Evolutionary Ecology Research, 1999, **1**: 173–188

Character displacement mediated by the accumulation of mutations affecting resource consumption abilities

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ABSTRACT

This article investigates models of ecological character displacement in which shifts in the relative resource-exploitation abilities of consumer species are driven by the accumulation of deleterious mutations with resource-specific effects. The models assume a simple ecological scenario in which there are two consumer species and two resource types. A mutation-selection balance determines the value of per-unit-resource consumption rates of each resource by each consumer species. A competitor that differentially reduces the abundance of the less-used resource of the focal consumer produces an increased equilibrium frequency of deleterious mutations affecting this resource. This results in divergent character displacement. If the reduction in the abundance of the less-used resource is sufficient, a process of mutational collapse may occur, in which the focal species becomes specialized on a single resource. Large magnitudes of displacement generally require high genomic deleterious mutation rates and mutations with a high degree of specificity to particular resources.

Keywords: character displacement, competition, deleterious mutations, ecological niche, specialization.

INTRODUCTION

Ecological character displacement is the evolutionary response of characters related to competition or resource exploitation as a consequence of interspecific competition. In nature, it is most commonly detected by a difference between the characteristics of a species in areas where it occurs allopatrically and where it is sympatric with a competing species (Grant, 1972; Schluter *et al.*, 1985; Schluter and McPhail, 1992; Taper and Case, 1992). However, recent work by Schluter (1994) has produced experimental evidence of the process in sticklebacks (*Gasterosteus aculeatus*). There have been a large number of theoretical explorations of character displacement since Brown and Wilson (1956) first introduced the idea; reviews of the theory may be found in Abrams (1986) and Taper and Case (1992). All of the extant models of which we are aware are based on the idea that the displacement arises from adaptive evolution in the face of a trade-off between the consumption rates of different resources. This article explores the alternative that character displacement arises

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for non-adaptive reasons based on the accumulation of deleterious mutations that have differential effects on a consumer's ability to exploit different resources.

Deleterious mutations with a late onset of expression have long been recognized as a potential evolutionary explanation of senescence (Medawar, 1952), complementary to antagonistic pleiotropy of genes affecting performance early and late in life (Williams, 1957). Models of character displacement ignored deleterious mutations despite analogies between evolution of senescence and evolution of ecological niches (Holt, 1996). One motivation for considering such models is the recent theory suggesting that deleterious mutations can play a role in the evolution of specialization within a species (Kawecki, 1994; Fry, 1996; Kawecki *et al.*, 1997). These works show that a positive feedback process generated by deleterious mutations can result in ecological specialization. Infrequent use of a resource allows the accumulation of deleterious mutations that affect utilization of that resource; this reduces the contribution of this resource to fitness, leading to still weaker selection against additional slightly deleterious mutations having similar resource-specific effects. A similar positive feedback process can be generated when use of a resource by a competitor initially reduces the abundance of that resource. However, it is not immediately clear whether this mechanism can occur under reasonable biological assumptions about mutation rates and resource use. Here we analyse several simple biological models that illustrate the magnitude of displacement that might be expected under different assumptions about these aspects of the system.

We consider two consumer species, both of which can use two resources. The use of such models to study character displacement has a long history (Lawlor and Maynard Smith, 1976; Abrams, 1986, 1987, 1990). This type of model represents the simplest food web configuration in which the resource dynamics that drive character displacement can be explicitly described. We assume that there is no fundamental trade-off within a species in its ability to consume the two resources; that is, an individual having the maximum consumption of resource 1 possible for its species may also have the maximum consumption of resource 2. However, we do assume that the consumption rates are affected by deleterious mutations. Each mutation is asymmetrical in its effects; it produces a larger decrease in the consumption rate of one resource than of the other. We refer to a species as being preadapted to the use of resource 1 if its maximum consumption of resource 1 (in the absence of mutations) is higher than its maximum consumption of resource 2. If consumption of resource 1 contributes more than resource 2 to a species' reproductive success, the species will accumulate more mutations that impair its ability to consume resource 2 than mutations that reduce its ability to consume resource 1. Moreover, an increased load of mutant alleles reducing consumption of resource 2 further lessens the relative importance of this resource for the species, and thus weakens selection against new mutations reducing consumption of resource 2. This results in a positive feedback mechanism that may cause partial or total loss of ability to consume resource 2.

The strength of selection against deleterious mutations that affect consumption rates unequally will depend on the contribution of each resource to fitness, which in turn will depend on the species' preadaptation and the availability of the two resources. Because the availability of the resources depends on exploitation by the consumers, the equilibrium frequency of mutations accumulated by the consumers should be different depending on whether the competing species is present. Different equilibrium mutation frequencies in turn translate into different mean consumption rates in sympatry versus allopatry (i.e. character displacement). We investigate the magnitude of such character displacement mediated by deleterious mutations under some simplifying assumptions about mutational effects.

THE MODEL

Recurrence equations

The two consumer species are labelled a and b with population densities N_a and N_b, while the resources are 1 and 2, with population densities R_1 and R_2. The evolutionary variables are the mean consumption rates (per unit resource density) of each consumer on each resource, denoted C_{ij}, where $i = 1$, 2 and $j = $ a, b. The consumption rates are given by the product of a maximum, mutation-free consumption rate, denoted A_{ij}, and a factor describing the decrease caused by mutations. The form of the mutation factor is described below.

The consumers have discrete generations, mating is random, and populations are large enough that stochastic effects can be ignored. The resource dynamics are assumed to be rapid relative to consumer generation length; consequently, the resource levels R_1 and R_2 can be assumed to be at a steady state with respect to the consumer population densities and consumption rates in the current generation. These assumptions imply that there is no between-generation effect of exploitation on resource abundance. For the sake of simplicity, we also assume that both resources follow identical chemostat dynamics with a constant inflow rate I and an outflow rate proportional to current density with proportionality constant O. On a short time-scale, the dynamics of resource type i is given by $\mathrm{d}R_i/\mathrm{d}t = I - OR_i - C_{ia}N_aR_i - C_{ib}N_bR_i$. The steady state concentration of resource i is found by setting $\mathrm{d}R_i/\mathrm{d}t = 0$, and is thus

$$R_i = I/(O + C_{ia}N_a + C_{ib}N_b) \tag{1}$$

The dynamics of the population of consumer j can be described by

$$N_j(t + 1) = N_j(t)B_j(C_{1j}R_1 + C_{2j}R_2) \tag{2}$$

where R_i is given by equation (1), C_{ij} is the mean consumption rate (per unit resource density) of resource i by individuals of species j, and B_j is a constant giving the rate of 'conversion' of consumed resources into offspring. In an iteroparous population, B_j incorporates both between-year survival and reproduction. In a more general model (not considered here), B_j could be a non-linear function of resource intake rate. The evolution of consumption rates will depend on the availability of the two resources, which in turn depend on the population densities (equation 1). We assume that the population dynamics are fast enough relative to evolutionary change that (ecological) equilibrium population densities may be used to calculate an evolutionary equilibrium of consumption rates. When both species are present, the equilibrium population densities satisfy the set of two equations,

$$B_jI\left(\frac{C_{1j}}{O + C_{1a}N_a + C_{1b}N_b} + \frac{C_{2j}}{O + C_{2a}N_a + C_{2b}N_b}\right) = 1, \tag{3}$$

for $j = $ a, b. When only species a is present, then its equilibrium density is given by a single equation of the above form with N_b set to zero. It can be shown that when a biologically meaningful equilibrium satisfying equation (3) exists and C_{ij} are constant, the equilibrium is always stable.

The consumption rate parameters are affected by deleterious mutations arising at n loci, with per-locus mutation rate u. Mutations at half of these loci (type-1 loci) reduce C_{1j} by the factor $(1 - s)$ and C_{2j} by the factor $(1 - ks)$, where $0 \leq k \leq 1$; mutations at the remaining $n/2$ loci (type-2 loci) reduce C_{1j} by $(1 - ks)$ and C_{2j} by $(1 - s)$. In most of our numerical analysis, the genetic parameters n, u, s and k are also assumed to be identical for the two species. The effects of the mutant alleles are multiplicative across loci. In modelling the dynamics of the mutations we make several simplifying assumptions: (1) linkage disequilibrium is negligible; (2) each mutant allele is sufficiently rare that homozygotes can be ignored; and (3) within a given species, the frequencies of different alleles within a particular type (1 or 2) are equal. The first and second assumptions are reasonable approximations when selection is weak (i.e. the deleterious effects of each mutant allele is small). The third follows from our assumption that the mutation rate and selection coefficients are the same for all loci of a given type. This equality of mutational rates and effects means: (1) if allele frequencies at different loci of type i are initially the same, they will follow the same dynamics; and (2) even if the frequencies are initially different, they will tend to the same equilibrium frequency (see analysis and discussion of these claims in Kawecki *et al.*, 1997).

Given these assumptions, mutations of type i at a particular locus in species j will reduce the consumption of resource i by a factor $(1 - 2q_{ij}s)$, where q_{ij} is the frequency of each of the mutations of type i in species j. The mean consumption rate constants are affected by $n/2$ loci of each type, and are therefore given by:

$$C_{1j} = A_{1j}(1-2q_{1j}s)^{n/2}(1-2q_{2j}ks)^{n/2} \cong A_{1j}\exp[-ns(q_{1j} + q_{2j}k)] \tag{4a}$$

$$C_{2j} = A_{2j}(1-2q_{2j}s)^{n/2}(1-2q_{1j}ks)^{n/2} \cong A_{2j}\exp[-ns(q_{1j}k + q_{2j})] \tag{4b}$$

for $j = a, b$. Recall that A_{ij} is the maximum consumption rate of resource i by species j. A_{1j} and A_{2j} reflect 'preadaptation' of species j to the two resources; that is, the relative consumption rates of a mutation-free genotype. These maximum rates are assumed not to evolve. Without loss of generality, we can assume $A_{1j} + A_{2j} = 1$; actual consumption rates could always be standardized to satisfy this assumption by rescaling other parameters.

To determine the equilibrium frequencies of deleterious mutations, we must first derive recurrence equations for the dynamics of these alleles. This requires expressions for mean fitness and for the fitness of a particular mutant type. The mean fitness of the population of species j is, from equation (2):

$$\bar{W} = B_j(C_{1j}R_1 + C_{2j}R_2) \tag{5a}$$

The mean consumption rate parameters in this expression incorporate the effects of deleterious mutations from equations (4). The fitness of an individual carrying a particular mutant allele (say, of type 1) can be determined based on the assumptions that led to equations (4). The consumption rate constant for resource 1 by such an individual is the product of the mutational effect $(1 - s)$ multiplied by the mean C_{1j} based on all other loci (i.e. $C_{1j}/(1 - 2q_{1j}s)$). Taking into account the effect of the mutation on the consumption of resource 2, the expected fitness of carriers of the mutant allele (heterozygotes) at a particular type-1 locus is:

$$W_{\text{mut}} = B_j\left(\frac{C_{1j}R_1(1 - s)}{1 - 2q_{1j}s} + \frac{C_{2j}R_2(1 - ks)}{1 - 2q_{1j}ks}\right) \tag{5b}$$

The frequency of the mutant allele after selection will be $q_{1j}W_{\text{mut}}/\bar{W}$, and after mutation, at the beginning of the next generation, it will be

$$q_{1j}' = q_{1j}\frac{W_{\text{mut}}}{\bar{W}}(1-u) + u \tag{6}$$

Because of our assumption of identical parameters for all mutations, a single recurrence equation can be used to find the equilibrium mutant allele frequencies at all type-1 loci in species j, q_{1j}. This equation is obtained by substituting (5a) and (5b) into (6), which yields

$$q_{1j}' = \frac{q_{1j}}{C_{1j}R_1 + C_{2j}R_2}\left(\frac{C_{1j}R_1(1-s)}{1-2q_{1j}s} + \frac{C_{2j}R_2(1-ks)}{1-2q_{1j}ks}\right)(1-u) + u \tag{7a}$$

The analogous equation for type-2 loci is

$$q_{2j}' = \frac{q_{2j}}{C_{1j}R_1 + C_{2j}R_2}\left(\frac{C_{1j}R_1(1-ks)}{1-2q_{2j}ks} + \frac{C_{2j}R_2(1-s)}{1-2q_{2j}s}\right)(1-u) + u \tag{7b}$$

where the mean consumption rates are given by equations (4) above.

Finding equilibrium mean consumption rates

Assuming that the mutant alleles are rare, terms of the order q^2 and qu can be ignored, and equation (7a) can be simplified to the following form:

$$q_{1j}' \cong q_{1j} + \frac{1-q_{1j}}{(1-2q_{1j}s)(1-2q_{1j}ks)}\left[u - q_{1j}s\frac{C_{1j}R_1 + C_{2j}R_2k}{C_{1j}R_1 + C_{2j}R_2}\right] \tag{8}$$

An analogous equation can be written for q_{2j}. From equation (8), the equilibrium frequency of type-1 mutant alleles is approximately

$$\hat{q}_{1j} \cong u\frac{[C_{1j}R_1 + C_{2j}R_2]}{C_{1j}R_1s + C_{2j}R_2ks} \tag{9}$$

Substituting equation (9) and the analogous equation for type-2 mutants into equations (4a,b) leads to implicit equations for the equilibrium consumption rates:

$$C_{1j} = A_{1j}\exp\left[-U\left(\frac{C_{1j}F + C_{2j}}{C_{1j}F + C_{2j}k} + \frac{C_{1j}F + C_{2j}}{C_{1j}F + C_{2j}/k}\right)\right] \tag{10a}$$

$$C_{2j} = A_{2j}\exp\left[-U\left(\frac{C_{1j}F + C_{2j}}{C_{1j}Fk + C_{2j}} + \frac{C_{1j}F + C_{2j}}{C_{1j}F/k + C_{2j}}\right)\right] \tag{10b}$$

where $F = R_1/R_2$ and $U = nu$ is the genomic mutation rate. At equilibrium, the mean consumption rates of the two resources are independent of the number of loci n and of the absolute magnitude of the mutational effects s.

In allopatry – that is, when only one consumer species (say, species a) is present – then, from equation (1):

$$F = \frac{R_1}{R_2} = \frac{O + C_{2a}N_a}{O + C_{1a}N_a} \tag{11}$$

To determine the consumption rate constants of species a in allopatry, we set $N_b = 0$ and $j = a$ in equation (3), solve this equation for N_a, and substitute the solution to equation (11) to get:

$$F = \frac{2C_{1a}C_{2a}(1 + C_{2a}B_a I/O) - C_{1a} - C_{2a} + \sqrt{(2C_{1a}C_{2a}B_a I/O)^2 + (C_{1a} - C_{2a})^2}}{2C_{1a}C_{2a}(1 + C_{1a}B_a I/O) - C_{1a} - C_{2a} + \sqrt{(2C_{1a}C_{2a}B_a I/O)^2 + (C_{1a} - C_{2a})^2}} \tag{12}$$

Equation (12) implies that the ratio of the concentrations of the two resources when species a is at equilibrium in allopatry is a function of $B_a I/O$. Equal increases in resource input and outflow rates do not affect the evolutionary equilibrium. Note that $B_a I/O$ is the net reproductive rate of the population free of the mutations when densities are close to zero. Thus $B_a I/O$ must be considerably higher than 1 for the population to persist. To find the equilibrium consumption rates in allopatry, we substitute equation (12) into equations (10a,b) and solve the latter equations for C_{1a} and C_{1b}.

When both consumer species are present (sympatry), the two equilibrium population densities and four consumption rates satisfy a set of six equations; that is, (3), (10a) and (10b) each for $j = 1$ and $j = 2$. Note, however, that in sympatry the equilibrium resource concentrations are independent of the resource output and input rate parameters, O and I, and are fully determined by the set of equations $N_j(t + 1) = N_j(t)$ for $j = a$, b. By solving this set of equations for R_1 and R_2, we find that, at equilibrium,

$$F = \frac{R_1}{R_2} = \frac{B_b C_{2b} - B_a C_{2a}}{B_a C_{1a} - B_b C_{1b}} \tag{13}$$

After expression (13) is substituted in equations (10a,b), the equilibrium consumption rates of the two species can be found by solving the set of equations (10a,b) with $j = a$, b (i.e. four equations) for the four consumption rates C_{ij}.

We can measure the degree of specialization of species j to resource 1 by the ratio of its consumption rate constant for resource 1 to the sum of its two consumption rate constants: $E_j = C_{1j}/(C_{1j} + C_{2j})$. Character displacement can thus be defined as the difference between E_j in sympatry and allopatry (Abrams, 1986). This ratio was calculated for a range of genomic mutation rates, U, correlated effects of each type of mutation, k, and a range of maximum net reproductive rates, BI/O. We carried out all numerical calculations using Mathematica (v. 2.2.3; Wolfram Research, 1994).

RESULTS

The equilibrium in allopatry

Because the sum of the two maximum consumption rates can be scaled to unity, we set $A_{1a} = h$ and $A_{2a} = 1 - h$. The departure of h from 0.5 is a measure of the degree of specialization of the species when present at low densities in the absence of mutations. Figure 1 shows the equilibrium degree of specialization of species a in allopatry as measured by E_a. This parameter is shown as a function of the degree of preadaptation to consumption of resource 1 (h) for three different values of the reproductive potential ($B_a I/O$). The higher the reproductive potential of the species, the stronger its impact on the concentration of resources at equilibrium. Therefore, if the species is preadapted to resource 1 ($h > 0.5$), higher $B_a I/O$ leads to a decrease in relative concentration of resource 1, or lower F (see also

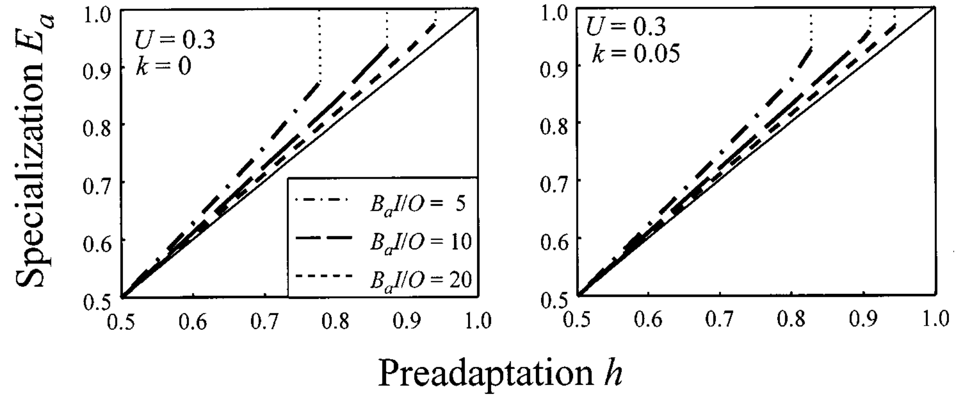

Fig. 1. The degree of specialization (E) of consumer species a at evolutionary equilibrium in allopatry as a function of preadaptation of the consumer to the use of resource 1, h, and the reproductive potential of the consumer, B_aI/O. The solid line is the diagonal ($E_a = h$). See text for further explanation.

Abrams, 1986). Thus, a high reproductive potential tends to equalize the contributions of the two resources to total fitness, which diminishes the differential accumulation of mutations affecting capture of the low-C resource. The thin diagonal line is $E_a = h$; that is, the expected specialization in the absence of mutations. The results in Fig. 1 are for a high genomic mutation rate ($U = 0.3$) and strongly asymmetric effects of the mutations ($k = 0$ and $k = 0.05$). For smaller U or larger k, the deviation from the diagonal – that is, the effect of the mutations on specialization – would be smaller. It can be shown that, under the assumptions of this model, E_a in allopatry can never be less than h.

An interesting feature of allopatric specialization, E_a, is that it is a discontinuous function of the degree of preadaptation. When mutations only affect one consumption rate ($k = 0$; Fig. 1a) and h is larger than a threshold value that depends on U, mutations reducing consumption of resource 2 become deterministically fixed, as symbolized by the vertical dotted lines in Fig. 1. These dotted lines correspond to the value of h above which equations (10a,b) do not have a solution. The degree of specialization resulting from the mutation fixation will depend on the number of loci involved and the magnitude of their effects. Such mutational collapse of the ability to consume one resource is analogous to the mutational collapse of fitness in a marginal habitat studied in more detail by Kawecki *et al.* (1997).

The degree of specialization E_a can also change discontinuously with h when $k > 0$, provided that k is small and U is large. In this case, the equilibrium for h larger than the threshold may correspond to a high equilibrium frequency of the mutant alleles rather than fixation. Fixation is prevented because, when $k > 0$, the mutant alleles also reduce consumption of resource 1, and thus are under selection even when $h = 1$. Whether they become fixed will depend on the relationship between the per-locus mutation rate u and the selection coefficient s. Results obtained with recurrence equations (7), which make fewer approximations than equations (10), suggest that the number of loci n and selection coefficient s have a negligible influence on the threshold h, as long as the per-locus mutation rate U/n is much less than the selective disadvantage s of carriers of a particular mutation (T.J. Kawecki, unpublished). Unless the mutation rate is high ($U > 0.1$), the mutations have

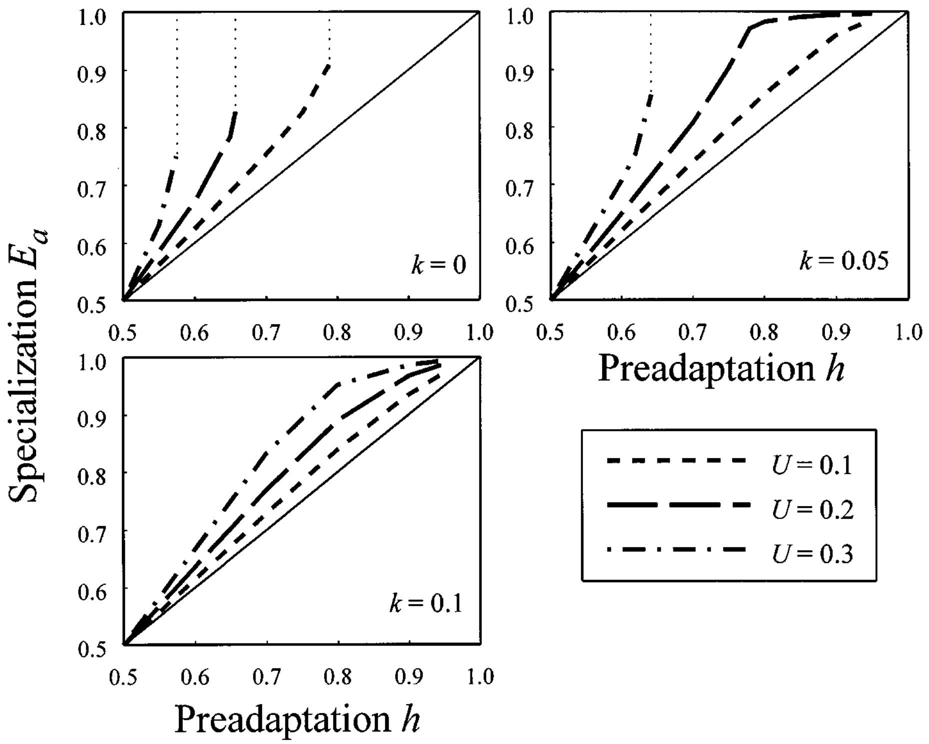

Fig. 2. The degree of specialization (E) of species a at evolutionary equilibrium in sympatry with species b under the 'mirror-image' scenario, as a function of h, U and k.

a strongly asymmetric effect on the consumption rates of the two resources ($k < 0.1$), and the species has a low reproductive potential ($B_aI/O < 10$), the mutational collapse of the ability to use resource 2 in allopatry requires very strong preadaptation to resource 1 ($h > 0.95$).

Sympatry: Mirror-image consumer species

The simplest type of sympatric system is one in which the two consumers have resource consumption traits that are mirror images of each other; this introduces symmetries that make the analysis much simpler (Abrams, 1986). Here we consider the case when both species have the same conversion coefficient $B_a = B_b = B$ and species a is preadapted to resource 1 to the same degree as species b is preadapted to resource 2 (i.e. $A_{1a} = A_{2b} = h$, $A_{2a} = A_{1b} = 1 - h$; $0.5 \leq h < 1$). With these assumptions, $N_a = N_b$ and $R_1 = R_2$ at equilibrium in sympatry. Equality of resource densities implies $F = 1$ in equations (10), which means that the equilibrium consumption rates in sympatry only depend on h, k and U. Consumption rates are independent of the reproductive potential of the consumers, because this does not affect the relative abundances of the two resources. It is important to realize that this is not true of systems that lack the symmetry assumed here. However, competitors that have very similar preadaptation (h) are unlikely to be able to co-exist. It is therefore likely that most

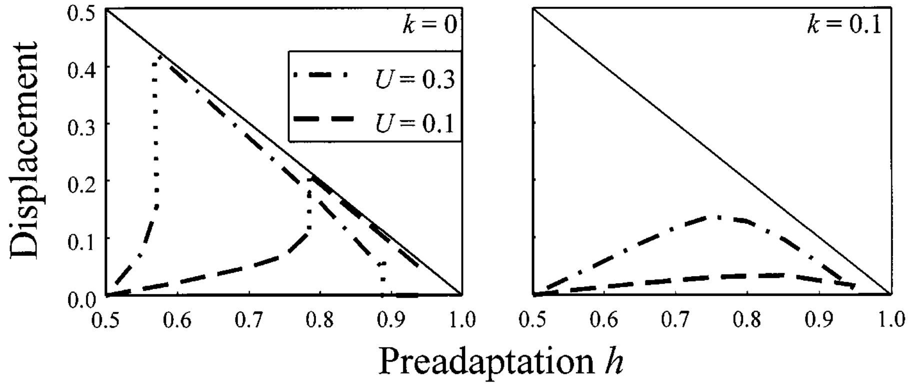

Fig. 3. The amount of character displacement as a function of preadaptation h in the mirror-image species case, for $k = 0$ (left) and $k = 0.1$ (right) and two genomic mutation rates. Displacement is defined as the difference between the degree of specialization E_a in sympatry and allopatry. The diagonal lines show the maximum displacement possible for a given h; the dotted lines mark discontinuities in the magnitude of displacement. The reproductive potential of the species, B_aI/O, is 10.

competitors that are able to co-exist are preadapted to different resources, and sympatry may often result in an approximate balancing of resource abundances.

Figure 2 shows the equilibrium specialization coefficient of species a, E_a, in sympatry with a mirror-image competitor as a function of the three parameters h, k and U. The diagonal line corresponds to $E_a = h$, which is the degree of specialization of species a in the absence of mutations. Because of the mirror symmetry, $E_b = 1 - E_a$. As expected, the consumption rate of the resource to which the species is less preadapted is more strongly affected by the mutations (i.e. $E_a > h$). This holds as long as the mutations affect consumption rate of the two resources differently ($k < 1$), but the deviation from $E_a = h$ is non-trivial only for $k \ll 1$. Recall that, in allopatry, E_a approaches h asymptotically as the reproductive potential, B_aI/O, increases. Therefore, the difference between the index of specialization, E_a, and the diagonal in Fig. 2 is the maximum character displacement for given U, k and h. More generally, the degree of displacement is measured by the difference between E_a in sympatry (Fig. 2) and allopatry (Fig. 1). Figure 3 shows this difference for a range of parameter values.

As in the allopatric case, E_a in the sympatric case is a discontinuous function of h. The threshold value of h, at which the discontinuity is located, is smaller than the analogous threshold in allopatry, even when BI/O is small. The greatest magnitudes of character displacement are expected when the preadaptation parameter is below the allopatric threshold for fixation, but above the sympatric threshold (see Fig. 3). In these cases, a species becomes nearly or completely specialized in sympatry, but can have an index of specialization only slightly larger than h in allopatry.

Sympatry: Species b only uses resource 2

Most competitive systems in nature are asymmetrical. We can gain some insight into the range of displacements possible under asymmetrical systems by considering competition between a focal generalist species and a specialist competitor. Therefore, in this second example, we assume that species b only consumes resource 2 ($C_{1b} = 0$). In this case, the ratio of densities of the two resources from equation (11) is:

$$F = \frac{B_b C_{2b}}{B_a C_{1a}} - \frac{C_{2a}}{C_{1a}} \tag{14}$$

This ratio depends on the ratio of the two species' conversion coefficients and on the consumption rate constants, but not on the input and output rate parameters. The specialist species, b, has a maximum consumption rate of the resource 2 given by $A_{2b} = 1$. This is reduced by deleterious mutations. From standard population genetics (e.g. Crow and Kimura, 1970), we know that the mutational effect depends only on the genomic mutation rate. If the genomic mutation rate to mutations affecting consumption of resource 2 by species b is U, the value of C_{2b} is:

$$C_{2b} = \exp(-2U) \tag{15}$$

We again set $A_{1a} = h$, $A_{2a} = 1 - h$. To find the equilibrium consumption rates of species a when species b is present, we substitute equations (14) and (15) in equations (10) and solve equations (10a,b) with $j = \text{a}$ for C_{1a}, C_{1b}. In contrast to the case of allopatry and that of mirror-image sympatric species, this case is not symmetric with respect to $h = 0.5$. We therefore also explore the results for $h < 0.5$; that is, for species a preadapted to resource 2.

The results are presented in Fig. 4. Because character displacement resulting from the presence of species b should be greater when species b has a relatively stronger impact on the resource density, we only explore cases with $B_b/B_a \geq 1$. If $B_b/B_a = 1$, species b is competitively excluded if species a is preadapted to resource 2 (h is less than 0.5). Lower ratios of efficiency ($B_b/B_a < 1$) would result in exclusion of species b under a wider range of conditions. If species b persists, species a accumulates more mutations at type-2 loci than at type-1 loci even when it is preadapted to resource 2. As a result, the degree of specialization of species a at equilibrium in sympatry E_a is always greater than h (all lines in Fig. 4 are above the diagonal). The difference between E_a and h is again the maximum possible displacement for $h > 0.5$. If $h < 0.5$, E_a in allopatry is less than h (by symmetry, in allopatry $E_a(h) = 1 - E_a(1 - h)$). However, for E_a in allopatry to deviate substantially from h, species a must have a low reproductive potential ($B_a I/O$), and a low $B_a I/O$ makes species a more likely to be eliminated in sympatry if it is strongly preadapted to resource 2. Thus, the deviation from the diagonal line in Fig. 4 is a close approximation of the degree of displacement expected in these systems. Significant magnitudes of displacement require that genomic mutation rates be relatively large or that mutations affecting exploitation of the jointly used resource in the specialist species have little effect on the consumption rate of the other resource.

DISCUSSION

In this paper, we have shown that character displacement due to interspecific competition can occur in the absence of genetic trade-offs in consumption of different resources. In our model, no loci show antagonistic pleiotropy; that is, the allelic effects on the two consumption rates are never negatively correlated. All genetic variation is assumed to be due to recurrent deleterious mutations that either reduce consumption of only one resource

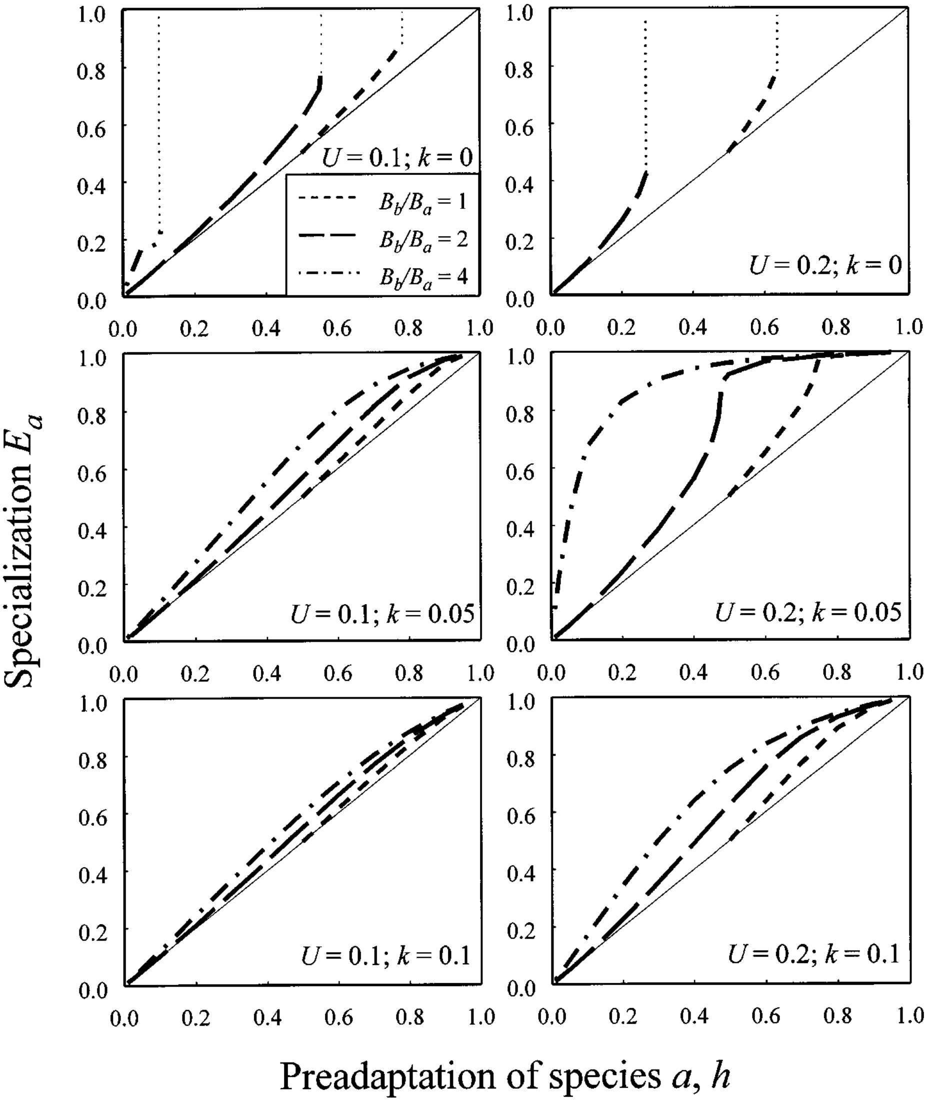

Fig. 4. The degree of specialization of species a, E_a, in sympatry with species b that only consumes resource 2. The results for $B_b/B_a = 1$ (short-dashed lines) do not extend to low h values because these conditions result in exclusion of species b.

($k = 0$), or reduce consumption rates of both resources but to a very unequal extent ($0 < k \ll 1$). Character displacement arises because of the different equilibria between mutation and selection that occur for species a in allopatry and in sympatry with a competing species b. For a given set of parameters, the differences between the relative consumption abilities of the two resources in allopatry and sympatry are entirely due to differential accumulation of the mutations. These results emphasize the need to consider the possibility of mechanisms for character displacement that are not based on negative genetic correlations in abilities to exploit different resources or habitats. Character displacement requires genetic variation that affects consumption of different resources differently, but the effects do not need to be negatively correlated; trade-offs are not essential. The models considered here examined deleterious mutations as the source of such variation, but single-species models of specialization (Kawecki, 1996, 1998) suggest that variation due to beneficial mutations or maintained by fluctuating selection would have a similar effect.

The simplifying assumptions of our model included multiplicative effects of the mutations across loci and no linkage disequilibrium, which allowed us to formulate the models in terms of allele rather than multi-locus genotype frequencies. Even though the effects of different loci on the consumption rates are multiplicative, their effects on the overall fitness $B_j(C_{1j}R_1 + C_{2j}R_2)$ are not. Therefore, some coupling-phase disequilibrium between loci of the same type, and repulsion-phase disequilibrium between loci of different types, would build up despite the random mating, but this disequilibrium should be small when selection is weak. Another assumption involved in derivation of our model was that all mutations of a given type arise at the same rate and have the same effect on consumption rates. In our approximate formulae, per-locus mutation rate u and selection coefficient s cancel out. Results obtained with equations (7), which make fewer assumptions than equations (10), show little sensitivity to u and s, as long as $u \ll s$. This makes it unlikely that a model with a range of mutational effects would have produced qualitatively different results. However, further work is needed on the consequences of relaxation of these assumptions.

Our model is deterministic and assumes infinite population size. In real populations, accumulation of deleterious mutations is a stochastic process. Analysis of the effects of drift on the process we describe above is beyond the scope of this paper, but some qualitative predictions can be made. The probability of fixation of a new deleterious mutation which reduces the relative fitness by r is approximately

$$Pr_{\text{fix}} \cong \frac{-2N_e r}{N[1 - \exp(4N_e r)]} \tag{16}$$

(Crow and Kimura, 1970), where N is the census population size and N_e is the effective population size. The probability of fixation of a deleterious mutation thus increases faster than linearly with decreasing selection coefficient r against the mutant allele. In our model, the overall selection coefficient against a type-2 mutation (affecting the lower-C resource) is approximately

$$r \cong s\,\frac{C_1Fk + C_2}{C_1F + C_2} \tag{17}$$

Two qualitative conclusions follow. First, the probability of fixation of a mutation that reduces the ability to consume resource 2 but has little effect on consumption of resource 1 increases with increasing preadaptation to resource 1. Second, accumulation of such mutations, which reduce the mean consumption rate of resource 2, results in an increased probability of fixation of similar mutations at other loci. We therefore conjecture that a process analogous to the one we are describing would work at least as effectively in small populations as in large ones.

Our numerical results suggest that, for deleterious mutations to play a non-trivial role in character displacement, mutations that reduce the ability to consume one resource but have little or no effect on consumption of other resources must arise with a genomic rate of the order of 0.1 per gamete or higher. Experimental data from *Drosophila melanogaster* suggest that mutations with mildly deleterious effects on viability under laboratory conditions arise with a genomic rate of the order of one per generation (Mukai *et al.*, 1972; Crow and Simmons, 1983; Keightley, 1994; reviewed in Lynch *et al.*, 1995). Mutation rates affecting fitness in nature may be considerably higher because more things can go wrong in the complex natural environment than in a fly bottle. Furthermore, the above-mentioned estimates did not include mutations affecting fecundity, male fertility or developmental time. It is also not clear whether the results from *Drosophila* can be generalized to other organisms (Peck and Eyre-Walker, 1997). Most importantly, we have no estimates of how often deleterious mutations affect the ability to use some resources but not others. If the figure of one mutation per gamete per generation is accurate, our models imply that at least about 10% of all mutations must have deleterious effects on consumption of specific resources, if mutations are to form the basis of significant character displacement. Mutations that are deleterious for the exploitation of some resources but neutral for others have long been used as markers of microorganisms, and have been identified in *D. melanogaster* (e.g. de Jong and Scharloo, 1976). In a recent experiment, lines of *D. melanogaster* that were genetically nearly identical except for spontaneous mutations accumulated over 200 generations showed considerable changes in productivity ranking on different media, indicating that many mutations had resource-specific effects on fitness (Fry *et al.*, 1996). The low genetic correlations in performance on different host plants typically found in studies of herbivorous insects (Jaenike, 1990; Via, 1990) provide more indirect evidence for the effect of mutations being resource- or habitat-specific. This and other theoretical studies that postulate that mutations with conditionally deleterious effects play a role in the evolution of specialization (Kawecki, 1994; Fry, 1996; Whitlock, 1996; Kawecki *et al.*, 1997) underscore the need for more empirical data on the interaction between deleterious mutations and environmental factors.

The present results should be compared with previous analyses of models with similar ecological assumptions, in which evolution was based on trade-offs between the two capture rate constants (Abrams, 1986). Although we know very little about either the nature of trade-offs or the mutation rates for loci with resource-specific effects, the conditions for significant magnitudes of character displacement driven by mutations seem likely (based on the mutation-rate studies reviewed above) to be much more restrictive than for displacement driven by trade-offs. The situations most likely to generate significant displacement due to mutations involve competition of a focal generalist species with a more abundant specialist species (Fig. 4). Significant displacement is generated under a wide range of conditions with specialist or generalist competitors in models based on trade-offs, provided the trade-off relationships are not too strongly non-linear (Abrams, 1986).

Unlike models based on trade-offs, the equilibrium degree of specialization in mutation accumulation models is a discontinuous function of the parameters when (as we have assumed) the mutations have strongly asymmetric effects on consumption of the two resources. If the preadaptation of a species to resource 1 exceeds a threshold value, natural selection on the ability to consume resource 2 becomes too weak to counter accumulation of mutations that reduce the consumption of resource 2, but have no effect on consumption of resource 1. This process, which may lead to effective specialization on resource 1, is analogous to the mutational collapse of fitness in a marginal habitat modelled by Kawecki *et al.* (1997) for a single species. That paper envisioned a different ecological setting with each individual spending its entire life either in the main or in the marginal habitat and passive random dispersal of propagules between the habitats. Here we consider two resources that are encountered simultaneously in a fine-grained environment. However, the dynamics of mutation accumulation is similar in these two types of models; in particular, our equation (8) is equivalent to equation (3) of Kawecki *et al.*, adjusting for the differences in notation. In the present paper, resource 2 is 'marginal' for a species in allopatry if the species is strongly preadapted to consumption of resource 1. However, in contrast to Kawecki and co-workers' (1997) density-independent models, we assume that consumption of the preferred resource (resource 1) reduces its concentration, thus decreasing the 'marginality' of resource 2. Therefore, the 'mutational collapse' of the ability to consume resource 2 in allopatry in this model requires stronger preadaptation to resource 1 than would be predicted by the model of Kawecki *et al.* (1997), especially when the consumer has a high reproductive potential. In sympatry, a resource can become marginal for a consumer species if it is depleted by a competitor. In the case of mirror-image consumer species, the two resources are always equally abundant at equilibrium. As a result, the accumulation of mutations is not affected by density dependence, and the degree of preadaptation required for the 'mutational collapse' of consumption of the less preferred resource is the same as would be predicted by the model of Kawecki *et al.* (1997). [When the resources are equally abundant, h in this paper is equivalent to $1/(1 + \varphi)$ in Kawecki *et al.* (1997).] When there is competition with an abundant specialist (Fig. 4), density dependence accentuates the rarity of the marginal resource, making the 'mutational collapse' of consumption of resource 2 by the focal consumer more likely than would be predicted by the model of Kawecki *et al.* (1997).

The present analysis has concentrated on models that assume that the resources under competition are nutritionally substitutable and that the per-capita growth rates of the consumer species depend solely on resource intake rates. We have also assumed that evolution (mutation accumulation) only influences resource consumption rates, and have not considered mutations affecting the ability to convert different resources to reproductive output (the parameters B). In models based on trade-offs, alternative assumptions (nutritional interactions between resources; presence of direct effects of consumer density on per-capita growth; evolution of conversion parameters) often result in parallel or convergent, rather than divergent, character displacement (Abrams, 1986, 1987, 1990). Qualitatively similar types of evolution are likely to occur under similar ecological assumptions when displacement is driven by mutation accumulation rather than by trade-offs. In both trade-off and mutation accumulation models, the driving force behind the displacement is a differential change, caused by the competitor, in the contribution of one of the resources to the fitness of the focal consumer. However, the magnitudes of displacement in these non-divergent scenarios are again likely to be relatively small without either high genomic mutation rates or relatively resource-specific mutations.

Traditional models of character displacement only consider variation along the outer boundary of the fitness set (the trade-off curve), assuming that any genes that do not show antagonistic pleiotropy should have become eliminated. In contrast, in our model, no loci show antagonistic pleiotropy in their effect on consumption of different resources. These are two extremes that are probably never realized in nature. Alleles segregating in natural populations will show all kinds of dependence on the environment, from being unconditionally deleterious, through affecting fitness in some environments but neutral in others, to improving fitness in some environments but reducing it in others. The relation between the environment and the fitness effect of an allele may be further complicated by epistatic interactions among loci. Future models of character displacement should take into account all these types of allelic variation and include forces – mutation, migration, temporal environmental variability – that maintain polymorphism at loci that do not show antagonistic pleiotropy. One conjecture we can make is that the two processes proposed for character displacement – optimizing selection along a trade-off curve and accumulation of mutations with conditionally deleterious effects – should facilitate each other. For example, if the population accumulates mutations that reduce its ability to digest a certain resource, optimizing selection will favour reduction of consumption of that resource if this can lead to increased consumption of other resources. This shift in the optimal consumption pattern will lead to weakening of selection against further mutations, reducing the ability to process the first resource. The resulting positive feedback between mutation accumulation and optimizing selection would lead to greater specialization than would either of these processes acting alone.

ACKNOWLEDGEMENTS

This study was supported by a grant from the National Science Foundation (DEB 9696049) to P.A. Abrams. We thank D. Queller for his comments on a previous draft of the manuscript.

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