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## GENETIC VARIATION FOR HABITAT PREFERENCE: EVIDENCE AND EXPLANATIONS

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*Abstract.*—Because adaptive shifts may often be initiated by evolutionary changes in behavior, it is of interest to determine the extent to which natural populations harbor genetic variation for ecologically important behaviors. Habitat preference is an especially significant behavior, because it determines the regime of natural selection acting on loci that affect adaptation to the environment. A survey of the literature reveals that genetic variation for habitat selection is common, especially in arthropods and mollusks, the groups that have been studied most frequently. Possible adaptive mechanisms by which this variation could be maintained within populations include a genetic correlation between density-independent fitness in a habitat and a preference for it; and soft selection, whereby density-dependent population regulation occurs independently in separate habitats. Several studies have documented a phenotypic correlation between preference and performance, but as yet, no such genetic correlations have been unequivocally demonstrated. We show theoretically that under hard selection, optimal habitat selection may often lower the probability of maintaining a polymorphism at a locus that affects adaptation to different habitats. Soft selection appears much more likely to promote variation for habitat preference. Mechanisms including resource competition and natural enemies whose numbers build up in a habitat-specific manner in response to host or prey density have the capacity to bring about selection favoring alleles whose carriers prefer relatively underused habitats. We believe that more progress in understanding the evolution of habitat preference will come from studies of these ecological mechanisms than from further demonstrations of the mere existence of genetic variation for such preferences.

A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior. . . . With habitat and food selection—behavioral phenomena—playing a major role in the shift into new adaptive zones, the importance of behavior in initiating new evolutionary events is self-evident. [MAYR 1963, p. 604]

Most discussions of the evolutionary importance of habitat preference are based on the assumption that animals actively select habitats to which they are best adapted morphologically or physiologically. Starting with Maynard Smith (1966), a number of workers have shown theoretically that the conditions for maintaining a multiple-niche polymorphism with soft selection are relaxed somewhat by such habitat selection (for review, see Hedrick 1986). Optimal habitat selection can filter the selective regime experienced by a population, and it can also influence effective population sizes and, therefore, the importance of drift and gene flow relative to natural selection as factors hindering local adaptation (Holt 1987*a*). However, as implied by Mayr's statement above, habitat selection

per se may be more important than specific adaptations to different environments in initiating evolutionary transitions. In view of its great potential evolutionary importance and its relative neglect in the literature, we focus primarily on genetic variation for habitat preference within populations.

Two laboratory examples serve to illustrate some possible evolutionary consequences of genetic variation in habitat selection in the absence of genotype-specific adaptation to different environments. Jones and Probert (1980) demonstrated in *Drosophila simulans* that a mutant eye-color allele that is competitively inferior in each of two habitats can nevertheless persist in a heterogeneous environment, because its bearers prefer the habitat that is avoided by wild-type flies. Thus, with habitat selection, habitat-specific adaptations are not required for the maintenance of genetic polymorphisms in variable environments. Habitat selection may also affect the genetic structure of a population. In laboratory populations of *Drosophila melanogaster*, disruptive selection on habitat selection in conjunction with genetically determined differences in fitness within habitats can bring about nearly complete reproductive isolation between the selected subpopulations (Rice and Salt 1988). The same result has been obtained even when there is selection on habitat preferences alone (W. R. Rice, personal communication). The key to these laboratory results is that habitat selection takes place before mating, thus ensuring assortative mating. Because mating occurs after dispersal and habitat selection in the life cycle of many species (Baker 1978), Rice's findings may be of great relevance to the real world.

The extent to which they are, of course, depends on the presence of genetic variation for habitat preference within natural populations. In this article, we review published data on such variation and explore several mechanisms that may be responsible for its maintenance. Because the environment is patchy at virtually all spatial scales, we take a liberal view of habitat selection and define it as any behavior that causes an individual to experience a set of environmental states different from that expected to be encountered by individuals moving at the same rate randomly through the environment. Thus, the scale on which habitat selection occurs clearly depends on the size and mobility of the species in question and on the spatial structuring of its environment.

#### EVIDENCE OF GENETIC VARIABILITY FOR HABITAT PREFERENCE

Our primary interest is in genetic variation for habitat preference *within* natural populations, since this is the level at which we believe most evolutionary changes occur. The following considerations guided our decisions about which empirical studies to include in our survey. (1) Because the vast majority of animals reproduce sexually and because sexual and parthenogenetic species evolve in fundamentally different ways, we have not considered clonal variation within parthenogenetic taxa (for review, see Gould 1983). (2) We also have not considered variants produced by laboratory mutagenesis; our concern is with naturally occurring variation. (3) Consistent differences among wild individuals in their fidelity to particular habitats does not necessarily mean that those differences have a genetic basis. We focus on examples for which there is at least some evidence

that the behavioral variation has a genetic component. (4) Many studies merely correlate variation in morph or karyotype frequencies with habitat characteristics. This tends to conflate the consequences of passive habitat sorting with those of active habitat selection, since such correlations could be due to variation among those types in habitat preference or due to variation among them in habitat-specific fitness (e.g., differential predation on morphs that do not match their background). Some cases (see, e.g., Curio 1965; Schoener and Schoener 1976; Coluzzi et al. 1977; Taylor and Powell 1978; Tabachnik et al. 1979) have been or could reasonably be interpreted as an outcome of genetically based differences in habitat preference. However, other examples of variation in morph frequencies among habitat types, as has been found, for example, in *Cepaea nemoralis* (Cain and Sheppard 1954) and the cricket frog *Acris crepitans* (Nevo 1973), are more likely due to differential mortality within habitats, leading to habitat sorting. (5) Finally, we focus primarily on studies documenting variation in habitat preference within, rather than among, populations. This seems reasonable, given that within-population variation provides the ultimate raw material for between-population differentiation.

We classify the studies reviewed into several, admittedly somewhat artificial, categories that are not mutually exclusive. We consider these in order of the increasing number of habitat choices of a given type made by an animal in its lifetime.

#### *General Residence*

Selecting a macrohabitat in which to live is a choice that may be made one or more times in an individual's lifetime. Several examples are presented in table 1.

In *Drosophila*, moderate degrees of variation among wild-caught individuals in their fidelity to different macrohabitats (e.g., dry, open woods vs. dense, moist woods) have been found in *Drosophila pseudoobscura* and/or *Drosophila persimilis* (Taylor and Powell 1978) and *Drosophila subobscura* (Kekic et al. 1980; Shorrocks and Nigro 1981), although negative results have also been obtained for these species (Atkinson and Miller 1980; Turelli et al. 1984). Taylor (1987) presented a general review of these findings and possible explanations for the discrepancies among studies. That the observed variation among individuals in habitat preference may have a genetic basis is suggested by differences in the behavior of flies whose ancestors were collected from different habitats (Kekic et al. 1980) and by differences among laboratory-reared strains when released in the field (Klaczko et al. 1986). Evidence for a genetic component of selection of a place to live has also been obtained for two species of intertidal mollusks (Giesel 1970; Byers 1983).

In some of these cases, the evidence for genetically based variation in macrohabitat selection is not very strong or consistent among replicate studies. A simple way to document such genetic differences would be to breed in the laboratory the offspring of individuals collected from different habitats and then to monitor their habitat preferences when released in the field. Taylor and Powell (1978), in fact, did this in one of their experiments but did not find that progeny preferentially returned to the habitats from which their parents were collected.

TABLE 1  
 SPECIES KNOWN TO HAVE GENETIC VARIATION  
 WITHIN POPULATIONS FOR GENERAL HABITAT SELECTION

Species	Habitats Distinguished	Genetic Evidence	Source*
<i>Drosophila:</i> <i>D. subobscura</i>	Dark spruce woods, open locust stand	Offspring of flies from locust stand more photopositive in lab assay	1
<i>D. persimilis,</i> <i>D. pseudoobscura</i>	Meadow, dense woods, open woods	Differences among released homokaryotic strains	2
Mollusks: <i>Tegula funebris</i>	Height in intertidal zone	Consistent differences in individual behavior correlated with leucine aminopeptidase in Oregon and with phosphoglucoisomerase in Washington	3
<i>Acmaea digitalis</i>	Gooseneck barnacle beds, high intertidal rock faces	Individual movements correlated with shell color pattern	4

\* 1, Kekic et al. 1980; 2, Klaczko et al. 1986; 3, Byers 1983; 4, Giesel 1970.

### Background Matching

Every day, around dawn, night-flying moths select a site on which to settle for the day. Because they are attacked by visually orienting predators, they have been subject to strong selection to settle upon a background against which they are cryptic. Endler (1984) has shown that day-resting moths are most cryptic at the time of year when they are active and on their normal resting sites, and Sargent (1966) has documented a strong correlation among species of moths between wing reflectance and preference for settling on light versus dark backgrounds. One might, therefore, expect an association between color morph and preference for different resting sites within species polymorphic for visually apparent characters. In quite a few species, there is such variation among wild-caught individuals or their offspring, with melanic morphs preferring darker substrates (table 2). In a few species, however, there appears to be no such association.

The positive associations between color morph and background preference suggest either that preference may be a pleiotropic manifestation of the genes affecting color or that it is influenced by loci closely linked to them. However, genetic studies on *Biston betularia* (Grant and Howlett 1988), one of the species in which wild-caught individuals of the typical and melanic morphs differ in preference, and *Allophyes oxyacanthae* (Steward, 1976, 1977, 1985) do not support this prediction. When laboratory-reared individuals are used, it appears that resting-site preference has a genetic component—there are indeed consistent dif-

TABLE 2  
BACKGROUND MATCHING IN INSECTS

Species	Individual Variation	Genetic Variation	Correlation with Color Morph	Source*
Acrididae:				
<i>Circotettix rabula</i>	+	?	+	1
Noctuidae:				
<i>Catocala ultronia</i>	+	+	+	2
<i>Brachionycha sphinx</i>	+	+	+	3
Geometridae:				
<i>Cosymbia pendulinaria</i>	?	?	-	4
<i>Philgalia titea</i>	?	?	-	5
<i>Philgalia pilosaria</i>	?	?	-	6
<i>P. pilosaria</i>	+	+	+	3
<i>Lycia hirtaria</i>	+	+	+	3
<i>Gonodontis bidentata</i>	+	+	+	3
<i>Biston betularia</i>	+	+	+	3,7-9
<i>B. betularia</i>	+	+	-	10
Caradrinidae:				
<i>Allophyes oxyacanthae</i>	+	+	-	9,11,12

NOTE.—Correlation between color morph and background preference or genetic evidence for variation in preference implies individual variation in preference. +, positive association; -, no association; ?, unknown.

\* 1, Gillis 1982; 2, Sargent 1966; 3, Kettlewell and Conn 1977; 4, Sargent 1968; 5, Sargent 1969; 6, Lees 1975; 7, Kettlewell 1955; 8, Boardman et al. 1974; 9, Steward 1985; 10, Grant and Howlett 1988; 11, Steward 1976; 12, Steward 1977.

ferences among individuals both within and among broods—but that this preference is independent of color morph. Thus, surprisingly, neither linkage nor pleiotropy would seem to account for the association between preference and color in wild individuals.

These apparently contradictory results may be reconciled if it is assumed that color and preference are governed by unlinked loci, and that selective predation had already acted on the wild-caught individuals before they were sampled; moths that preferred a substrate against which they were not cryptic would be eliminated before collections were made. The survivors would be individuals that genetically prefer the “right” background. Haldane’s (1956) calculation of a 50% selective difference between morphs of *B. betularia* lends credibility to this notion.

The best-documented example of a correlation between color morph and background preference is in the grasshopper *Circotettix rabula* (Gillis 1982), in which individuals preferred substrates that matched their body color. It is not known, however, whether variation in body color is genetically determined in this species.

#### *Routine Daily Activities*

Animals are attracted to and settle at potential food resources in order to carry out a variety of activities, such as feeding, courtship, mating, oviposition, and grooming. The frequency with which individuals move among such sites is generally not known.

TABLE 3  
SPECIES IN WHICH INTRAPOPULATION VARIATION IN PREFERENCE FOR HABITATS  
IN WHICH TO CARRY OUT ROUTINE ACTIVITIES HAS BEEN DEMONSTRATED

Species	Resources Distinguished	Genetic Evidence	Source*
<i>Drosophila:</i>			
<i>D. buzzatii</i>	5 naturally occurring yeast strains	Correlation between esterase genotypes and yeast attracted to	1
<i>D. melanogaster</i>	Apples, peaches, plums	Consistent differences in olfactory responses of flies originating from different fruit types	2
<i>D. pseudoobscura</i>	Saccharomyces, <i>Kloeckera</i> (yeasts)	Differences among strains when released in the wild	3
<i>D. tripunctata</i>	Mushrooms, tomatoes	Consistent differences among isofemale strains	4
Crustaceans:			
<i>Gammarus palustris</i>	<i>Enteromorpha</i> , <i>Ulva</i> (algae)	Consistent differences among amylase genotypes	5
<i>Asellus aquaticus</i>	Beech and willow leaves	Consistent differences among amylase genotypes	6
Mollusks:			
<i>Cepaea nemoralis</i>	Height in vegetation (or time of activity)	Consistent differences among banded and unbanded snails	7
<i>Arianta arbustorum</i>	Time of activity or position in vegetation	Differences between yellow and brown morphs	8

\* 1, Barker et al. 1981; 2, Hoffman et al. 1984; 3, Klaczko et al. 1986; 4, Jaenike 1985; 5, Borowsky et al. 1985; 6, Christensen 1977; 7, Jones 1982; 8, Abdel-Rehim 1983.

In *Drosophila*, small but consistent differences among wild individuals in their resource use (or settling behavior) have been found in *Drosophila melanogaster* and/or *Drosophila simulans* (Turelli et al. 1984), *Drosophila falleni*, and *Drosophila tripunctata* (Jaenike 1986a). That this behavioral variation is at least in part genetically based has now been demonstrated or is strongly suggested in a number of species (table 3). In *D. melanogaster*, lab-reared descendants of individuals collected from different fruit types in an orchard exhibit generally consistent preferences in a wind tunnel for the appropriate fruit odors (Hoffmann et al. 1984). Two isofemale strains of *D. tripunctata*, descended from a single natural population, show consistent and very large differences in preference for two resource types when flies are released in the field (Jaenike 1985).

In *Drosophila buzzatii*, the frequencies of various esterase-2 alleles have been found to vary as a function of the yeast strain used in baits (Barker et al. 1981). However, the association between particular esterase alleles and yeast strains changed from one experiment to the next over an 18-mo period. Furthermore, within experiments, esterase-allele frequencies in flies captured at baits were

influenced by significant yeast-by-site interactions, showing that the preference of flies carrying a given allele varied from one site to another. These results suggest that a locus linked to esterase indeed affects a fly's preference for different yeasts but that esterase itself is not important.

Consistent associations between food preference and allozymes have also been discovered in the crustaceans *Gammarus palustris* (Borowsky et al. 1985) and *Asellus aquaticus* (Christensen 1977). It is suggestive that in both species the allozymes studied were amylases and that the foods were different species of plants, which may vary in the amount and kind of starch they contain.

Finally, in the snails *C. nemoralis* (Jones 1982) and *Arianta arbustorum* (Abdel-Rehim 1983) individuals of different morphs vary in how much they expose themselves to sunlight. However, the relative importance of differences in habitat selection per se versus differences in the temporal pattern of activity in causing this is not known.

It is worth noting that in some species, including many *Drosophila*, mating, as well as feeding and other activities, occurs at patches of food resources. Thus, to the extent that preference has a genetic basis, there will tend to be assortative mating between individuals with similar preferences, and this can increase the genetic variance for preference and its heritability (Nagylaki 1982).

#### *Oviposition-Site Preference*

For species in which juveniles are relatively immobile, the selection of an appropriate oviposition site by adult females is very important. In essence, oviposition-site preferences of females determine the habitats used by their offspring. There is now abundant evidence that, at least in insects, variation in oviposition-site preference frequently has a genetic basis (table 4). In fact, species in which such variation has not yet been found, such as the tortoise beetle *Deloyala guttata* (Rausher 1983), stand out as exceptions to the general rule.

Most of the evidence on genetic variation for oviposition behavior has been obtained on various species of Diptera and Lepidoptera. In many species of Diptera, such as most *Drosophila*, oviposition frequently occurs at the same sites as feeding and mating. One might expect, therefore, that the determinants of oviposition-site preference would be the same as those that govern site selection for the routine daily activities covered in the previous section. However, this is not always the case; prior experience affects settling behavior and oviposition in different ways in *D. melanogaster* (Hoffmann 1985), and these two behaviors are under independent genetic control in *D. tripunctata* (Jaenike 1986*b*). Among Lepidoptera, adults and larvae feed on different types of resources, and therefore one might not expect a correlation between oviposition-site preference and selection of sites for other activities (see, e.g., Wiklund 1977).

The studies cited in table 4 reveal a number of patterns in the nature of changes in oviposition-site preference and the populations in which they occur. These include the following.

1. Behaviors affected by genetic variation for oviposition-site preference:
  - (a) the rank order of preferences for different substrates (*D. tripunctata* and



TABLE 4

INSECTS KNOWN TO HAVE WITHIN-POPULATION GENETIC VARIATION FOR OVIPOSITION-SITE PREFERENCE

Species	Oviposition Sites Discriminated	Genetic Evidence	Source*
Diptera:			
<i>Drosophila buzzatii</i>	Microbial communities (yeast species)	Correlation with each of 7 allozyme loci	1
<i>Drosophila mojavensis</i>	Acceptance of novel substrate, agria cactus	Significant sire component in half-sib design	2
<i>Drosophila tripunctata</i>	<i>Amanita muscaria</i> , <i>Russula compacta</i> , <i>Leccinum scabrum</i>	Differences among isofemale strains	3
<i>D. tripunctata</i>	<i>Agaricus bisporus</i> , tomatoes	Crosses between isofemale strains	4
<i>Liriomyza brassicae</i>	3 species of introduced crucifers	Differences among flies reared from different host plants	5
<i>Liriomyza sativae</i>	Tomatoes, peas	Differences among individuals collected from different populations	6
Lepidoptera:			
<i>Colias eurytheme</i>	Alfalfa, vetch	Differences among laboratory-reared full-sib families	7
<i>Euphydryas editha</i>	<i>Collinsia parviflora</i> (native), <i>Plantago lanceolata</i> (introduced)	Correlation between mother and female offspring	8
<i>Laspeyresia pomonella</i>	Apples, walnuts, plums	Differences among laboratory-reared individuals	9
<i>Papilio oregonius oregonius</i>	3 species of umbellifers, 1 composite	Differences between 2 isofemale lines	10
<i>Papilio zelicaon</i>	3 species of umbellifers, 1 composite	Differences among 4 isofemale lines	10
Coleoptera:			
<i>Callosobruchus maculatus</i>	Azuki beans, pigeon peas	Response to selection	11

\* 1, Barker et al. 1986; 2, Lofdahl 1986; 3, Jaenike and Grimaldi 1983; 4, Jaenike 1987; 5, Tavormina 1982; 6, Via 1986; 7, Tabashnik et al. 1981; 8, Singer et al. 1988; 9, Phillips and Barnes 1975; 10, Thompson 1988; 11, Wasserman and Futuyma 1981.

*Laspeyresia pomonella*); (b) the degree of specificity for different hosts within the same rank order of preference (*Drosophila mojavensis*, *Liriomyza brassicae*, *Liriomyza sativae*, *Colias eurytheme*, *Euphydryas editha*, *Papilio zelicaon*, and *Papilio oregonius*). Changes in specificity appear to be more common than changes in rank-order preference.

- Types of breeding sites for which genetically based variation in oviposition behavior has been found: (a) native, naturally occurring breeding sites (*Drosophila grimshawi*, *D. tripunctata*, *P. oregonius*, and *P. zelicaon*); (b) introduced weeds (*L. brassicae*, *E. editha*); (c) agricultural crops (*L. sativae*, *C. eurytheme*, *L. pomonella*, and *Callosobruchus maculatus*); (d) novel substrates (e.g., *D. mojavensis*).

TABLE 5  
HABITAT SELECTION BY *DROSOPHILA* LARVAE

Species	Genetic Evidence	Consequences	Source*
Foraging-site selection:			
<i>D. pseudoobscura</i>	Differences among strains in preference for various artificial media	Correlation among strains between habitat choice and developmental rate	1
<i>D. melanogaster</i>	Differences between ADH genotypes in preference for ethanol-containing medium	Correlation between ADH activity and ethanol content of media	2,3
Pupation-site selection:			
<i>D. melanogaster</i>	Differences among isofemale lines in pupation height and among lab stocks established from pupae collected on or away from larval breeding site	May affect probability of survival as function of soil-water content and probability of parasitism	4,5

\* 1, Taylor and Condra 1983; 2, Cavener 1979; 3, Parsons and Spence 1981; 4, Sokolowski 1985; 5, Sokolowski 1986.

3. Areas where such genetic variation has been found: (a) populations within the original geographic range of the species (e.g., *D. mojavensis*, *D. tripunctata*, *C. eurytheme*, *E. editha*, *P. oregonius*, and *P. zelicaon*); (b) introduced populations (e.g., *D. buzzatii*, *C. maculatus*, and *L. pomonella*).

Given this abundant evidence for intraspecific genetic variation for oviposition behavior, this component of breeding-site use is unlikely to limit the capacity of insects to undergo evolutionary changes in host specificity.

#### *Larval Habitat Selection*

Even if the behavior of ovipositing females determines to a large degree the types of food resources consumed by their offspring, these offspring can often (to the extent permitted by their mobility) select particular microhabitats within the general vicinity of their birthplace. Several studies of *Drosophila* indicate that such larval habitat selection can have a genetic component (table 5). Larvae of *D. pseudoobscura* move preferentially to media on which individuals of their strain develop best (Taylor and Condra 1983). The reaction of *D. melanogaster* larvae to medium containing ethanol varies as a function of their *Adh* genotype, such that those with higher adenine dehydrogenase (ADH) activity showing a greater preference for ethanol (Cavener 1979; Parsons and Spence 1981). These observations suggest some sort of a genetically based preference-performance correlation in larvae.

Larval behavior also determines where an individual will undergo pupation. Variation for pupation-site selection, either on or away from the larval food, has recently been demonstrated among strains of *D. melanogaster* (Sokolowski 1985,

1986). Strains that behave differently in the laboratory do so in the field. Sokolowski (1985) suggested that survival through the pupal stage may depend in a site-specific manner on the soil-water content in the vicinity of the larval food. The risk of predation or parasitism might vary among pupation sites as well.

The fact that larvae can choose among microhabitats near a given oviposition site underscores the notion that the environment is, from the point of view of a particular species, patchy on a number of spatial scales and that one should seek genetic variation in habitat selection on each of these scales.

### *Methodological Problems*

Although the studies reviewed above strongly suggest that genetic variation for habitat selection is widespread, a number of questionable procedures lessen our confidence in the conclusions of some studies. The following are some of the problems that appear to be generic in studies of habitat selection, but could easily be remedied.

1. *Failure to distinguish sibling species.*—It is unlikely that sympatric sibling species will be identical with respect to habitat selection. After all, competition, whether real or apparent (Holt 1977), may be expected to cause their ecological divergence. Thus, if one failed to distinguish sibling species, one might conclude that a population under study harbored intraspecific variation for habitat selection. This problem should be easiest to get around when it is known that the organisms under study in fact comprise two or more sibling species. We question the practice of lumping individuals from different sibling species after preliminary work fails to reveal a significant difference between them in their distribution across habitats.

Even when a taxon consists of only one described species, it is frequently the case, especially in insects, that it may actually consist of two or more sibling species. Enzyme electrophoresis can be a quick and effective method for testing this possibility, although, for very closely related sibling species, more sensitive methods may be needed (e.g., analysis of highly repetitive DNA).

2. *Failure to distinguish male from female behavior.*—Adult males and females of most species for a variety of reasons might be expected to differ in some aspects of habitat use (e.g., because of differences in body size or reproductive strategies). Thus, if the sexes are lumped for analysis, one might often find consistent individual differences in habitat preference that reflect nothing more than differences between males and females in their behavior.

3. *Problems with replication.*—In some of the studies that included true, independent replicates, there were occasionally substantial inconsistencies among them. For instance, there may be a highly significant effect of genotype on habitat preference in one replicate, but no effect in the next. There are also inconsistencies among research groups carrying out essentially identical experiments on the same species. These inconsistencies underscore the necessity of replication.

One possible cause of these inconsistencies is that populations are often highly structured genetically even within habitats (see, e.g., Selander and Kaufman 1975). As a result, samples collected from a limited area within each of two habitats may not accurately reflect the average degree of genetic divergence between the two populations.

4. *Assessing levels of interpopulation variation.*—Although we have focused our concern on genetic variation found within populations, several studies documented interpopulation heterogeneity. However, just as in an analysis of variance, the significance of differences among populations can be assessed only when levels of intrapopulation variation are also determined. What is needed is more extensive work on geographic variation in habitat preference, with equal attention being given to the documentation of within- and between-population variation.

#### MAINTENANCE OF THE VARIATION

Despite our reservations about the methods employed in some studies, it is nevertheless clear that genetic variation for various types of habitat selection is quite common, at least in the groups that have been subject to the most study. The question thus arises as to how this variation is maintained within populations. We focus here on the adaptive significance of genetic variation for habitat selection. The possibility that such variation is maintained by mutation-selection balance is explored in some detail elsewhere (Jaenike 1990). Adaptive explanations of variation in habitat selection fall into two general categories.

1. *Preference-performance correlations.*—Genetic variation for habitat selection can, under some circumstances, be maintained if it is correlated, via linkage or pleiotropy, with genetic variation affecting adaptation to different habitats. For the case of linkage, Bush (1974) has sketched a two-locus model—one locus affects the host preference of ovipositing females, and the other determines larval survival in a density-independent manner on alternative hosts—in which host races of insects could be formed as a result of such preference-performance correlations. However, if a population is initially monomorphic for alleles allowing use of only the ancestral host, it is implausible to postulate the selective increase of rare alleles at both loci if the selective advantage of each depends on the presence of the other in an individual. Thus, it would be more reasonable to assume that a population is initially polymorphic at a locus that affects either preference or performance and that this facilitates the spread of rare alleles affecting the other trait, thus bringing about a preference-performance correlation. Garcia-Dorado (1986) has explored such a situation theoretically, but her model assumes strong density-dependent regulation within each habitat, which in itself promotes genetic variation for habitat preference, even if individuals are not specifically adapted to the habitats they chose (see 2 below). We should point out that, if preference and performance are polygenically controlled traits, then it is very unlikely that linkage could maintain genetic correlations between them, unless there is very strong assortative mating.

An alternative and simpler means by which a preference-performance correlation could be achieved is through pleiotropic effects of a single locus or set of genes. Any mechanism that allows an animal to monitor and respond to its present well-being could, in conjunction with genetic variation in adaptation to different habitats, bring about such a genetic correlation. We explore the theoretical consequences of this possibility later.

2. *Density-dependent regulation within different habitats.*—If population sizes

are regulated independently in different habitats, then frequency-dependent selection favors alleles that confer upon their carriers a preference for underused habitats, even if there is no genetic variation in how well individuals are adapted to the different habitats. In this manner, polymorphisms for habitat selection can be maintained quite easily (Templeton and Rothman 1981; Rausher 1984; Rausher and Englander 1987). In these models, it is assumed that each habitat contributes a constant fraction of the breeding adults to the general population each generation. This is an extreme form of density dependence, which gives a great advantage to rare types. However, it is reasonable to assume that less extreme forms of density dependence would also promote genetic variation for habitat selection (see, e.g., the models of genetic polymorphism in heterogeneous environments in Arnold and Anderson 1983; Wilson and Turelli 1986). We consider below the evidence for these possibilities, genetic correlations between preference and performance and density-dependent regulation within habitats.

#### *Preference-Performance Correlations*

Probably the most widely recognized correlation between habitat selection and differential adaptation within populations concerns the resting-site preferences of pale and melanic moths (table 4). The variation in preference between morphs was attributed by Kettlewell (1955) to a form of pleiotropy: moths were hypothesized to select a resting site that minimized contrast with their circumocular scales. However, experimental manipulations of moths by Sargent (1968) and Grant and Howlett (1988) have failed to support this conjecture. The genetic crosses carried out by Steward (1976, 1977, 1985) and Grant and Howlett (1988) not only fail to support the pleiotropy hypothesis but also demonstrate that, even though preference appears to be genetically influenced, the loci affecting preference are not linked to the gene that governs body color. As mentioned previously, the observed difference in resting-site preference between color morphs of wild-caught individuals may be due to selective predation's having already taken place on the cohort of individuals in the field. In the grasshopper *Circotettix rabula*, body color clearly influences the type of background substrate preferred (Gillis 1982). However, it is not known whether its body coloration is genetically based.

The finding that *Drosophila* larvae prefer the medium in which they develop fastest (Taylor and Condra 1983) or for which they may have appropriate allozymes (Cavener 1979; Parsons and Spence 1981) is probably due to pleiotropy. Because the strains studied had not been selected for their ability to use the various media considered, one would not expect linkage disequilibrium between the loci affecting preference and those governing larval growth rate or enzyme activity (unless strong selection had acted during the course of the experiment, killing larvae that chose the "wrong" medium). It would be interesting to determine whether larvae within individual breeding sites in the field genetically segregate themselves into different microhabitats where they develop best.

There is growing interest in the possibility that there may be genetic correlations in insects between female oviposition-site preference and offspring performance on different hosts. Associations between female host preference and larval

TABLE 6  
STUDIES DEMONSTRATING CORRELATIONS BETWEEN OVIPOSITION-SITE PREFERENCE AND  
LARVAL PERFORMANCE IN INSECTS

Species	Breeding sites	Correlation	Source*
<i>Liriomyza sativae</i>	Tomatoes, peas	Positive	1
<i>Drosophila tripunctata</i>	Mushrooms, tomatoes	Not significant	2
<i>D. tripunctata</i>	Medium with or without amanitin	Not significant	2
<i>Euphydryas editha</i>	<i>Collinsia parviflora</i> (native host), <i>Plantago lanceolata</i>	Positive	3
<i>Colias philodice</i>	Alfalfa and vetch	Not significant	4

\* 1, Via 1986; 2, Jaenike 1988; 3, Singer et al. 1988; 4, Tabashnik 1986.

performance have been found between populations of some insects. For instance, two populations of *Euphydryas editha* that differ greatly in oviposition behavior (Singer 1971) also vary in larval performance on the host plants used by these populations (Rausher 1982). Larvae from each population grew faster and had higher survival on the host preferred as oviposition sites by females of that population. Similarly, adult females of the tobacco budworm *Heliothis virescens* from Mississippi have a greater oviposition preference for cotton, and the larvae grow better on cotton, than do individuals from the Virgin Islands, where cotton is rarely used as a host plant (Schneider and Roush 1986). However, because evolution proceeds in large measure by changes within populations, it is important to determine whether such correlations are also found at this level.

A small number of studies have now been carried out to address this question (table 6). Positive correlations between female oviposition-site preference and offspring performance within populations or geographic regions were found in *Liriomyza sativae* and *E. editha*, whereas in *Drosophila tripunctata* and *Colias philodice* these correlations were not significantly different from zero. Oviposition behavior in *Liomyza*, *Euphydryas*, and *Colias* was measured in individuals collected as larvae or adults from the field. Because it is possible that environmental conditions (such as the food type a larva or adult has fed upon) or a female's age could influence both her oviposition behavior and the quality of the eggs she produces (Wellington 1965), the sign and magnitude of a phenotypic correlation will not necessarily be the same as those of a genetic correlation. For instance, an induced preference for the food type that an individual consumed as a larva and on which it is probably fitter than average (as evidenced by the fact that it survived on that host) could produce a correlation between oviposition-site preference and offspring performance, even if there were no genetic variation for oviposition behavior. Such a preference might be induced in young adults if they emerge in the vicinity of their larval food. Thus, the existence of a positive genetic correlation between oviposition-site preference and offspring performance within populations is not yet firmly established for any insect species. Given the potential evolutionary importance of such correlations, further studies are certainly warranted.

In sum, there does not appear to be much evidence to support the idea that genetic variation for habitat preference within populations is maintained by a correlation with adaptation to different habitats. In the last section of this article, we explore a theoretical model that indicates that correlations between habitat preference and density-independent, habitat-specific fitness are unlikely to provide a general explanation for the widespread occurrence of genetic variation in preference. We find, in fact, that optimal habitat choice may often make polymorphisms affecting habitat choice or adaptation to different habitats *less* likely to be stable.

*Ecological Processes Bringing about Density-Dependent Regulation  
within Habitats*

The other major possibility for explaining genetic variation in habitat preference is that density-dependent population regulation occurs separately in different habitats, thus bringing about selection favoring alleles whose carriers prefer underused habitats.

Most of the examples we found to document genetic variation for habitat selection concerned insects. However, variation for habitat selection and the density-dependent ecological factors that may influence it have not been studied concurrently within the same population of a species. The following is a discussion of some ecological factors that may be important for insects.

Competition for food resources is generally considered relatively unimportant in most insects (Andrewartha and Birch 1954; Strong et al. 1984). However, it may be significant in species that breed in discrete, ephemeral resources, such as carrion, dung, dead wood, decaying fruits, and so on (Beaver 1984). In *Drosophila*, larval competition has been demonstrated in both fruit- and mushroom-breeding species (Atkinson 1979; Grimaldi and Jaenike 1984). In these species, individuals that prefer relatively underused resources might suffer less competition.

Natural enemies—predators, parasites, parasitoids, and diseases—are generally thought to keep many insect populations well below levels at which competition for food occurs. Frequently, these enemies seem to regulate insect populations in a density-dependent manner (Strong et al. 1984), and because time delays and spatial variation in the intensity of predation or parasitism may obscure their regulatory effects, density-dependent regulation by natural enemies may be even more pervasive than is generally believed (Hassell 1985).

Some indirect evidence suggests that many enemies may affect their phytophagous insect prey in a host-plant-specific manner. Redfearn and Pimm (1988) analyzed several large data sets on the population dynamics of aphids and moths and found that year-to-year variation in population sizes (log-transformed) tends to be inversely correlated with the degree of polyphagy in these species. In other words, monophagous species tend to fluctuate more in their abundance than do polyphagous species. Although not mentioned by Redfearn and Pimm, one possible explanation of this pattern is that some component of the variability in abundance is an outcome of host-parasite or predator-prey interactions. If the enemies that attack a given insect species vary as a function of its host plant, as is often

the case (Lawton 1978), and if there are asynchronous fluctuations in the abundance of these different enemies, then, by an averaging process, populations of polyphagous insects should vary less in total size than those of monophagous species.

An important component of the concept of enemy-free space (Lawton 1978, 1983; Lawton and Strong 1981; Jeffries and Lawton 1984) is that in the initial phases of their search, predators and parasites select a particular habitat, host plant, or part of a plant before searching for prey or hosts. Because many parasitoids are specific to particular species of plants rather than to insect hosts (Lawton 1978), an abundance of an insect on one host plant could cause a population increase in the parasitoids there and favor individuals that prefer less used host plants.

The behavior of general predators can have similar effects. Martin (1988) demonstrated that predators, primarily chipmunks and red squirrels, that prey on birds' eggs concentrate their search in habitats where they have previously discovered nests with eggs. Martin concluded that nest predation could favor the coexistence of bird species that differ in the sites preferred for nesting. Holt (1984, 1987*b*) examined the implications of aggregation by general predators for prey species' coexistence in a spatially heterogeneous environment. Such a mechanism might also promote genetic variation in nest-site preference within species, especially those that are important items in the diet of mobile, general predators.

Natural enemies, such as internal parasites or phoretic, predatory mites, that are carried among habitats by their hosts or prey could also bring about frequency-dependent selection for habitat selection. For example, several species of mycophagous *Drosophila* are parasitized, and often rendered infertile as a result, by the nematode *Howardula aoronymphium* (Welch 1959; Montague and Jaenike 1985). Inseminated females of this parasite infect larval *Drosophila* and produce hundreds of offspring within the fly when it becomes an adult. These offspring then escape through the anus or ovipositor when the fly visits a mushroom, where they can infect the next generation of larvae. It seems very likely that mushrooms attracting the most flies also have the highest densities of parasitic nematodes associated with them.

Finally, a disease that undergoes local epidemics when a critical threshold density of its host is surpassed could favor the use of alternative habitats by the host. For instance, the use of a secondary host plant, pitch pine, by the gypsy moth may be caused in part by high probabilities of mortality resulting from infection with nuclear polyhedrosis virus in larvae feeding on oaks, the primary hosts (Rossiter 1987).

It would seem, then, that a variety of ecological processes could bring about frequency-dependent selection for individuals that prefer less crowded habitats. These processes are usually invoked to explain stable coexistence of different species, particularly via habitat partitioning (Schoener 1974; Holt 1984), but they could also promote genetic variation for habitat selection within species. We would expect to find such variation most often in species subject to spatially localized, strongly density-dependent regulation, whether this regulation occurs by competition for resources or control by natural enemies. In species subject



only to weakly density-dependent regulation at most times, factors favoring the maintenance of genetic variation for habitat selection ought to be less important. In fact, the difficulty of finding a mate may actively select for habitat specialization and monomorphism in rare species (Colwell 1986). Note that, if variation in habitat selection were maintained solely by a density-independent preference-performance correlation, then we would not expect to find an association between the strength of density-dependent regulation and a tendency to be genetically variable for habitat selection.

A MODEL FOR THE MAINTENANCE OF GENETIC VARIATION IN HABITAT PREFERENCE  
WITH DENSITY-INDEPENDENT FITNESSES

Ecological models of habitat selection (e.g., Fretwell 1972; Rosenzweig 1981; Pulliam and Danielson 1991) assume that each individual prefers the habitat in which it is most fit. Several distinct kinds of genetic machinery could underlie any given example of habitat-selection behavior. For instance, there could be tight linkage between loci that separately govern fitness and habitat preferences. Alternatively, allelic variation at a single locus could pleiotropically influence both local adaptation and habitat preferences. Such pleiotropy might arise in a variety of ways. One general mechanism leading to pleiotropy is for all individuals in a population to behave according to rules that tend to increase their fitness. For instance, a rule might be "remain in habitats in which body temperature stays within  $X\%$  of the physiological optimum of  $Y^\circ\text{C}$ ." Variation at a locus that directly influences body color, and thus an individual's temperature in a given habitat, would indirectly lead to behavioral differences in habitat use between individuals differing in body color. The model developed below assumes this sort of pleiotropic relation between habitat use and within-habitat fitnesses.

Consider a species with the following life cycle: (start of generation  $t$ ) zygote formation  $\rightarrow$  dispersal and habitat choice  $\rightarrow$  habitat residence and selection (differential mortality)  $\rightarrow$  random mating across the entire population (start of generation  $t + 1$ ). Two discrete habitat types are present, and following an episode of dispersal early in the life cycle, individuals are restricted to a single habitat. Following habitat choice, the fraction of individuals with genotype  $ij$  found in habitat 1 is  $D_{ij1}$ . The realized fitnesses of individuals with genotype  $ij$  in these two habits are  $W_{ij1}$  and  $W_{ij2}$ , respectively. The average fitness of individuals with genotype  $ij$  is thus

$$W_{ij} = W_{ij1} D_{ij1} + W_{ij2} (1 - D_{ij1}). \quad (1)$$

Thus, genotypic fitnesses are determined simply by the fitnesses of their carriers in each habitat, weighted by the fraction of these carriers found in each habitat. In general,  $D_{ij1}$  will increase monotonically with both the availability of habitat 1 and the selectivity of the genotype for that habitat. We assume that such selectivity is relatively constant for a given genotype. This may be appropriate for insects but is doubtless far too simple for vertebrates.

This expression could encompass a wide variety of natural-selection schemes,

including frequency dependence, density dependence, and soft selection. Here we examine the simplest kind of spatially structured selection, in which the realized fitness of genotype  $ij$ , once an individual is settled in a habitat, is a habitat-specific constant. The average genotypic fitnesses are thus also constant, and the model reduces to the classical model of natural selection in a constant environment (see, e.g., Nagylaki 1977). A polymorphism will be protected (in the sense of Prout 1968) if and only if  $W_{12} > W_{11}$  and  $W_{12} > W_{22}$ .

In this model, a gene locus has pleiotropic effects on both within-habitat fitnesses (the  $W_{ij}$ ) and habitat preferences ( $D_{ij}$ ). To what extent does the maintenance of variation in one of these characters depend on variation in the other? To explore this question, we use a simple graphic representation of the relation between average genotypic fitness and habitat preference. In figure 1, we plot the average fitness of each genotype as a function of  $D_{ij2}$ , the fraction of individuals with genotypes  $ij$  which reside in habitat 2, for a variety of different cases. The straight lines represent families of genotypes that have identical within-habitat fitnesses but differ in their habitat preferences. A given genotype thus corresponds to a point along this line. By inspection, one can ascertain whether a given heterozygote has greater fitness than both homozygotes. As noted above, the parameter  $D_{ijk}$  conflates relative habitat availabilities and behavioral preferences into a single compound measure of realized habitat selectivities. We assume here that the two habitats are equally abundant; thus, any deviation in  $D_{ij}$  from 0.5 indicates habitat preference.

One simple case is for all genotypes to have the same within-habitat fitnesses but to differ in their habitat preferences. For variation in habitat preferences to persist stably, the heterozygote must occupy the better habitat more often than do either of the two homozygotes (fig. 1A), a result also obtained by Templeton and Rothman (1981). In essence, overdominance in fitness reflects the heterozygote's superior ability at selectively occupying the better habitat. In this case, genetic variation in habitat preference will obviously exist, even though there is no intrinsic variation in adaptive capabilities among the genotypes. It is not clear on mechanistic grounds why one should expect this kind of overdominance in ability to select habitats to be at all common. If by contrast the heterozygote has an intermediate preference, the population will become fixed for one allele.

If both habitats lead to the same realized fitnesses for all three genotypes, variation in habitat preference may exist, but it will be selectively neutral. The amount of such variation in a given population in this case reflects a mutation-migration-drift balance. This contrasts with the case of soft selection, in which even in a haploid model without intrinsic fitness differences among genotypes, genetic variation in fixed habitat preferences may be maintained stably. In the following paragraphs, we assume that there are both spatial and genotypic variations in fitness, such that the heterozygote has both intermediate within-habitat realized fitnesses and intermediate habitat preferences.

First, assume that all genotypes have the same degree of habitat preference and that all genotypes are fittest in habitat 1. However, the rank order of realized genotypic fitnesses is reversed between the two habitats. Our graphic model then

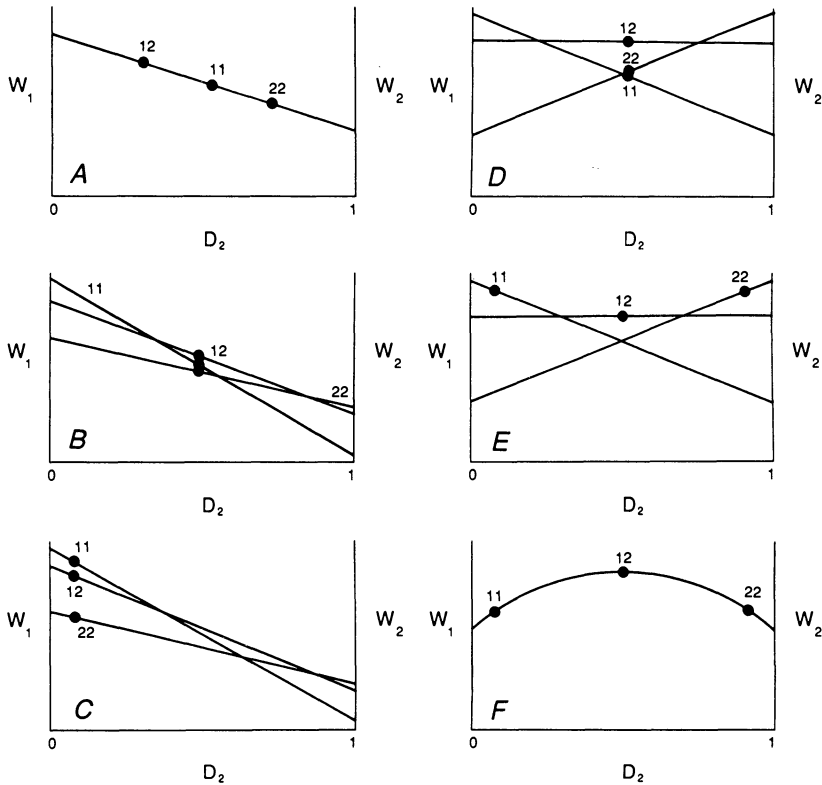


FIG. 1.—Graphic model of the effect of habitat selection and habitat-specific, density-independent fitnesses on the stability of genetic polymorphisms. The average fitness of a genotype (11, 12, or 22) is indicated by the height of the dots along the lines in the figures. This fitness is a function of  $W_1$  and  $W_2$ , the fitnesses in habitats 1 and 2, respectively, and  $D_2$ , the fraction of individuals of a given genotype that select habitat 2 (see expression [1] in text). Polymorphisms are stable if the mean heterozygote fitness is greater than that of either homozygote. *A*, All genotypes have the same within-habitat fitnesses (the fitness curves are coincident), but they differ in their habitat preferences. In the case shown, the heterozygote has the highest preference for the better habitat, thus maintaining a stable polymorphism for preference. *B–E*, The fitness of the heterozygote is greater than the mean of the homozygote fitnesses within each habitat. *B–C*, Habitat 1 is better for each of the three genotypes; *D–E*, the two homozygotes are fittest in different habitats. With no habitat selection (*B, D*), half of the individuals of each genotype end up in each of the two habitats, and because of marginal overdominance the polymorphism is stable. With optimal habitat selection, in which individuals prefer the habitat where their own fitness is greatest, allele 1 goes to fixation in *C*, whereas alternative stable monomorphic conditions are possible in *E*. Prospects for a stable polymorphism are thus diminished by optimal habitat selection. *F*, If having a strong preference for a particular habitat reduces fitness, perhaps because of excessive time spent searching for that habitat, and if homozygotes have stronger preferences than heterozygotes, then a stable polymorphism for preference may be maintained.

provides a restatement of the classical model of Dempster (1955) for the maintenance of polymorphism in a spatially variable environment. If the heterozygote exhibits marginal overdominance, such that in each habitat its fitness exceeds the arithmetic-mean realized fitness of the two homozygotes, and if there is a uniform distribution of individuals between the two habitats, then the polymorphism is stably protected (fig. 1*B*). This is because, when averaged over space, the heterozygote's fitness exceeds that of either homozygote.

Now assume that individuals tend to choose the habitat in which their fitness is greater and do so equally (i.e., there is little or no genetic variation in habitat preference). Given that there is no within-habitat overdominance in fitness, this favors the fixation of the allele that is most favored in homozygous condition in the better habitat (fig. 1*C*). Thus, habitat selection tends to *destroy* the conditions needed for the maintenance of a stable adaptive polymorphism in a spatially variable environment.

As noted in our review above, there is not much evidence suggesting the existence of strong preference-performance correlations. In our graphic model, such a correlation is expressed by allowing the two homozygotes to be differentially superior in different habitats (figs. 1*D,E*). Once again, if there is marginal overdominance in each habitat, without habitat selection an adaptive polymorphism may be maintained (fig. 1*D*). However, if individuals can selectively reside in the habitat conferring greater expected fitness, a polymorphism tends to be unstable (fig. 1*E*). An interesting difference between this case and that depicted in figure 1*C* is that alternative stable states are now possible. Because the heterozygote is inferior to each of the homozygotes, if either allele is sufficiently common, the alternative allele is excluded. Therefore, a population will be expected to specialize genetically in one or the other of the two habitat types, and the habitat in which it is observed to specialize will largely reflect its past history. In any case, once again habitat selection makes it more difficult to maintain an adaptive polymorphism. In particular, it is difficult to retain genetic variation simultaneously in adaptive characteristics and habitat preference when individuals select the habitat that provides the greatest expected fitness.

The situation sketched in figure 1*E* provides a possible explanation for the observation that different populations of herbivorous insects sometimes specialize in different host plants, even though all have access to a similar array of potential hosts (Fox and Morrow 1981). Recall that the fraction of individuals found in a given habitat (or host plant) is assumed to be a function not only of an individual's innate preference for it but also of the availability of that habitat. Suppose a population is initially monomorphic for allele 1, which confers preference for and adaptation to host plant 1. If this host becomes rare and hard to find, then  $D_{ij2}$  will increase, bringing about a decline in the average fitness of genotype 11. This could then allow the spread and eventual fixation of allele 2, a state which could persist even if host plant 1 should again become more common. This mechanism could, in principle, bring about the formation of geographically isolated host races. Limited gene flow among such populations could lead to modest degrees of preference-performance correlations within populations.

Note that figures 1C and 1E are genetic analogues of the cases of "shared" and "distinct" preferences explored by Rosenzweig (1987) for habitat-selecting, competing species. However, as with the genetic models of Rausher (1984), habitat selection in our model reflects fixed individual preferences, rather than the labile behavior, sensitive to local population density, that is assumed by Rosenzweig and other ecological theorists of habitat selection.

We have been assuming implicitly that the within-habitat fitnesses are independent of the degree of habitat preference. But what if there is a cost to being too choosy? If having a strong preference for either habitat reduces an individual's fitness, perhaps because more time is spent searching for the preferred habitat, then the straight lines of figures 1A–E become bowed. If this cost is great enough, heterozygote intermediacy in preference promotes the maintenance of genetic variance in habitat use, even without inherent variation in adaptive characteristics (fig. 1F).

Putting aside for a moment the details of these models, we might distinguish between *ecological* and *genetic* mechanisms promoting the stable maintenance of genetic variation. An ecological mechanism can also enhance the coexistence of distinct species. The soft-selection model with fixed preferences analyzed by Rausher (1984) provides an example of such a mechanism. By contrast, a genetic mechanism operates by virtue of the genetic machinery of a species to maintain variation, in essence through a constraint on adaptive evolution. Average overdominance in a spatially variegated environment is one example of a genetic mechanism promoting polymorphism. If a mutation produces a new allele whose carriers in both heterozygous and homozygous conditions are equal or superior in fitness to the currently favored heterozygote, then the polymorphism for habitat preference will no longer be protected. Thus, strictly genetic mechanisms promoting variation are unlikely to be stable evolutionarily.

In general, our models of hard selection acting in a habitat-specific manner indicate that optimal habitat selection actually makes it less likely that polymorphisms for selection of or adaptation to specific habitats will be stable evolutionarily. Under soft selection, on the other hand, habitat selection clearly facilitates the maintenance of such polymorphisms (Taylor 1976; Templeton and Rothman 1981; Rausher 1984; Hoekstra et al. 1985).

Although further demonstrations of genetic variation for habitat selection will be useful, especially among vertebrates, we believe that it is more important now to turn our attention to the ecological factors that can promote such variation through soft selection. Just as behavior may be the key to initiating evolutionary transitions, ecological interactions may be the prime determinants of behavioral evolution.

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