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Niche shifts and expansion due to sexual selection

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ABSTRACT

Several theoretical studies have shown that niche breadth evolution is weighted by gene flow and selection pressures to maintain adaptation within the current niche. However, these studies have assumed that mating pairs form at random within demes. I extend previous models to include sexual selection and find that non-random mating can alter the likelihood of niche expansion in mainland/island structured populations. Under random mating, an allele that improves fitness on the island will only spread if individuals are more than compensated in island fitness for any loss of mainland fitness. In contrast, under sexual selection, an island-adapted allele can spread even when it causes a complete loss of fitness on the mainland.

Keywords: evolution, mating systems, niche breadth, sexual selection.

INTRODUCTION

Habitat that cannot support population growth may be found at the edges of a species' range or interspersed with favourable habitat as a mosaic. For instance, many plant species' ranges are limited by low temperatures that change on a large spatial scale, while phytophagous insects may find some host plants unsuitable and experience habitat variability at a small spatial scale. Populations in unsuitable habitat can only be maintained by dispersal from source populations (Shmida and Ellner, 1984; Pulliam, 1988), unless evolution results in increased adaptation to the unsuitable habitat. When evolution acts to increase the set of habitats that promote growth, then niche breadth has evolved.

The evolution of a species' niche is likely to be influenced by changes in the environment, competition from other species, the spatial structure of the environment and the evolutionary lability of traits affecting niche breadth. In a previous paper (Proulx, 1999) I showed that under a unidirectional dispersal from source to sink, the mating system can alter the evolution of niche breadth. This paper extends this work to spatial environments where individuals disperse in both directions between a large mainland (ancestral) population and a small island (peripheral) population. By including mainland/island dynamics, the spread of mutant alleles will depend on fitness in both habitats, so the trade-off between success in the two environments will determine which strategies can invade.

The novel environment may represent an unused habitat which is part of a mosaic, a

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habitat which is located beyond a sharp environmental transition, or a literal island. For example, the blue tit (*Parus caeruleus*) has a range that includes southern France and the island of Corsica. The tits breed in both deciduous oak and evergreen oak forests that vary in the timing of bud break by more than a month (Dias and Blondel, 1996). The timing of bud break controls the emergence time of caterpillars, which are the primary food item for young tits. The mainland is primarily deciduous while Corsica is mostly evergreen, a difference that is reflected in the mean laying dates in the two locations (Dias and Blondel, 1996). Thus, the island of Corsica represents a peripheral population with different selection pressures than on the European mainland. In this system, it is likely that there is little gene flow because the island and mainland are separated by a large barrier, which has allowed local adaptation to develop on the island. In this same system, habitat variation occurs at a small scale on both the mainland and on Corsica, but large differences in breeding timing only develop when barriers to gene flow exist (Lambrechts *et al.*, 1997).

In another example, the desert spider *Agelenopsis aperta* inhabits mostly desert grasslands but has peripheral populations in narrow riparian zones. The riparian zones have more bird predators and less competition for food and web sites (Riechert, 1993b). Riparian populations differ from arid-land populations in their diet choice, fighting behaviour and reaction to predation cues (Riechert, 1993a; Riechert and Hall, 2000). Furthermore, these differences are genetically based, as demonstrated by transplant experiments (Riechert and Hall, 2000). In this system, movement of individuals appears to be mostly from the arid habitat (mainland) to the riparian zone (island) (Riechert, 1993a), which probably accounts for the poor fit between behaviours in the riparian zone and those of experimentally evolved riparian populations (Riechert and Hall, 2000).

To understand how evolution proceeds in peripheral populations, it is useful to consider the fate of a neutral allele in a spatially structured population as a limiting case. If a single neutral allele were followed through time, it would be found in individuals in both habitats, but it would be found more often in the habitat with the lowest per capita emigration rate and the highest reproductive rate. Thus, a small phenotypic change will be favoured if it has a positive effect on fitness in the habitat that the allele most often experiences. This increases the strength of selection on the habitat with low emigration and high reproductive output, which will often be the mainland (source) habitat. This process tends to lead to niche conservatism (Holt and Gaines, 1992; Holt, 1996a,b).

Over the last decade, several authors have investigated the roles of dispersal, density dependence and unstable population dynamics in determining the likelihood of niche expansion in a source–sink system (Brown and Pavlovic, 1992; Holt and Gaines, 1992; Kawecki, 1995, 2000; Holt, 1996a,b, 1997; Kawecki *et al.*, 1997; Gomulkiewicz *et al.*, 1990; Proulx, 1999). In the simplest models, two habitat types are connected through fixed dispersal rates without density dependence in population growth parameters (Holt and Gaines, 1992). In this situation, selection acts more strongly on adaptation to habitats that already have high fitness, as long as there is only partial dispersal (Holt and Gaines, 1992). This resistance to niche expansion can be increased because the original habitat will often have greater population density than the peripheral habitat (Kawecki, 1995). Holt (1996a) expanded the theory by including ideas about trade-offs between populations and density-dependent dispersal. When passive dispersal operates, then adaptation to the peripheral habitat will only proceed if the benefit in absolute fitness in the peripheral habitat is greater than the cost in relative fitness on the mainland habitat (Holt, 1996a). Kawecki *et al.* (1997) noted that an additional bias against niche expansion comes from the reduction in

peripheral population size due to fixation of deleterious mutations, leading to mutational meltdown of adaptation to peripheral habitats. Temporal variability can increase the likelihood of niche expansion if the peripheral habitat yields greater offspring production than the mainland in some years (Holt, 1997). However, these analyses typically assume that only small changes in phenotype are likely through a single mutation, but this belief may not be imperially justified (Orr and Coyne, 1992). When larger shifts are possible, an even larger proportional increase in peripheral fitness is required for adaptation to the periphery to increase (Kawecki, 2000, fig. 1).

When females choose mates with high fitness in the current environment, however, invasion of the new niche becomes more probable. I previously introduced the 'locally adapted male mating advantage', or LAMMA, which describes cases in which males with the highest viability in the current habitat receive the most matings (Proulx, 1999). This could occur as a result of male–male competition or through female choice of healthy males. It is not meant to describe a particular process, but rather to describe an outcome. The female choice interpretation relies on a 'truth in advertising' or good genes type of male display, either arising through handicap evolution (Zahavi, 1975; Grafen, 1990; Iwasa *et al.*, 1991) or through revealing indicators (Hamilton and Zuk, 1982; Maynard Smith, 1985; Iwasa *et al.*, 1991). Male–male competition can also result in LAMMA, if general condition alters competitive ability (Borgia, 1979; Andersson, 1994). If males develop in the environment in which they will mate, then male phenotype, or display, will reflect the fit between their genes and the environment. General characteristics that cause habitat-specific viability will often operate in both males and females, so that males with high viability in a given environment are likely to have offspring, either female or male, with high viability in the same environment (Merkel, 1977; Watt *et al.*, 1985; Simmons, 1987; Simchuk *et al.*, 1999). In other words, general viability alleles have a pleiotropic effect on male mating success.

Although males with higher viability should be favoured in mating when LAMMA operates, it is unrealistic to expect small differences in viability, or phenotype, to have the same effects on mating success as large differences. To incorporate this property, I have extended my model of the mating system to include perceptual error, so that the probability of confusing two males decreases as the two males become less similar. This differs from many models of mate acquisition, which implicitly assume that small phenotypic changes have significant effects on mate choice (Seger, 1985; Laland, 1994; Kirkpatrick and Servedio, 1999), which causes a discontinuity in the mating success function and can destabilize the system.

The spread of a new allele depends on the viability of the mutant allele in each environment and on the mating success of males bearing the mutant allele. A mutation that increases viability on the island and decreases viability on the mainland will reduce male mating success on the mainland but increase male mating success on the island. Thus the net effect of LAMMA will depend on the balance of increased cost on the mainland with increased benefit on the island. I show that, under most conditions, LAMMA will increase the spread of a mutant allele with higher viability on the island, making invasion of the new niche more likely.

Previous work in this area has focused on unidirectional migration without perceptual error (Proulx, 1999) or bidirectional migration with random mating (Holt, 1996a,b; Holt and Gaines, 1992). Without perceptual error, small changes in male display can have a large effect on mating success, which is potentially destabilizing. Models that include only one-way migration are important both because they reflect some actual population

structures, including real mainland/island dynamics, and because they are a limiting case of the bidirectional migration models. Including bidirectional migration increases our understanding of more complex population structure, but produces more equivocal results.

This paper is concerned with evolution of increased niche breadth in peripheral populations, which can occur through the spread of new alleles that will eventually be fixed in both habitats or through the spread of alleles that will reach high frequency in the peripheral population but remain polymorphic in the species as a whole. Under random mating, an allele can generally spread only if it reduces fitness on the mainland less than it amplifies it on the island. When there is only a small survival cost on the mainland, the mutant will still pay a mating cost on the mainland and so may be less likely to spread under LAMMA than under random mating. However, when LAMMA is strong, the benefits on the island are guaranteed to outweigh the costs on the mainland, so that, in this limit, niche breadth is certain to increase.

NICHE EXPANSION UNDER RANDOM MATING

Several previous studies have explored niche expansion under random mating and have generally concluded that evolution is biased towards habitats that currently support large populations (Holt, 1996a, Holt and Gaines, 1992). In this section, I reproduce these results, with the more restrictive assumption that density on the mainland is regulated exactly, to establish a baseline for comparison.

I consider a simple population dynamic scenario in which a mainland population is in density-dependent equilibrium and an island sink population experiences no density dependence. Migrants are exchanged as juveniles and experience viability selection and phenotypic development in the patch they settle in. This is an idealization of the population and life-history structure of lepidopterans and other insects in which females lay eggs in multiple distinct habitats. I also assume that the proportion of individuals that emigrates is constant regardless of the population size.

Given these conditions, a set of recursion equations can be defined. The dynamics on the mainland can be represented by a single equation describing the changes in allele frequencies, as density dependence ensures that there is a constant population size on the mainland:

$$p_{I,m}(t+1) = \left(N_m(1-d_m)p_{I,m}(t) + n_{I,i}(t)d_i \right) \frac{W_I}{\bar{W}} \tag{1}$$

where $\bar{W} = \Sigma_j W_j N_m p_{j,m}(1-d_m) + n_{j,i}d_i$, the subscript I refers to island-adapted alleles, the subscript A refers to the ancestral allele, the subscript i refers to the island, the subscript m refers to the mainland, p refers to a proportion of individuals, n refers to a number of individuals, W is relative fitness on the mainland and d is a dispersal probability. Thus $n_{I,i}$ indicates the number of island-adapted individuals on the island (see Table 1 for a complete list of variables). For simplicity, the relative fitness of the ancestral allele on the mainland is assumed to be 1. The frequency of the island-adapted allele is increased by local production of offspring (the first term in parentheses) and by immigration of individuals from the island (the second term in parentheses) that survive with frequency $W_I/\bar{W}$. The dynamics on the island require two equations because both allele frequencies and population size are variable:

Table 1. Definitions of variables

Variable	Definition
N_m	Carrying capacity of the mainland
$p_{I,m}(t)$	Proportion of mutants on the mainland
$d_m(t)$	Proportion of individuals that leave the mainland each generation
$d_i(t)$	Proportion of individuals that leave the island each generation
W_I	Relative fitness of the mutant on the mainland
$\bar{W}$	Mean fitness of individuals on the mainland
$n_{I,i}$	Number of locally adapted individuals on the island
$n_{A,i}$	Number of ancestral individuals on the island
R_I	Absolute fitness of the mutant on the island
R_A	Absolute fitness of ancestral type individuals on the island
$M_m(p)$	Probability that a female on the mainland mates with a mutant male
$M_i(p)$	Probability that a female on the island mates with a mutant male
λ	Average number of males observed per female
v	Accuracy of female perception

$$n_{I,i}(t+1) = n_{I,i}(t)(1-d_i)R_I + N_m p_{I,m}(t) d_m R_I \tag{2}$$

$$n_{A,i}(t+1) = n_{A,i}(t)(1-d_i)R_A + N_m(1-p_{I,m}(t)) d_m R_A \tag{3}$$

where R is the absolute fitness on the island. Thus, the number of individuals of each class on the island grows because of local reproduction and immigration. Note that the growth of the island allele is not affected by the number of immigrants carrying the ancestral allele.

If the population is initially genetically homogeneous, an equilibrium island density will develop. This equilibrium is given by

$$\tilde{n}_{A,i} = \frac{N_m R_A d_m}{1 - R_A(1-d_i)} \tag{4}$$

When a mutant allele arises, it will be rare and a linear matrix describing the growth dynamics can be found by substituting equation (4) into the equations for the dynamics (equations 1, 2 and 3). This matrix is given by

$$\mathbf{A} = \begin{pmatrix} \dfrac{N_m(1-d_m)W_I}{N_m(1-d_m)+\tilde{n}_{A,i}d_i} & \dfrac{N_m d_m W_I}{N_m(1-d_m)+\tilde{n}_{A,i}d_i} \\ R_I d_i & R_I(1-d_i) \end{pmatrix}$$

where R_I (mutant reproductive rate on the island) and W_I (mutant relative fitness on the mainland) are assumed to be less than 1. The elements of the first row represent the number of new alleles a single mutant individual on the mainland will leave on the mainland (first column) and on the island (second column). Thus, production of offspring on the mainland is density dependent, while the absolute fitness determines the number of offspring produced on the island (second row). For a mutant to spread, the dominant eigenvalue of **A** must be greater than 1, implying

$$R_I > \frac{(1-d_m)(1-W_I) + R_A(W_I(1-d_i)(1-d_m) - (1-d_i-d_m))}{(1-d_m)(1-d_i)(1-R_A) + R_A d_i(1-d_i) - W_I(1-d_m-d_i)(1+R_A(1-d_i))} \tag{5}$$

The critical island fitness that allows the mutant to spread is defined as R_I*. When there is no cost to increasing island adaptation ($W_I = 1$), any allele that increases island adaptation will spread ($R_I^* = R_A$). If there is a cost to increasing fitness on the island, then this cost will retard the spread of the mutant allele.

Adaptation at the edge of the current niche

A species fundamental niche includes habitats that produce positive growth when population size is small. Islands that are just on the edge of the fundamental niche neither allow small populations to grow nor decay ($R_A = 1$). A new allele that increases the growth rate on the island will only spread if it does not greatly reduce fitness on the mainland.

Substituting $R_A = 1$ into equation (5) yields

$$R_I > \frac{W_I(d_m - 1) + 1}{W_I(d_i + d_m - 1) + (1 - d_i)} \tag{6}$$

Taking the derivative with respect to fitness on the mainland, we get

$$\left.\frac{\mathrm{d}R_I^*}{\mathrm{d}W_I}\right|_{W_I=1} = -\frac{d_i}{d_m} \tag{7}$$

where R_I* is the critical island fitness above which a mutant allele spreads. This means that, for an allele which causes a small decrease in fitness on the mainland to spread, it must increase island fitness by more than the ratio of the dispersal rates. If dispersal is density independent ($d_i = d_m$), local adaptation will occur when the trade-off between island and mainland fitness has a slope greater than –1, as in Holt's model (Holt, 1996a). So, for habitats on the edge of the current niche, an equal gain in fitness in the new environment will compensate an equal loss on the mainland.

Dispersal is both observed and predicted to be density dependent (McPeek and Holt, 1992; Travis *et al.*, 1999; Aars and Ims, 2000; Wilson, 2001), so that mainland dispersal rates will often be higher than island dispersal rates. Increases in the relative dispersal rate out of the mainland make the maximum trade-off less severe. When mainland dispersal is higher than island dispersal, greater losses on the mainland can be tolerated. This is because local adaptation is able to develop on the island, where dispersal is low.

Adaptation outside the current niche

Because environmental conditions are often patchy, a species may encounter habitats that are well outside its fundamental niche ($R_A < 1$). For instance, dispersing butterflies may encounter a wide variety of microhabitats that vary in temperature and humidity, even over a contiguous area. If R_A is not equal to 1, then the derivative of R_I* becomes

$$\left.\frac{\mathrm{d}R_I^*}{\mathrm{d}W_I}\right|_{W_I=1} = \frac{(R_A^2(1-d_i)(d_i-(1-d_m)) + R_A((2-d_i)(2-d_m)-2) - (1-d_m))}{(d_m d_i)} \tag{8}$$

This will be greater than −1 for R_A less than 1, as can be seen by taking another derivative, this time with respect to R_A, as follows:

$$\frac{\mathrm{d}}{\mathrm{d}R_A}\frac{\mathrm{d}R_I^*}{\mathrm{d}W_I}\bigg|_{W_I=1,R_A=1}=\frac{2-2d_i-d_m}{d_m} \tag{9}$$

which is strictly positive in the range of interest, d_m, $d_i \in (0, 0.5)$. This means that a decrease in R_A makes the necessary trade-off function steeper. In other words, a large benefit on the island is required to offset any loss on the mainland when the initial island fitness is low.

Again, the issue of density-dependent dispersal is interesting, although the results for habitats well outside the fundamental niche are more complicated. Whether or not increased emigration from the island will relax the trade-off depends on the ancestral island fitness and the magnitude of the mainland dispersal rate. To find the range of parameters for which increases in d_i result in a relaxed trade-off, I first take the derivative of the right-hand side of equation (8) with respect to d_i, set it equal to 0 and solve for R_A. This yields the minimum ancestral island fitness for which small increases in d_i relax the trade off:

$$R_A > \frac{d_i\sqrt{1-d_m}-(1-d_m)}{d_i^2-(1-d_m)} \tag{10}$$

If the ancestral island fitness is high, then increases in d_i tend to relax the trade-off.

These results can be combined to provide an idea of the set of alleles that can spread, for a particular spatial structure. The set of alleles that invades is shown in Fig. 6. Alleles that have either mainland fitness or island fitness above the curve will invade. It is important to note that, after an allele invades, two outcomes are possible. The mutant allele could globally replace the ancestral allele, or the two alleles could co-exist. In the former case, the species has evolved increased niche breadth, as each individual is better adapted to both habitats. If two alleles co-exist, then the species as a whole may exhibit greater niche breadth, or simply speciate.

NICHE EXPANSION WITH LAMMA

Locally adapted male mating advantage (LAMMA) describes a result, not a mechanism, and as such could be modelled in many ways. I adopt a modified version of the 'best of n' mating system (Janetos, 1980; O'Donald, 1980), in which each female examines n males and mates with the male most closely matching her preference. Males are assumed to produce a trait that is related to male quality (survivorship) in the current environment. This can occur because revealing indicators exist or because of honest advertisement by males (Zahavi, 1975; Grafen, 1990). Many recent studies have identified condition-dependent displays used by females in mate choice (Merkel, 1977; Simmons, 1987; Clark *et al.*, 1997; Simchuk *et al.*, 1999). I adopt a system in which females examine a variable number of males by searching a fixed area and mate with the male with the highest observed trait. Each male is assumed to be distributed randomly (with a uniform density) in space, without regard to their genotype. Thus, each female examines a Poisson number of males, with the expected number of observed males equalling the product of the area searched and the density of males. I will refer to this mating system as the 'fixed search effort' model. The search effort can be described by a single variable, λ, the average number of males each female examines before choosing a mate (Table 1).

Both the best of n and fixed search effort models have a discontinuity that limits their applicability. These models assume that females have complete information about the males they observe, so that if one male has a slightly larger trait than another, she will choose the higher quality male. This difficulty can be overcome by introducing an element of error into female perception, so that although males of high quality are likely to be perceived as having higher quality than males of low quality, two males of similar quality are approximately equally likely to be chosen. I refer to this extension of the fixed search effort model as the 'perceptual error' model. Female behaviour for this model requires two parameters: λ is still the average number of males observed by each female and v is the perceptual accuracy of females.

The probability a female mates with a male of each quality will depend on the frequencies of each type of male and the ranking or differences in male qualities. The mating frequencies for each type of male are derived in the Appendix and are explained in more detail elsewhere (Proulx, 2001). The success of a rare, island-adapted allele will be determined by both male and female components of success. The spread of a new allele adapted to the island will be generically described by the matrix

$$\mathbf{B} = \begin{pmatrix} \dfrac{N_m W_I (1-d_m)(1+M'_m(0))/2}{N_m(1-d_m)+\tilde{n}_{A,i}d_i} & \dfrac{N_m W_I (d_m)(1+M'_m(0))/2}{N_m d_m+\tilde{n}_{A,i}(1-d_i)} \\ R_I d_i (1+M'_i(0))/2 & R_I(1-d_i)(1+M'_i(0))/2 \end{pmatrix}$$

Here, $M'_m(0)$ and $M'_i(0)$ are derivatives, with respect to mutant frequency, of the function that describes the probability of mating with the mutant allele on the mainland and the island, respectively. Thus, $M'_i(0)$ is the per capita mating success of a rare favoured allele and $M'_m(0)$ is the per capita mating success of a rare disfavoured allele. Again, the first row shows the number of offspring a single mutant individual on the mainland will leave on the mainland (first column) and island (second column). This matrix is very similar to the random mating matrix (**A**), with the addition of terms for male mating success. Thus, each entry now includes a term that averages female mating success (which is assumed to be independent of genotype and, therefore, is 1) with male mating success. For example, on the mainland, this term is $(1 + M'_m(0))/2$.

The forms of the male mating success function for the two models are shown in Table 2. For the fixed search effort model, only the ordering of male qualities affects mating frequencies. The perceptual error model incorporates the concept that it should be difficult to discriminate among very similar males, and so mating frequencies depend on the actual qualities of each genotype.

The mating systems described here provide a logically consistent method for determining the relationships between the fitnesses of mutant alleles and the mating success of those alleles. This system could accommodate any relationship between the M''s and the allele fitnesses, or arbitrary values for all four parameters. Because a general solution for the critical level of island fitness is unavailable, I will consider several special cases. First, I explore several limiting cases, where LAMMA is extreme or mutants have large fitness effects. Second, when LAMMA is not extreme and fitness effects are smaller, some analytical results can be worked out for the fixed search effort model. Finally, I explore the effects of perceptual error for several intermediate cases.

Table 2. Linearized mating success for the two models

	Male genotype	
Mating system	Favoured: $M'_i(0)$	Disfavoured: $M'_m(0)$
Fixed search effort	$\lambda + e^{-\lambda}$	$e^{-\lambda}(\lambda + 1)$
Perceptual error	$\frac{1 - e^{-\lambda e^{v(\mu_{A,i} - \mu_{I,i})}} + e^{-\lambda + v(\mu_{A,i} - \mu_{I,i})}}{e^{v(\mu_{A,i} - \mu_{I,i})}}$	$\frac{(\lambda + 1)(e^{v\mu_{A,m}} - e^{v\mu_{I,m}}) + e^{\lambda + v\mu_{I,m}}}{e^{\lambda + v\mu_{A,m}}}$

Complete loss of fitness on the mainland

One extreme class of mutants has a complete loss of fitness on the ancestral environment and a gain of fitness on the island. Under these conditions, LAMMA will always improve the spread of such new alleles. The mating success of mutants on the mainland is irrelevant because they all die. On the other hand, LAMMA of any flavour will have a positive effect on mating success on the island. Thus LAMMA does not reduce the spread of the mutant on the mainland but increases the spread of the mutant on the island, so mutant alleles will have larger eigenvalues in LAMMA populations and will spread under a wider range of island fitnesses than the same mutants in randomly mating populations.

The critical island fitness required to offset complete loss of fitness on the mainland for the fixed search effort model is:

$$R_I > \frac{2e^{\lambda}}{(e^{\lambda}(\lambda + 1) + 1)(1 - d_i)} \tag{11}$$

Figure 1 plots critical fitness as a function of the average number of males observed per female (λ). The island dispersal rate (d_i) acts as a source of mortality, because all dispersing individuals die once they reach the mainland. When λ is 0, random mating occurs and the the critical island fitness must be greater than $1/(1 - d_i)$. In other words, under random mating, reproduction on the island must compensate for loss due to migration. As λ increases, the critical island fitness decreases towards zero (Proulx, 1999). So, increased female mate choice increases the likelihood that a mutant which reduces mainland fitness to zero will spread.

Strong female preference

When LAMMA becomes very strong, all females mate with the males they prefer. This means that on the mainland, island-adapted males are never mated with, and on the island, all females mate with island-adapted males. Female reproduction, however, proceeds normally. This means that, under extreme LAMMA, the new island-adapted allele produces half as many copies on the mainland as under random mating. On the island, however, the rare island-adapted allele produces as many copies of itself as there are females on the island. In the limit of rarity, this is an infinite proportional increase, which will always outweigh the 50% reduction on the mainland. However, even under the logical restriction of there being at least one individual mutant on the island, the advantage is N_i-fold. This means that, whenever females have a high probability of mating with their preferred

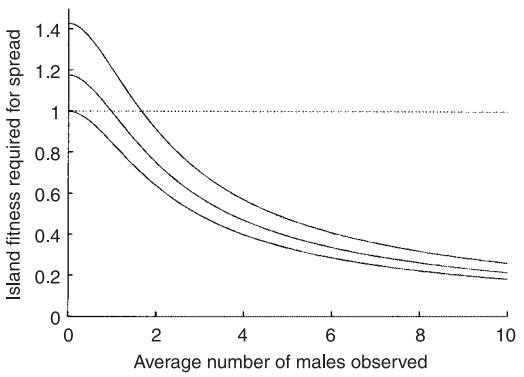

Fig. 1. Critical island fitness for a mutant allele to spread as a function of the average number of males observed. The three curves represent the three different dispersal rates (island to mainland) of 0, 0.15 and 0.3, in increasing order.

males, mutants that increase island fitness are likely to spread. This will be true even when the mutant allele has a large cost on the mainland.

Intermediate levels of female choice

The above argument works to show that an infinite amount of LAMMA will always improve a new island-adapted allele's chances of spreading, but what about a small amount of LAMMA? We can evaluate the effect of a small amount of LAMMA by taking the derivative of the eigenvalue with respect to λ. If it is positive, then a small amount of LAMMA is beneficial; if it is negative, a small amount of LAMMA is detrimental. For the fixed search effort model, this derivative is always 0, so the second derivative governs the behaviour of the function near 0. We find that, for low mainland fitness, even a small amount of LAMMA is beneficial, but for high mainland fitness it is not. For a small amount of LAMMA to be beneficial, the mainland fitness must be below a critical value:

$$W_I < \frac{R_I R_A (1-d_i)(1-d_i-d_m) + R_I (1-d_i)(1-d_m)}{R_A (1-d_i)(1-d_m) - (1-d_m)} \tag{12}$$

Figure 2 shows the maximum mainland fitness for which small amounts of LAMMA are beneficial. Even when small amounts of LAMMA are detrimental, it only takes a small amount of LAMMA for it to become beneficial, as is shown in Fig. 3.

Perceptual error: complete loss of fitness on the mainland

The condition for the spread of mutants that cause complete loss of fitness on the mainland is similar with perceptual error. Because these types of mutants do not survive on the mainland, their mating success there is irrelevant. The probability that a female on the island mates with a mutant, however, will be reduced through perceptual error, a reduction that depends on the difference in fitness between wild-type and mutant alleles on the island. The critical island fitness can be found by solving the inequality

$$\tfrac{1}{2}(1-d_i)R_I\left(1+\frac{e^{vR_I}}{e^{vR_A}}-\frac{e^{-\lambda e^{-v(-R_A+R_I)}+vR_I}}{e^{vR_A}}+e^{-\lambda}\right)>1 \tag{13}$$

Figure 4 shows how increased perceptual accuracy (v) reduces the critical island fitness. Similar to the case without perceptual error, decreased migration from the island, increased island fitness and increased female choice all increase the likelihood that the island habitat is colonized. Additionally, increased perceptual accuracy and decreased fitness of the ancestral allele on the island increase the likelihood of niche expansion. The

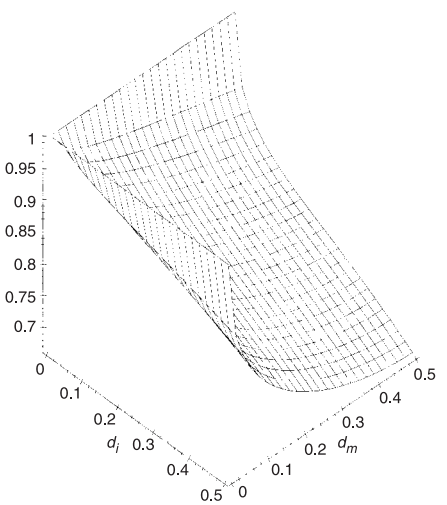

Fig. 2. If the mainland fitness of a mutant allele is less than a critical value, then any amount of LAMMA will increase the spread of this allele. The z-axis shows the value that mainland fitness must be below for LAMMA to increase the spread of a mutant allele. The only free parameter is the ancestral island fitness, which is set to 0.5.

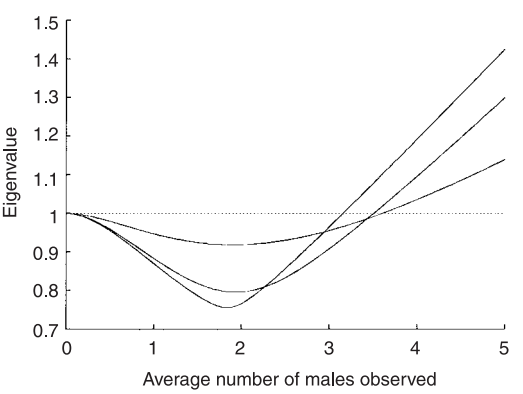

Fig. 3. The reduction in spread of a mutant allele at low levels of LAMMA depends on the spatial and selective structure. For relatively severe conditions, λ must only be greater than about 4 for the allele to spread. The parameters are $R_A = 0.5$, $R_I = 0.5001$, $W_I = 1$ for all curves. The dispersal rates are set equal ($d_i = d_m$) and vary from 0.05, 0.15 to 0.5. Increases in the dispersal rate increase the λ at which the allele spreads.

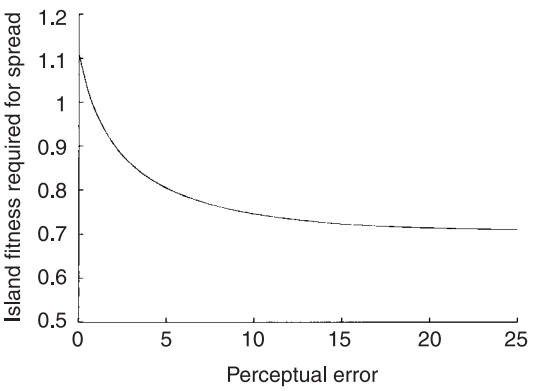

Fig. 4. Critical island fitness varies between that of a randomly mating population and of a LAMMA population without error as v increases. The parameters are $R_A = 0.5$, $\lambda = 2$, $d_i = 0.1$, $d_m = 0.1$. Under random mating, a mutant allele must have a fitness of greater than about 1.1 to increase, whereas under LAMMA without perceptual error, the fitness must only be greater than about 0.71.

fitness of the ancestral allele now has an effect because females cannot distinguish between ancestral and mutant males if they have similar phenotypes.

Perceptual error: strong female preference

Once perceptual error is included, increasing the strength of female choice is no longer guaranteed to increase the spread of island-adapted mutants. This is because increased search time cannot eliminate perceptual error. The limit of mutant mating success on the mainland and island, as search effort (λ) goes to infinity, is

$$m_m = \mathrm{e}^{-v(1-W_I)} \tag{14}$$

$$m_i = \mathrm{e}^{-v(R_I-R_A)} \tag{15}$$

When v is large, and female perception is very accurate, then $m_m \to 0$ and $m_i \to 1$, which guarantees that the mutant spreads. When v takes on an intermediate value, however, the mating cost on the mainland can outweigh the mating benefit on the island (Fig. 5).

Null fitness isoclines

For random mating, we can find the critical mainland fitness that a mutant allele must supersede for a mutant to spread, given fitness on the island:

$$W_I > \frac{(1-R_I(1-d_i))(1-R_A(1-d_i)-d_m(1-R_A))}{(1-R_A(1-d_m))(1-R_I(1-d_i)-d_m(1-R_I))} \tag{16}$$

This curve, the null fitness isocline, separates the set of all alleles into those that spread (greater W_I or greater R_I) and those that do not (Fig. 6). If we imagine the set of alleles that can be achieved through a few or a single mutational step as a contiguous set of points in the graph, then niche expansion is more likely when most of the achievable alleles are above the curve. If we further consider two species that are similar in their ecology and genomic

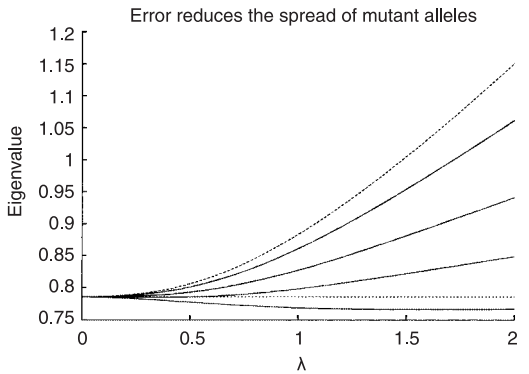

Fig. 5. If the mainland fitness of a mutant is sufficiently low, then a small increase in LAMMA will result in an increase in the rate of spread of the mutant allele. Decreasing perceptual accuracy can reduce the spread even below that of a randomly mating population. The parameters are $d_i = 0.1$, $d_m = 0.1$, $R_A = 0.8$, $R_I = 0.81$, $W_I = 0.7$ for all curves. The lower dashed curve is for randomly mating populations, whereas the upper dashed curve is for a population with no perceptual error. The solid curves are for different amounts of accuracy, v, at 10, 50, 100 and 200. The higher solid curves are for larger v.

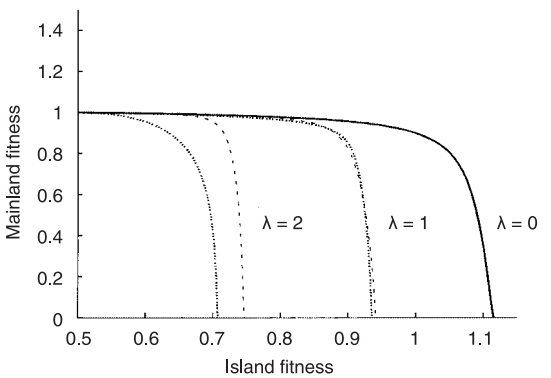

Fig. 6. This figure shows the set of alleles which are neutral. The three curves are for different values of λ, where the dotted curves are for the fixed search effort model and the dashed curves are for the perceptual error model. The parameters are $R_A = 0.95$, $d_m = 0.1$, $d_i = 0.1$, $v = 10$.

architecture but differ in their mating system, then they will have two different null fitness isoclines but the same set of feasible alleles. The species that has the most area above the null fitness isocline is more likely to expand into the island habitat, for a given set of feasible alleles.

Unfortunately, there is no analytical solution for this curve for LAMMA populations. However, some of the special cases allow us to understand how LAMMA affects these null fitness isoclines. First, any allele that increases both island and mainland fitness will always spread. This means that the null fitness isocline will always be below the line where mainland fitness is 1. Second, LAMMA always increases the rate of spread of mutants that cause complete loss of fitness on the mainland, but increase fitness on the island. This means that the point where the curve intersects the x-axis must be moved to the left for LAMMA

populations compared to randomly mating populations (Fig. 6). Thus, LAMMA will always cause a new set of alleles with high island fitness, but low mainland fitness, to spread. LAMMA can have a negative effect on the spread of mutants that have smaller effects on island fitness, but this causes only small changes in the amount of area above the null fitness isocline, because the random mating curve is already quite close to 1 when the mutant island fitness is low.

CONCLUSIONS

Increased adaptation to peripheral habitats can only evolve if it is not outweighed by selection to maintain adaptation for habitats within the current niche. If the new habitat is similar to the ancestral niche, then the balance of selection is determined by the ratio of the island and mainland dispersal rates, which corresponds to the proportion of mutants in each environment. This is related to the idea that the current fitness and number of individuals within a habitat determine the strength of selection on maintaining or increasing adaptation towards that habitat (Holt, 1996b; Holt and Gaines, 1992). This reasoning applies to mutations that are only slightly different from the dominant strategy, because slightly different mutations will develop the same spatial distribution as the wild-type individuals. However, when considering new mutants that may be very different from the ancestral allele, the success of the mutant will depend on the spatial distribution that develops because of the new allele's qualities. Thus, a new allele can spread by increasing in only one habitat, even if that is not the habitat with the most individuals or highest current fitness. This can lead to the development of a polymorphism of the mutant and ancestral alleles instead of a gradual shift in niche.

If the island dispersal rate is large compared to the mainland dispersal rate, then a new neutral allele will experience the mainland environment more than it experiences the island environment. This puts more weight on the selective costs in the mainland than on the selective benefits in the island. Because the island is a peripheral habitat and expected to be at low density, one possibility is that island dispersal is much lower than mainland dispersal (McPeek and Holt, 1992; Travis *et al.*, 1999; Aars and Ims, 2000; Wilson, 2001). This suggests that niche breadth will be larger for species where dispersal increases as density increases.

Any mechanism that increases the mating success of locally adapted males will alter the likelihood of niche shifts or niche expansion. In particular, a strong locally adapted male mating advantage (LAMMA) will guarantee the spread of alleles that are beneficial on the island and detrimental on the mainland. This happens because extreme LAMMA will only reduce the success of the novel allele by 1/2 on the mainland (male function) but can increase the success on the island without bound. Under extreme LAMMA, all island females mate with mutant males and, since mutant males only represent an infinitesimal proportion of the island population, their proportion increases by an infinite factor. Even when mutant frequencies are restricted to reasonable values (greater than $1/N$, for instance), the island mating advantage can easily outweigh any mainland fitness cost. When these conditions occur, the mutant allele will either replace the ancestral allele or reach some polymorphic equilibrium. If the ancestral allele is replaced, then the species niche has become broader. On the other hand, if a polymorphism develops, then individuals will be habitat specialists, but as a species niche breadth will still have expanded. Furthermore, because LAMMA does not interfere with the dispersal ability of females, gene flow at loci

unlinked to habitat ability can still be high. Thus, species with LAMMA are likely to evolve increased niche breadth, either through specialist individuals or generalist individuals.

The effects of non-random mating on niche expansion depends on both the fitnesses and mating success of alleles in both habitats. If there is a fitness trade-off between the two habitats, then an allele that has a natural and sexual selection advantage in one habitat will, under LAMMA, have a natural and sexual selection disadvantage in the other habitat. The form of the mating system will determine whether the mating advantage can tip the balance of selection towards spread of the new allele. This makes it difficult, except in the limiting cases discussed above, to make broad generalizations about how increasing the strength of sexual selection alters the likelihood of niche expansion.

It is possible, however, to numerically investigate how a particular form of sexual selection alters the likelihood of niche expansion. For intermediate levels of female choice, increases in the strength of female choice can either increase or decrease the spread of an island-adapted allele. In the limit, as female choice becomes perfect the island-adapted allele always spreads. I have numerically investigated how increasing the strength of female choice has a beneficial effect on island-adapted alleles once the strength of female choice passes a threshold. Although I have no analytical results for this threshold, it appears to be rather small, as illustrated in Fig. 3.

Decreasing perceptual accuracy can reduce, or even reverse, the effects of LAMMA, even when LAMMA is extreme. When error is complete, random mating occurs and the effect of LAMMA is entirely eliminated, regardless of its strength. On the other hand, as accuracy increases ($v \to \infty$), the effect of LAMMA is completely recovered, as long as the allele has an appreciable effect in both habitats. For intermediate accuracy, increased LAMMA can have a negative effect on the spread of the mutant allele.

The results presented here suggest a picture of niche jumps induced by LAMMA. Sexual selection can allow alleles to increase in frequency locally even when they do not have high enough reproductive output to persist without immigration (Proulx, 1999). This allows niche evolution to occur through the evolution of local adaptation rather than through the spread of a single generalist genotype. After this has occurred, the species may continue to maintain local adaptation through LAMMA without speciating because, unlike assortative mating, LAMMA allows gene flow to continue through female dispersal.

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APPENDIX: DERIVATION OF THE MATING PROBABILITIES

Fixed search effort

In the fixed search effort model, females spend a fixed amount of time examining males and then choose the male with the largest phenotype. Because there is no perceptual error in this model, a female will always mate with a single preferred male in a group of observed males. Thus, the per capita mating success of a rare preferred male is just the probability that a male of the preferred genotype is observed. When males are distributed randomly in space, the number of observed males follows a Poisson distribution. The probability that a female observes a group consisting of n_A ancestral genotype males and n_I island genotype males is

$$\Pr[n_A, n_I] = \frac{\lambda^{n_A+n_I} p^{n_A}_A p^{n_I}_I \mathrm{e}^{-\lambda}}{n_A! n_I!} \tag{A1}$$

where p_A is the frequency of the ancestral allele and p_I is the frequency of the island allele.

Because the island allele is preferred on the island, any female who observes an island male will mate with him. The probability of mating with an island male is then just the probability of observing one or more island males:

$$\sum_{n_A=0}^{\infty} \sum_{n_I=1}^{\infty} \Pr[n_A, n_I] = 1 - \mathrm{e}^{-\lambda p_I}$$

Because there is a probability $\mathrm{e}^{-\lambda}$ that no males are observed during the search period, I assume that females will continue to search and mate with the first male found, so that the term $\mathrm{e}^{-\lambda p_I}$ must be included in the total probability of mating with an island male. Thus the total probability a given female on the island will mate with an island male is

$$M_i(p_I) = 1 - \mathrm{e}^{-\lambda p_I} + p_I \mathrm{e}^{-\lambda} \tag{A2}$$

We can find the per capita mating probability for a rare island allele by taking the derivative when $p_I = 0$:

$$M'_i(0) = \lambda + \mathrm{e}^{-\lambda} \tag{A3}$$

On the mainland, the island allele is disfavoured, so a female will only mate with an island male if she observes no ancestral males, which occurs with probability

$$\sum_{n_I=1}^{\infty} \Pr[n_A = 0, n_I] = (1 - e^{-\lambda p_I})\, e^{-\lambda(1-p_I)}$$

Again, there is a probability $e^{-\lambda}$ that no males are observed during the search period. The total probability a given female on the mainland will mate with an island male is

$$M_m(p_I) = (1 - e^{-\lambda p_I})\, e^{-\lambda(1-p_I)} + p_I e^{-\lambda} \tag{A4}$$

Again, the derivative of the mating function gives the per capita success of a rare island male:

$$M'_m(0) = e^{-\lambda}(\lambda + 1) \tag{A5}$$

Perceptual error

The perceptual error model builds on the fixed search effort model by including perceptual error. When a group of males is observed by a female, each male phenotype is perturbed by an independant random variable. Although there are many plausible distributions for the perceptual error, I was only able to calculate mating frequencies using an exponential distribution. Thus, male phenotype is assumed to be coded by the random variable

$$\Pr[\xi_i] = v e^{-v(\xi_i - \mu_i)} \tag{A6}$$

for ξ_i greater than μ_i, where v is the level of perceptual accuracy. In other words, μ_i is the phenotype coded by genotype i, but the realized phenotype is perturbed by an exponentially distributed random variable. Note that this paper assumes that the value μ_i is the fitness of genotype i in the given habitat, but other relationships are possible. Given that $\mu_{I,i} > \mu_{A,i}$, the probability that a female observing a group of n_I and n_A males mates with an island male depends on the probability that one island male has a perceived phenotype greater than all the other males in the sample. This can be restated as the probability that the best island male has an observed phenotype greater than some value x and all ancestral males have observed phenotypes of less than x, integrated over all possible values of x. So, the probability a female on the island mates with an island male is

$$\Pr[M_{I,i} | n_I, n_A] = \int_{x=\mu_{I,i}}^{\infty} \frac{v e^{-v(x-\mu_{I,i})}}{1 - e^{-v(x-\mu_{I,i})}} n_I (1 - e^{-v(x-\mu_{I,i})})^{n_I} (1 - e^{-v(x-\mu_{A,i})})^{n_A}\, dx \tag{A7}$$

The total probability that a female mates with a male of a given genotype can now be calculated by summing up the mating probabilities, conditioned on a set of observed males, over all possible sets of observed males. As in the fixed search effort, a term must be added to account for the possibility that no males are observed during the search period. The probability that a female on the island mates with an island male is

$$M_i(p_I) = p_I e^{-\lambda} + \sum_{n_I=0}^{\infty} \sum_{n_A=0}^{\infty} \Pr[M_I | n_I, n_A] \Pr[n_A, n_I] \tag{A8}$$

which can be evaluated to

$$M_i(p_I) = p_I e^{-\lambda} + p_I e^{v\mu_{I,i}} \frac{1 - e^{-\lambda(p_A e^{v(\mu_{A,i} - \mu_{I,i})} + p_I)}}{p_A e^{v\mu_{A,i}} + p_I e^{v\mu_{I,i}}} \tag{A9}$$

As in the fixed search effort model, the per capita mating success of an island male is determined by the derivative of the mating function.

$$M_i'(0) = \frac{1 - e^{-\lambda e^{v(\mu_{A,i} - \mu_{I,i})} + e^{-\lambda + v(\mu_{A,i} - \mu_{I,i})}}}{e^{v(\mu_{A,i} - \mu_{I,i})}} \tag{A10}$$

The probability a female on the mainland mates with an island male is simply 1 minus the probability she mates with an ancestral male:

$$\Pr[M_{I,m} | n_I, n_A] = 1 - \int_{x = \mu_{A,m}}^{\infty} \frac{v e^{-v(x - \mu_{A,m})}}{1 - e^{-v(x - \mu_{A,m})}} n_A (1 - e^{-v(x - \mu_{A,m})})^{n_A} (1 - e^{-v(x - \mu_{I,m})})^{n_I} \, dx$$

Summing up the mating probabilities over all possible sets of observed males and including the term for the case when no males are observed gives the mating probability, $M_m(p_I)$. As in the fixed search effort model, the per capita mating success of an island male is determined by the derivative of the mating function:

$$M_m'(0) = \frac{(\lambda + 1)(e^{v\mu_{A,m}} - e^{v\mu_{I,m}}) + e^{\lambda + v\mu_{I,m}}}{e^{\lambda + v\mu_{A,m}}} \tag{A11}$$