

EVOLUTION OF MATE CHOICE FOR GENOME-WIDE HETEROZYGOSITY

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The extent to which indirect genetic benefits can drive the evolution of directional mating preferences for more ornamented mates, and the mechanisms that maintain such preferences without depleting genetic variance, remain key questions in evolutionary ecology. We used an individual-based genetic model to examine whether a directional preference for mates with higher genome-wide heterozygosity (H), and consequently greater ornamentation, could evolve and be maintained in the absence of direct fitness benefits of mate choice. We specifically considered finite populations of varying size and spatial genetic structure, in which parent-offspring resemblance in heterozygosity could provide an indirect benefit of mate choice. A directional preference for heterozygous mates evolved under broad conditions, even given a substantial direct cost of mate choice, low mutation rate, and stochastic variation in the link between individual heterozygosity and ornamentation. Furthermore, genetic variance was retained under directional sexual selection. Preference evolution was strongest in smaller populations, but weaker in populations with greater internal genetic structure in which restricted dispersal increased local inbreeding among offspring of neighboring females that all preferentially mated with the same male. These results suggest that directional preferences for heterozygous or outbred mates could evolve and be maintained in finite populations in the absence of direct fitness benefits, suggesting a novel resolution to the lek paradox.

KEY WORDS: Compatible genes, genetic quality, good genes, inbreeding depression, sexual selection.

Identifying the mechanisms that drive the evolution of directional mating preferences for more ornamented mates, and that maintain such preferences over evolutionary time, remain key aims in evolutionary ecology (Neff and Pitcher 2005; Kokko et al. 2006; Kempenaers 2007; Kotiaho et al. 2008a). Clear knowledge of the nature and operation of these mechanisms is critical to understanding the evolution of costly, ornamental secondary sexual traits (Mead and Arnold 2004; Tomkins et al. 2004; Kokko et al. 2006; Radwan 2008).

Directional mating preferences are relatively easy to understand when preferred mates provide direct fitness benefits, for example through increased resources or parental care (Andersson 1994; Kokko et al. 2003). In contrast, the continued expression of directional preferences is much harder to explain when mate choice provides no direct fitness benefit, or incurs a direct cost. In such cases, the fitness benefits driving preference evolution are presumably solely genetic. Two key questions remain to be definitively answered with regard to this scenario (Kempenaers 2007): are genetic benefits sufficient to explain the evolution of costly mate choice mechanisms, and if so, what is the nature of these genetic benefits?

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In general, mate choice could provide two broad categories of genetic benefit (Colegrave et al. 2002; Neff and Pitcher 2005). First, choice could provide additive genetic benefits, reflecting the direct inheritance of beneficial alleles by offspring from the preferred parent. Such beneficial alleles could increase any component of offspring survival or reproductive success (Kokko et al. 2002; Radwan 2008), and an individual's quality as a mate has correspondingly been defined as its additive genetic breeding value for fitness (Hunt et al. 2004). The immediate benefit of choosing a mate of high breeding value for fitness is intuitively clear. Furthermore, because breeding value is a fixed property of an individual within a local episode of mate choice, a general mating preference for high breeding value could cause directional sexual selection for specific individuals, and consequently drive the evolution of costly secondary sexual traits that indicate individual breeding value. However, the hypothesis that directional mating preferences confer additive genetic benefits poses a major theoretical problem. Any such mating preference is predicted to deplete additive genetic variance for fitness, meaning that net selection for the preference will be weak (Kirkpatrick and Barton 1997). Although several resolutions to the resulting "lek paradox" have been proposed, their generality and relative importance remain the subject of considerable debate (Kirkpatrick and Ryan 1991; Rowe and Houle 1996; Tomkins et al. 2004; Kokko et al. 2006; Kotiaho et al. 2008a; Radwan 2008).

Second, mate choice could provide nonadditive genetic benefits, reflecting beneficial combinations of maternal and paternal alleles. Such "compatible" allele combinations could operate at key individual loci, or at the level of genome-wide heterozygosity or degree of inbreeding (Tregenza and Wedell 2000; Mays and Hill 2004; Neff and Pitcher 2005; Thom et al. 2008). Given the latter situation, the fitness benefit of choosing a genetically dissimilar or unrelated mate is again intuitively clear, because resulting heterozygous or outbred offspring are typically relatively fit (Crnokrak and Roff 1999; Keller and Waller 2002; Coltman and Slate 2003; Oh and Badyaev 2006, but see Kokko and Ots 2006). However, in contrast to its breeding value, the quality of any potential mate with respect to nonadditive genetic benefits is generally expected to be contingent on the genotype of the chooser. Mate choice for offspring heterozygosity, for example, is expected to lead to individual preferences for specifically dissimilar or unrelated mates rather than a consistent, directional preference for any one particular individual (Tregenza and Wedell 2000; Mays and Hill 2004; Neff and Pitcher 2005; Kotiaho et al. 2008b). It is therefore unclear how mate choice for nonadditive genetic benefits could contribute to the evolution of unanimous directional mating preferences, or therefore of costly secondary sexual traits in which substantial mating success is required to outweigh direct costs of expression.

Mate choice for additive and nonadditive genetic benefits are frequently viewed as two distinct processes, mediated by directional preferences for more ornamented mates and individual choice for specifically "compatible" mates, respectively (Colegrave et al. 2002; Mays and Hill 2004; Neff and Pitcher 2005; Oh and Badyaev 2006). However, the expression of ornamental secondary sexual traits can be correlated with male heterozygosity and/or coefficient of inbreeding (f), suggesting that females could express a directional preference for relatively heterozygous or outbred mates (Reid et al. 2005; Kempnaers 2007, see also Thom et al. 2008). Such sexual selection for heterozygous mates may not deplete genetic variance (Irwin and Taylor 2000). However, because heterozygosity and f do not show simple Mendelian inheritance, it is not immediately clear how a directional preference for heterozygous mates could confer an indirect genetic benefit in terms of increased offspring fitness, or therefore why such a preference should evolve in the absence of direct fitness benefits of mate choice.

In contrast to this basic expectation, it is increasingly apparent that some degree of parent-offspring resemblance in heterozygosity and f can arise. Whenever uneven allele frequencies arise due to mutation, selection, or stochastic sampling variance (drift), some individuals will carry alleles that are globally rare across the whole population. Precisely because such alleles are rare, they are likely to occur in a heterozygous state in both parents and in offspring that inherit them, causing parent-offspring resemblance in heterozygosity (Mitton et al. 1993). Such resemblance may be further amplified in small or structured populations in which immigration and/or variance in fecundity or recruitment generates high variance in relatedness and local allele frequencies (Bensch et al. 2006; Reid et al. 2006). In such cases, relatively homozygous or inbred individuals may be more closely related to the set of potential mates, and hence more likely to inbreed themselves (as observed in free-living song sparrows, *Melospiza melodia*, Reid et al. 2006). Furthermore, the combination of inbreeding depression in ornament expression and parent-offspring resemblance in f resulting from population structure can cause a correlation between ornamentation and the expected f of a male's offspring (Reid 2007). Such empirical patterns suggest a need to reassess aspects of mate choice theory, and particularly to examine the evolutionary dynamics of directional mating preferences for more heterozygous or outbred (and hence more ornamented) mates in small or structured populations in which substantial parent-offspring resemblance in heterozygosity and f is likely to arise.

Given a correlation between male ornamentation and offspring f plus inbreeding depression in offspring fitness, the evolution of a directional mating preference for more ornamented mates might seem inevitable. However, one rarely noted consequence of any directional female mating preference will be the

production of large groups of paternal half siblings, which will in turn create high local relatedness and an increased risk of close inbreeding among offspring of choosy females. Although large paternal sibships and the associated risk of close inbreeding will arise in any situation in which females express a strongly directional mating preference, this potential downstream cost of mate choice is of particular relevance when inbreeding avoidance is suggested to be the main force driving the original mating preference. Given this situation, models that track fitness across multiple generations are required to investigate whether choice for relatively heterozygous or outbred (and therefore relatively ornamented) mates can evolve despite any downstream cost of increased inbreeding among offspring.

We used individual-based simulations to examine whether a costly mating preference for mates with high genome-wide heterozygosity and hence increased ornamentation could evolve and be maintained in the absence of direct fitness benefits of mate choice. We specifically considered this problem in the context of finite populations with varying degrees of spatial genetic structuring in which substantial parent–offspring resemblance in heterozygosity is expected. We thereby consider whether directional mating preferences for one component of nonadditive genetic variance could in principle evolve and be maintained, suggesting an additional resolution to the lek paradox.

The Model

The hypothesis of directional mate choice for mate and hence offspring heterozygosity has been verbally formulated in an “island model” context in which a focal population receives occasional unrelated immigrants (Reid 2007). However, such sharp divisions between small subpopulations may be relatively uncommon in the wild (Kempnaers 2007). Therefore, to maximize generality and applicability, we modeled a situation in which spatial genetic structure emerged through a continuous distribution of dispersal distances within relatively large and continuous populations (creating isolation-by-distance) rather than through migration between discrete subpopulations. Simulations proceeded as follows.

POPULATION SIZE AND STRUCTURE

A population was initiated with N individuals that were randomly defined as male or female and located in finite two-dimensional space. Each individual's initial location along each spatial dimension was specified by a random number drawn from a uniform distribution between 0 and 1. Available space therefore comprised a square of edge length 1. Individuals whose subsequent dispersal (see below) took them over an edge reentered from the opposite side of space, following a standard “toroid” model formulation to avoid edge effects. This spatial structure, together with limited

dispersal of individuals, created genetic isolation by distance that applied to all individuals independent of their location.

INDIVIDUAL GENOTYPE

Each individual had 50 unlinked diploid loci at which the identity of both alleles was tracked, and that were used to measure each individual's genome-wide heterozygosity. The identities of all alleles at all loci were initially defined as random numbers, meaning that all N initial population members were heterozygous at all loci and completely genetically distinct from each other. The numeric value of each allele did not specify the phenotypic effect of that allele. Rather, the almost guaranteed uniqueness of random allelic values allowed the subsequent identification of homologous pairs of alleles that were identical by descent. Given this formulation, individual genome-wide heterozygosity (H ; the proportion of an individual's loci that were heterozygous) can also be interpreted as an inverse measure of individual coefficient of inbreeding (f), defined as the probability that a pair of homologous alleles will be identical by descent (Falconer and Mackay 1996).

All individuals also carried an unlinked mating preference locus that was assumed to be haploid (see Kokko 2007 for justification), with allelic values of 1 or 0 coding for the presence or absence of a directional mating preference for more ornamented mates. The initial probability of carrying the preference allele was x_0 , drawn independently for every individual. Although all individuals carried the mating preference locus, it was expressed only in females. We thereby consider the common scenario in which females are the choosy sex, but our model could in principle apply equally well to choosy males.

ORNAMENTATION

Males expressed an ornamental secondary sexual trait to a degree that depended on their own heterozygosity (H) and on stochastic effects, reflecting developmental or environmental variation. Each male's ornamentation value was calculated as $(1 - S)H + SR$, where S specifies the degree of stochasticity and R was a random number drawn from a uniform distribution between 0 and 1 for every individual male. Across a population, ornamentation was therefore more tightly correlated with H when S was small. When $S = 1$, ornamentation conveys no information about a male's heterozygosity H .

MATE CHOICE AND REPRODUCTION

At each time step, each female selected a mate. Females carrying the preference allele (hereafter “choosy” females) selected the male with the largest ornament among the n nearest males in two-dimensional space, whereas nonchoosy females randomly selected one of the n nearest males. Each female mated only once, whereas males could mate with multiple females or remain unmated. Each female then produced four offspring, which were

randomly defined as male or female. Although a fecundity of four is low compared to that of many organisms, it suffices to describe the number of offspring that may typically recruit. Each offspring randomly inherited the haploid preference allele from either its mother or its father. The 50 diploid loci followed normal Mendelian inheritance, such that offspring inherited a randomly selected allele (out of two options) from each parent at each of the 50 diploid loci. The preference allele mutated to no preference, and vice versa, with a probability of 0.001. Individual alleles at diploid loci mutated into unique new alleles (an “infinite alleles” assumption) with probability μ . To model a cost of mate choice, each offspring of choosy females died with an independent probability c . A value $c = 0.01$ therefore imposed a 1% cost of mate choice in terms of reduced fecundity.

VIABILITY SELECTION ON HETEROZYGOSITY

Of the remaining offspring of both choosy and nonchoosy females, N were selected to recruit to the next generation with an individual probability of survival that increased in proportion to an individual offspring's own H (thereby imposing survival selection on individual heterozygosity). If the total number of offspring was lower than or equal to N then all offspring recruited, meaning that selection on H was zero. However, the female fecundity of four limited this scenario to rare occasions in which stochastic variation produced a strongly male-biased sex ratio. All adults died after each breeding event, meaning that generations were nonoverlapping. Individual H , as measured across the 50 unlinked loci, therefore influenced both offspring survival and male mating success.

DISPERSAL

Recruited offspring dispersed in a random direction from their mother's location in space, with each individual's dispersal distance drawn from a negative exponential distribution with mean d . When d was small compared to the size of space, most offspring remained relatively close to their natal location, with a low frequency of long-distance dispersal. This formulation produced a positive correlation between the spatial and genetic distance between pairs of individuals (isolation by distance, r_{id}) that became weaker with increasing d . Genetic distance was measured as the expected H of offspring that would be produced by any particular pairing of recruits. This method is justified because more genetically distinct parents tend to produce relatively heterozygous offspring. To compare results with a scenario with no spatial genetic structure ($r_{id} = 0$), we also used an alternative dispersal formulation in which offspring locations along each spatial dimension were assigned as random numbers drawn from a uniform distribution between 0 and 1. This situation is referred to as “panmixia,” and no value of d is specified.

BASELINE EXPECTATION

Evidence of net selection favoring mating preference evolution requires that the preference allele stabilized at higher frequencies than expected under baseline mutation–selection balance with costs of choice as the only source of selection. To quantify this baseline, we ran control simulations in which the preference allele was replaced by a “control” allele that caused females to pay the fecundity cost of mate choice while mating exactly as nonchoosy females.

DOWNSTREAM INBREEDING

To quantify the downstream cost of mate choice in terms of increased risk of close inbreeding among offspring of choosy females, we quantified the proportion of matings that occurred with paternal half siblings among offspring of choosy and nonchoosy females. We then ran a final set of simulations in which a male's ornamentation was uncorrelated with male H (i.e., where $S = 1$), but where the mating preference was still expressed. This formulation exposes the full cost of expressing a directional mating preference in the absence of any indirect genetic benefit, thereby enabling us to quantify the total downstream cost of mate choice.

Each simulation was run for t_{\max} generations, when key output metrics describing the degree of parent–offspring resemblance in H , the frequency of the mating preference allele, and population genetic diversity were recorded. Table 1 summarizes the input parameters that were varied among sets of simulations and all recorded output metrics. Final t_{\max} was sufficient to ensure that all metrics had reached equilibrium. The rare simulations in which populations went extinct before t_{\max} (because a generation contained only one sex) were excluded. Each simulation was replicated 500 times for each set of input parameter values.

Results

After initial transient dynamics, all metrics converged to stable equilibria. Figure 1 illustrates convergence for a representative set of parameter values. Equilibrium values were in all cases independent of the initial frequency of the mating preference allele (x_0).

PARENT–OFFSPRING CORRELATION IN HETEROZYGOSITY

The parent–offspring correlation in heterozygosity (r_{po}) varied markedly among generations within each replicate population. This is reflected in the “spiky” trajectory of mean r_{po} (Fig. 1C), and in the large variation in r_{po} among replicate populations at any given time (Fig. 2A provides a “snapshot”). However, mean r_{po} was positive across a wide range of values of N and d (Fig. 3A). Relatively heterozygous parents therefore produced relatively heterozygous offspring on average. As expected, r_{po} was greatest in

Table 1. Summary of (A) specified input parameters and (B) recorded output metrics.

(A) Input parameters	
N	Population size (total number of individuals)
x_0	Initial frequency of mating preference allele
c	Cost of mate choice (the probability of premature death of offspring of females that carry the mating preference allele)
S	Stochasticity in expression of male ornament
d	Mean dispersal distance
n	Number of males sampled by each female at each mating event
μ	Mutation rate at each diploid locus
t_{\max}	Total number of generations within each simulation
(B) Recorded metrics	
H	Individual genome-wide heterozygosity (proportion of 50 diploid loci that were heterozygous).
x	Observed frequency of the mating preference allele within a given population
\bar{x}	Mean equilibrium frequency of the mating preference allele (averaged across replicate populations)
r_{po}	Correlation between parent and offspring heterozygosity, measuring the degree of parent-offspring resemblance in H .
r_{id}	Correlation between spatial and genetic distance between all possible pairs of individuals, measuring the degree of genetic isolation by distance.
\bar{a}	Mean equilibrium number of alleles per locus across the 50 diploid loci, measuring mean allelic diversity.
b_H	Regression of the number of recruited offspring on parent H , measuring the total magnitude of heterozygote advantage or inbreeding depression.

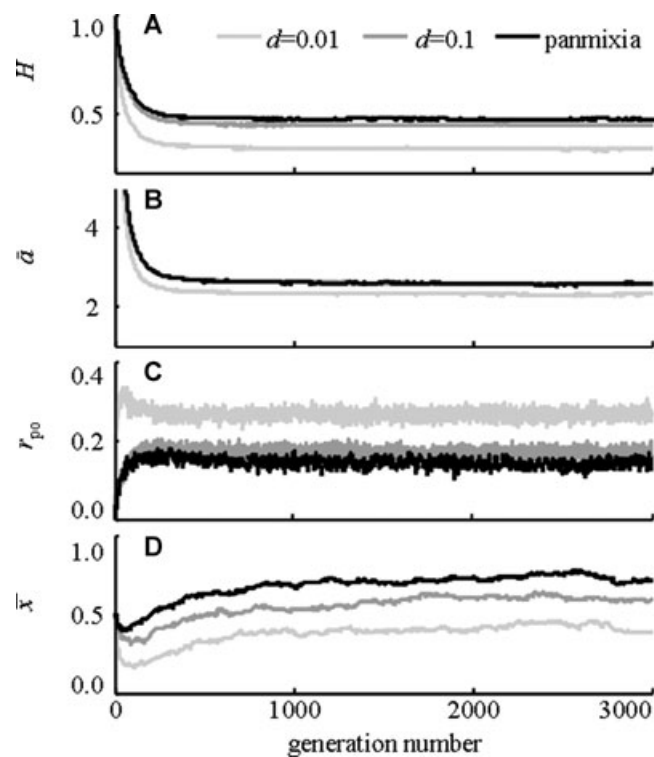


Figure 1. Example trajectories of mean (A) individual heterozygosity H , (B) allelic diversity \bar{a} , (C) parent-offspring correlation in heterozygosity r_{po} , and (D) preference allele frequency \bar{x} across 500 replicate populations for three dispersal scenarios. In (B), \bar{a} is virtually identical for $d = 0.1$ and panmixia. Other parameter values were $N = 100$, $n = 10$, $\mu = 0.0005$, $c = 0.01$, $S = 0.25$, and $x_0 = 0.5$.

small populations with short dispersal distances and hence high genetic isolation by distance (Fig. 3).

MATING PREFERENCE EVOLUTION

In all but the largest populations (e.g., $N = 1000$), the female-mating preference for more ornamented (and hence relatively heterozygous) males was typically either fixed or extinct in any individual population after t_{\max} generations (Fig. 2B). The mean

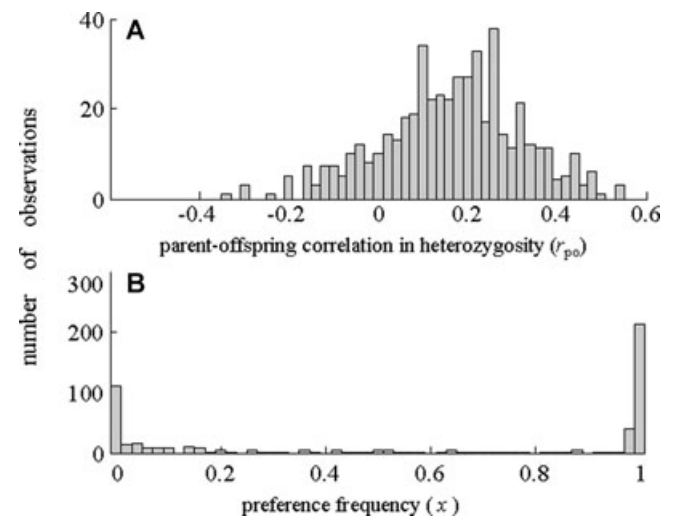


Figure 2. Distributions of parent-offspring correlation in heterozygosity r_{po} and the equilibrium frequency of the mating preference allele x after $t_{\max} = 2000$ generations across 500 replicate populations. Parameter values were as in Figure 1 with panmixia.

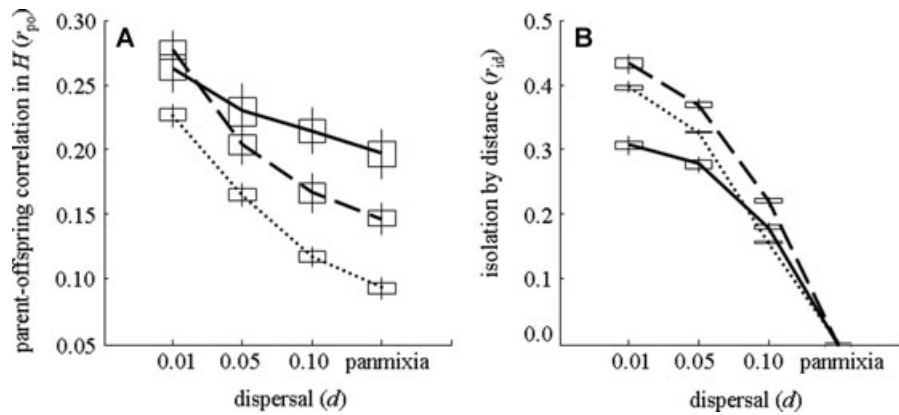


Figure 3. The mean (A) parent–offspring correlation in heterozygosity r_{po} and (B) genetic isolation-by-distance r_{id} given various population sizes ($N = 50$: solid line; $N = 100$: dashed line; $N = 300$: dotted line) and dispersal scenarios. Boxes and whiskers indicate mean \pm 1SE and the associated 95% CI across 500 replicate populations after $t_{max} = 2000$ generations. Other parameter values were $n = 10$, $\mu = 0.0005$, $c = 0.01$, $S = 0.25$ and $x_0 = 0.5$.

equilibrium frequency of the preference allele across replicate populations (\bar{x}) therefore primarily reflects the proportion of replicate populations in which the mating preference became fixed.

Equilibrium frequencies exceeded baseline expectation across a wide range of parameter values (Fig. 4). As expected, \bar{x} was higher when the cost of mate choice c was lower (Fig. 4C) and when ornamentation indicated male heterozygosity more accurately (i.e., when S was small, Fig 4A). Equilibrium \bar{x} was generally higher in smaller populations, but still exceeded baseline expectation in larger populations if ornamentation was tightly correlated with male heterozygosity (Fig. 4A). Surprisingly, \bar{x} increased with dispersal distance (d) and was highest in panmictic populations with zero isolation by distance (although this pattern was less pronounced in smaller populations, Fig. 4B). Finally, \bar{x}

was relatively insensitive to variation in mutation rate μ (Fig. 4D). These results remained qualitatively similar when the degree of female sampling (n) was varied in proportion to N rather than being held constant.

CONSEQUENCES OF MATING PREFERENCE EVOLUTION

Mating preference evolution reduced mean allelic diversity (\bar{a}) slightly below that observed in the absence of the preference (Fig. 5A). However, even when μ was small, \bar{a} was never depleted to the theoretical minimum of 1, and the effect of preference evolution was small compared to the overarching decrease in \bar{a} with decreasing N (Fig. 5A). Preference evolution also reduced the equilibrium parent–offspring correlation in heterozygosity (r_{po}), but did not reduce it to zero (Fig. 5B). The magnitude of

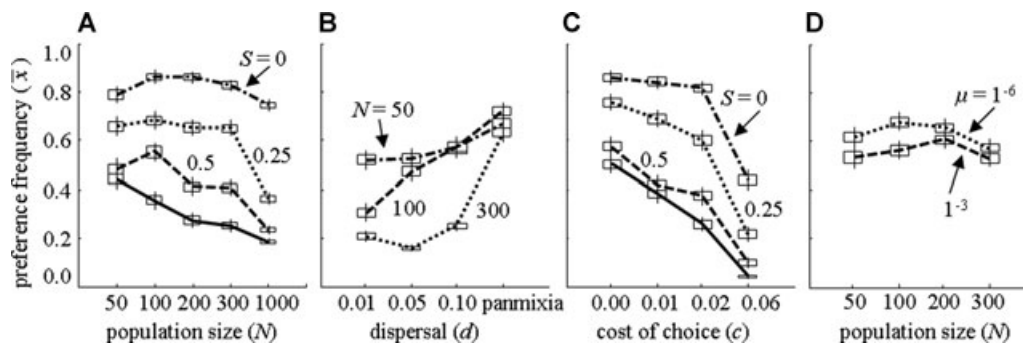


Figure 4. Equilibrium frequency of mating preference allele given variation in pairwise combinations of population size (N), stochasticity in ornament expression (S), dispersal distance (d), cost of mate choice (c), and mutation rate (μ). In (A), the values $S = 0.5$, 0.25 and 0.0 produced heterozygosity–ornament correlations of about 0.2 , 0.5 , and 1.0 respectively. Solid lines show the baseline expectation (not shown in panels B and D for the sake of visual clarity, because each line would have to be compared to its own baseline expectation). Boxes and whiskers indicate mean \pm 1SE and the associated 95% CI across 500 replicate populations after $t_{max} = 2000$ generations (panels A–C), or after $t_{max} = 20,000$ generations (panel D, in which convergence is slowed down by low μ), respectively. Default parameter values were $n = 10$, $\mu = 0.0005$, $c = 0.01$, $S = 0.25$, and panmixia.

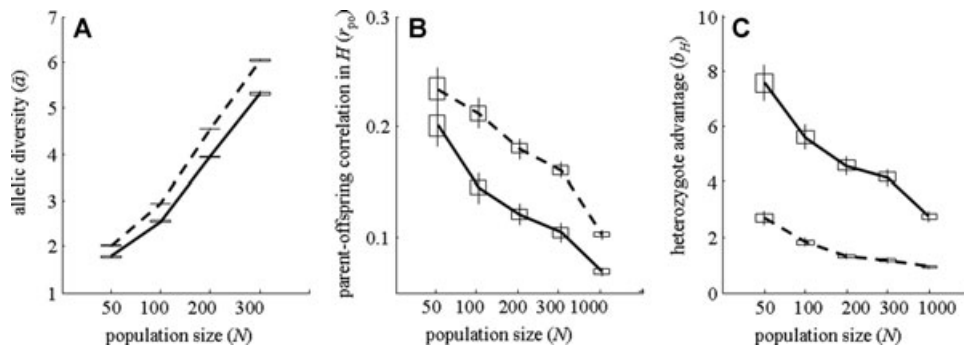


Figure 5. Consequences of the female-mating preference when allowed to evolve freely (solid lines) and held fixed at $\bar{x} = 0$ (dashed lines), on mean (A) population-wide allelic diversity \bar{a} , (B) parent-offspring correlation in heterozygosity r_{po} , and (C) heterozygote advantage (b_H). Boxes and whiskers indicate mean \pm 1SE and the associated 95% CI across 500 replicate populations after $t_{max} = 2000$ generations. Other parameter values were $n = 10$, $\mu = 0.0005$, $c = 0.01$, $S = 0.25$, and panmixia.

heterozygote advantage or inbreeding depression (b_H) increased in the presence of the preference (Fig. 5C).

DOWNSTREAM COSTS

Offspring of females that expressed the mating preference were more likely to mate with a paternal half sibling than offspring of females that did not express the preference (Fig. 6A). This difference in inbreeding risk was greater in populations with greater spatial genetic structure (Fig. 6A), but remained greater than zero even given panmixia. Furthermore, the mating preference for an uninformative ornament was selected against even in the absence of a direct cost ($c = 0$), again to a greater degree in populations with greater spatial genetic structure (Fig. 6B). Indeed, Figure 6B indicates that the intergenerational cost of preferentially mating with any specific male also preferred by others in a highly structured population equated to an additional 1–2% fecundity cost of mate choice.

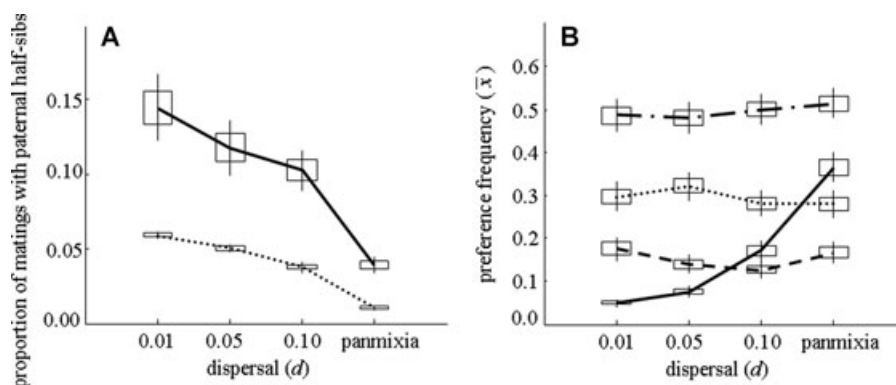


Figure 6. Costs of mate choice in terms of downstream inbreeding measured as (A) the proportion of matings that occur with paternal half siblings in offspring of choosy (solid line) and nonchoosy (dotted line) females, and (B) the equilibrium frequency of a mating preference allele (solid line) for an uninformative ornament ($S = 1.0$) given zero fecundity cost ($c = 0.0$). Baseline expectations given cost $c = 0.0$ (dash-dotted line), $c = 0.01$ (dotted line), and $c = 0.02$ (dashed line) are shown for comparison. Boxes and whiskers indicate mean \pm 1SE and the associated 95% CI across 500 replicate populations after $t_{max} = 2000$ generations. Other parameter values were $N = 200$, $n = 10$, $\mu = 0.0005$.

Discussion

Recent empirical studies show that the expression of secondary sexual ornamentation can be correlated with individual heterozygosity or coefficient of inbreeding (e.g., Aspi 2000; van Oosterhout et al. 2003; Reid et al. 2005; Mariette et al. 2006), suggesting a means by which females could express a directional mating preference for relatively heterozygous or outbred mates. We considered whether a directional mating preference for a more ornamented male with high genome-wide heterozygosity could evolve and be maintained in the absence of direct fitness benefits. We focused explicitly on finite populations with varying degrees of spatial genetic structure in which substantial parent-offspring correlations in heterozygosity or f might be expected to arise (see Bensch et al. 2006; Reid et al. 2006), potentially providing an indirect genetic benefit of mate choice. Our simulations showed that the equilibrium frequency of the mating preference often exceeded baseline expectation (taking the cost of choice

into account), and in some cases even exceeded the frequency of 0.5 expected if mate choice had neither benefit nor cost. Furthermore, although the mating preference reduced equilibrium allelic diversity slightly below that observed in the absence of the preference, genetic variance was not depleted entirely and the mating preference was maintained indefinitely.

Preference evolution occurred in our model because parent and offspring heterozygosity were positively correlated and offspring fitness increased with heterozygosity. Choosy females therefore accrued an indirect fitness benefit in terms of increased offspring fitness. Preference evolution occurred under a broad range of biologically plausible conditions although, as expected for beneficial traits in finite populations, the preference did not go to fixation in all populations (Falconer and Mackay 1996). Crucially, the preference evolved despite a direct fecundity cost of a magnitude that typically prevents the evolution of mating preferences in models focusing on additive genetic benefits (Kirkpatrick 1996; Mead and Arnold 2004; Radwan 2008). Furthermore, the preference also evolved when the expression of the ornamental trait guiding mate choice showed stochastic variation and was therefore imperfectly correlated with male heterozygosity. There was therefore no requirement for choosy individuals to have either perfect or self-referential knowledge of the genotype of potential mates, biological difficulties that have plagued verbal and quantitative models of mate choice for aspects of genetic “compatibility” (Tregenza and Wedell 2000; Reinhold 2002; Neff and Pitcher 2005). Empirical evidence shows that ornamentation can be correlated with individual heterozygosity or f to the degree that our model assumes (Reid et al. 2005; Mariette et al. 2006; Kempnaers 2007, but see Drayton et al. 2007).

Preference evolution was also robust to variation in mutation rate, and still occurred given realistically low values. In contrast, models of mate choice for additive genetic benefits often explicitly require particularly high mutation rates and/or large mutational targets to maintain additive genetic variance under directional sexual selection (e.g., “genetic capture,” Rowe and Houle 1996; Tomkins et al. 2004; Radwan 2008; see also Petrie and Roberts 2007). It is difficult to quantitatively compare the equilibrium levels of heterozygosity (H) and per locus allelic diversity (\bar{a}) that emerged from our model with those observed in natural populations, because empirically observed H and \bar{a} vary enormously depending on locus type, selection regime, and current and previous population dynamics. Allozyme diversity, which reflects diversity at coding loci under selection, may provide a more suitable comparison than the more commonly reported heterozygosity and allelic diversity at neutral microsatellite loci. Output H and \bar{a} were broadly similar to levels of allozyme heterozygosity and allelic diversity commonly observed in the wild (e.g., Hamrick and Murawski 1991; Charlesworth and Yang 1998; Batista and Sosa 2002), and slightly lower than levels estimated for major histo-

compatibility complex (MHC) loci that are well known to be unusually diverse (e.g., Aguilar et al. 2004). Finally, the magnitude of heterozygote advantage (or inbreeding depression) emerging from our model was of the same order of magnitude as that observed in empirical studies. For example, compared to maximally outbred individuals ($H = 1$), individuals with $H = 0.75$ (representing offspring of matings between first-order relatives) incurred a fitness reduction of about 30% in the absence of the mating preference or 30–60% in the presence of the preference depending on other parameter values. These effect sizes are comparable to those observed given close inbreeding in wild populations (e.g., Crnokrak and Roff 1999; Keller and Waller 2002). In summary, our model indicates that a directional female mating preference for relatively heterozygous and hence more ornamented males can in principle evolve and persist under biologically reasonable conditions, and specifically given genetic structuring in continuous space rather than necessarily requiring immigration of unrelated individuals into an “island” situation.

Mating preferences for heterozygous mates have been repeatedly hypothesized (e.g., Brown 1997; Irwin and Taylor 2000; Reinhold 2002). However, earlier theoretical studies concluded that such preferences are relatively unlikely to evolve for purely indirect genetic benefits except under rather restricted environmental or genetic conditions (Partridge 1983; Charlesworth 1988; Irwin and Taylor 2000; Lehmann et al. 2007). Why do we reach a different conclusion? Our model differs from most previous studies in important ways. First, we measure individual heterozygosity across 50 unlinked multiallelic loci rather than at a single diallelic locus. Second, we consider finite populations with varying degrees of internal genetic structure rather than unstructured populations of infinite size. These conditions create relatively high parent–offspring correlations in H , reflecting both global and local variation in allele frequencies and relatedness. In previous models, rare alleles that conferred high fitness in heterozygotes conferred low fitness in homozygotes (assuming asymmetric overdominance as opposed to symmetric overdominance, where both homozygotes have equal fitness); otherwise they would not be rare. By preferentially choosing a heterozygous mate, females therefore increased the chance of producing unfit offspring that were homozygous for the rare deleterious allele (Lehmann et al. 2007). This cost does not apply in our model in which homozygous carriers of rare alleles were no less fit than homozygous carriers of common alleles (symmetric overdominance).

Lehmann et al. (2007) have previously noted that symmetric overdominance in combination with uneven allele frequencies can select for choice of heterozygous mates. However, they suggested that to be stable this situation requires biased mutation; otherwise the rare allele would increase in frequency. In our model, the presence of rare alleles is not caused by biased mutation, but arises from dynamic and stochastic variation in allele frequencies.

Such variation is inevitable in finite populations, especially if selection on individual loci is weak. This is where the number of loci considered becomes relevant: if selection targets many loci simultaneously, its effect on any one locus is reduced. Indeed, further simulations showed that the mating preference does not evolve when our model was restricted to one rather than 50 diploid loci (results available on request).

A different route to the evolution of choice for heterozygous mates was suggested by Charlesworth (1988), based on a one-locus two-allele model without overdominance. In this model, choice for heterozygotes (as compared to random monogamous mating) lead to increased offspring diversity, which is advantageous in a temporally fluctuating environment (genetic bet-hedging). However, this scenario appears less compatible with choice for exaggerated male ornaments. Charlesworth (1988) did not model ornamentation explicitly, but noted that secondary sexual characteristics are unlikely targets of temporally fluctuating selection because they are detrimental traits with respect to natural selection. Later views on condition-dependence of ornaments (e.g., Rowe and Houle 1996) might be used to challenge this particular conclusion. However, even if Charlesworth's (1988) results were interpreted such that they apply to ornament evolution, heterozygotes in his scenarios were assumed to have intermediate fitness compared to either homozygote type, and it therefore does not appear plausible to assume that they should express better ornaments than any homozygote type.

In our simulations, parent–offspring correlations in heterozygosity (r_{po}) were generally weakest in larger and less-structured populations. This is expected because sampling variance that is contingent on population size causes homologous alleles to occur at relatively equal frequencies in larger populations, thus limiting the magnitude of parent–offspring correlations in H that can arise (Mitton et al. 1993). Consistent with this pattern of variation in r_{po} , the mating preference for heterozygous males generally became fixed less often in larger populations. Unexpectedly, however, the preference became fixed most frequently in unstructured populations in which relatives became randomly distributed in space after each breeding event and hence where r_{po} was lower than in structured populations of the same size. This counter-intuitive pattern shows that, even though mating preference evolution requires a positive r_{po} , the magnitude of r_{po} does not on its own determine the net indirect benefit of mate choice. In structured populations with limited dispersal and hence high local relatedness among individuals, the fitness benefit of mate choice in terms of increased offspring heterozygosity (as captured by r_{po}) was partly counteracted by a future cost in terms of increased inbreeding among offspring of choosy females. Specifically, any directional female preference for the most ornamented local male (for whatever direct or indirect benefit) will inevitably produce relatively large groups of paternal half siblings. Given restricted

dispersal, these half siblings will remain adjacent in space and therefore be relatively likely to inbreed and produce relatively homozygous offspring in the next generation (see Amos et al. 2001). In our simulations, this cost of homozygous grand-offspring was reduced in panmictic populations in which half siblings became dispersed in space before mating. This complex interplay of intra- and intergenerational effects suggests that the net benefit of preferentially mating with a heterozygous mate will be difficult to predict through verbal arguments rather than quantitative modeling.

In indicating that a directional mating preference for mate (and therefore offspring) heterozygosity could arise and be maintained in the absence of direct fitness benefits, our model suggests an intriguing new dimension to genetic models of sexual selection. Neff and Pitcher (2008) recently reached largely similar conclusions. However, their model incorporated neither spatial genetic structure nor any uncertainty in female assessment of male heterozygosity (as we did through stochastic variation in ornament expression), and therefore ignores potentially critical drivers and constraints on mate-choice evolution. However, further theoretical and empirical work is required to examine the extent to which our framework may generally resolve the lek paradox.

Because one factor limiting preference evolution appears to be the cost of inbreeding in the next generation, one obvious extension to our current model would be to introduce some additional mechanism of inbreeding avoidance. This could comprise sex-biased dispersal, which is common in nature, can coevolve with mate choice (Lehmann and Perrin 2003), and may reduce the likelihood of local inbreeding while retaining sufficient genetic structure to create parent–offspring correlations in heterozygosity. Alternatively, direct recognition and avoidance of mating with close kin could be assumed (as postulated by Reid 2007). Models could also be extended to consider specific additive or dominance effects of individual alleles, for example relaxing the assumption of symmetric overdominance. Kempnaers (2007) states that “one pressing question is whether female choice for ornamented males equals choice for heterozygous males rather than choice for good alleles.” However, mate choice for additive and nonadditive components of genetic variance is not necessarily mutually exclusive. Future models should strive to combine the two into a single integrated framework.

Finally, further empirical data on the occurrence, magnitude, and form of parent–offspring correlations in heterozygosity or f , and on correlations between ornamentation and heterozygosity or f , are required to substantiate model assumptions. Our model, however, predicts that preference evolution can occur robustly over time despite substantial stochastic variation in r_{po} among replicate populations and among generations. Such variation, resulting from stochastic variation in demography and genetic variance, is expected in small populations. Empiricists may therefore

need to measure r_{po} across multiple populations or years rather than expecting to always observe instantaneously high positive values (see also Reid et al. 2006). High-quality, long-term population studies are therefore likely to be required to quantify these effects in the wild.

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