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The effect of competition between prey species on the evolution of their vulnerabilities to a shared predator

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ABSTRACT

Here, we use some simple models to investigate the impact of between-prey competition on the nature of the indirect evolutionary interaction between prey species via shared predators. Sympatry with a second prey species is likely to alter the population size of the shared predator population(s) and thereby affect the adaptive evolution of anti-predator (vulnerability) traits in the first prey species. Such predation-driven character shift has been investigated previously in models that either assumed no resource-based competition between prey species, or complete overlap in resource use by prey. This study examines the intermediate situation in which prey species compete, but are able to co-exist in the absence of the predator. This scenario is capable of producing either of the two most common responses observed in the limiting cases: parallel change in anti-predator characteristics or divergent change in those characteristics. Parallel change characterizes situations with relatively low competition, and those with high competition when the asymmetry in competition coefficients is less extreme than the asymmetry in the ratio of values of the two prey to the predator. Divergent change occurs with high competition or with moderate competition given sufficient asymmetry in competition coefficients. The factors determining the magnitude of character shifts are explored. Potential examples of such evolutionary responses to sympatry with additional prey species are discussed.

Keywords: apparent competition, character displacement, competition, food web, predation.

INTRODUCTION

Ecologists have a long history of studying indirect interactions, in which a change in the density of one species affects a second species as the result of some change produced in a third species (or population) that interacts with both of the other two. Exploitative interspecific competition for resources is the best known of these indirect effects, but many others have been documented (Schoener, 1993; Menge, 1995; Abrams *et al.*, 1996). Holt's (1977) theoretical examination of 'apparent competition' stimulated many subsequent studies showing that species on a single trophic level affect one another's densities via effects on the behaviour or population density of shared natural enemies. These are only two of a large variety of indirect effects that have been documented in natural communities

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(Schoener, 1993; Wootton, 1994; Menge, 1995), and a much wider variety that have been predicted by theory (Abrams *et al.*, 1996).

Because changes in the density of an interacting species are likely to alter natural selection on a focal species, ecological indirect effects are likely to be accompanied by evolutionary responses. In contrast to ecologists, evolutionary biologists have seldom searched for such indirect effects. There have been several studies of character displacement in which the effects of one consumer species on the relative abundance of resources produce an evolutionary shift in resource-related traits in another consumer (e.g. Brown and Wilson, 1956; Grant, 1972; Taper and Case, 1992; Schluter, 2000a,b). However, most other possible types of evolutionary indirect effects remain unexplored. Following a simple model in Holt (1977), there have been a few theoretical studies of indirect effects on the evolution of anti-predator traits (Brown and Vincent, 1992; Matsuda *et al.*, 1994; Abrams, 2000a; Abrams and Chen, in press). The lack of empirical attention to such potential effects is surprising, given that field studies of natural selection have been more successful in detecting evolutionary change when predation, rather than competition, is the selective agent (Endler, 1986; see discussion in Abrams, 2000b). At least one potential example has recently been described (Vamosi, 2001).

The recent theoretical studies by Abrams (2000a) and Abrams and Chen (in press) have examined systems in which two prey species share a common predator, and either do not compete or compete for a single resource. In the former case, anti-predator traits in either of two prey species usually increase in response to an increase in the density of (or sympatry with) the other prey. In the latter case, the most common outcome is that the anti-predator trait of one prey species increases in response to increased numbers of the second prey, but the anti-predator trait of the second decreases in response to increased numbers of the first. More rigorously stated, the ratio of the effect of predator density on fitness to the effect of resources on fitness in each of the two prey species will diverge in sympatry, as a result of the changes in their anti-predator traits.

Differences in resource utilization can allow two or more prey species to co-exist in the absence of the predator; such differences also increase the likelihood that they will co-exist in the presence of the predator. It is clear that both parallel and opposite shifts in anti-predator characters of the two species in sympatry are possible in this case, because these are the most common outcomes in the limiting cases when there is either no resource competition or complete resource overlap. However, there has been no exploration of the relative probabilities of these two different responses. How much interspecific competition is needed before the most likely response is divergent shifts? Does one or the other type of response predominate for those parameters that are most likely to allow co-existence of the two prey species in the presence of the predator? These are the sorts of questions that will be examined for a range of simple models in the following sections.

A THREE-SPECIES MODEL OF THE EVOLUTION OF ANTI-PREDATOR TRAITS IN TWO PREY SPECIES COUPLED BY A PREDATOR

The population dynamics of the three-species system described above will be modelled by the following simple equations:

$$\mathrm{d}P/\mathrm{d}t = P(e_1C_1N_1 + e_2C_2N_2 - d) \tag{1a}$$

$$\mathrm{d}N_1/\mathrm{d}t = N_1(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - C_1P) \tag{1b}$$

$$dN_2/dt = N_2(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2 - C_2P) \tag{1c}$$

where r_i is the maximum per capita population growth rate of prey species i and α_{ij} is the effect of an individual of species j on the per capita growth rate of species i. The predator encounters and consumes prey species i at a rate C_iN_i, and converts that consumption into new predators with a conversion efficiency e_i. The predator has a per capita death rate d. We assume that each of the two prey species has a trait that increases both its maximum per capita growth rate, r_i, and its vulnerability to the predator, C_i. We will express r_i as the sum of a component r_{0i}, which is independent of the trait, and a component r_{ii}, which is functionally related to the trait, C_i. Following previous work (see Taper and Case, 1992; Abrams *et al.*, 1993; Abrams, 2000a), we assume that C_i changes at a rate proportional to the rate at which individual fitness changes with C_i. Here we assume that there is a narrow distribution of trait values in the population. Thus, the fitness of an individual in population i with trait value C can be approximated by the per capita growth rate, evaluated at the mean trait value, C_i. The rate of change of C_i is, therefore, proportional to $d/dC_i[(1/N_i)(dN_i/dt)]$, so that the trait dynamics are described by:

$$dC_i/dt = v_i[dr_{ii}/dC_i - P] \qquad \{i = 1, 2\} \tag{1d}$$

where v_i is the additive genetic variance of C_i. We will assume that per capita growth rate is a unimodal or monotonically increasing function of the individual's vulnerability, and that $d^2r_{ii}/dC_i^2 < 0$. This condition is possible on biological grounds; increasing vulnerability is likely to have less of an effect on growth rate when vulnerability and growth rates are both already high. Because d^2r_{ii}/dC_i^2 is also the second derivative of fitness with respect to C_i, a negative value of this derivative also implies that trait values maximize fitness for each of the two species at an evolutionary equilibrium. In the stability-determining Jacobian matrix, diagonal elements, $v_i(d^2r_{ii}/dC_i^2)$, are associated with each of the two trait dynamic equations (1d). Negative values of these elements increase the likelihood that the equilibrium of the entire system will be stable.

The form of equations (1) makes some implicit assumptions regarding the nature of the anti-predator traits. One assumption is that a prey phenotype can be specified by the predator's per capture rate of that prey. This is not the case when there are many potentially different ways to evade or defend against the predator. The model will apply to the level of defence in such cases, but will not be able to describe the variety of different defences. Thus, it is incomplete as a model of the evolution of the phenomenon of aspect diversity in prey (e.g. Ricklefs and O'Rourke, 1975). A second assumption is that the trait does not affect the per capita strength of inter- or intra-specific competition in the prey. Furthermore, the predator is assumed not to alter its foraging based on prey defence, either evolutionarily or behaviourally. These latter assumptions are discussed below in the section on 'Other models'.

It follows directly from equation (1d) that the change in the equilibrium trait of prey species i, $\hat{C}_i$, as the result of some change in a parameter of species j, x_j, depends solely on how x_j affects the predator density. Implicit differentiation of equation (1d) at equilibrium gives

$$\frac{\partial \hat{C}_i}{\partial x_j} = \frac{\partial \hat{P}/\partial x_j}{d^2r_{ii}/dC_i^2} \tag{2}$$

The fact that the equilibrium trait maximizes fitness implies that the denominator of the

right-hand side of equation (2) must be negative, and the equilibrium vulnerability trait, $\hat{C}_i$, will change in a direction opposite to the change in predator density. The Appendix outlines some of the mathematical analysis of the dynamic system given by equations (1), and shows that the effect of an increase in the trait-independent growth rate of species j, r_{0j}, on the equilibrium vulnerability trait of species i is given by the sign of the quantity,

$$C_i e_i \alpha_{ij} - C_j e_j \alpha_{ii} \tag{3}$$

Note that expression (3) implies that vulnerability in one species must decrease in response to an increased trait-independent growth rate of the other prey species, when competition between the prey is sufficiently low relative to competition within prey species. It also implies that, when competition within and between species is identical (all α's are unity), then the traits in the two species, C_1 and C_2, must change in opposite directions; the species characterized by the larger value of the product, $C_i e_i$, will increase vulnerability in response to increased growth in the other prey, whereas the prey characterized by the smaller $C_i e_i$ will decrease vulnerability in response to increased growth of the first species. The product $C_i e_i$ is the slope of the relationship between the density of prey i and the predator's per capita growth rate; we will refer to this as the value of prey i to the predator. When all α's are equal to 1, equation (3) states that the prey that is more valuable to the predator will become more vulnerable when the less valuable prey increases in density. This result is intuitive, because the high interspecific competition when $\alpha_{ij} = \alpha_{ii} = 1$ means that increases in the less valuable prey decrease the more valuable prey's density and, therefore, decrease predator density. The end result is relaxed selection for defensive traits (increased vulnerability).

The results have been framed in terms of how the vulnerability/growth trait of prey species i changes when there is an increase in the trait-independent growth rate of prey species j. If the sign of this effect does not depend on the magnitude of the other prey's growth rate, the results can be extended to predict what occurs when one of the two prey species is added to, or removed from, a system with the other prey. Addition of prey j is equivalent to a large magnitude change in r_{0j} starting from a value just sufficient to allow species j to exist. It is theoretically possible for the sign of expression (3) to change as r_{0j} increases, particularly if the two species differ greatly in the curvature of their relationships between r_{ii} and C_i. The lack of measurements of the relevant trade-off relationships in nature makes it difficult to know if this could happen frequently, but it at least appears to be uncommon using most functional forms that have been applied in previous theory. It is likely, therefore, that condition (3) usually gives the sign of the change in vulnerability of species i when it becomes sympatric with species j.

When two similar prey species are able to co-exist in the absence of the predator, they generally experience some interspecific competition, but must be characterized by the condition, $\alpha_{ij}\alpha_{ji} < \alpha_{ii}\alpha_{jj}$. In this case, it is possible for either mutual (parallel) reductions or opposing changes in vulnerability to occur in sympatry, depending on parameter values. By rewriting condition (3) after taking into account the co-existence requirements, we can say that the conditions for divergence in sympatry are that, either

$$\alpha_{21}/\alpha_{22} < C_1 e_1/(C_2 e_2) \text{ and } \alpha_{12}/\alpha_{11} > C_2 e_2/(C_1 e_1) \tag{4a}$$

or

$$\alpha_{21}/\alpha_{22} > C_1 e_1/(C_2 e_2) \text{ and } \alpha_{12}/\alpha_{11} < C_2 e_2/(C_1 e_1) \tag{4a}$$

Parallel change in sympatry occurs when

$$\alpha_{21}/\alpha_{22} < C_1e_1/(C_2e_2) \text{ and } \alpha_{12}/\alpha_{11} < C_2e_2/(C_1e_1) \quad (4b)$$

We will use R_{ij} to denote the ratio of the value of prey j to the predator relative to the value of prey i (i.e. $R_{ij} = C_je_j/C_ie_i$), and will use α'_{ij} for the competition coefficient of species j on i (i.e. the ratio of inter- to intra-specific effects: $\alpha'_{ij} = \alpha_{ij}/\alpha_{ii}$). Inequalities (4a,b) then mean that divergence occurs when either $\alpha'_{12} > R_{12}$ and $\alpha'_{21} < R_{21}$, or $\alpha'_{21} > R_{21}$ and $\alpha'_{12} < R_{12}$. Parallel change occurs if both competition coefficients are less than the corresponding ratios of values to the predator. In the simplest case, if each prey is equally valuable to the predator ($R = 1$) – competition is symmetrical – and both competition coefficients ≤ 1, parallel change is the only type of response that will be observed. Some asymmetry, either in values to the predator or in competitive effects, is required for divergence

SUMMARY OF RESULTS

The outcomes that follow from conditions (4a,b) may be summarized as follows. First, divergence is most likely when: (i) interspecific competition is relatively high ($\alpha_{12}\alpha_{21}$ is close to $\alpha_{11}\alpha_{22}$), given the existence of some asymmetry in either values to the predator or in competitive effects; or (ii) interspecific competition is moderate, but the asymmetry in competition coefficients is either significantly more extreme or significantly less extreme than the asymmetry in values to the predator. This can occur when competition is symmetrical, provided that one of the two species is significantly more easily caught by, or nutritious to, the predator. Second, parallel change to greater defence is most likely when: (i) interspecific competition is relatively low ($\alpha_{12}\alpha_{21} << \alpha_{11}\alpha_{22}$); or (ii) interspecific competition is moderate to high, and asymmetrical, and the asymmetry in competition coefficients corresponds to the asymmetry in values to the predator, such that the competition coefficient of species j on species i is less than the ratio of the values of j to i to the predator, for both $i = 1, j = 2$ and $i = 2, j = 1$.

AN EXAMPLE

It is possible to quantify the parameter ranges that result in parallel and opposite responses in the two vulnerability traits if we make some assumptions to decrease the number of parameters involved. For simplicity, we assume both prey have identical energetic values to the predator. It is common for both inter- and intra-specific competitive effects to reflect rates of consuming resources. Here we assume species 2 is the better resource exploiter, and has a functional response slope equal to $\sqrt{k}$ times that of species 1 (where $k > 1$). If we scale α_{11} to unity, then the derivation of competition coefficients first given by MacArthur (1970) implies that $\alpha_{22} = k > 1$ and that $\alpha_{21} = \alpha_{12} = \sqrt{k}\,\alpha$, where α is less than 1, and reflects similarity in resource use. It is also common for the species with the higher exploitation rate to be more vulnerable to predators (Leibold, 1996). Thus, we scale C_1 to unity and assume $C_2 \geq 1$. The above results imply that opposite responses to sympatry occur if

$$\alpha > \text{Min}(\sqrt{k}/C_2,\ C_2/\sqrt{k}) \quad (5)$$

Parallel change in vulnerability is expected if condition (5) is not satisfied. One implication of this result is that there must be a significant difference between the asymmetry in vulnerability (C_2) and the asymmetry in resource consumption rates ($\sqrt{k}$) for opposite changes

in the vulnerabilities to be favoured in sympatry. If these two quantities are equal, the above condition for opposite responses becomes $\alpha > 1$, which cannot be satisfied if the species are to co-exist in the absence of the predator. Figure 1 shows the parameter ranges of k and α producing parallel and opposite shifts for the case when $C_1 = C_2$ and the comparable ranges for a case where $C_2 = 2C_1$, meaning that $R_{12} = 2$ and $R_{21} = 1/2$. Cases with a larger ratio of the two vulnerabilities produce diagrams similar in form to the case of $C_2 = 2C_1$, except that the point at which all values of α produce parallel change moves to a higher value of k when C_2/C_1 increases. Opposite responses in the two vulnerabilities occur over a relatively wide range of strengths of interspecific competition when the asymmetry in resource competition is slight (k close to 1) and asymmetry in vulnerability is relatively high ($C_2 >> 1$). The areas of parameter space in Fig. 1 are somewhat misleading as indicators of the relative probabilities of the two different outcomes. The Appendix shows that the range of growth rates, r, allowing co-existence in the presence of the predator diminishes as the interspecific competition coefficients approach their maximum values; this is also true of co-existence in the absence of the predator (e.g. MacArthur, 1970). Thus, parameters that could lead to opposite shifts in vulnerability traits are more likely to produce exclusion of one prey before any significant evolutionary change occurs.

THE FREQUENCIES OF OCCURRENCE AND MAGNITUDES OF CHARACTER SHIFT

It is likely that parallel change towards lesser vulnerability (greater defence) in both species represents a more common consequence of sympatry than does opposite change in the two species' vulnerability. Parallel changes are especially likely when interspecific competition is relatively low. Low interspecific competition is probably more common than high

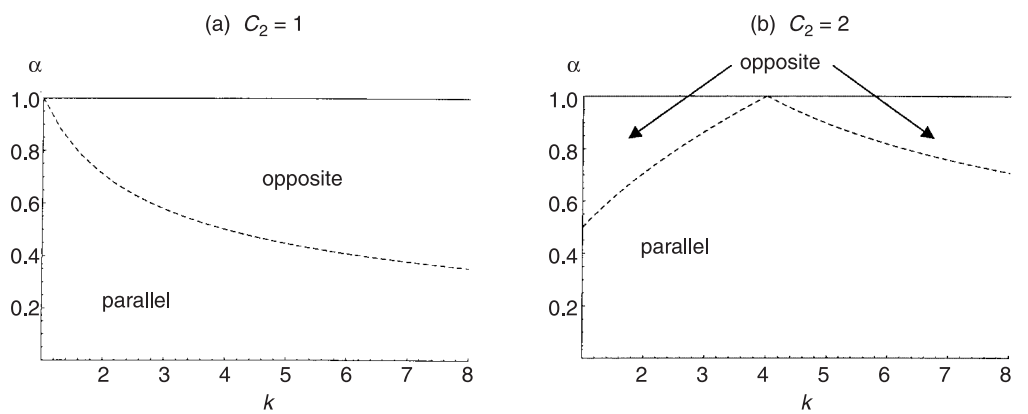

Fig. 1. Ranges of parameter space in which sympatry produces parallel or opposite changes in the vulnerabilities (defensive traits) of two competing prey species. The x-axis is the ratio of the resource consumption rate of prey species 2 to prey species 1, which results in α_{22} being k times as large as α_{11}. The parameter C_2 is the relative vulnerability of prey 2 to the predator (i.e. the slope of the predator's functional response to prey 2, given that C_1 is measured in units such that $C_1 = 1$). Panel (a) assumes that the two prey species have identical vulnerabilities, whereas (b) assumes that prey 2 is consumed at twice the rate of prey 1. Competition coefficients above the solid line do not permit co-existence of the prey in the absence of the predator.

competition, both because co-existence is most likely in this case and because evolution of the relative use of different resources usually tends to reduce interspecific competition (Lawlor and Maynard Smith, 1976; Abrams, 1986).

The above results provide some insight into factors affecting the magnitude of the difference in trait values between allopatry and sympatry. Equation (2) suggests that a relatively slight curvature of the relationship between r_i and C_i favours a large magnitude response, as does a large change in predator density caused by the addition of the competitor. The latter is more likely to be measurable in the field. The formulae for equilibrium predator densities in allopatry and sympatry given in the Appendix can be used to show that the largest magnitudes of change in predator density for a focal prey when going into sympatry with a second prey occur when the second prey is very different in its vulnerability to predation, competes relatively little with the focal prey, and has a relatively large maximum growth rate.

OTHER MODELS

This section will present a cursory overview of the effect of alternative models on the preceding conclusions.

One of the limitations of equations (1) is the lack of an explicit representation of the competition for resources that is embodied in the competition coefficients. It is possible to expand the model considered in the preceding section to include resources by following the framework used by Abrams and Chen (in press). Here, the trait of each prey species increases both its rate of resource capture and its rate of being captured by the predator. As a consequence, both maximum growth rate and per capita density dependence in the prey are affected by the anti-predator trait. We have performed some numerical analyses of this sort of model in which there are two resources, the prey display some degree of resource partitioning, and the trait of a given prey causes proportional increases in its consumption of both resources as well as increases in predator vulnerability (X. Chen and P.A. Abrams, unpublished). In models with linear functional responses of both predator and prey species, the results are generally similar to those outlined above. Parallel change to greater defence occurs when the prey do not differ much in their inherent vulnerability, and interspecific competition is relatively weak. Opposite changes in vulnerability occur when competition between species is stronger and there are significant differences in the inherent vulnerabilities of the two species. Figure 2 is an example of parallel displacement in such a model, showing that greater similarity in the relative use of the two resources decreases the magnitude of character shifts in sympatry. This is in accord with our findings, based on equations (1), that greater interspecific competition reduces the magnitude of parallel character shifts.

Most predators have saturating functional responses. The possibility of population cycles resulting from such a functional response significantly reduces the range of parameters that permit two prey species to co-exist when there is only a single resource (Abrams, 1999). The presence of sustained cycles also means that the rates of evolutionary change (the constants, v_i, in equation 1d) have an effect on the mean values of both traits and population densities (Abrams, 1997), so that the potential range of results is much greater. Finally, the population cycles often produce a mutualistic interaction between prey species that would otherwise exhibit apparent competition (Abrams *et al.*, 1998). This scenario has again only been explored numerically and to a limited extent, and will be treated in more detail elsewhere. It

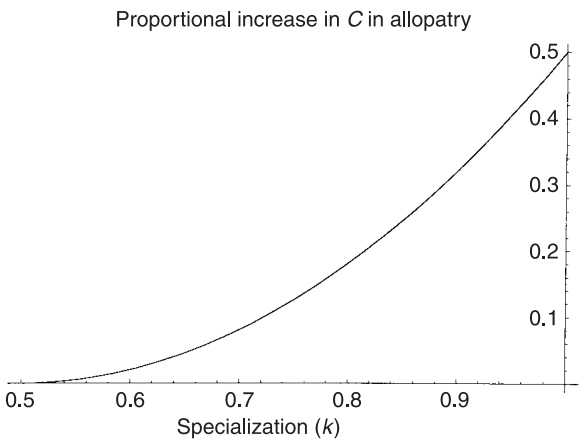

Fig. 2. The magnitude of parallel shifts towards greater vulnerability in allopatry in a model in which two consumer species share one predator and two resources. The consumers and predator both have linear functional and numerical responses, and the resources have logistic growth. The parameters C_{ij} describe the consumption rate of resource j by consumer i. The per capita consumption of consumer (prey) species i by the predator is proportional to the square of $C_{i1} + C_{i2}$. The consumers have identical predator vulnerabilities when their two trait values are equal. They have 'mirror-image' consumption rates of the two resources such that $C_{11} = C_{\max 1}k$, $C_{12} = C_{\max 1}(1 - k)$, $C_{21} = C_{\max 2}(1 - k)$, $C_{22} = C_{\max 2}k$. When the two $C_{\max i}$ parameters are equal, both prey species shift their trait value by identical amounts in going from sympatry to allopatry. The graph shows the magnitude of the increase in the vulnerability traits C_i in allopatry as a function of the degree of specialization of the two consumers ($k = 0.5$ means both are complete generalists, while $k = 1$ means that each consumer only uses its own resource).

is possible to have parallel evolution to reduced levels of defence following sympatry of two prey species because of a decrease in the average effective risk of predation. This reduction occurs because the increased amplitude of cycles means that the predator is often either rare or, when common, is often satiated by temporarily abundant prey. Large differences in the strengths of intraspecific competition between the two prey species can produce a change from stability to cycling, or vice versa, when going from allopatry to sympatry. These changes in dynamics can have a major impact on the evolutionarily favoured change in character values.

Sustained fluctuations can occur in equations (1a–c) if the prey species are characterized by greater interspecific than intraspecific competition. Gilpin (1979) has discussed the chaotic dynamics that can occur in this case. We have not considered such high interspecific competition here for two reasons: (1) exploitative competition is unlikely to produce such large magnitudes of interspecific competition, and (2) these magnitudes of interspecific competition make it impossible for the competitors to co-exist in the absence of the predator. Nevertheless, it would be of theoretical interest to determine how prey species would affect each other's dynamics and vulnerability traits in such a case.

Adaptive predator foraging behaviour can have a major impact on the results discussed above. Abrams and Matsuda (1993) discuss a model in which two non-competing prey both adjust anti-predator effort in response to predation pressure, and the predator exhibits adaptive switching between the two prey. This leads to very different responses of

anti-predator traits in one prey to the presence of the second prey than when there is no predator adaptation. Magnitudes of character shifts are often less than for the corresponding system with fixed predator behaviour. The same is likely to be true for models that include prey competition, but this requires further study.

All of the models discussed thus far have assumed that there is only a single type of predator. We can understand the case with two predator types by examining the limiting cases of specialist and generalist predators. If each predator is a specialist on a different prey species, each consumer has an independent limiting factor (its specialist predator) in addition to its resources. Sympatry with a second prey that is also a resource competitor is expected to decrease equilibrium resource and predator densities for each of the two prey species. In general, the reduction in predator densities favours parallel evolution of increased vulnerability in each of the two species. On the other hand, if the two predators are identical generalists, and if defensive traits have the same relative effectiveness against each predator, then the model is equivalent to the single-predator system analysed above, and both parallel and opposite shifts in sympatry are possible. If the predators are generalists, but differ in their relative consumption rates of the two prey species, then the directions of change of prey traits in sympatry depend on how closely the system resembles one of these two limiting cases, with greater differences between predators tending to produce parallel change rather than strict divergence.

Direct density dependence in the predator population reduces the change in its population density that occurs as the result of adding or removing a second prey species. This also reduces the magnitude of the character shifts in a prey species that occur as a consequence of sympatry with a second prey. The combination of predator density dependence and a type-2 predator functional response can lead to mutual reductions in predation risk when two prey species become sympatric. The reduction in the predator's available search time can more than compensate for its increased population size in such a system (Holt, 1977; Abrams and Matsuda, 1996). Parallel evolution of increased vulnerability in sympatry is then possible. Direct density dependence may also lead to alternative attractors in such a system in the absence of evolution (Abrams and Matsuda, 1996), and is likely to produce alternative evolutionary outcomes in models that permit such responses.

Both our simple model (equations 1) and the alternatives discussed here have implicitly assumed that the prey have a 'unidirectional' axis of adaptation for reducing predator vulnerability (*sensu* Abrams, 2000a,b). Increases in the prey's trait increase vulnerability regardless of the predator's phenotype. Abrams (2000a) discusses the case of bidirectional axes when the two prey species do not compete with each other. In this case, a given prey individual may reduce its vulnerability by either increasing its trait (if it is above the corresponding trait that is most vulnerable to the predator) or by decreasing its trait (if it is below the most vulnerable trait value). Body size may often operate as such a bidirectional trait; prey may escape by becoming too large or too small for their predator. The results for bidirectional traits under the present model are very similar to those presented above, if the trait is measured simply by the vulnerability (consumption rate) that it produces. However, a bidirectional axis introduces the possibility that the actual phenotype may change in different directions to produce similar reductions or increases in vulnerability. Brown and Vincent (1992) analyse a more elaborate model with a bidirectional axis based on size. Multidimensional traits are also possible and may be involved in the evolution of diverse cryptic colour patterns of prey species ('aspect diversity'; Ricklefs and O'Rourke, 1975).

DISCUSSION

The simple model (equations 1) that forms the core of the above analysis is consistent with several different mechanisms that produce different levels of inter- and intra-specific competition. One possibility is that there are intraspecific limiting factors other than the shared resources, but no difference in resource use between the two prey species. It could be that there are several resources that are consumed with different relative efficiencies by different prey species. It is also possible that each of the prey species has some exclusive and some shared resources. The analysis of the models considered here differs from analyses of food webs in which there is only a single resource (Abrams and Chen, in press). In particular, it is much more likely that both prey species exhibit parallel changes in their trait when they come into sympatry. Because co-existence of the prey is much more likely when they have some differences in their resource use (or in their sets of limiting factors), it is possible that parallel change in anti-predator traits may be the most likely response of prey species when they come into sympatry, given the assumption of a unidirectional axis of vulnerability.

Although the present models are not designed to describe a particular type of trait, several characteristics are known to affect both resource acquisition rate and vulnerability to predation. Body size usually affects vulnerability to predation, as well as the use of resources of different sizes (Cohen *et al.*, 1990). However, body size may also affect the absolute rate of acquiring resources, for example when larger individuals are able to move faster and thus encounter more prey individuals. There are also many organisms that use the same structures for resource acquisition and defence against predators (e.g. Vermeij, 1994). On a behavioural time-scale, choice of habitat often constrains both exposure to resources and exposure to predators. It would be interesting to compare the anti-predator adaptation of prey species that occur in isolated systems which differ in number of co-occurring prey species. Such comparisons are extremely rare.

Almost all work on character shifts in sympatry has been based on the presumption that shifts are driven by changes in the abundance of species on lower trophic levels rather than higher levels. Recent work by Vamosi (2001) has produced some evidence for parallel change to reduced defensive traits in the three-spined stickleback, which seems to exhibit resource-based character displacement between benthic and pelagic morphs in several lakes in British Columbia (Schluter, 2000a,b). Although the observed values of defensive traits are consistent with a scenario in which predators have inflexible population sizes combined with significant handling time, it is as yet unclear what historical selective pressures have produced the present-day differences described by Vamosi.

Most work on resource-based character displacement has stressed divergence of traits (Schluter, 2000a,b). However, non-divergent responses to resource competition are also expected under a wide range of conditions, including self-limitation of consumers and nutritional interactions between resources (Abrams, 1986, 1987, 1996). Although it has received surprisingly little study, direct density dependence in consumer species can arise in many ways and appears likely to be very common (Abrams, 1986; Abrams and Ginzburg, 2000). The lack of empirical cases of parallel displacement in systems involving resource competition is an evolutionary puzzle, whether or not it is driven by indirect interactions via shared predation.

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APPENDIX: EQUILIBRIA AND STABILITY FOR EQUATIONS (1) AND VARIATIONS

The equilibrium densities for equations (1a–c) are given by:

$$N_1 = \frac{C_2^2 e_2 (r_{01} + r_{11}) - C_2 (C_1 e_2 (r_{02} + r_{22}) + d\alpha_{12}) + C_1 d\alpha_{22}}{C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22}}$$

$$N_2 = \frac{C_1^2 e_1 (r_{02} + r_{22}) - C_1 (C_2 e_1 (r_{01} + r_{11}) + d\alpha_{21}) + C_2 d\alpha_{11}}{C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22}}$$

$$P = \frac{C_2 e_2 (r_{02}\alpha_{11} + r_{22}\alpha_{11} - (r_{01} + r_{11})\alpha_{21}) + C_1 e_1 (-r_{02}\alpha_{12} - r_{22}\alpha_{12} + (r_{01} + r_{11})\alpha_{22}) - d(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})}{C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22}}$$

The conditions for the population dynamical equilibrium of equations (1a–c) to be locally stable (given that these are positive densities) include the necessary condition,

$$C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22} > 0 \qquad \text{(A1)}$$

Condition (A1) is both necessary and sufficient for stability when combined with our assumption that $\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$, which is itself a necessary condition for the two prey species to co-exist in the absence of the predator.

The effects on the predator's equilibrium population, P, of increasing the baseline growth parameter, r_{0i}, of each prey are given by:

$$\frac{\partial P}{\partial r_{02}} = \frac{C_2 e_2 \alpha_{11} - C_1 e_1 \alpha_{12}}{C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22}}$$
$$\frac{\partial P}{\partial r_{01}} = \frac{C_1 e_1 \alpha_{22} - C_2 e_2 \alpha_{21}}{C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22}} \quad \text{(A2)}$$

The denominator of each of these expressions must be positive based on inequality (A1). These two formulae determine the direction of the response of the vulnerability trait in each prey species in response to a greater growth rate – and, therefore, higher density – of the other prey species. Equation (2) in the text shows that C changes in a direction opposite to the change in predator population. Thus, C_2 will decrease with an increase in r_{01} provided $C_2 e_2 \alpha_{21} < C_1 e_1 \alpha_{22}$; C_2 will increase if the inequality is reversed. Similarly, C_1 will decrease with an increase in r_{02} provided that $C_1 e_1 \alpha_{12} < C_2 e_2 \alpha_{11}$; it will increase if the inequality is reversed. It is immediately clear that if there is no interspecific competition, both prey species decrease vulnerability, C, in response to an increase in the other prey's population, because such an increase also increases the predator population.

The magnitude of the character shift caused by introducing a second prey species is largely determined by the change in predator density in going from sympatry to allopatry. The magnitude of the allopatric predator population (when only prey species i is present) is given by

$$P^* = \frac{1}{C_i}\left(r_{0i} + r_{ii} - \frac{d\alpha_{ii}}{C_i e_i}\right) \quad \text{(A3)}$$

The text discusses conditions that make this very different from the sympatric equilibrium density given above.

The range of conditions allowing co-existence can be measured by the range of growth rates, r_i, that will allow both prey species to co-exist in the presence of the predator. The range of r_i that allows co-existence is:

$$\frac{d(C_2^2 e_2 \alpha_{11} - C_1 C_2 (e_1 \alpha_{12} + e_2 \alpha_{21}) + C_1^2 e_1 \alpha_{22})}{C_j^2 C_i e_1 e_2} \quad \text{(A4)}$$

This shows that co-existence is promoted by either low interspecific competition or by significant differences in the two vulnerability parameters, C_1 and C_2.