Levins 1979			x	x
Sale 1982			x	x
Turelli and Petry 1980			x	x
Three-factor models:				
Brown and Rosenzweig 1986	x	x	x	
Pimm and Rosenzweig 1979	x	x	x	
Pimm et al. 1985	x	x	x	
Rosenzweig 1979, 1981, 1987	x	x	x	
Lawlor and Maynard Smith 1976	x		x	x
Lynch and Gabriel 1987	x		x	x
May and MacArthur 1972	x		x	x
Slatkin and Lande 1976	x		x	x
Templeton and Rothman 1981		x	x	x

NOTE.—The four factors are (1) the shape of the fitness set, (2) activity (usually habitat) selection, (3) negative density dependence, and (4) intergeneration stochastic environments.

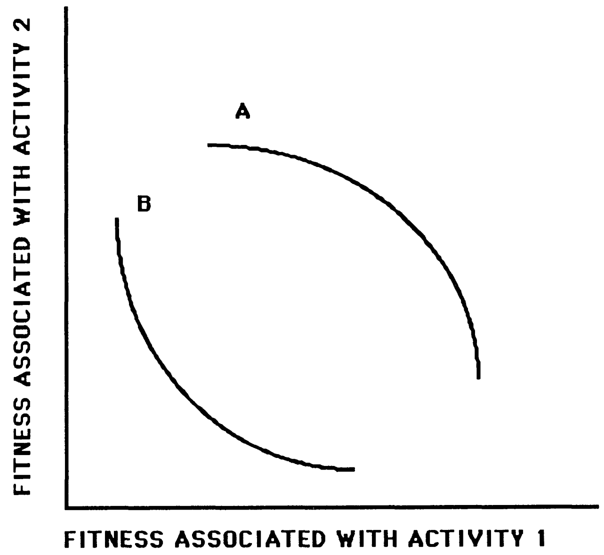

FIG. 1.—Levins's fitness set. Each *point* on the graph shows the fitness of a genotype associated with two activities. Each *line* represents the set of genotypes that can potentially exist in the population. Fitness sets *A* and *B* both have negative slopes, which signifies a trade-off in the ability of genotypes to perform the two activities. Fitness set *A* is concave outward, which indicates that the costs of generalization are slight. Fitness set *B* is concave inward, which signifies that the costs of generalization are great.

fraction *g* of the individuals perform their preferred activity while the remainder are nonselective. The degree of selectivity can then be altered by varying *g* from zero to one (see, e.g., Lawlor and Maynard Smith 1976; Templeton and Rothman 1981). Alternatively, we can assume that individuals adopt a degree of selectivity that maximizes their fitness, as specified by an appropriate optimization model (see, e.g., Morishita 1950, 1952, 1954; Fretwell and Lucas 1970; Fretwell 1972; Rosenzweig 1979, 1981, 1987).

Third, negative density dependence may also affect generalist and specialist fitness. Fitness associated with a given activity depends not only on the abilities of the organisms but also on the number of other organisms performing the same activity. As with activity selection, negative density dependence has been modeled in two ways. First, we can assume that individuals choose activities without respect to the density-dependent consequences (e.g., the "soft selection" model of Levene 1953, in which the numbers of individuals emerging from each habitat is held constant). Alternatively, we can assume that individuals adaptively monitor density along with other aspects of their environment and adjust their activities accordingly (e.g., the "environmental density" of Morishita 1950, 1952, 1954, and the "ideal free distribution" of Fretwell and Lucas 1972).

The final factor is temporally varying environments. Seasonal fluctuations and stochastic variation are thought to favor generalists by forcing all genotypes to perform a range of activities (see, e.g., Schoener 1969; Roughgarden 1972; Slatkin and Lande 1976; Taper and Case 1985; Lynch and Gabriel 1987; Seger and Brockman 1987). According to Rosenzweig (1987, p. 327), "Population sizes are not often at equilibrium. Neither are other aspects of the environment. The effect of such variance is straightforward and intuitively reasonable . . . extreme specialists become less likely."

Although each of these factors has received considerable attention (table 1), they have seldom been studied in combination. In this note we examine the effects of temporal variation on a community of specialists and generalists that can adaptively choose between two habitats and that experience negative density dependence. We show that temporal variation often does not drive extreme specialists extinct but rather allows all three types to coexist at a stable equilibrium.

THE MODEL

Consider three species that occupy two habitats. The absolute individual fitness of species i in habitat j is

$$W_{ij} = e^{r(1-(N_{ij}+N_{2j}+N_{3j})/K_{ij})} . \tag{1}$$

The terms r, N_{ij}, and K_{ij} are the rate of increase (assumed to be the same for all species), the number of species i in habitat j, and the carrying capacity of species i in habitat j, respectively. Thus, fitness declines with the number of individuals occupying the habitat. Fitness is coupled to population growth by the equation

$$N_{ij,t+1} = N_{ij,t} W_{ij,t} , \tag{2}$$

where t is time measured in generations. This is the standard stock recruitment equation that is used for discrete-time population-dynamics models (see, e.g., May and Oster 1976; Yodzis 1989).

We assume that species 1 and 2 are specialized to exploit habitat 1 and 2, respectively, and that species 3 is a generalist. Let

$$K_{1,1} = K_1, \quad K_{2,1} = aK_1, \quad \text{and} \quad K_{3,1} = bK_1 \tag{3}$$

and

$$K_{2,2} = K_2, \quad K_{1,2} = aK_2, \quad \text{and} \quad K_{3,2} = bK_2 , \tag{4}$$

where $1 > b > a > 0$. The performance trade-off is represented by the a and b terms. For example, values of $b = 0.95$ and $a = 0.1$ indicate a convex fitness set in which generalists are only slightly inferior to the specialist in each habitat. Values of $b = 0.3$ and $a = 0.1$ indicate a concave fitness set in which generalists fare poorly in both habitats.

In this model, the competitive abilities of the specialists and generalists are represented by differences in carrying capacity. For example, if $K_1 = 100$, $a = 0.1$, and $b = 0.9$, each species by itself in habitat 1 will attain a density of $N_1 = 100$, $N_2 = 10$, and $N_3 = 90$. If all three species are introduced into habitat 1, species 1 will displace species 2 quickly and species 3 more gradually. Strictly speaking, however, all three species have the same per capita effect on each other because the N terms in equation (1) are not weighted by interaction coefficients. Another way to model competitive abilities is with a matrix of interaction coefficients, α_{ijk}, which gives the per capita effect of species k on species j in habitat i. For example, we could let $K_1 = 100$ for all species, $\alpha_{121} = 10$, $\alpha_{112} = 0.1$, $\alpha_{113} = 0.9$, and so on. In this case each species by itself in habitat 1 will attain a density of 100, but species 1 will displace the others as in the first model. We use the first model for convenience but have also explored the effects of using the second model for a subset of the parameter space (see Results).

Temporal heterogeneity is modeled by randomly varying the values of K_1 and K_2 according to the following equations:

$$K_1 = K_{1,\min} + rnd_1(K_{1,\max} - K_{1,\min}), \tag{5}$$

where rnd_1 is a random number uniformly distributed between zero and one. Thus, in any particular time interval the value of K_1 ranges uniformly between $K_{1,\min}$ and $K_{1,\max}$. In some simulations we assumed that the second habitat varied in a reciprocal fashion, such that

$$K_2 = K_{2,\min} + (1 - rnd_1)(K_{2,\max} - K_{2,\min}). \tag{6}$$

In other simulations we assumed that the second habitat varied independently, such that, if rnd_2 is a random number chosen independently from rnd_1,

$$K_2 = K_{2,\min} + rnd_2(K_{2,\max} - K_{2,\min}). \tag{7}$$

All individuals were assumed to select the habitat that maximizes their fitness, which resulted in the ideal free distribution of Fretwell and Lucas (1972). Let $N_{i,1} = p_iN_i$ and $N_{i,2} = (1 - p_i)N_i$, where N_i is the total number of species i and $0 < p_i < 1$. Then the negative density effect on species i in habitat j (D_{ij}) is

$$D_{i1} = (p_1N_1 + p_2N_2 + p_3N_3)/K_{i1} \tag{8}$$

and

$$D_{i2} = [(1 - p_1)N_1 + (1 - p_2)N_2 + (1 - p_3)N_3]/K_{i2}. \tag{9}$$

Starting with species 1, all individuals choose habitat 1 if $D_{11} < D_{12}$ when $p_1 = 1$. All individuals choose habitat 2 if $D_{11} > D_{12}$ when $p_1 = 0$. Otherwise, individuals of species 1 distribute themselves into both habitats at a value of p_1 that achieves $D_{11} = D_{12}$. The other species behave similarly.

The simultaneous distributions of all three species were determined by first calculating p_3 based on arbitrary values of $p_1 = 1$ and $p_2 = 0$. We then successively calculated p_1, p_2, and p_3 until their values equilibrated. Equilibration always occurred within a few iterations of the procedure, and the final values did not depend on the initial values of p_1 and p_2.

To summarize, our model consists of the following steps: (1) Specify parameter values of r, a, b, $K_{1,\max}$, $K_{1,\min}$, $K_{2,\max}$, and $K_{2,\min}$; (2) specify initial values of N_1, N_2, and N_3; (3) calculate values of K_1 and K_2 from equations (5)–(7); (4) calculate habitat choice (p_i) from equations (8)–(9); (5) calculate fitness in each habitat from equation (1); (6) calculate new values of N_1, N_2, and N_3 from equation (2); and (7) repeat steps 3–6.

RESULTS

The basic dynamics of the model can be illustrated with an example in which $r = 1.3$, $a = 0.1$, $b = 0.90$, $N_1 = N_2 = 0$, $N_3 = 3$, $K_{1,\mathrm{min}} = K_{1,\mathrm{max}} = 200$, and $K_{2,\mathrm{min}} = K_{2,\mathrm{max}} = 100$. In other words, habitat 1 is twice as large as habitat 2, temporal variation is absent, and the community initially consists entirely of a few generalists. The population dynamics and habitat choice of species 3 over 10 generations is shown in figure 2*A*. It quickly reaches an equilibrium of $N_3 = 270$ and $p_3 = 0.66$. Note that the habitat choice of the generalist (p_3) matches the relative size of the two habitats. In figure 2*B* we introduce the two specialists in small numbers ($N_1 = N_2 = 1$). The generalist is less fit than each specialist in its preferred habitat. The low value of $a = 0.1$ is irrelevant because the specialists are free to avoid their nonpreferred habitat ($p_1 = 1$ and $p_2 = 0$). Thus, *any* value of $b < 1$ allows the specialists to replace the generalist, even when $a = 0$. Adaptive habitat selection coupled with negative density dependence is a powerful force favoring the evolution of specialization (Rosenzweig 1974, 1991).

In figure 2*C* we add reciprocal temporal variation (K_2 governed by eq. [6]) by letting $K_{1,\mathrm{min}} = 170$, $K_{1,\mathrm{max}} = 230$, $K_{2,\mathrm{min}} = 70$, and $K_{2,\mathrm{max}} = 130$. Each specialist is now unpredictably either under- or overcrowded depending on the relative values of N_1, N_2, K_1, and K_2. Given the low value of $a = 0.1$, however, the specialists are never so overcrowded that they choose to enter their nonpreferred habitat (i.e., p_1 and p_2 remain at one and zero, respectively). In figure 2*D* we reintroduce the generalist in small numbers ($N_3 = 3$). The generalist is inferior to the specialist in each habitat, but its ability to exploit both habitats relatively well allows it to choose the underpopulated habitat during every generation. Thus, the specialists must endure feast and famine, while the generalist can hop from feast to feast.

Temporal variation allows the specialists to be invaded by the generalist but not to be replaced. Rather, figure 2*D* shows that all three species coexist at a stable equilibrium that varies slightly with the particular values of the random numbers that are chosen. In figure 2*E* we increase the magnitude of temporal variation by letting $K_{1,\mathrm{min}} = 110$, $K_{1,\mathrm{max}} = 190$, $K_{2,\mathrm{min}} = 10$, and $K_{2,\mathrm{max}} = 190$. The equilibrium frequencies of the specialists decline, but they remain in the community despite very high degrees of temporal variation.

To understand the persistence of the specialists, recall from figure 2*C* that temporal variation causes the density of the specialists to fluctuate without changing their habitat choice. Figure 2*F* shows that temporal variation has exactly the opposite effect on a population of generalists; density remains constant, while habitat choice fluctuates. Habitat choice in generalists acts as a regulator that adjusts the number of consumers to the carrying capacities of the two habitats. As a result, the values of p_3N_3/K_1 and $(1 - p_3)N_3/K_2$ are constant despite environmental variation in K_1 and K_2, which eliminates temporal variation from the

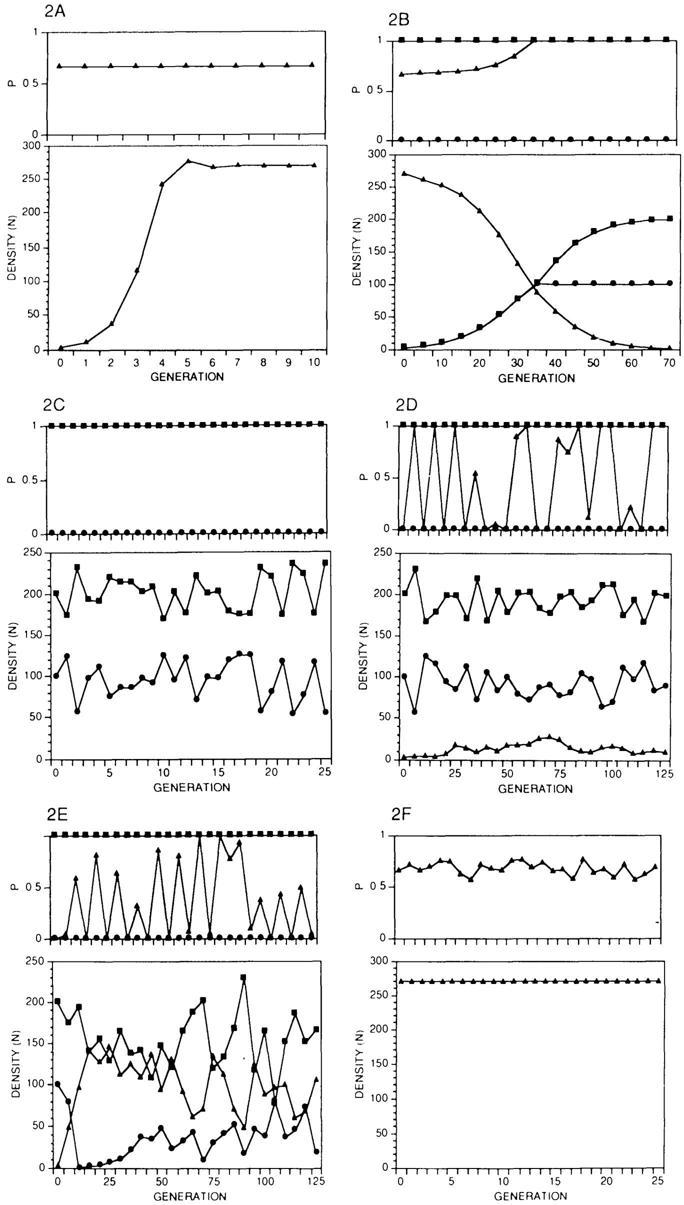

FIG. 2.—The effects of habitat choice, negative density dependence, and temporal variation on the coexistence of specialists and generalists. *Squares*, *circles*, and *triangles* represent the specialist on habitat 1, the specialist on habitat 2, and the generalist, respectively. The *upper graph* in each diagram gives the proportion of individuals that choose habitat 1. The *lower graph* gives the combined density in both habitats (N_i). Fig. 2*A* shows the generalist species in a constant environment. Note that the proportion of individuals in each habitat ($p_3 = 0.66$) mirrors the relative sizes of the habitats ($K1 = 200$, $K2 = 100$). Fig. 2*B* shows that the generalist is excluded by the specialists in a constant environment. Note that the generalist's habitat choice shifts from $p_3 = 0.66$ to $p_3 = 1.00$ as habitat 2 becomes saturated with species 2, but habitat 1 is not yet saturated with species 1. Fig. 2*C* show the two

standpoint of invading specialists. The statement "temporal variation favors generalists" is correct but must incorporate the fact that temporal variation in habitat *availability* is influenced by the activities of animals in addition to the external environment. The joint effect of adaptive habitat choice, negative density dependence, and temporal variation therefore allows all three types to coexist.

With this example in mind, we can now systematically explore the parameter space.

Reciprocally versus Independently Varying Habitats

Our example assumed that the two habitats vary in a reciprocal fashion, such that their combined carrying capacities remain constant. This is plausible for some ecological situations, but in other cases habitats can be expected to vary independently. Figure 3 shows the effects of reciprocally versus independently varying habitats on the average density of specialists and generalists. The average carrying capacities of the two habitats were equal ($K_1 = K_2 = 100$), and the range of temporal variation ($K_{\max} - K_{\min}$) was varied from 0 to 200. The basic patterns are similar in both cases, but generalists are more abundant when temporal variation is reciprocal. This makes sense because habitat choice can only be exercised when the habitats *differ* in their degree of overpopulation, which is always the case with reciprocal variation but only sometimes the case with independent variation. It follows that a positive correlation between habitats should favor specialists over generalists. To test this prediction, we ran simulations in which the same random number was used in equations (5) and (7). As expected, generalists could not invade even with extreme temporal variation ($K_{\max} - K_{\min} = 200$).

Relative Abundance of the Two Habitats

In some theoretical models, coexistence is possible only when the two habitats are relatively equal in size (see, e.g., Maynard Smith and Hoekstra 1980). We therefore altered the relative sizes of K_1 and K_2 in our model by fixing the average value of K_2 at 100 and varying the average value of K_1 from 100 to 1,000 (fig. 4). Temporal variation was independent, and the range of variation in both habitats was $K_{i,\max} = 2K_i$ and $K_{i,\min} = 0.5K_i$. Coexistence does not require relative equality of K_1 and K_2. In addition, a 10-fold increase in K_1 increases the average density of the generalist by less than a factor of two. This is because the smaller habitat 2 acts as a bottleneck for the generalist during periods when the larger habitat 1 is overpopulated by species 1.

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specialists in a varying environment. Note that their densities fluctuate but their habitat choices remain constant at $p_1 = 1$ and $p_2 = 0$, respectively. Fig. 2*D* shows that the generalist can invade the community of specialists in a temporally varying environment. Note that generalist continuously shifts habitats, depending on which is least inhabited. Fig. 2*E* shows that all three species continue to coexist despite extreme temporal variation, although species 2 periodically reaches low densities. Fig. 2*F* shows the generalist by itself in a temporally varying environment. Note that density remains constant while habitat choice varies, in contrast to the specialists in fig. 2*C*.

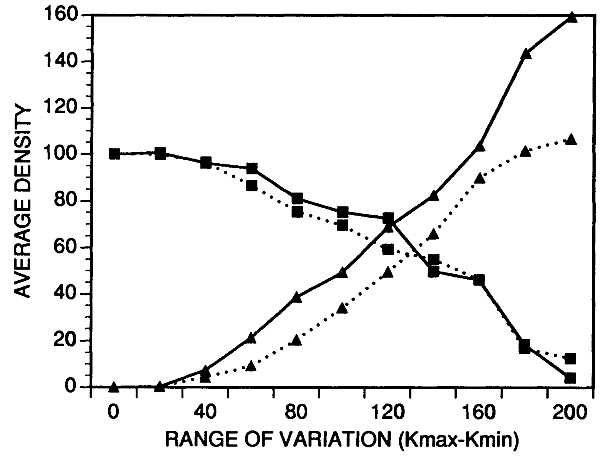

FIG. 3.—The effects of reciprocal vs. independent temporal variation on the average density of specialists (*squares*) and generalists (*triangles*). The average carrying capacities of both habitats are equal ($K_1 = K_2 = 100$), which allows both specialists to be represented by a single line. The range of variation (K_{max}–K_{min}) is varied from 0 to 200 along the X-axis. Other parameter values were $r = 1.3$, $a = 0.1$, and $b = 0.9$. Densities are averaged over 100 generations. The *solid lines* indicate reciprocal variation, in which K_1 is a random variable and $K_2 = (200 - K_1)$. The *dashed lines* indicate independent variation, in which $K1$ and $K2$ are independent random variables.

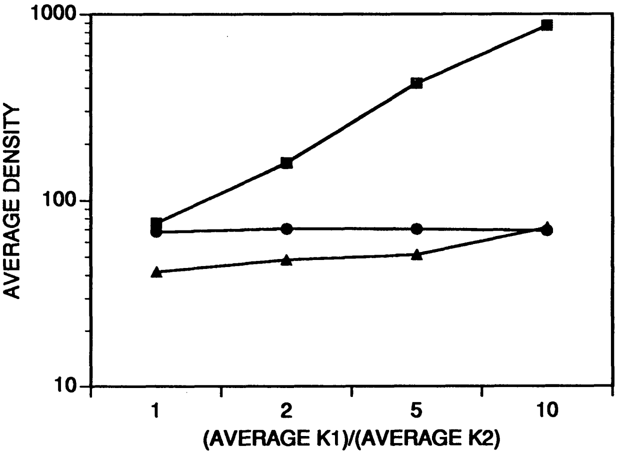

FIG. 4.—The effects of relative habitat abundance on the average density of species 1 (*squares*), 2 (*circles*), and 3 (*triangles*). The average carrying capacity of the second habitat was held constant at $K_2 = 100$, while the average carrying capacity of the first habitat was increased from $K_1 = 100$ to 1,000 along the X-axis. Variation was independent and ranged from $K_{min} = 0.5K$ and $K_{max} = 1.5K$ for both habitats. Densities were averaged over 100 generations. Other parameter values are listed in fig. 3.

Severity of the Trade-Off

The shape of the fitness set was altered by holding a constant at 0.1 and varying b from 0.99 to 0.3. The *solid line* in figure 5 represents moderate variation ($K_{1,\min} = K_{2,\min} = 50$, $K_{1,\max} = K_{2,\max} = 150$), and the *dashed line* represents more extreme variation ($K_{1,\min} = K_{2,\min} = 10$, $K_{1,\max} = K_{2,\max} = 190$). Not surprisingly, N_3 declines as the cost of generalization increases. With extreme variation, species 3 can persist in low numbers even when the fitness set is concave ($b < 0.5$). Finally, despite the existence of temporal variation, species 1 and 2 persist even when the advantages of specialization are minute ($b = 0.99$).

Degree of Adaptive Habitat Choice

Our model assumes that the species can perfectly assess their fitness in each habitat and modify their habitat choice accordingly. To explore departures from the ideal free distribution, we first calculated ideal values of p_i and then randomly distributed a proportion $1 - g$ of all species into both habitats, based on the relative values of K_1 and K_2. When $g = 1$, the ideal free distribution is attained; and when $g = 0$, a fraction $K_1/(K_1 + K_2)$ of all species enter habitat 1. Figure 6 shows the results of a simulation run in which $a = 0.1$, $b = 0.9$, and $r = 1.3$, with moderate reciprocal environmental variation ($K_{1,\min} = K_{2,\min} = 50$, $K_{1,\max} = K_{2,\max} = 150$). As expected, decreasing g favors the generalist, but the specialists remain in the system even when g is as low as 0.75 (representing a quarter of all individuals entering habitats randomly). To understand this result, note that generalists can be favored relative to specialists by either decreasing g or increasing b. We have already shown that, when $g = 1$, specialists can persist even when b is increased from 0.9 to values close to one (e.g., $b = 0.99$). It follows that, when $b = 0.9$, specialists can persist when g is decreased from one to moderately low values. It also follows that the effect of g will depend on the relative values of a and b, which we have confirmed with spot simulations. Although a complete exploration of the parameter space is beyond the scope of this note, moderate departures from the ideal free distribution do not alter our qualitative results, except for very high b:a ratios (representing fitness sets that are very highly convex).

Modeling Density Dependence with Interaction Coefficients

We have repeated the simulations using modified versions of equations (1)–(9) in which carrying capacities (K_1, K_2) are the same for all species and competitive effects are represented by a matrix of interaction coefficients (see The Model). The qualitative results are unaltered. The coexistence of specialists and generalists depends on negative density dependence and not on the particular way that it is modeled.

DISCUSSION

When considered apart, the four factors listed earlier tend to promote either specialists or generalists but not both. In fact, none of the models listed in table

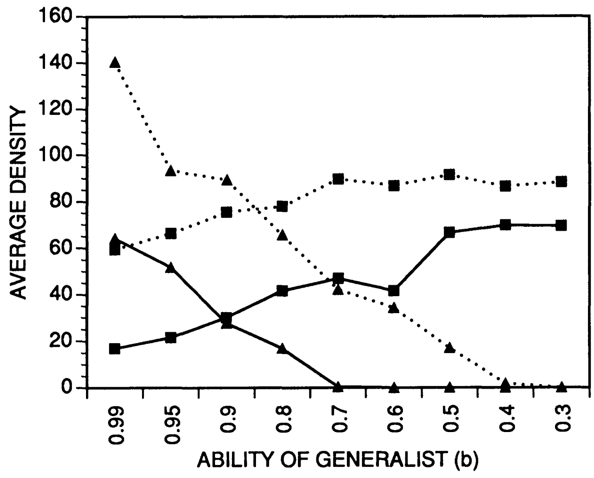

FIG. 5.—The effects of altering the shape of the fitness set on the average densities of specialists (*squares*) and generalists (*triangles*). The average carrying capacities of both habitats are equal ($K_1 = K_2 = 100$), which allows both specialists to be represented by a single line. The *solid line* represents moderate independent variation ($K_{\max} - K_{\min} = 100$), and the *dashed line* represents more extreme independent variation ($K_{\max} - K_{\min} = 180$). Densities were averaged over 100 generations. Other parameter values are listed in fig. 3.

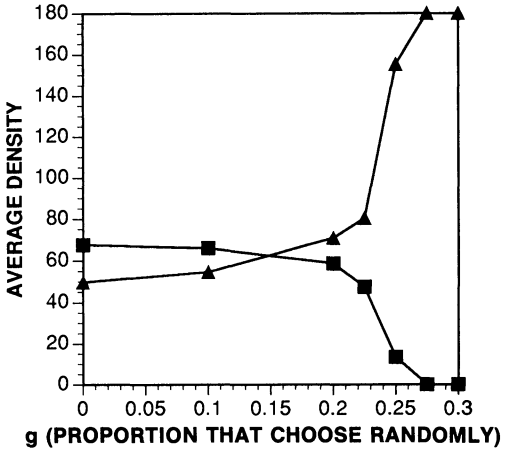

FIG. 6.—The effects of nonadaptive habitat choice (g) on the average densities of specialists (*squares*) and generalists (*triangles*). The average carrying capacities of both habitats are equal ($K_1 = K_2 = 100$), which allows both specialists to be represented by a single line. Parameter values are $r = 1.3$, $a = 0.1$, $b = 0.9$, $K_{1,\max} = K_{2,\max} = 150$, and $K_{1,\min} = K_{2,\min} = 50$.

1 predicts the coexistence of two specialists and a generalist at equilibrium. Nevertheless, coexistence emerges as a robust conclusion when the four factors are considered together. As expected from the earlier models, habitat choice and negative density dependence favor specialists while temporal variation favors generalists. Coexistence is made possible by the adaptive switching behavior of the generalists, which reduces temporal variation in habitat availability experienced by the specialists.

It is important to emphasize that the model depends critically on *flexible* habitat choice rather than on habitat choice per se. If we assume that the species merely enter habitats with fixed probabilities (e.g., $p_1 = 0.9$, $p_2 = 0.1$, $p_3 = 0.5$), the generalists do not counteract environmental variation, and the potential for coexistence is lost. It might seem that flexible habitat choice requires sophisticated cognitive abilities and therefore is restricted to a small subset of animal species (e.g., the higher vertebrates). We disagree for three reasons. First, adaptive habitat choice in the generalist merely requires that the proportion of individuals in each habitat match the relative size and/or quality of each habitat ($p_3/[1 - p_3] = K_1/K_2$). This kind of matching does not necessarily require sophisticated cognitive abilities and has even been demonstrated for so-called lower animals such as insects (see, e.g., Hassell 1978). Second, even though we assumed that the specialists could adaptively choose habitats, they virtually always "chose" the habitat that they were specialized to exploit. Our results would be the same if we assumed that specialists are "mindlessly" programmed to choose a single habitat and that only the generalists are capable of choice. Third, our basic results hold even when adaptive habitat choice is sloppy, with a sizable fraction of individuals behaving nonadaptively. Our model therefore potentially applies to a large number of animal taxa. Also, even though our model assumes that negative density dependence is caused by competition for resources, the basic dynamics might also apply when negative density dependence is caused by other factors (e.g., predation).

In the absence of temporal variation, habitat choice and negative density dependence favor extreme specialization, even when the costs of generalizing are trivial (e.g., $b = .99$). Most authors (see, e.g., Rosenzweig 1987, quoted above) have assumed that temporal variation will counter this trend, which will lead to intermediate degrees of specialization. Our model suggests an alternative possibility in which temporal variation merely reduces the frequency of extreme specialists rather than their degree of specialization. To fully explore this possibility, however, it will be necessary to build models in which many types are distributed along the entire fitness set rather than three types that occupy the middle and the two extremes.

The implications of our model for species coexistence are straightforward, and we hope that community ecologists will test some of the specific predictions (e.g., generalists should switch activities more than specialists, and their switching behavior should have a modulating effect on resources). In addition, our model may explain patterns of intraspecific variation if coexisting genotypes can be construed as specialists and generalists. For example, consider four genotypes

(G1–G4) with the following properties: G1 and G2 are developmentally canalized to produce specialized phenotypes A and B; G3 is developmentally canalized to produce generalized phenotype C; G4 is developmentally plastic and can produce phenotypes A′ and B′ depending on an environmental cue. The A′ and B′ phenotypes are slightly different from the A and B phenotypes because they are produced by different developmental pathways.

At the phenotypic level, G1, G2, and G4 are specialists, and G3 is a generalist. At the developmental level, however, G1, G2, and G3 are specialists that can only produce one phenotype, while G4 is a generalist that can produce two phenotypes. If the basic principle of specialization applies to the process of development, the two phenotypes (A′, B′) produced by G4 should be inferior to the corresponding phenotypes (A, B) produced by G1 and G2. Our model suggests that even a small cost of developmental plasticity would allow the specialists to exist. We might therefore expect a mixture of G1, G2, and G3 or G1, G2, and G4 depending on the relative advantages of phenotypic versus developmental generalization.

This prediction is based on selection pressures at the phenotypic level and needs to be confirmed by an explicitly genetic version of the model presented here. Nevertheless, the ecological forces that maintain balanced genetic polymorphisms within species are basically the same as the forces that allow interspecific coexistence, barring genetic complexities such as heterozygote advantage. Empirical studies often do reveal a mixture of developmentally plastic and developmentally canalized genotypes that coexist in single populations (see, e.g., Parejko and Dodson 1991). To our knowledge, however, no one has actually demonstrated that the principle of specialization operates for development, such that a developmentally canalized genotype can produce a better phenotype than a developmentally plastic genotype.

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