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Introgression of sexually selected traits in lek-mating species

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ABSTRACT

Questions: Do sexually selected traits cross species boundaries faster in species with lek or lek-like mating systems in which mating success is highly skewed? Can introgression of alleles take place even if selected against when rare?

Mathematical methods: Here we use a population genetic model and consider an unstructured population in which males form leks at random and females choose mates within leks based on phenotypic differences. We then expand the model and add metapopulation structure.

Key insights: When a novel allele is associated with phenotypic traits in males that are preferred by females, we show that the initial speed of introgression increases with lek size and strength of female preference. In our metapopulation model, we show that a novel allele can invade a species even if sexual selection works against the allele when rare (a form of positive frequency dependence).

Conclusions: The speed of introgression of a novel allele increases with lek size and female bias. Immigration of an allele from subpopulations in which it is common into subpopulations in which it is rare can make it frequent enough to overcome sexual selection against it at low frequencies. In such cases, introgression is more likely and occurs faster with larger lek size.

Keywords: female choice, hybrid zones, invasion, leks, *Manacus*, manakins, migration, population structure, sexual selection, travelling wave, unidirectional introgression, gene flow.

INTRODUCTION

Hybrid zones are viewed by evolutionary biologists as active sites of evolutionary change (Harrison, 1993). Although selection against hybrids can lead to the formation of pre-zygotic barriers to gene flow and reinforcement of species boundaries (Harrison, 1993; Grant and Grant, 1997), selection for hybrids can lead to the generation of new recombinant types, particularly in habitat transitions (Good *et al.*, 2000), in novel climate regimes (Grant and Grant, 1996; Grant *et al.*, 2004), or through exploitation of vacant niches or habitats (Lewontin and Birch, 1966; Grant and Grant, 1992). Consistent selection for recombinant types can even lead to the generation of new species (Rieseberg, 1997; Reich *et al.*, 1999; Seehausen, 2004; Mavárez *et al.*, 2006; Patterson *et al.*, 2006; Mallet, 2007). Understanding the causes and consequences of genetic interactions between differentiated

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populations provides insights into a range of important problems in evolution (Harrison, 1993) and conservation (Rhymer and Simberloff, 1996).

One consequence of hybridization is the incorporation of alleles from one taxon into the gene pool of another. This is caused by backcrossing of hybrids to one or both parental types in a process known as 'introgression'. Hybridization need not always lead to introgression, but once the first hybrid cross has been made, backcrossing of F1 hybrids is almost always easier, from a genetic standpoint, than initial hybridization itself (Mallet, 2005). Introgression is often characterized by the bidirectional flow of neutral alleles into either parental species, leaving intact parts of the genome which are under selection and which define species identity (Buerkle *et al.*, 2000). However, selection across the hybrid zone for traits held by the opposite species may lead to unidirectional introgression (Harrison, 1993). Traits from one species that confer an advantage to the other should be expected to sweep to fixation in the receiver (Barton, 1979; Hewitt, 1988), fundamentally changing the appearance or make-up of the receiver. Thus, it is important to recognize hybrid zones not only as conduits for advantageous traits and for evolutionary change (McDonald *et al.*, 2001), but also as places where genetic diversity can be lost, especially in hybrid zones caused by recent anthropogenic habitat modification (Rhymer and Simberloff, 1996; Seehausen, 2004).

Given the potential of introgression to introduce new alleles (advantageous or not), and in some cases generate new forms, there is considerable interest in predicting the speed (e.g. distance travelled by a given allele or genotype frequency per generation) and the extent to which introgression of genes might occur when two species come into contact. Some of the many factors likely to influence the rate of introgression include: generation time, reproductive output, dispersal distance, frequency of hybridization and backcrossing, strength of reproductive barriers, vigour of hybrids, relative and absolute sizes of hybridizing populations, structure of mixing between the two populations where they meet, and strength of environmental selection for backcross individuals (Wolf *et al.*, 2001; Hails and Morley, 2005). Although there has been much recent work on introgression rates in plants (e.g. Wolf *et al.*, 2001; Hooftman *et al.*, 2007), particularly with respect to introgression of transgenes into wild populations, there has been relatively little work with respect to animals. One important and often overlooked factor in animals that may influence introgression rates is the mating system.

If the mating system involves the choice of mates of one sex by the other, then sexual selection is possible. The differences in mating success among members of the selected sex may have a profound effect on the rate of introgression of genes affecting the phenotypic basis for sexual selection. All else being equal, in systems where few males obtain most copulations (high mating skew), genes that code for preferred traits should be expected to sweep more rapidly to fixation than in systems where mating success is more evenly distributed among males. This is because a male in a highly skewed system, if preferred, could sire a significant fraction of the offspring in a given breeding season, and quickly change the make-up of the local population. In contrast, when mating success is more evenly distributed among males (e.g. systems approaching monogamy), a novel male's offspring would only constitute a smaller fraction of the total number of offspring produced and introgression of those novel genes would proceed much more slowly. In this paper, we develop a general model that contrasts rates of introgression in systems that differ in the degree of reproductive skew, from lek-like systems with the most extreme skew to systems approaching monogamy. The strength of female preference for a trait affects the mating success of males possessing that trait. Thus, the stronger the female preference for a particular male trait, the greater the resulting reproductive skew towards males possessing that trait will be. Conversely, the weaker the preference for a particular trait, the more even male reproductive success will be.

The stimulus for this work comes from a well-known hybrid zone between two lek-mating species in western Panama, the Golden-Collared Manakin (*Manacus vitellinus*) and the White-Collared Manakin (*M. candei*). The most striking feature of this particular hybrid zone is a shifted plumage cline caused by the unidirectional introgression of yellow *vitellinus*-like plumage. Plumage brightness is an important cue in female choice in Golden-Collared Manakins and reproductive skew is high (Stein and Uy, 2006a). Recent work with mixed yellow and white populations suggests that White-Collared females also prefer more brightly coloured yellow males when given a choice between white and yellow. Thus, the introgression of yellow plumage into white-plumaged *M. candei* populations is likely due to strong sexual selection for yellow males across the centre of the hybrid zone (Parsons *et al.*, 1993; Brumfield *et al.*, 2001; McDonald *et al.*, 2001; Stein and Uy, 2006b). In the absence of any historical documentation on the speed of introgression of the genes for a yellow collar, we develop here a mathematical model to explore introgression from a theoretical perspective. The model is sufficiently general to be of interest to researchers studying introgression and sexual selection in other animal systems.

MODEL

Consider a species in which males form leks of size n. Suppose that there is a single autosomal genetic locus that controls a sexually selected trait in males (e.g. yellow and white plumage in the case of the *Manacus* system). Let the alleles at this locus be given by $\boldsymbol{E}$ and $\boldsymbol{e}$. Thus, the three genotypes are $\boldsymbol{EE}$, $\boldsymbol{Ee}$, and $\boldsymbol{ee}$. In what follows, we shall think of $\boldsymbol{E}$ as the newly imported allele in a focal species (e.g. an allele corresponding to yellow plumage within *M. candei* coming originally from *M. vitellinus*). The frequencies of these genotypes in generation t are $x(t)$, $y(t)$, and $z(t)$, respectively (where $z(t) = 1 - x(t) - y(t)$). We assume that genotypic frequencies are the same in males and females and there is no viability selection.

We assume that males form leks at random and that leks are randomly encountered by females. Thus, the probability that a female finds a lek with a $\boldsymbol{EE}$ males, b $\boldsymbol{Ee}$ males, and $n - a - b$ $\boldsymbol{ee}$ males is given by the following trinomial term:

$$\Gamma(a,b,x(t),y(t)) = \binom{n}{a,b,n-a-b} x(t)^a y(t)^b [1 - x(t) - y(t)]^{n-a-b}. \tag{1}$$

Given that a female has found a lek with a $\boldsymbol{EE}$ males, b $\boldsymbol{Ee}$ males, and $n - a - b$ $\boldsymbol{ee}$ males, we assume she will mate with a male of genotype $\boldsymbol{EE}$, $\boldsymbol{Ee}$, or $\boldsymbol{ee}$ with the following respective probabilities:

$$\Phi_{EE}(a,b) = \frac{a[1 + \pi + \beta(\{a-1\} + \gamma b)]}{D}, \tag{2a}$$

$$\Phi_{Ee}(a,b) = \frac{b[1 + \delta(\pi + \beta(a + \gamma\{b-1\}))]}{D}, \tag{2b}$$

$$\Phi_{ee}(a,b) = \frac{n-a-b}{D}, \tag{2c}$$

where $D = n + (a + b\delta)[\pi + \beta(a + \gamma b)] - \beta(a + \gamma b\delta)$. The parameter π measures base female preference for males of the genotype ***EE*** and δ measures the dominance of the ***E*** allele with respect to female preference. Female preference for a particular ***E***-carrying male can depend on the presence of other ***E***-carrying males. For a lek with a ***EE*** males and b ***Ee*** males, a given ***EE*** male is surrounded by $a - 1$ ***EE*** lek-mates and b ***Ee*** lek-mates; whereas a given ***Ee*** male is surrounded by a ***EE*** lek-mates and $b - 1$ ***Ee*** lek-mates. These other ***E***-carrying males are assumed to raise female preference for a focal ***E***-carrying male by the rate of β, which we call the 'preference slope'. Because ***Ee*** males may not raise female preference as much as ***EE*** males, we discount the contribution of heterozygotes by the factor γ. For instance, in the *Manacus* system, if heterozygotes are intermediate in plumage colour, a particular ***E***-carrying male may experience greater mating success when surrounded by a certain number of ***EE*** males as opposed to an equivalent number of ***Ee*** males (such that $\gamma < 1$). This idea is supported by research showing that mating success of yellow males increases above a threshold level of yellow males on initially white dominated leks (Stein and Uy, 2006b).

Given equations (1) and (2), we can describe genotype dynamics with the following recursions:

$$\begin{aligned} x(t+1) = {} & x(t)\sum_{a=0}^{n}\sum_{b=0}^{n-a}\Gamma(a,b,x(t),y(t))\left[\Phi_{EE}(a,b) + \frac{1}{2}\Phi_{Ee}(a,b)\right] + \\ & y(t)\sum_{a=0}^{n}\sum_{b=0}^{n-a}\Gamma(a,b,x(t),y(t))\left[\frac{1}{2}\Phi_{EE}(a,b) + \frac{1}{4}\Phi_{Ee}(a,b)\right], \end{aligned} \tag{3a}$$

$$\begin{aligned} y(t+1) = {} & x(t)\sum_{a=0}^{n}\sum_{b=0}^{n-a}\Gamma(a,b,x(t),y(t))\left[\frac{1}{2}\Phi_{Ee}(a,b) + \Phi_{ee}(a,b)\right] + \\ & y(t)\sum_{a=0}^{n}\sum_{b=0}^{n-a}\Gamma(a,b,x(t),y(t))\left[\frac{1}{2}\Phi_{EE}(a,b) + \frac{1}{2}\Phi_{Ee}(a,b) + \frac{1}{2}\Phi_{ee}(a,b)\right] + \\ & [1 - x(t) - y(t)]\sum_{a=0}^{n}\sum_{b=0}^{n-a}\Gamma(a,b,x(t),y(t))\left[\Phi_{EE}(a,b) + \frac{1}{2}\Phi_{Ee}(a,b)\right]. \end{aligned} \tag{3b}$$

The preceding model applies to a single unstructured population. To incorporate population structure, we consider a set of S subpopulations, each with the genotypic dynamics described by equations (3). The frequencies of genotypes ***EE***, ***Ee***, and ***ee*** in subpopulation i at time t are given by $x_i(t)$, $y_i(t)$, and $z_i(t)$, respectively. Let m_{ij} be the fraction of subpopulation i that migrates to subpopulation j. For simplicity, we consider a one-dimensional world where migration takes place between nearest neighbours:

$$m_{ij} = \begin{cases} m/2, & \text{if } j = i - 1 \\ 1 - m, & \text{if } j = i \\ m/2, & \text{if } j = i + 1 \\ 0, & \text{otherwise} \end{cases} \tag{4}$$

where m is the fraction of a subpopulation migrating out of most subpopulations (migration out of the first and last subpopulations in the linearly arranged set is $m/2$, since these subpopulations exchange individuals only with the single neighbouring adjacent subpopulation). We model migration as preceding sexual selection such that

$$x'_i(t) = \begin{cases} (1-m)x_i(t) + \frac{m}{2}[x_{i+1}(t) + x_{i-1}(t)], & \text{for } 1 < i < S \\ \left(1 - \frac{m}{2}\right)x_i(t) + \frac{m}{2}x_{i+1}(t), & \text{for } i = 1 \\ \left(1 - \frac{m}{2}\right)x_i(t) + \frac{m}{2}x_{i-1}(t), & \text{for } i = S \end{cases} \tag{5}$$

where the prime denotes the frequency of the ***EE*** genotype before sexual selection. We use a similar equation for the ***Ee*** genotype ($y'_i(t)$). We then allow for sexual selection by applying equations (3) to all subpopulations (with primed state variables on the right-hand sides). Through such repeated rounds of migration and selection, we can track genotypic frequencies within the metapopulation.

RESULTS

Imagine that the ***E*** allele has just entered our focal species through a hybridization event. Under what circumstances does this rare allele invade? The point $(\hat{x},\hat{y}) = (0,0)$ is an equilibrium of the system described by equations (3), which corresponds to the fixation of the ***ee*** genotype. To investigate the circumstances under which the ***E*** allele can invade a population composed of ***ee*** individuals, we perform a linear stability analysis. Let $\varepsilon_x(t)$ and $\varepsilon_y(t)$ be very small frequencies of the ***EE*** and ***Ee*** genotypes, respectively. Ignoring higher-order terms, we have

$$\vec{\varepsilon}(t+1) \approx \mathbf{J}\vec{\varepsilon}(t), \tag{6}$$

where

$$\vec{\varepsilon}(t) = \begin{bmatrix} \varepsilon_x(t) \\ \varepsilon_y(t) \end{bmatrix}, \tag{7}$$

and the relevant Jacobian matrix is

$$\mathbf{J} = \begin{bmatrix} 0 & 0 \\ \frac{2n + (n+1)\pi}{n + \pi} & \frac{2n + (n+1)\delta\pi}{2n + 2\delta\pi} \end{bmatrix}. \tag{8}$$

The Jacobian is a triangular matrix, so the eigenvalues line the diagonal. The dominant eigenvalue is:

$$\lambda_d = \frac{2n + (n+1)\delta\pi}{2n + 2\delta\pi}, \tag{9}$$

which is always greater than unity if $n > 1$, $\delta > 0$, and $\pi > 0$. This means that in an unstructured population, the ***E*** allele can invade if lek size is greater than one and there is preference for males with an ***E*** allele. Furthermore, we have the following:

$$\frac{\partial \lambda_d}{\partial n} = \frac{\delta\pi(1+\delta\pi)}{2(n+\delta\pi)^2}, \tag{10}$$

$$\frac{\partial \lambda_d}{\partial \pi} = \frac{n\delta(n-1)}{2(n+\delta\pi)^2}, \tag{11}$$

$$\frac{\partial \lambda_d}{\partial \delta} = \frac{n\pi(n-1)}{2(n+\delta\pi)^2}. \tag{12}$$

When $n > 1$, $\pi > 0$, and $\delta > 0$, we have $\partial\lambda_d/\partial n > 0$, $\partial\lambda_d/\partial\pi > 0$, and $\partial\lambda_d/\partial\delta > 0$ (see Fig. 1). Thus, the rate of invasion of the ***E*** allele increases with lek size, base female preference for males with an ***E*** allele, and the degree of dominance of the ***E*** allele with respect to female preference (Fig. 1). Applying L'Hopital's rule to equation (9) shows that $\lambda_d \to 1 + \delta\pi/2$ as $n \to \infty$ and $\lambda_d \to (n+1)/2$ as $\pi \to \infty$ or as $\delta \to \infty$. That is, the dominant eigenvalue does approach an asymptote as these parameters increase.

Note that the preference slope (β) does not appear in the expression for the dominant eigenvalue. Although β does not influence initial speed of invasion, it does influence introgression rates after the ***E*** allele has increased to higher frequencies (see below). Stein and Uy (2006b) showed a positive relationship between the frequency of yellow males within a mixed lek and their mean mating success (their figure is reproduced in Fig. 2a). This is consistent with $\beta > 0$ in the context of our model. If a regression line is fit to their data, the prediction is that yellow males would actually experience *negative* sexual selection at very low frequencies within the lek. Of course, the relationship between frequency and mating success of yellow males need not be linear, but the possibility of sexual selection acting antagonistically towards a rare ***E*** allele merits theoretical attention. We can model such frequency-dependent selection by setting $\pi < 0$ and $\beta > 0$ in equations (2) (see Fig. 2b). In

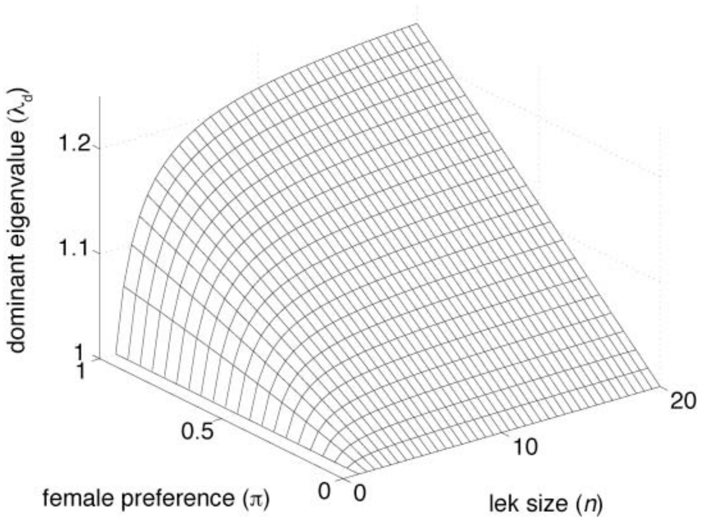


Fig. 1. The dominant eigenvalue as a function of lek size (n) and base female preference (π). Here $\delta = 0.5$. Invasion of the ***E*** allele can occur in regions of the n/π plane where the dominant eigenvalue is greater than one. In an unstructured population, the ***E*** allele can invade if lek size is greater than one and there is preference for males with an ***E*** allele ($\pi > 0$).

our model of an unstructured population, when $\pi < 0$, the dominant eigenvalue is less than unity and the $\boldsymbol{E}$ allele cannot invade (equation 9). What happens in a structured population?

Population structure is readily apparent at species boundaries. Here we assume that two related species hybridize at the edge of their ranges, and that the $\boldsymbol{E}$ allele has fixed at the edge of our focal species. We can investigate introgression using the metapopulation extension to our model [through numerical iteration of equations (3) and (5)]. We initialize the metapopulation by fixing allele $\boldsymbol{E}$ in subpopulation 1 (e.g. $x_1(0) = 1$), and fixing allele $\boldsymbol{e}$ elsewhere (e.g. $x_i(0) = y_i(0) = 0$, for $1 < i \leq S$). In cases where there is always female preference for males with the $\boldsymbol{E}$ allele (e.g. $\pi > 0$ and $\beta \geq 0$), introgression occurs as a single travelling wave (e.g. a given genotype frequency moves from one side of the metapopulation to the

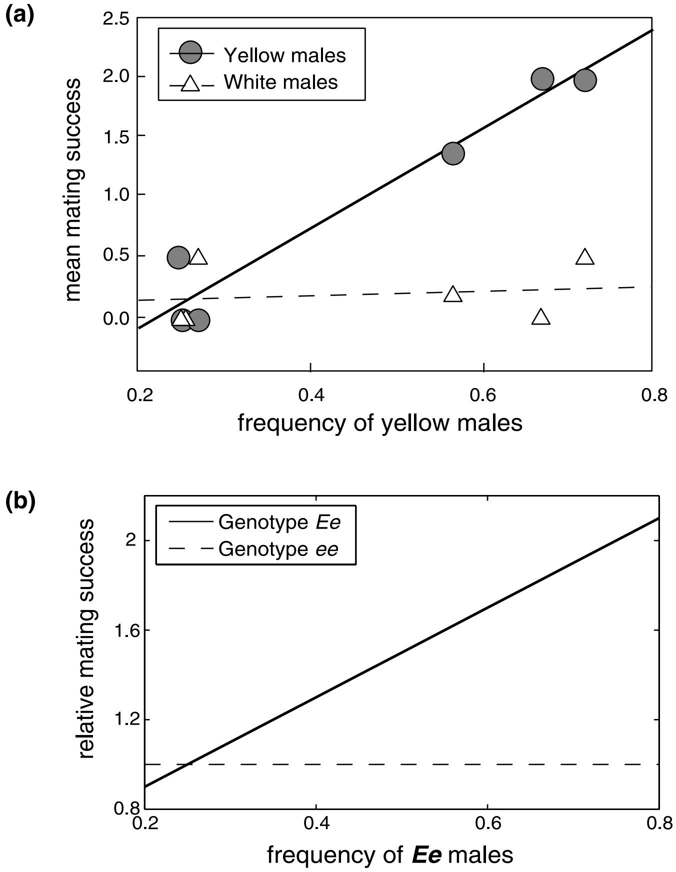
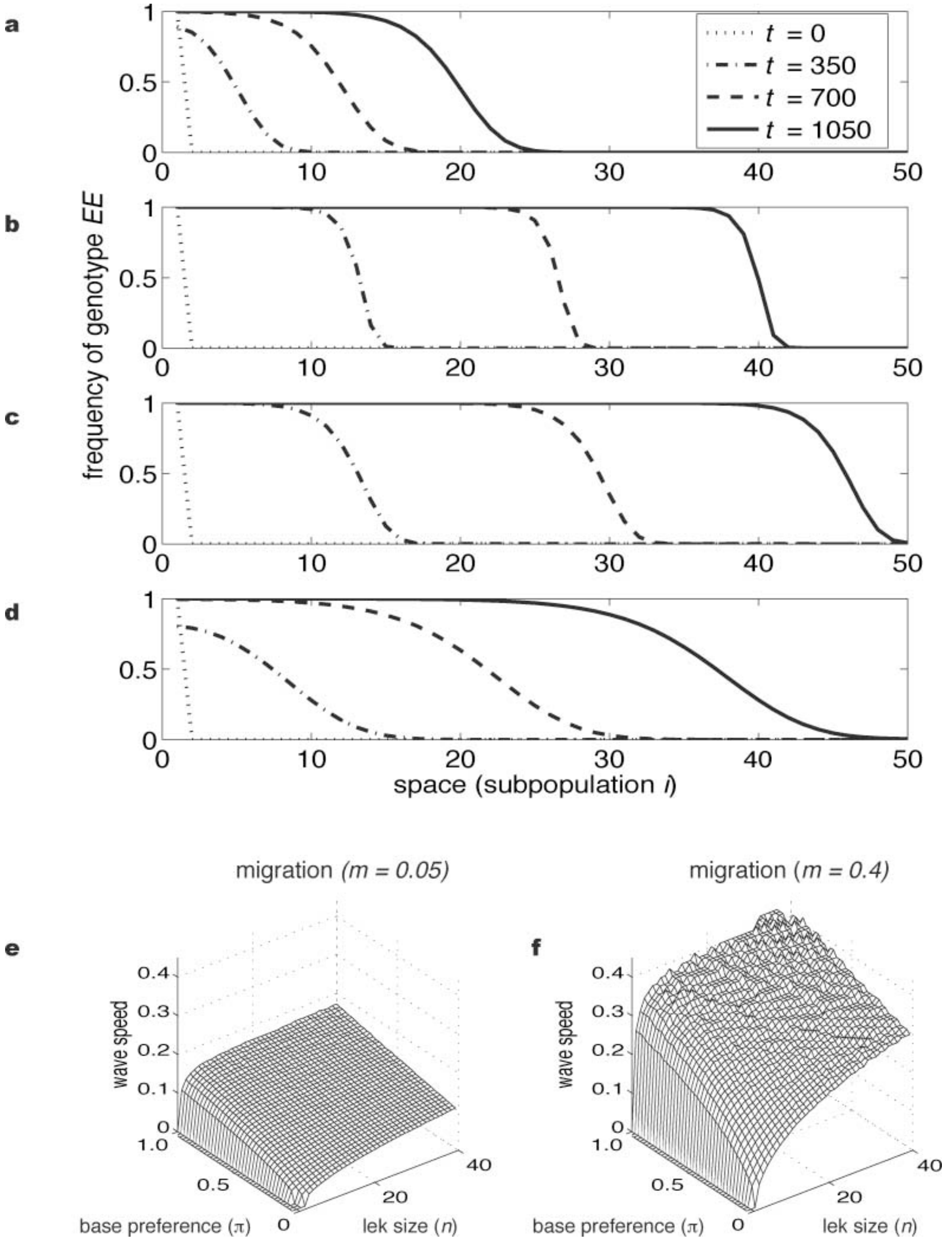


Fig. 2. (a) Relationship between the frequency of yellow males in a mixed lek and mean mating success (reprinted with permission from John Wiley and Sons, Inc.). (b) Relative mating success of genotypes ***Ee*** and ***ee*** as a function of the frequency of ***Ee*** males using equations (2b) and (2c) (assuming $a = 0$, $n = 20$, $\pi = -0.8$, $\delta = 0.5$, $\beta = 0.2$, and $\gamma = 1$). We define the mating success of ***Ee*** relative to ***ee*** as $\frac{\Phi_{Ee}(0,b)/b}{\Phi_{ee}(0,b)/(n-b)}$ and the frequency of ***Ee*** males in the lek is b/n. Note that part (a) shows the average of the *absolute* number of copulations, whereas part (b) displays the mating success of the heterozygote males *relative* to the white homozygote males. Thus, (b) captures qualitative relationships present in (a) rather than precise functional forms.

other; Fig. 3a). Consistent with equation (9), wave speed increases with lek size (n; Fig. 3b) and strength of initial female preference (π; Fig. 3c). Wave speed also increases with migration rate (m; Fig. 3d). Figures 3e and 3f provide more details on how the speed of the travelling wave changes with lek size, female preference, and migration rate.



We now return to our earlier question: Can the ***E*** allele invade a structured population, even if selected against when rare? The answer is yes (Fig. 4a). If the ***EE*** genotypes that are initially fixed in subpopulation 1 are evenly spread across a large metapopulation, no introgression will take place. Thus, initial structure in the spatial distribution of genotypes is important to introgression under this form of positive frequency-dependent sexual selection. Stronger base female preference for ***ee*** males ($\pi \to -1$) slows or prevents the invasion of allele ***E*** (Figs. 4b and 4c). Similarly, a shallower slope of increased preference for ***E***-carrying males ($\beta \to 0$) slows or prevents ***E*** invasion (Figs. 4d and 4e). Figures 4f through 4i provide more details on how the speed of the travelling wave is affected by π and β for different combinations of lek size (n) and migration rate (m).

To understand these metapopulation dynamics, we focus on genotypic preference within leks. A compact way to visualize such preference involves the use of de Finetti diagrams. Each of the vertices of an equilateral triangle is labelled with one of the three genotypes. A single point inside or on the triangle gives the frequencies of the three genotypes inside a lek. The frequency of a specific genotype is given by the normalized distance from the point to the edge opposite the relevant vertex. Thus, as the point approaches a given vertex, the corresponding genotype increases in frequency. We consider how female preference for a genotype deviates from the probability of randomly picking that genotype from the lek. Specifically, for genotype g within a lek with a ***EE*** males and b ***Ee*** males, we define the preference deviation as follows:

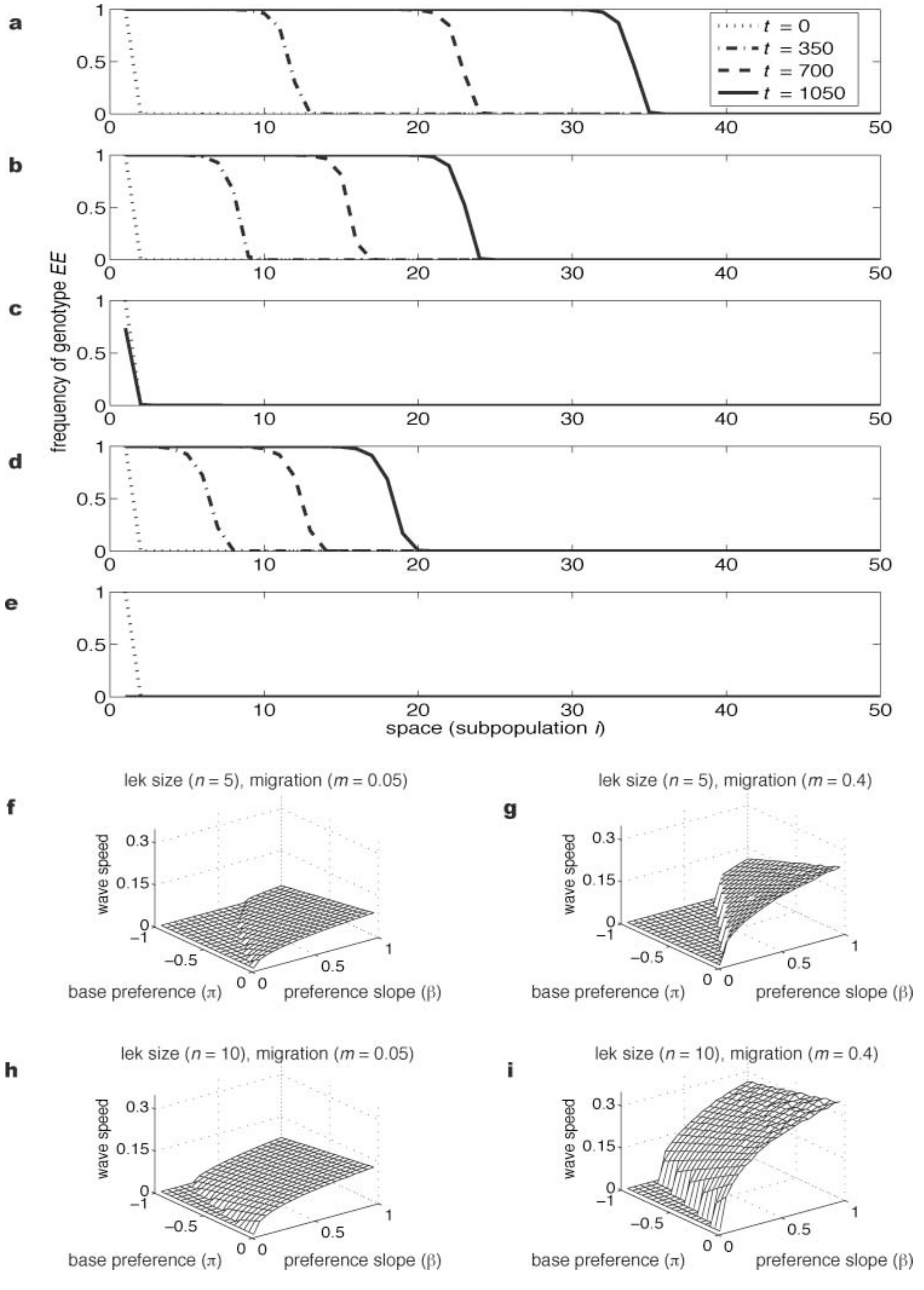
$$\Delta_g(a,b) = \Phi_g(a,b) - f_g(a,b), \tag{13}$$

where $f_g(a,b)$ is the frequency of genotype g (i.e. $f_{EE}(a,b) = a/n$, $f_{Ee}(a,b) = b/n$, and $f_{ee}(a,b) = (n - a - b)/n$), and $\Phi_g(a,b)$ is defined in equations (2). We plot the preference deviation for genotypes ***EE***, ***Ee***, and ***ee*** in Figs. 5a, 5b, and 5c, respectively, for a case of positive frequency-dependent selection. If $\Delta_g(a,b) > 0$, then sexual selection is working for genotype g within the lek, whereas if $\Delta_g(a,b) < 0$, then sexual selection is working against genotype g.

Now, to return to our case of positive frequency-dependent selection in a metapopulation: When genotypes ***EE*** and ***Ee*** are rare in a subpopulation (e.g. in the tail of the travelling wave), then a and b are likely to be small. This concentrates most leks near the ***ee*** vertex of the de Finetti diagram. In this region of the triangle, sexual selection is working against ***E***-carrying genotypes ($\Delta_{EE} < 0$ in Fig. 5a and $\Delta_{Ee} < 0$ in Fig. 5b) and favouring ***ee*** genotypes ($\Delta_{ee} > 0$, Fig. 5c). So, how can the ***E*** allele increase in such a subpopulation? Besides sexual selection, there is another evolutionary force operating on this subpopulation: migration.

Fig. 3. The spatial spread of the ***EE*** genotype. The spatial frequency distribution of ***EE*** is shown at several time points in a linear metapopulation. Initially, genotype ***EE*** is fixed in subpopulation 1 while all other subpopulations are fixed for genotype ***ee***. Over time, the spread of the ***EE*** genotype occurs as a travelling wave moving from left to right. (a) A typical travelling wave with $n = 2$, $\pi = 0.2$, $m = 0.05$, $\delta = 0.5$, $\beta = 0.1$, and $\gamma = 1$. (b) Increasing the lek size ($n = 10$) speeds up the invasion (all other parameters are as in part (a)). (c) Increasing female preference ($\pi = 0.8$) has a similar effect (all other parameters are as in part (a)). (d) Increasing migration rate ($m = 0.2$) speeds up invasion as well (all other parameters are as in part (a)). (e) The speed of the travelling wave is expressed as subpopulations per generation (where the distance between adjacent subpopulations is fixed). Wave speed is shown as a function of lek size (n) and female preference (π) for $m = 0.05$. (f) Wave speed is shown for $m = 0.4$. All other parameters in parts (e) and (f) are as in part (a).

Immigration of the ***E*** allele (from subpopulations where it is more frequent) tends to move leks away from the ***ee*** vertex (i.e. by increasing a and b). Thus, there are two evolutionary processes that are initially in conflict: sexual selection and migration (Fig. 5d). Sufficiently strong migration can raise the frequency of ***E*** in a subpopulation such that many leks have



entered the region of preference for ***E***-carrying males (below the dotted line in Fig. 5d). Then both of the evolutionary forces work together for fixation of the ***E*** allele.

DISCUSSION

Our model predicts that the rate of invasion of a sexually selected introgressed allele increases asymptotically with lek size (Fig. 1). To understand why lek size matters, it helps to think in terms of finite populations. Imagine a population of 100 manakins with only one yellow bird. All else being equal, as leks become larger the probability that a female will encounter the lek with the yellow male increases. However, the probability that she will mate with the preferred yellow male decreases as leks become larger, because successful mating is diluted by the larger number of males competing in the lek (see equations 2). Nevertheless, as leks become larger, the increased probability of the yellow male being in the encountered lek overwhelms the decreased probability of the yellow male being chosen as a mate. Consequently, the speed of invasion of a sexually selected allele increases with lek size (n). Of course, this speed also increases with the base female preference for males with the allele (π) (Fig. 1), assuming that female preference is also a proxy for male mating success. The wave speed of the sexually selected ***E*** allele in a structured population also increases with lek size and base female preference (Fig. 3). Furthermore, wave speed increases with preference slope (β) and migration rate (m). In these cases, wave speed increases because of a higher probability that an ***E***-carrying male resides in the encountered lek (as n increases), a higher mating success of ***E***-carrying males in mixed leks (as π or β increase), or a higher rate of dispersal of the ***E*** allele into subpopulations where it is rare (as m increases).

Even if selected against when rare, the ***E*** allele can invade as long as the population is structured (Fig. 4). The build up of ***E*** occurs when migration of ***E***-carrying males into a subpopulation dominated by genotype ***ee*** is a stronger evolutionary force than sexual selection against ***E***-carrying males in that subpopulation (Fig. 5d). As the ***E*** allele increases further in frequency, sexual selection for the ***E*** allele becomes positive, such that migration and selection work in tandem and ***E*** becomes fixed. A travelling wave is the result of this process operating over a set of contiguous subpopulations. With positive frequency-dependent sexual selection, parameter values exist where introgression does not occur (e.g. when base female preference strongly favours ***ee*** and when the preference slope is small; see Fig. 4f–i). Careful inspection of Fig. 4 shows that lek size can make a qualitative difference to introgression: for certain parameter combinations, introgression will only occur when lek size has surpassed a critical value.

Our results are pertinent to the *Manacus* system. Stein and Uy's (2006b) data show that when yellow males increase in frequency, their mean mating success also increases. Stein

Fig. 4. The spatial frequency distribution of ***EE*** is shown at several time points in a linear metapopulation. Initially, genotype ***EE*** is fixed in subpopulation 1 while all other subpopulations are fixed for genotype ***ee***. (a) Even though selected against when rare ($\pi = -0.2$), invasion of ***EE*** occurs as a travelling wave when $\beta = 0.25$ (here $n = 10$, $m = 0.05$, $\delta = 0.5$, and $\gamma = 1$). (b) Decreasing female preference ($\pi = -0.5$) slows down the travelling wave and (c) invasion is completely prevented when $\pi = -1$. (d) Decreasing the preference slope ($\beta = 0.1$) also slows down the speed of invasion and (e) introgression is prevented with $\beta = 0.01$. (f) The speed of the travelling wave as a function of base preference (π) and preference slope (β) is shown for $n = 5$ and $m = 0.05$, (g) $n = 5$ and $m = 0.4$, (h) $n = 10$ and $m = 0.05$, and (i) $n = 10$ and $m = 0.4$. All other parameters in parts (f)–(i) are as in part (a).

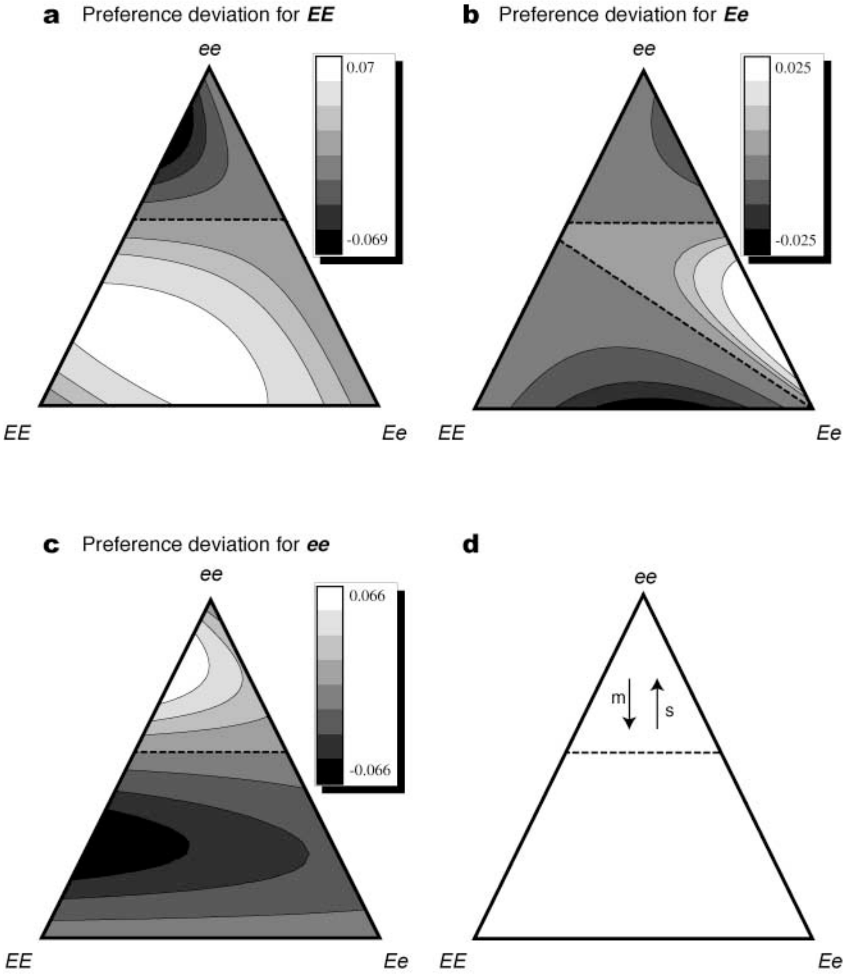


Fig. 5. Strength of sexual selection on each genotype as a function of lek composition. In each de Finetti diagram, different points in the triangle refer to different frequencies of the three genotypes in a lek. For a given point (lek composition), the frequency of each genotype is given by the normalized distance from the point to the edge opposite the relevant labelled vertex. The contours give the preference deviation (equation 13) for different lek compositions. Each triangle diagram corresponds to deviations for one genotype (i.e. the force of sexual selection on that genotype). Negative deviation values correspond to lek combinations where the genotype is less preferred than by chance, while positive values correspond to positive sexual selection (the zero contours are dashed). (a) Preference deviation for the ***EE*** genotype, (b) the ***Ee*** genotype, and (c) the ***ee*** genotype when there is positive frequency-dependent sexual selection ($n = 20$, $\pi = -0.8$, $\delta = 0.5$, $\beta = 0.1$, and $\gamma = 1$). (d) Under positive frequency-dependent selection in a metapopulation, two evolutionary processes can be in conflict in a subpopulation when leks are mostly composed of ***ee*** genotypes. Sexual selection (s) and migration (m) are shown as arrows pointing in opposite directions for the upper region of the de Finetti diagram. Although sexual selection works against the ***E*** allele when it is rare (see parts (a)–(c)), migration can work for it. Specifically, migration from subpopulations where ***E*** is common can raise its frequency in subpopulations where it is rare. Thus, migration can help leks cross the zero contour (dotted line), where both evolutionary forces work in tandem for fixation of the ***E*** allele.

and Uy's data are also consistent with the possibility that yellow males are selected against when rare. When hybrids are first formed across a species boundary, they are, of course, rare. Given their initial rarity, how can we account for the invasion of *M. vitellinus* into *M. candei* populations? Our model provides a possible explanation. Imagine that in our structured population the ***E*** allele is fixed in subpopulation 1 while rare everywhere else. Then, subpopulation 1 represents a population composed entirely of yellow males (e.g. *M. vitellinus*), while subpopulations 2 through S correspond to populations composed entirely of white males (e.g. *M. candei*). The line separating subpopulations 1 and 2 corresponds to the species boundary. Given enough migration, the establishment of yellow males in white-dominated leks across the species boundary may eventually overcome selection against them. Once they become frequent enough, both selection and migration work together to further increase the frequency of yellow male alleles into the white population. The result will be a travelling wave of *M. vitellinus* genes invading the *M. candei* species (see Figs. 3 and 4).

Other processes, in addition to migration, may aid the establishment of a critical number of yellow males on white-dominated leks. Yellow males may be more aggressive (McDonald *et al.*, 2001) than white males, thus conferring them an advantage when they invade white-dominated leks. This advantage may be compounded by the fact that *Manacus* manakins seem to recognize kin, and may group together to bolster each other's mating success through kin selection (Shorey *et al.*, 2000; Höglund and Shorey, 2003). The latter two factors may work in tandem with the process outlined in our model to facilitate introgression. Thus, the dispersion of yellow males across the hybrid zone may influence the rate at which a critical number of yellow males on any one lek is reached, such that female choice shifts from white to yellow.

The mechanisms and factors underlying rates of trait introgression should be of interest to evolutionary and conservation biologists. For evolutionary biologists, hybridization and introgression are responsible for diversifying the gene pool on which natural selection might act (Grant and Grant, 2005). For conservation biologists, especially those dealing with endangered populations of animals with lek or lek-like mating systems, extinction of native populations via introgression is of utmost concern.

Evolutionary implications

If a novel male ornament is preferred by females, that ornament will invade the population as the 'sexy sons' of that male are encountered and mate successfully (Weatherhead and Robertson, 1979). This type of selection in which rare or novel types are preferred is known as negative frequency-dependent selection. Our model is flexible enough to explore this case. By setting base female preference positive ($\pi > 0$) and preference slope negative ($\beta < 0$), we can model negative frequency-dependent selection. Under such circumstances, we would expect novel ornaments to invade initially. With time, however, as they become more common, the novelty wears off and females may switch their preference to the other type. Eventually, these back-and-forth changes in trait frequency may lead to the evolution of polymorphism. These results apply to both structured and unstructured populations.

In the *Manacus* system, the genes for yellow collar appear to have swept to fixation up to the southeast bank of the Changuinola River. Northwest of the river, white-collared males still dominate. While the river may present a barrier to further gene flow, environmental differences across the river may also influence further introgression of *M. vitellinus* plumage into *M. candei* populations. Uy and Stein (2007) detected differences in light environments north of the Changuinola River such that white collars may stand out more in the ambient light of the forest than yellow collars, making white collars more conspicuous to females in this environment and potentially slowing or preventing the further spread of yellow plumage. Many sexually selected traits function as signals and, as a result, should be shaped not only by the sensory biases of the intended receiver (Ryan and Rand, 1993) but also by the environments in which they are transmitted (Endler, 1992, 1993). Such environmental effects could be incorporated into our metapopulation model by allowing parameters of female preference (π, δ, β) to differ across subpopulations.

Conservation implications

As habitat modification allows formerly isolated species to come into contact and hybridize, and as endangered species managers and land managers intentionally hybridize small populations with other populations to prevent inbreeding depression and restore population sizes, the issue of damaging introgression cannot be ignored (Avise and Nelson, 1989; Hedrick, 1995; Garant *et al.*, 2003). In extreme cases, the introgression and fixation of unwanted alleles in a given species may represent the effective extinction of that species (Rhymer and Simberloff, 1996). In endangered populations of lek mating species, such as Greater and Gunnison's Sage-Grouse (*Centrocercus urophasianus* and *C. minimus*) or Lesser Prairie Chickens (*Tympanuchus pallidicinctus*), introgression of non-adaptive traits, as well as sexually selected ornaments that are representative of other populations or species, should be of utmost concern, especially if land managers are faced with the prospects of transplanting individuals to bolster local population sizes (Young *et al.*, 2000). In our model, we have shown that once a species boundary breaks down and introgression takes place at the boundary, invasion of sexually selected traits can spread to whole populations, effectively rendering the invaded species extinct at relevant genetic loci. Even in systems without strong inter-sexual selection, such as that of hybridizing Barred Owls (*Strix varia*) and Northern Spotted Owls (*S. occidentalis caurina*), investigating the role of intra-sexual selective forces, such as aggressive asymmetries, will help us to understand the potential for introgression of unwanted alleles into threatened populations (Dark *et al.*, 1998; Kelly *et al.*, 2003).

We have shown that mating system, in particular the skew in reproductive success of the selected sex, has profound effects on invasion rates. However, there is nothing intrinsic in our model that restricts it to lek-mating systems. Indeed, our results apply to any system in which female preference operates (e.g. species with uneven sex ratios, resource polygamy, or socially monogamous species in which extra-pair copulations are common). Nevertheless, our model is most appropriate to lek-mating systems in which female choice and sexual selection are particularly strong.

Hybridization has the power to generate novel traits and combinations of traits that can be acted upon by sexual and natural selection. Here we have shown that the speed of introgression of novel genes into pre-existing populations, especially animal systems in which mating success is highly uneven, depends on lek size and female preference for those genes. Finally, our model shows that traits under positive frequency-dependent sexual selection may invade structured populations even if selected against when rare.

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