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ADAPTIVE CHANGE IN THE RESOURCE-EXPLOITATION TRAITS OF A GENERALIST CONSUMER: THE EVOLUTION AND COEXISTENCE OF GENERALISTS AND SPECIALISTS

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Abstract.—Mathematical models of consumer-resource systems are used to explore the evolution of traits related to resource acquisition in a generalist consumer species that is capable of exploiting two resources. The analysis focuses on whether evolution of traits determining the capture rates of two resources by a consumer species produce one generalist, two specialists, or all three types, when all types are characterized by a common fitness function. In systems with a stable equilibrium, evolution produces one generalist or two specialists, depending on the second derivative of the trade-off relationship. When there are sustained population fluctuations, the nature of the trade-off between the consumer's capture rates of the two resources still plays a key role in determining the evolutionary outcome. If the trade-off is described by a choice variable between zero and one that is raised to a power n , polymorphic states are possible when $n > 1$, which implies a positive second derivative of the curve. These states are either dimorphism, with two relatively specialized consumer types, or trimorphism, with a single generalist type and two specialists. Both endogenously driven consumer-resource cycles, and fluctuations driven by an environmental variable affecting resource growth are considered. Trimorphic evolutionary outcomes are relatively common in the case of endogenous cycles. In contrast to a previous study, these trimorphisms can often evolve even when new lineages are constrained to have phenotypes very similar to existing lineages. Exogenous cycles driven by environmental variation in resource growth rates appear to be much less likely to produce a mixture of generalists and specialists than are endogenous consumer-resource cycles.

Key words.—Coexistence, competition, cycles, environmental variation, generalist, nonlinearity, specialist.

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Most previous theory suggests that evolution within a species that exploits two resources but faces a trade-off in its ability to exploit those resources can result in the evolution of either a single generalist or two specialists (Levins 1963; Lawlor and Maynard Smith 1976; Abrams 1986; Meszéna et al. 1997; Kisdi and Geritz 1999; Kisdi 2002; Rueffler et al. 2006). Ecologically, the competitive exclusion principle (Armstrong and McGehee, 1980) suggests that the only other outcome possible in a stable system with only two resources is a generalist and a specialist, and this evolutionary outcome has been shown to be possible in some of the models listed above (e.g., Kisdi 2002). Although most previous theory has dealt with stable systems, Kisdi's (2002) analysis shows that stochastic variation can alter the outcomes predicted by stable models. This work was preceded by Wilson and Yoshimura's (1994) purely ecological study of coexistence in systems where there was stochastic environmental variation in the maximum abundances of two resources. They showed that, given moderate variation in carrying capacities associated with each habitat, a generalist could coexist with two spe-

cialists in a system with habitat-related density dependence in two habitats. Wilson and Yoshimura's (1994) work has been modified and extended to determine whether evolution in a single generalist lineage could result in all three species (Egas et al. 2004). Egas et al. (2004) argued that coexistence was unlikely if traits affected both the intrinsic growth rate and a carrying capacity of a habitat and that only under very restrictive conditions could gradual evolution produce both a generalist and two specialists from a single ancestral type. Kisdi (2002) used a somewhat different framework to examine this question and found that a variety of evolutionary outcomes were possible but that all three types could only persist for an extremely narrow range of parameters.

Wilson and Yoshimura (1994), Kisdi (2002), and Egas et al. (2004) all analyzed models in which explicit resource dynamics are lacking; variation in resource abundances was produced by stochastic variation in the consumers' carrying capacities, intrinsic growth rates, or both parameters. This leaves open the possibility that the negative conclusions about evolution of coexisting specialists and generalists may

not apply to the case of competition for renewable resources. Consumer-resource models provide a means to relate composite parameters like carrying capacities to consumer traits and therefore provide a better basis for understanding both competitive coexistence and coevolution (Abrams 1986; Schoener 1986). Abrams (2006a) explored a model of non-evolving consumers of two resources in fluctuating environments and found that two specialists and a generalist could coexist under a fairly wide range of conditions. This suggests that these three types might also be able to evolve in such a system. Thus, the present article will address the question of whether adaptive evolution in a lineage that is characterized by a fixed trade-off relationship between two resource consumption rates is likely to give rise to both generalist and specialist consumers in variable environments. It examines models in which resource cycles are driven by consumer-resource interactions and models in which the cycles are driven by environmental forcing of resource growth rates.

MODEL OF ECOLOGICAL AND EVOLUTIONARY DYNAMICS

The models treated here assume that two independent resources can both be exploited by a generalist consumer. The consumer is characterized by multiple-species Holling type 2 functional responses (Holling 1959), which assume that the two resources can be encountered in a fine-grained manner. In practice, this means that time spent handling one resource reduces the foraging time available for both. This is true when the two resources are well mixed within a single habitat. It also applies when the two types occur in different habitats or at different times, provided that food processing time is the main component of handling time and the movement between habitats is frequent enough that food consumed in one habitat reduces searching in both. Consumer-resource cycles are possible in such a system if the resources have biotic growth (i.e., are self-reproducing). In the main case considered here, the resources are assumed to have logistic population growth with the addition of immigration from outside the system and (in some cases) competition between the two resources. To avoid the complications of optimal diet choice, the two resources are assumed to have equal handling times and equal conversion efficiencies. Consumers have constant per capita death rates. A trade-off relationship determines the resource attack rates of the consumer, such that the attack rates on resources 1 and 2 are given respectively by $C_1 p^n$ and $C_2(1 - p)^n$, where p , an index of specialization, is the evolutionary variable. If $p = 1$, the consumer has a maximal consumption of resource 1, and if $p = 0$, it has a maximal consumption of resource 2. The parameter C_i is the maximum attack rate on resource i , corresponding to complete specialization. The positive exponent, n , determines the shape of the trade-off. Distinct, reproductively isolated lineages of the consumer are assumed to exist and to have independent evolution of their respective specialization indices, p_i , where i is the index of the lineage. The number of lineages varied between analyses, as explained below. The ecological dynamics of the two-resource, multiple-consumer model is thus,

$$\frac{dR_1}{dt} = I_1 + r_1 R_1 \left(1 - \frac{R_1 + \alpha_{12} R_2}{K_1} \right) - \sum_{i=1}^{i_{\max}} \frac{(C_1 p_i^n) N_i R_1}{1 + h\{(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2\}}, \quad (1a)$$

$$\frac{dR_2}{dt} = I_2 + r_2 R_2 \left(1 - \frac{R_2 + \alpha_{21} R_1}{K_2} \right) - \sum_{i=1}^{i_{\max}} \frac{[C_2(1 - p_i)^n] N_i R_2}{1 + h\{(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2\}}, \quad (1b)$$

and

$$\frac{dN_i}{dt} = N_i \left[\frac{b(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2}{1 + h\{(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2\}} - d \right]. \quad (1c)$$

In the preceding equations, resource populations are denoted R_j for resource j , and consumer populations are N_i for the i th reproductively isolated lineage of the consumer. The resources have logistic growth with parameters r_j and K_j , and external immigration given by I_j . Immigration rates are assumed to be small and reflect the fact that resources are generally more widely distributed than are their consumers (Abrams and Holt 2002). Competition between the resources is described by the Lotka-Volterra competition coefficients, α_{ij} ; these are set to zero in models that assume noninteracting resource populations. Because they are assumed to share a common fitness function, all consumers share the same handling time, h , maximum capture rate constants, C_1 and C_2 , conversion efficiency, b , and per capita death rate, d .

The trait p_i is assumed to evolve independently in each of the consumer lineages. This could describe situations in which isolated subpopulations of an ancestral consumer species evolve reproductive isolation and reinvade the ancestral location. At that point different lineages are likely to have somewhat different values of the trait, p , due to genetic drift or differences in the selective environments they experienced in allopatry. The same model could apply to mutation-limited evolution with rare mutants having a large effect on the character and more frequent mutations of small effect altering the phenotypes of these major strains. The dynamics of the trait, p_i , within each lineage is described by an equation having the form,

$$\frac{dp_i}{dt} = v \left(\frac{dW_i}{dp_i} \right) + \frac{\varepsilon}{p_i^2} - \frac{\varepsilon}{(1 - p_i)^2}, \quad (2)$$

where the first term is the product of a rate constant, v , and the derivative of the fitness of a mutant individual within that lineage with respect to its trait value. This first term on the right side of equation (2) is a reasonable approximation to a number of genetic models when the trait distribution is narrow relative to the fitness function (Abrams et al. 1993; Gomulkiewicz 1998; Abrams 2001). The constant, v , reflects the additive genetic variance for the trait and is much smaller than one. The second and third terms in equation (2) are a phenomenological representation of the effects of biased mutation. This process pushes the trait away from its limiting values of zero or one when it is close to one of those values. Mutation must logically become biased when a trait approaches an extreme value. Pomiankowski et al. (1991) sum-

marized evidence for the existence of biased mutation even at nonextreme trait values. The constant ε is typically several orders of magnitude less than one. The evolutionary effect of the biased mutation is similar to the effect of density-independent stabilizing selection on the traits, p_i , with a broad flat selective surface centered around a generalist phenotype of $p_i = 1/2$. It is likely that genetic variance would decline if the mean value of the trait approached either of the two limiting values or if population size became very small. Simulations suggested that neither of these changes had a large impact on the results described below. The major results are also insensitive to the exact value of ν , provided it is small enough to represent evolutionary change.

Numerical integrations of equations (1) and (2) using Mathematica 5.1 (Wolfram Research 2005) were used to investigate the combined population and trait dynamics. A particular system was studied by initially simulating its dynamics with two lineages respectively having initial values of the trait p close to the maximum and minimum values of zero and one. After the system had reached its ultimate dynamics, the resource populations obtained from that simulation were used to calculate the fitness of each possible invading phenotype. If any invading phenotype had a positive invasion fitness, a new lineage was introduced at very low density with an initial value of p equal to that which gave the largest invasion fitness. The new system was allowed to reach its final dynamical state, and the procedure was repeated until it was not possible to introduce any additional lineages. At this point, invasion fitness is negative for all types differing from those already present. The extant types then represent an evolutionarily stable coalition. In the systems explored below, the maximum number of lineages observed in a coalition was three. In a second set of simulations, initial runs assumed a single lineage with a randomly chosen initial trait value. After the system reached its ultimate dynamics, a new lineage was introduced at very low density and was assumed to have a phenotype that differed by 1% from (one of) the resident type(s). This process was repeated for all possible invaders until all possible invasions proved unsuccessful or the system reached its evolutionarily stable coalition. This allowed a determination of whether the final coalition found earlier could be attained if new lineages were constrained to arise from existing ones by mutations of small effect or any other process that restricted new lineages to be phenotypically close to existing ones. This assumption of small steps is made by most studies employing adaptive dynamics (reviewed in Waxman and Gavrillets 2005). In the following text, a brief consideration of systems having a stable equilibrium is followed by analysis of several related models exhibiting population cycles.

Evolution of p in a System with a Stable Equilibrium

The competitive exclusion principle (Armstrong and McGehee 1980) ensures that at most two species (or reproductively isolated lineages) can coexist on two resources at a stable equilibrium. The trade-off relationship incorporated into equations (1a–c) ensures that the fitness of a type with a particular p can have an extremum at only three points: an interior point at which $dW/dp = 0$ or the points at which p

$= 0$ or $p = 1$. If the exponent $n < 1$, there is a value of $0 < p < 1$ at which $dW/dp = 0$ and $d^2W/dp^2 < 0$ for any set of resource densities. The value of p that satisfies these conditions and that results in population dynamical equilibrium will exclude any other type. If $n = 1$, then C_1R_1 must equal C_2R_2 at the equilibrium p -value. Although all p -values confer equal fitness at this equilibrium point, any increase in the population mean p decreases R_1 and results in evolution of lower p (i.e., returns to the equilibrium). Thus, this equilibrium p is evolutionarily stable. When $n > 1$, the equilibrium at which $dW/dp = 0$ is a minimum in fitness for any set of resource densities, and two lineages introduced with p -values on either side of this equilibrium will increase if the carrying capacity of each resource is high enough to support a specialist consumer. Each of the two lineages will experience selection for more extreme values, and the final evolutionary state will be a dimorphic population of two specialists. Starting with a single type having a value of p close to 1 or 0, it may be impossible to reach the dimorphic state if n is large and all new lineages must have p -values close to the resident. These results are similar to those obtained for a closely related model by Rueffler et al. (2006), where a more rigorous justification of these results may be found. The results were also confirmed by simulations of equations (1) and (2) using parameters that produced a stable equilibrium.

Evolution of p in a System with Consumer-Resource Cycles

If the handling time, h , is above a threshold value, then the system described by equations (1a–c) will undergo cycles, provided that the resource densities at the equilibrium point are sufficiently low (stability conditions for the model lacking evolution are given in Abrams et al. 1998). Because there is no closed form solution for the population dynamics of the two-prey, one-predator system, the combined population and evolutionary dynamics were investigated numerically, using the procedure described above. Because evolution cannot lead to three types unless it is possible for three nonevolving types to coexist, the analysis focuses on parameter values shown to permit coexistence of at least three types that share the same fitness function (Abrams 2006a). Coexistence does not necessarily imply evolutionary stability; evolution may result in the characteristics of one or more lineages converging, yielding a system with fewer types, even when three (or more) are capable of coexisting. Abrams (2006a) showed that coexistence of two specialists and one or more generalist types based on the population dynamics in equations (1a–c) requires some difference in the form of the population cycles of the two resources. Asynchrony gives the generalist an advantage when it is rare, due to its decreased variance in food intake. However, that advantage disappears when the generalist becomes more common, because it then synchronizes the cycles of the resources (Abrams 2006a). In the present model, such asynchrony can arise if the resources differ in their growth parameters or if the two maximum attack rates, C_1 and C_2 , differ (Abrams 2006a). Asynchrony can also arise due to competition between resources (Vandermeer 2004). In addition to asynchronous resource dynamics, coexistence of three nonevolving consumers under equations (1a–c) requires that the product of attack rate, handling

time, and carrying capacity (ChK) is relatively high (Abrams 2006a); $ChK > 3.69$ for the main example considered below. Given these prerequisites, coexistence of at least three forms was possible for a large fraction of the range of consumer efficiencies (measured by d/b), that allowed population cycles.

The approach to quantifying different evolutionary outcomes taken here was to investigate the impacts of the parameters that seemed most likely to affect coexistence based on the ecological results in Abrams (2006a): (1) the trade-off exponent, n ; (2) the consumer's per capita death rate, d ; and (3) the value of the factor producing asynchrony (e.g., the difference between resources in their growth parameters). The simulation procedure described above determines the number and characteristics of lineages (species) in a coalition that cannot be invaded by other lineages. It also reveals whether this coalition could be reached by a process in which additional lineages were initially required to have phenotypes nearly identical to those of resident types.

Many of the numerical analyses below are based on a standard parameter set. This is characterized by a high proportion of the consumer's time spent handling resources when the resources are at their carrying capacities (this proportion is given by $\bar{C}\bar{K}h$, where \bar{C} and \bar{K} denote the means of the two parameters). The standard parameters are: $I_1 = I_2 = 0.001$; $r_1 + r_2 = 2$; $K_1 + K_2 = 2$; $h = 1$; $C_1 + C_2 = 10$; $\alpha_{12} = \alpha_{21} = 0$; $b = 0.1$; $v = 0.05$. This implies no competition between resources, a consumer conversion efficiency of 10%, and a moderate rate of evolutionary change. Higher conversion efficiency, b , has essentially the same effect on evolutionary outcome as does a lower death rate, and smaller evolutionary rate constants, v , have very little effect on the evolutionary outcome. The following section concentrates on the remaining factors that have a stronger effect on the sets of evolving lineages that can persist.

Impact of the trade-off exponent, consumer mortality, and factors producing resource asynchrony on the evolutionary outcome

The initial set of simulations examined the impact of the trade-off exponent, n , on the evolutionary outcome. To illustrate the mechanism involved in the evolution of trimorphism, I begin with the standard parameter set presented in the preceding paragraph with a particular asymmetry due to unequal resource carrying capacities: $K_1 = 0.8$; $K_2 = 1.2$. The consumer death rate was initially set at $d = 0.03$, which is intermediate in the interval producing population cycles in a pure specialist system ($0 < d < 0.067$). Given these parameters, simulations were run for a range of values of the trade-off exponent. As in the case of stable systems, when $n < 1$ (a weak trade-off), the outcome is independent of the initial value of p and is independent of the initial number of distinct lineages; all lineages eventually converge to a common intermediate value of p . The common trait p then undergoes very small amplitude cycles around a value slightly less than 0.5. The cycles are similar in form to those shown in Figure 1A, which assumes a larger trade-off exponent ($n = 1.5$) but restricts the consumer to a single lineage. This outcome is observed up to a value of approximately $n =$

1.03; this threshold value is greater than one in part because the biased mutation effectively results in a weak stabilizing force and in part because the resource cycles seem to have a small effect of favoring a generalist over two specialists when n is only slightly greater than one.

When the trade-off exponent, n , is greater than 1.03, the evolutionary outcome in this example always depends on the number of lineages and may depend on their initial trait values. When $n > 1.03$, the evolutionarily stable coalition, which would be observed if the number of independent lineages were unrestricted, consists of either two or three types. Values of n between 1.03 and approximately 1.77 have an evolutionarily stable coalition that is trimorphic, consisting of a generalist and two (relative) specialists. Larger values of n (> 1.77) have a dimorphic coalition of two specialists. Dimorphism is also the outcome for $1.03 < n < 1.77$ when the initial number of lineages is restricted to two. The dimorphic outcome for $n = 1.5$ is shown in Figure 1B; the trimorphic coalition for this same exponent is shown in Figure 1C. For values of n larger than 1.77, the evolutionarily stable coalition always consists of two specialists, with phenotypes similar to those shown in Figure 1B. If there are three or more lineages and n is only slightly greater than 1.77, a generalist may evolve, but it gradually goes extinct, leaving a system that consists of two specialists. The fact that the coalition of two specialists and a generalist is evolutionarily stable for $n = 1.5$ is illustrated in Figure 2, which shows the invasion fitness for lineages with every possible value of p . The three points where invasion fitness is equal to zero are the (approximate) phenotypes of the three resident types. The values of p close to zero or one having positive invader fitness are not attainable because of the biased mutation terms in equations (1). The general form of the invader fitness curve in Figure 2 is similar for all trade-off exponents between 1.03 and 1.77.

It is of interest to determine whether the evolutionarily stable coalition (e.g., Fig. 1C for the case of $n = 1.5$) can be reached if there is initially a single lineage and whether new lineages arise seldom and must have phenotypes p that differ only slightly from the resident phenotypes. For the system having standard parameters with $K_1 = 0.8$ and $K_2 = 1.2$ and $1.03 < n < 1.77$, a single lineage always evolves to the generalist state, illustrated for $n = 1.5$ in Figure 1A. In adaptive dynamics (Geritz et al. 1998), this is referred to as a branching point. If this generalist is invaded by a new lineage having a slightly different value of p , subsequent evolution always leads to the dimorphic system with two specialists for the full range of exponents where the trimorphic coalition exists. If the dimorphic system, such as that shown in Figure 1B, is invaded by mutants that are slightly different from each of the two resident forms, one or both mutants persist and diverge from the resident type, resulting in the evolutionarily stable coalition for trade-off exponents $1.03 < n < \sim 1.6$. Fitness landscapes for two exponents within this range are shown in Figure 3, which confirms that an invader that is similar to the specialist on the slower-growing resource (or intermediate between the two specialists) will increase in abundance. It will subsequently diverge, producing the trimorphic system with both specialists and the generalist.

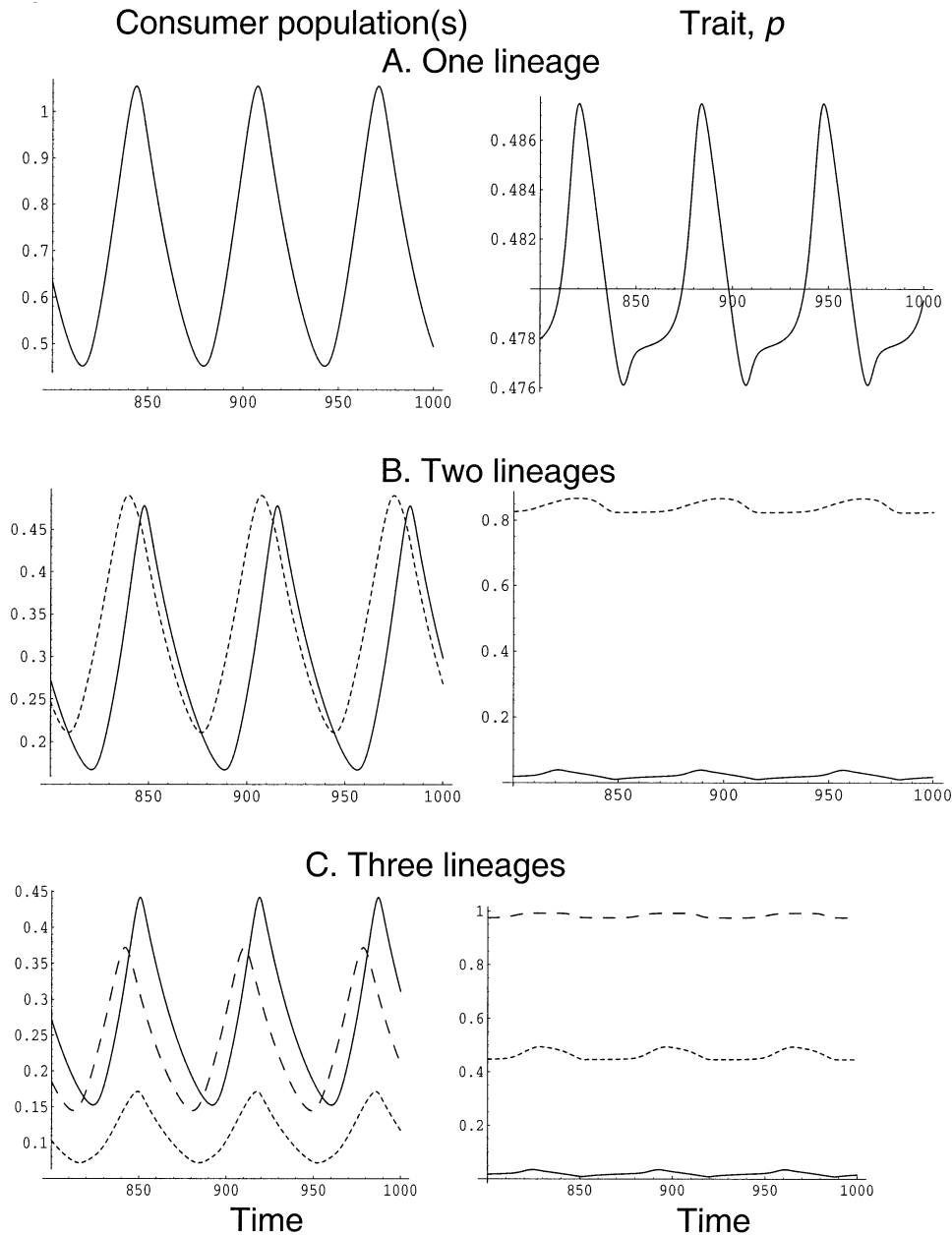


FIG. 1. The outcomes of evolution given equations (1) and (2). The three panels show the ultimate dynamics of both traits and populations given different numbers of lineages in a system with parameter values: $n = 1.5$; $v = 0.05$; $b = 0.1$; $d = 0.03$; $K_1 = 0.8$; $K_2 = 1.2$, $r_1 = r_2 = 1$; $I_1 = I_2 = 0.001$; $h = 1$; $C_1 = C_2 = 5$; $\epsilon = 10^{-7}$. In each case the line style used for different population sizes in the left graphs correspond to the line styles used for the corresponding phenotypes, p , in the right graphs. Comparing panels (B) and (C) shows that the presence of the generalist has very little effect on the abundance of the specialist on the higher- K resource, while decreasing the abundance of the specialist on the lower- K resource; the generalist reverses the relative abundances of the two specialists.

Dimorphic systems having exponents significantly larger than 1.6 cannot be invaded by mutants that are close to one of the residents, but can be invaded if the invader has a phenotype, p , sufficiently close to the intermediate value of $p = 0.5$, provided $n < 1.77$. A fitness landscape for one such case is shown in Figure 4E; here invasion can occur if the invader's p is between 0.39 and 0.63, but invasion would not occur if potential invaders were constrained to have trait values close to those of the two residents. When $n > 1.77$, the dimorphic state is the evolutionarily stable coalition, as

shown by Figure 4F. The question of the smallest exponent where trimorphic coalitions exist and can be reached by small steps is somewhat more complicated, due to the fact that there are two alternative dimorphic pairs of phenotypes for values of the trade-off exponent close to $n = 1.6$. The two dimorphic states differ in the dynamics and mean values of the specialist phenotypes (Figs. 4C,D). This difference results in the invasion diagrams shown in Figures 4A,B. The first attractor (Figs. 4A,C) does not allow invasion by types having p -values very similar to the residents, although it can be

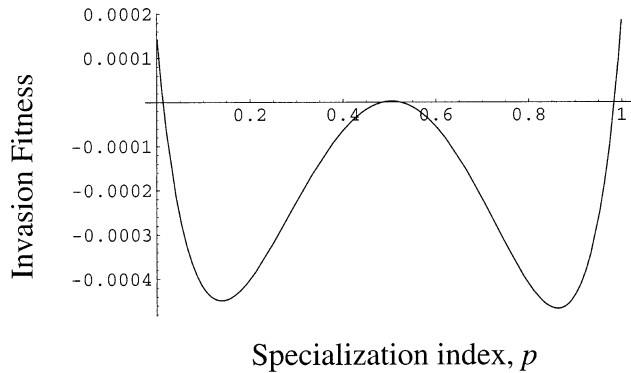


FIG. 2. Invasion fitness for a system with the parameter values of Figure 1, having two specialists and a generalist present at evolutionary equilibrium, as in Figure 1C. The mean values of the three resident phenotypes have the p -values where the invasion fitness is equal to zero. All invasion fitnesses are negative, other than the unattainable p -values very close to zero or one.

invaded for most of the range of potential intermediate types. The second attractor (Figs. 4B,D) can be invaded by mutants similar to the resident with the lower p -value, and evolution of the three types will then produce the trimorphic coalition that resists further invasion. Note that there is disruptive selection at the lower resident p -value. The range of exponents when there are alternative dimorphic states is approximately $1.57 < n < 1.67$. For $n > 1.67$, invasion by lineages having a p -value very close to that of one of the two specialist residents will not occur for the remaining dimorphic attractor. It is worth noting that reducing the evolutionary rate constant, v , reduces the range of exponents with alternative dimorphic states. The first attractor appears to result from an interaction of the evolutionary change with the population dynamics, which does not persist at very slow rates of evolutionary change.

The conclusion from the investigation of different trade-off exponents is that, given that coexistence of three reproductively isolated lineages is possible, evolution will always produce trimorphism for a broad range of exponents with weakly to moderately concave trade-offs ($1.03 < n < 1.6$). Trimorphism can evolve for a somewhat larger range of exponents (up to $n = 1.77$) if new lineages that are sufficiently different in their resource use trait, p , from either specialist resident can arise. This could happen by mutations of large effect or by the invasion of individuals from an isolated population having only a single lineage (which would evolve to become a generalist).

If n becomes sufficiently large ($n > \sim 3.2$ for the other parameters considered here), the generalist state is no longer an evolutionary attractor for a single lineage. If only one lineage is present, it will evolve to be a specialist on resource 1 or resource 2, depending on initial conditions; low initial p -values tend to lead to specialization on resource 2, while a lineage having a large initial p -value becomes specialized on resource 1. Similarly, invasion of either of these specialist states by a lineage that is close to the resident results in convergence, so that even the dimorphic state is not produced unless the invader has an initial p -value that is far from that of the resident. A trade-off exponent of $n = 3$ implies that

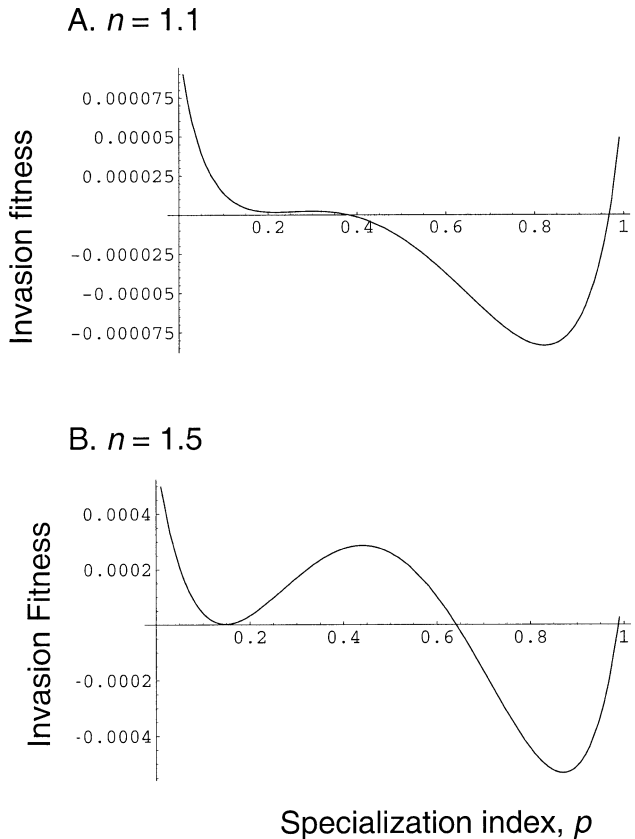


FIG. 3. The invasion fitness versus p for the dimorphic resident state for two values of the trade-off exponent, n , with other parameters as in Figures 1 and 2. Both exponents are within the range where the trimorphic coalition can be reached even if new lineages are constrained to have phenotypes similar to those of the one of the two resident specialists. The two resident phenotypes are at the values where invasion fitness is zero. In (A), the calculated fitness of the invader equivalent to the lower resident phenotype (near $p = 0.2$) is slightly positive because of the error entailed by assuming a fixed value of p for the invader (which would undergo small amplitude fluctuations following introduction). In both panels, an invader with a p -value slightly greater than that of the resident with the lower p -value can invade. An invader that is slightly smaller than the larger resident p -value cannot increase when rare. Although the figure indicates the mutants with larger p can invade, such phenotypes are unattainable because of the biased mutation terms.

a generalist with $p = 0.5$ has a consumption rate $1/8$ that of the corresponding specialist. This is a huge disadvantage, and it seems unlikely that any lineage would persist in a generalized state with a trade-off exponent of this magnitude or larger.

The previous results show that trimorphism can evolve for a relatively wide range of trade-off exponents given the set of parameters explored. The question immediately arises whether the ranges of trade-off exponents producing different evolutionarily stable coalitions in the preceding example is representative of parameter sets having different values of the consumer death rate or different degrees of or factors causing asynchronous resource dynamics. The fact that coexistence of two specialists and a generalist on two resources is ecologically possible for a wide range of parameters (Abrams 2006a) suggests that it is also likely to be an evo-

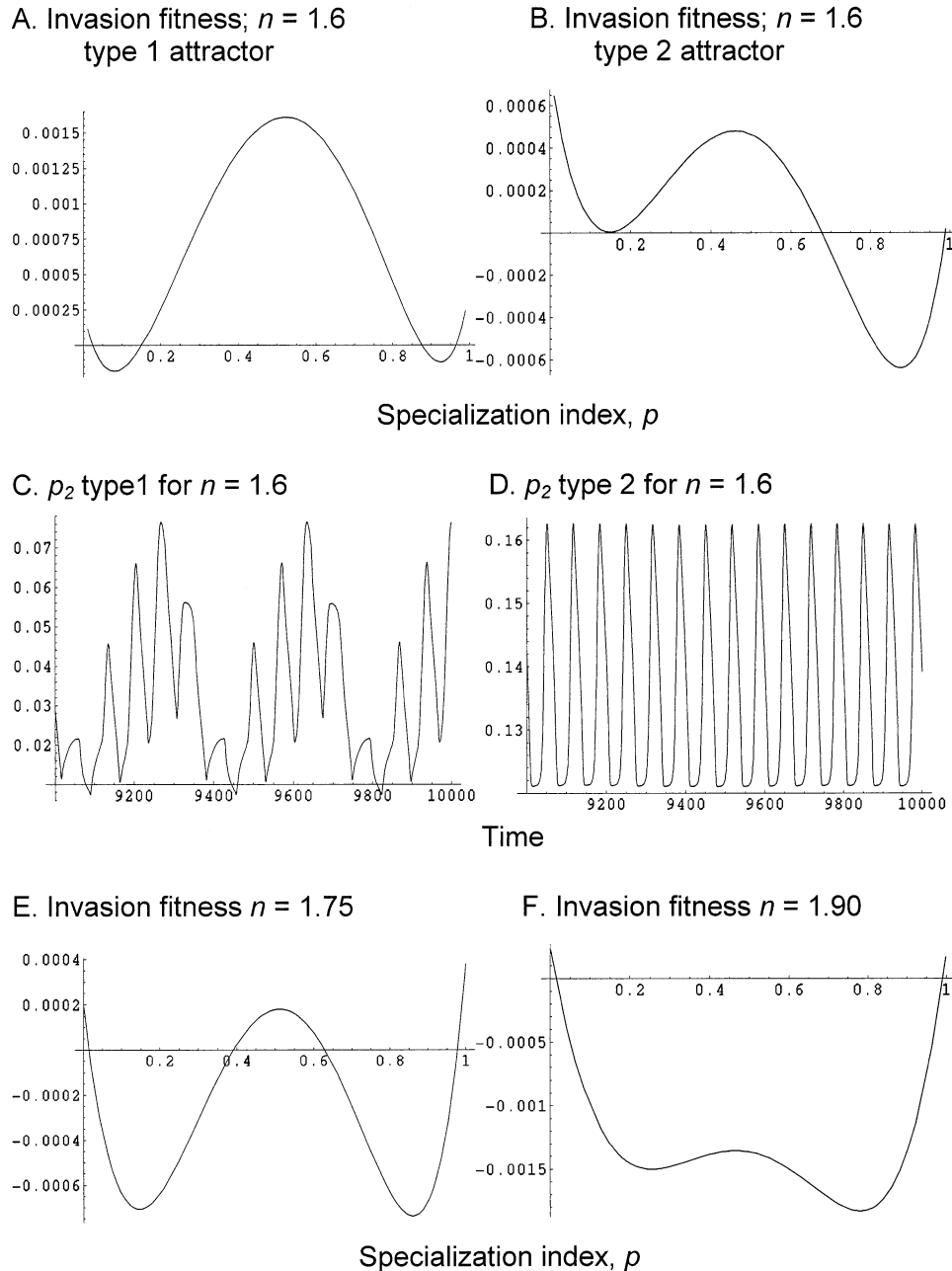


FIG. 4. The fitness of an invader at the dimorphic equilibrium as a function of its trait, p , for systems with the same parameters as Figure 3 except that the trade-off exponent is close to the upper end of the range where the evolutionarily stable coalition is trimorphic (A, B, E) or just above that range (F). (A) and (B) show invasion fitness for the two alternative dimorphic states that exist when n is close to 1.6, and (C) and (D) show the dynamics of p for the R_2 specialist for these two states. The residents are given by the upper- and lowermost of the intersections and tangency points of the invasion curve with the x-axis. It is clear that the specialist residents at the attractor described by (A) and (C) (attractor 1) cannot be invaded by a somewhat less specialized type (and more specialized phenotypes are prevented by biased mutation). For the second attractor at $n = 1.6$ invasion is possible for p -values close to the lower resident phenotype. In (E), $n = 1.75$, which is close to the maximum where trimorphic coalitions occur. Here invasion is only possible if the invader has a phenotype fairly close to $p = 0.5$. In (F), $n = 1.9$, and no invader can increase in the dimorphic community.

lutionarily stable coalition for a significant range of systems. This speculation can be tested by exploring variations on the parameter set described above.

The consumer per capita mortality rate is monotonically related to the equilibrium resource density, and the latter is the main determinant of the outcome of competition between

species (Abrams and Holt 2002; Wilson and Abrams 2005; Abrams 2006a). The range of mortality rates allowing trimorphism is therefore a good indicator of whether trimorphism is robust or fragile. The range of mortality rates for which there is a trimorphic coalition for the preceding example with $n = 1.5$ (as in Fig. 1) can be shown (numerically)

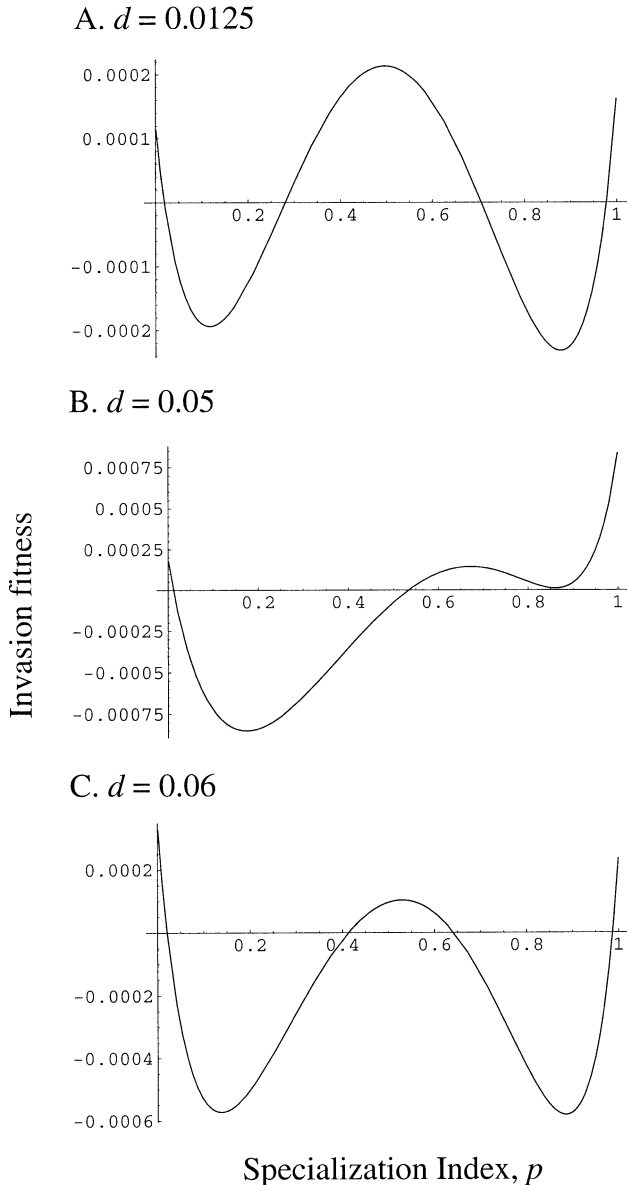


FIG. 5. The fitness of an invader at the dimorphic state for a system $r_1 = 0.8$, $r_2 = 1.2$; $K_1 = K_2 = 1$; and other parameters as in Figure 1, except for the per capita death rate d . The lower (0.0125) and upper (0.06) death rates illustrated in (A) and (C) are close to the limits where a trimorphic coalition exists, and these panels show that such a coalition cannot be reached from the dimorphic state if new lineages must have phenotypes similar to the existing one.

to be $0.0132 < d < 0.564$. This represents a substantial fraction of the range of death rates allowing consumers to persist in the absence of competition; specialists on resource 1 cannot persist, even in the absence of competition, if $d > 0.08$. Figure 5 shows the invasion fitness when two specialists are present for three mortality rates in a similar system where r rather than K differs between resources. Most mortality rates yield invasion plots as in Figure 5B, where rare mutants that are similar to one specialist can increase.

The analysis of factors leading to trimorphism in the preceding example was expanded in three ways. First, the range of mortality rates producing trimorphic evolutionarily stable

coalitions was examined for a range of resource growth asymmetries based on each of the two main resource growth parameters, r and K ; the results are shown in Figure 6A,B for $n = 1.5$. Clearly, trimorphism is common in systems where the asymmetry is not extreme. Asymmetry in the consumer's two maximum resource capture rates in the absence of asymmetry in resource growth rates will also produce asynchronous resource dynamics, and therefore allow the evolution of trimorphism. Assume the two maximum capture rates are $C_1 = 6$ and $C_2 = 4$, the two resource growth equations are equivalent, and the remaining parameters are as in the standard set with $n = 1.5$ as in Figures 6A,B. Trimorphic evolutionary coalitions exist for values of d from 0.013 to 0.049. This somewhat reduced range compared to the examples in Figures 6A,B appears to be attributable to the near-stability of the subsystem with the specialist on resource 2 (with $C_2 = 4$) when consumer death rates significantly exceed 0.05. Larger differences in the capture rates resulted in similar ranges of d -values yielding trimorphism ($0.014 < d < 0.048$ when $C_1 = 7$ and $C_2 = 3$; $0.016 < d < 0.062$ when $C_1 = 8$ and $C_2 = 2$). Simulations (P. A. Abrams, unpubl. results) have also shown that significant (e.g., order of magnitude) differences in the two resource immigration rates allow coexistence over a range of mortality similar to the largest of those shown in Figures 6A,B, when all other pairs of resource growth parameters are identical.

The next step in exploring the parameter ranges yielding trimorphic coalitions was to examine the range of trade-off exponents producing this outcome as a function of resource growth asymmetry. Because asymmetries in r and K have similar effects, only the latter is shown in Figure 6C. Finally, the range of mortalities producing trimorphism is presented as a function of the trade-off exponent in Figure 6D. All of the panels in Figure 6 suggest that, except for highly asymmetrical systems or exponents near the limits of the range of potential values, trimorphic coalitions represent a common evolutionary outcome. The figures involving mortality should be interpreted in light of the fact that mortalities greater than a threshold value between 0.08 and 0.09 cause extinction of specialist consumers in the absence of any competition. Trade-off exponents must be greater than one to produce any diversification and must be less than ~ 3.2 for a generalist to persist in any environment. Thus, the ranges shown represent large fractions of the potential values of this exponent for generalist lineages. In Figure 6C exponents below the lower bound that produces trimorphism usually have a single generalist as the evolutionarily stable coalition, while exponents above the upper bound produce two specialists. The one exception is that at $K = 1.9$ there is a band of exponents between 1.43 and 1.63 for which a generalist and a specialist on the high- K resource represents the stable coalition. (At $K_1 = 1.9$ this range is between 1.43 and 1.63.) In any event, these results make it clear that variation favors generalists; in corresponding systems with no variation, generalists would be excluded by specialists for any exponent above approximately 1.02 (with the exact value depending on the mutational bias terms).

Figure 6 clearly does not represent a complete sampling of potential parameter space. However, most combinations of parameters simulated supported the conclusion that tri-

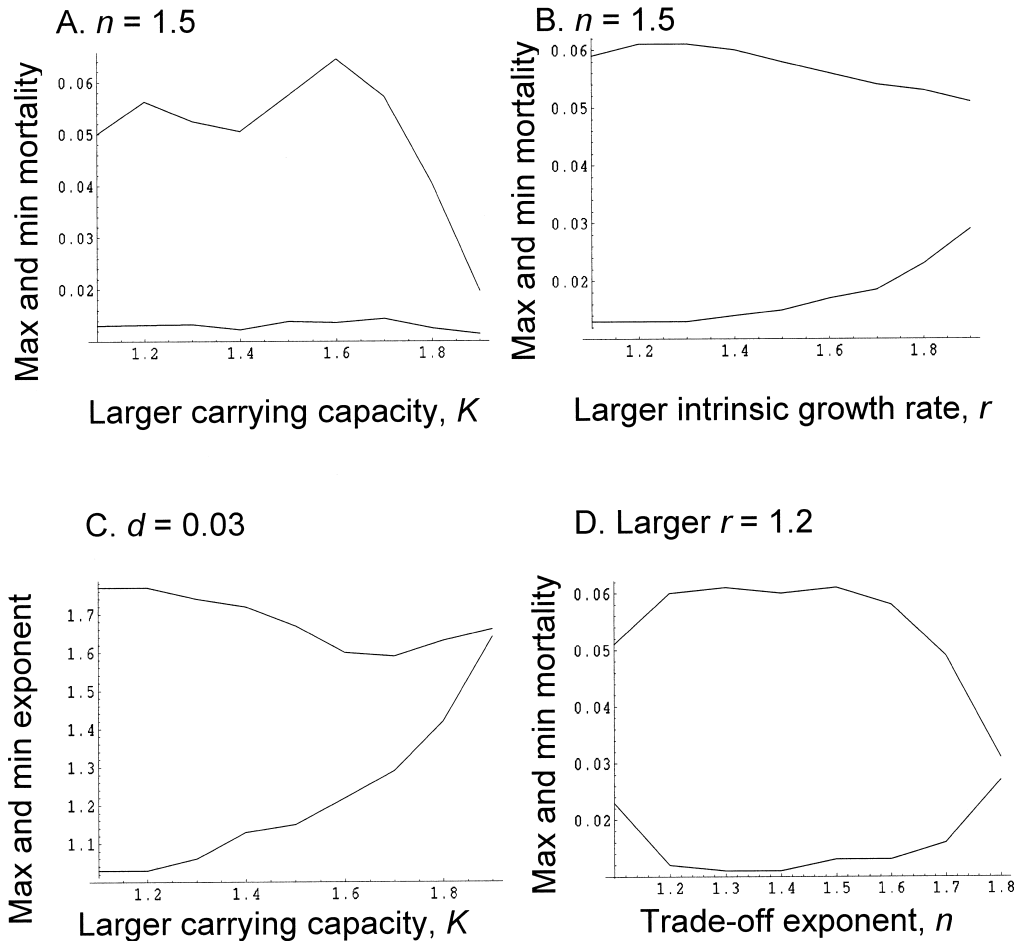


FIG. 6. The parameter ranges allowing trimorphic evolutionarily stable coalitions for various combinations of parameters. In each case the maximum and minimum value of either consumer mortality or the trade-off exponent yielding a trimorphic coalition is plotted as a function of the parameter given by the x-axis, for fixed values of other parameters given in the heading. If a growth parameter is on the x-axis, it is subject to the constraints: $r_1 + r_2 = 2$ or $K_1 + K_2 = 2$.

morphism (with a generalist and two specialists) was a common outcome of evolution in the model investigated here, provided the resources undergo asynchronous cycles. Figure 7 illustrates two significant features that were observed in the additional simulations. Figure 7A plots the maximum and minimum mortalities in systems having different levels of asymmetry in the resource intrinsic growth rate; it is comparable to Figure 6B except that the trade-off exponent is $n = 1.25$ rather than 1.5. This and other exponents closer to one do not lead to the evolution of trimorphism in systems with high asymmetry in resource growth rates. Instead, the evolutionarily stable coalition is a generalist plus a specialist on the more productive resource. The same pattern is seen in systems with asymmetry in the carrying capacities. Figure 7B explores the consequences of competition between resources. Competition represents another mechanism for producing asynchronous cycles in the two resources (Vandermeer 2004). Resource competition allows consumer coexistence even when the resources have identical growth parameters (Abrams 2006b). As Figure 7B shows, resource competition generally allows consumer coexistence over a

broader range of trade-off exponents than do differences in resource growth parameters.

The results in Figures 6 and 7 are both based on finding the evolutionarily stable coalition without restricting the number of lineages or their initial trait values. Simulations were also used to study the possibility of attaining each of these coalitions when new lineages were constrained to have an initial phenotype very similar to one of the existing phenotypes. Results generally paralleled those described for the first example considered in this section (Fig. 5). Parameter values close to a limiting value for the existence of a trimorphic coalition often made that coalition evolutionarily unattainable when new lineages were restricted to having phenotypes similar to the residents. Determining the parameter bounds for the success of nearby invasion was very time-consuming, preventing analysis of a large number of model variants and parameter sets. However, in most cases simulated, the majority of the range of a single parameter for which a trimorphic coalition was the evolutionarily stable state also allowed evolution of that coalition purely via the introduction of new lineages having a phenotype close to that of one of the resident forms.

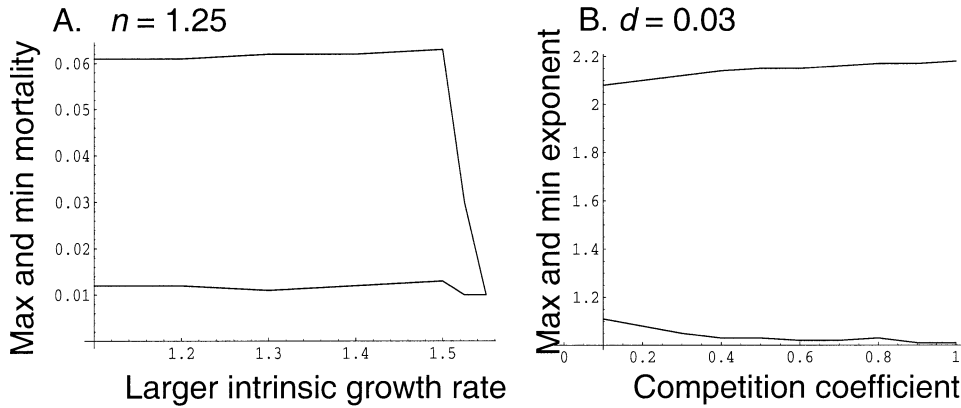


FIG. 7. Two examples of how different parameters affect the existence of an evolutionarily stable coalition with two specialists and a generalist. (A) The maximum and minimum death rates for which such a coalition is the evolutionarily stable state, as a function of the asymmetry in maximum resource per capita growth rates, given a trade-off exponent $n = 1.25$. (B) The maximum and minimum trade-off exponents for which trimorphism is the stable coalition for a model in which both resources have the same growth parameters and competition between resources described by equal competition coefficients. Other parameters have standard values given in the legend of Figure 1.

Some examples of the change in the range of parameters producing trimorphism under the constraint of phenotypic steps no larger than 1% are as follows. In the Figure 6A example with $K_1 = 1.5$, the range of mortality rates is reduced from 0.014–0.057 to 0.014–0.030. In the Figure 6B example with $r_1 = 1.5$, the range of mortality rates is reduced from 0.015–0.058 to 0.018–0.051. In the Figure 6C example for $K_1 = 1.2$, the range of exponents is reduced from 1.03–1.77 to 1.03 to ~ 1.60 (this is the initial example analyzed in this article). In the Figure 6D example for $n = 1.3$, the full range of mortality rates that has a trimorphic coalition (0.011–0.061) can reach that coalition from a dimorphic state via new lineages that are similar to the existing ones. In most cases, trade-off exponents closer to one have smaller (or non-existent) parameter ranges where evolution by tiny steps fails to lead to the trimorphic coalition. The only case where the dimorphic specialist state resisted invasion by slightly different phenotypes over the entire range of one of the parameters determining coexistence was the case where the trade-off exponent was relatively large (> 1.5) and the asynchronous dynamics were due entirely to competition between the resources. Relatively large values of the trade-off exponent imply that there is locally strong stabilizing selection toward the specialist states for phenotypes near the extremes.

MODELS WITH EXOGENOUS VARIATION
IN RESOURCE GROWTH

The cycles in resource abundances that are required for coexistence of three consumer lineages on two resources can also arise by exogenous variation in resource growth rates. To separate the effects of exogenous and endogenous cycles, equations (1a–c) are modified to make endogenous cycles impossible. This is done by assuming MacArthur’s (1972) classic model of an abiotic (nonreproducing) resource for both resources in equations (1a–c), as follows:

$$\frac{dR_1}{dt} = I_1 \left[1 + \gamma_1 \sin\left(\frac{2\pi t}{q_1}\right) \right] - E_1 R_1 - \sum_{i=1}^{i_{\max}} \frac{(C_1 p_i^n) N_i R_1}{1 + h\{(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2\}} \quad (3a)$$

and

$$\frac{dR_2}{dt} = I_2 \left\{ 1 + \gamma_2 \sin\left[\frac{2\pi(t - L)}{q_2}\right] \right\} - E_2 R_2 - \sum_{i=1}^{i_{\max}} \frac{[C_2(1 - p_i)^n] N_i R_2}{1 + h\{(C_1 p_i^n) R_1 + [C_2(1 - p_i)^n] R_2\}}. \quad (3b)$$

The parameters I_j and E_j are the mean input rate of resource j and the per-unit-resource exit rate of resource j . The cycles in input rate are sinusoidal and are characterized by an amplitude γ_j and a period q_j . There is also a phase difference between the cycles in the two resources given by L , which is less than q_2 . The remainder of the model is given by equations (1c) and (2).

Abrams (2006a) investigated the impact of exogenous cycles on coexistence of nonevolving species and found that coexistence required that the environmental variation of input rates differ substantially between the two resources. Given this prerequisite, coexistence of specialists and generalists was possible, but it required that parameter values fall within a relatively narrow range. Similar conclusions apply to the evolutionary model considered here; trimorphic evolutionary coalitions are possible, but require rather precise balancing of parameters. In general, antisynchrony (i.e., equal periods with a 180° phase shift; $q_1 = q_2 = q$; $L = q/2$) in resource variation was most conducive to trimorphic coalitions. As in the model with endogenous cycles, it is necessary for the trade-off exponent to be greater than one for more than a single lineage to evolve. However, exponents that are only moderately greater than one in this case lead to the evolution of a single generalist. An evolutionarily stable coalition of three types only occurs for trade-off exponents $1.18 \leq n \leq$

1.23 given parameters $d = 0.03$; $I_j = E_j = 0.25$; $\gamma_j = 0.8$; $q_j = 100$; $L = 50$; and other consumer parameters as in Figure 1. However, this trimorphic state cannot be reached by small phenotypic steps starting with a single type at the monomorphic generalist equilibrium (where p undergoes small amplitude cycles around the value 0.5). The monomorphic generalist is the only other evolutionary attractor for exponents up to and including $n = 1.21$, while the dimorphic set of two specialists is an alternative attractor for exponents of 1.22 and 1.23 and is the stable coalition for $n > 1.23$. When dimorphism is an alternative attractor, it is not possible to reach the trimorphic coalition when new lineages are constrained to have values similar to one of the two specialist phenotypes at the dimorphic attractor. Larger amplitude variation in resource input results in a trimorphic coalition for a narrow range of larger trade-off exponents: if $\gamma_j = 0.99$ in this example, the trimorphic coalition is found from $1.30 < n < 1.38$. Trimorphism is either absent or more restricted in parameter space when the two resources are not completely antisynchronized; that is, when the lag, L , is not exactly $1/2$ of the period, q . While it is difficult to rule out the possibility that a particular set of values for some parameters would allow trimorphic coalitions to occur for a wide range of other parameters, such combinations were not found in a large number of simulations of this system. Evolutionarily stable trimorphism cannot occur without the possibility of coexistence, and earlier results (Abrams 2006a) indicated that coexistence of two specialists and a generalist only occurs for a narrow range of parameters in the model given by equations (3a,b). This was due to the limited ability of a generalist to synchronize the resource cycles.

THE CONSEQUENCES OF LARGER CHANGES IN THE MODEL

Evolution When Lineages Differ in Fitness Functions

The above analysis has assumed that lineages share identical fitness functions; their population dynamics equations are identical except for the initial values of p . It is more likely that lineages that are separated for some time will also evolve differences in some parameters of, and perhaps the functional forms of, their fitness components. If the two specialists are present and have little or no genetic variation for resource use, then any generalist with an evolutionarily flexible resource use trait, p , that does not converge toward one of the specialists will coexist over a broad range of mortality rates, based on the ecological analysis in Abrams (2006a). The present results for trimorphic systems show that generalists with trade-off exponents n between one and approximately two diverge from specialists. Generalists with exponents $n < 1$ will evolve to an intermediate trait value even in the absence of specialists, so both of these categories of generalists will coexist with nonevolving specialists over a wide range of values of other parameters. When $n < 1$, it is necessary that the generalist mortality rate be larger than those of the specialists for coexistence (Abrams 2006a). However, such a difference could easily have come about via decreases in the specialists' death rates or increases in the generalist's death rate when the species were evolving in allopatry. Models that allow such differences also have evolutionarily stable systems consisting of the generalist and two

specialists over a much broader range of the values of other parameters than the models considered in the previous section.

The Impact of More Rapid Rates of Adaptive Change in p on the Generation of Diversity

The above results have all assumed that the adaptive rate constant, v , was less than or equal to 0.05, values that are appropriate for evolutionary change. However, if they are based on similar costs and benefits, behavioral or developmental changes can also be modeled using equation (2) with a greater rate constant v (e.g., Abrams 2003; Abrams and Matsuda 2004). In the limiting case of $v \gg 1$, the lineages can be considered to be subsets of the consumer population that are characterized by different initial resource use behaviors. In this case, all lineages converge quickly to a common value unless the trade-off exponent is much greater than two. Intermediate rates of adaptive change (v on the order of one) can result in a wide variety of alternative outcomes and complex dynamics, although there is not space to analyze these fully here. Trimorphism seems to be impossible with large enough v , since all types eventually become entrained to closely follow the cycles in resource densities.

DISCUSSION

The results presented here argue that evolution in systems undergoing sustained fluctuations can produce two specialist and one generalist types from reproductively isolated lineages that share a common fitness function. This can occur in cases where two lineages would each evolve to become a specialist on a different resource. The generalist in this case can gain an advantage by experiencing a reduced variance in resource intake, even when its mean capture rates of each resource are less than the mean of the two specialists' capture rates (Abrams 2006a). This represents a novel mechanism by which competition can lead to increased diversity. Although the role of population fluctuations in past adaptive radiations is not well known (Schluter 2000), West-Eberhard (2003) argued that a fluctuating environment was associated with some adaptive radiations, and it is certainly possible that the mechanism discussed here has been involved in some of those cases. Most present-day biological communities are formed by immigration of types from other areas rather than in situ evolution. Furthermore, the individuals that arrive, even if derived from the same ancestor as the resident, are likely to have experienced different recent selective pressures and therefore to differ in a number of ways, including the shapes of their trade-offs for traits related to resource capture. As noted above, divergence and coexistence of three types sharing two fluctuating resources is more likely to occur when the original consumer lineages have different fitness functions. The results presented here also show that there are some circumstances under which two specialists and a generalist can only evolve when new lineages initially have phenotypes substantially different from existing types. This is contrary to the assumptions of most adaptive dynamics models (e.g., Waxman and Gavrillets 2005), but is consistent with the gradual accumulation of many differences in allopatry in the normal scenario for allopatric speciation (Abrams 2005).

While there is no doubt that evolution of reproductively isolated lineages sharing a common fitness function and competing for two resources can lead to trimorphism, it is less clear whether this outcome is common in natural communities. Several conditions must be satisfied, given the basic models considered here. The trade-off must be strong ($n > 1$), but not too strong. Total time spent handling resources when they are abundant must be large relative to one (meaning that the product of per item handling times, capture rates, and resource carrying capacities must be large relative to one). Some asynchrony in the resource cycles in the presence of two relatively specialized consumers is required for the generalist to have a resource-intake-rate advantage when it is rare; without such an advantage, coexistence will not occur. In the absence of competition between resources, this asynchrony is eliminated if specialist phenotypes consume significant amounts of the other resource (Abrams 2006a). In the model considered here, divergence of one or both specialists from an ancestral generalist will produce the high levels of specialization required. Although environmentally driven cycles in resource densities are capable of producing asynchrony, they do not seem to result in generalist-specialist coexistence or the evolution of such a trimorphism over a broad range of parameters, at least in the model considered here.

Whether the conditions outlined in the previous paragraph are biologically restrictive is currently unknown. There are many predators characterized by spending a small fraction of their time actively searching for prey, when the latter are close to their carrying capacities, implying $ChK \gg 1$ (reviewed in Abrams and Holt 2002). Long-term datasets suggest that endogenous cycles may be common (Kendall et al. 1998), and it is certainly possible that trade-off exponents most often fall within the range between one and two. These imply that generalist pay some price for being able to capture both resources, but that a perfect generalist (with $p = 1/2$) does not suffer more than a 50% disadvantage when resources are equally common. It has been difficult to measure trade-offs, but at least several seem to be weakly concave, as required (O'Hara Hines et al. 2004).

It is important to note that the presence of variation leads to an evolutionary coalitions consisting of a single generalist type for a range of trade-off exponents slightly above $n = 1$. These exponents produce dimorphism in stable systems. Thus, while temporal variation can lead to the evolution of greater diversity in some cases, it does not always do so.

The type of coevolution of generalists and specialists described here can also operate when there are larger numbers of resources and consumers. It is most likely when evolution initially promotes divergent specialization, but the presence of specialists then leads to asynchronous fluctuations in resources, which favor generalists. At present, the impact of resource fluctuations on the evolution of resource-use characters appears not to have been studied. There are systems in which it is likely to operate. For example, seed production by plants is frequently variable, and this is thought to often be an adaptation to reduce the density of specialist seed predators (Satake and Bjørnstad 2004). At the same time, the variability may allow the existence of generalist seed predators when different plant species have asynchronous fluctua-

tions in seed production. Cycling mammals having both specialist and generalist predators include both arvicoline rodents (Hanski et al. 2001) and the snowshoe hare (Krebs et al. 2001). Further study of the long-term dynamics of specialists and generalists in such systems might reveal the mechanism proposed here.

Adaptive behavior is a feature that greatly expands the range of conditions allowing coexistence in models of specialist-generalist competition having sustained temporal variation in resource abundances (Wilson and Yoshimura 1994; Abrams 2006a). The analysis presented here has not considered the possibility that resource use by the consumer is influenced by rapid behavioral switching between resources as well as by evolution of morphological or physiological traits. Other work suggests that this also increases the opportunity for coalitions including two specialists and one or more generalists (P. A. Abrams, unpubl. ms.).

The theoretical question of the diversification of resource use in a generalist consumer lineage was addressed by Egas et al. (2004), who reached a conclusion that is nearly opposite to the one reached here. They argued that the coexistence of generalists and specialist on two resources could very seldom be attained by gradual evolution. In contrast, in the present model such a three-species coalition could be reached by gradual evolution from the two-specialist starting point for most (but not all) parameter sets examined. Egas et al. (2004) pointed out that generalists that are initially quite different from either specialist can often invade and coexist with the specialists in their model. The conclusions presented here differ in suggesting that a wide range of ecological circumstances allow the evolution of two specialists and a generalist from a single generalist lineage, whether or not new lineages are constrained to have phenotypes close to those of existing ones. Because both the model and the methods of analysis used by Egas et al. (2004) differed from those used here, several factors are likely to contribute to this difference in conclusions. The model examined here assumes a single habitat, whereas Egas et al. (2004) used a model that assumed each resource was found in a different habitat. Egas et al. (2004) assumed that adaptive behavior redistributed individuals between habitats each generation, but no similar behavior is assumed here. Egas et al. (2004) assume stochastic environmental variation, whereas the current models examine consumer-resource cycles or environmental seasonality. Finally, the models differ in the lack of explicit resource dynamics in Egas et al. (2004) and the presence of such dynamics here. Additional work will be required to determine how each of these differences between the models affects the evolution of resource capture traits.

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