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SHORT COMMUNICATION

Mate choice for nonadditive genetic benefits and the maintenance of genetic diversity in song sparrows

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Abstract

The lek paradox asserts that strong directional selection via female choice should deplete additive genetic variation in fitness and consequently any benefit to females expressing the preference. Recently, we have provided a novel resolution to the paradox by showing that nonadditive genetic effects such as overdominance can be inherited from parent to offspring, and populations with females that express a mating preference for outbred males maintain higher genetic variation than populations with females that mate randomly. Here, we test our dynamic model using empirical data previously published from a small island population of song sparrows (*Melospiza melodia*). The model assumes that fitness and male trait expression display overdominance effects. The results demonstrate that female choice for outbred males mediated by directional selection on song repertoire size provides a heritable benefit to offspring through reduced inbreeding depression. Within the population, we estimate the heritability of the inbreeding coefficient to be 0.18 ± 0.08 (SD). Furthermore, we show that mate choice for outbred males increases fitness-related genetic variation in the population by 12% and thereby reduces inbreeding depression by 1% per generation in typical years and upwards of 15% in severe years. Thus, mate choice may help to stave off population extinction in this and other small populations.

Introduction

The 'lek paradox' has interested biologists for many years (Kirkpatrick & Ryan, 1991; Tomkins *et al.*, 2004). Leks occur when males congregate to display their elaborate secondary sexual traits, such as the large trains of peacocks, to females. Females typically prefer the male with the most elaborate trait, and because females receive only sperm from males, biologists have assumed that choosy females must benefit by obtaining additive genetic benefits ('good genes') for their offspring (e.g. Petrie, 1994). However, strong directional selection for males with good genes should rapidly deplete additive genetic variance in fitness and eliminate any benefit to differentiating among males (Taylor & Williams, 1982).

Several resolutions to the paradox have been proposed (reviewed in Tomkins *et al.*, 2004; Kotiaho *et al.*, 2008; Radwan, 2008) including sexual ornaments are condition dependent because they are linked to many loci or expressed in proportion to male genetic quality (Rowe & Houle 1996); mutations are able to create substantial new genetic variation in sexually selected traits (Pomiankowski & Møller, 1995; Petrie & Roberts, 2007); direct selection is more important than indirect selection (Reynolds & Gross, 1990); maternal phenotypes influence the condition and expression of secondary sexual traits in sons (i.e. indirect genetic effects, Miller & Moore, 2007); and inheritance of nonadditive genetic benefits such as heterozygosity or genetic diversity (Irwin & Taylor, 2000; Lehmann *et al.*, 2007; Neff & Pitcher, 2008). The resolution proposed by Rowe & Houle (1996) arguably has received the most support. However, it relies on mutation to maintain additive genetic variation in fitness, which may be unlikely in small populations.

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Instead, directional selection for nonadditive genetic benefits may be more applicable to small populations.

Using mathematical models, Lehmann *et al.* (2007) examined the evolution of female preferences for nonadditive genetic benefits conveyed by heterozygous males (i.e. overdominance; see also Irwin & Taylor, 2000; Reinhold, 2002; Neff & Pitcher 2005). The authors assumed an infinite population size and showed that a preference allele for heterozygous males can be selected for when there is symmetric overdominance and a biased mutation rate at the viability locus. Biased mutation rates at fitness loci may be common in many populations (e.g. Lynch *et al.*, 1999) and it ensures that the homozygous genotypes are not equally frequent in the population. In this case, females that mate only with heterozygous males produce more heterozygous offspring than females that mate randomly and, as such, sire heterozygosity is inherited from parent to offspring.

We recently extended the work of Lehmann *et al.* (2007) to address populations of finite size and genetic drift (Neff & Pitcher 2008). We used dynamic models to show that genetic drift can lead to the necessary deviations in frequency of the homozygous genotypes to result in inheritance of nonadditive effects. Because drift is stronger in small populations, the inheritance of the nonadditive effect is greater in small than in large populations. We also showed that a preference allele for heterozygous males can invade populations even when the allele is associated with a fecundity cost. Furthermore, populations with females that express a mating preference for heterozygous males maintain higher genetic variation than populations with females that mate randomly.

Although the paradox has emerged from lek mating systems, its application is much broader and comprises any mating system in which there is directional sexual selection. For instance, one important example comes from the inbred population of song sparrows on Mandarte Island, Canada, which consists of about 35 breeding pairs (Reid, 2007). Song sparrows are socially monogamous with both parents provisioning young, but more than a quarter of the young are sired by extra-pair males (O'Connor *et al.*, 2006; Smith *et al.*, 2006). Females select mates in part based on the complexity of males' courtship song; females prefer more complex songs (Reid *et al.*, 2004). Thus, there is directional selection on song complexity and inasmuch as song complexity is heritable, the preference should deplete any underlying additive genetic variance in the trait. However, because outbred males produce more complex songs, the preference results in females selecting outbred males as mates (Reid *et al.*, 2005). Importantly, the inbreeding coefficient f appears to be heritable as there is a positive correlation between parent and offspring f (Reid *et al.*, 2006).

Here, we test a dynamic model (Neff & Pitcher, 2008) using empirical data based on the Mandarte Island song sparrow population and investigate the effect of mate

choice on population genetic diversity. The population has been extensively studied for decades (see Smith *et al.*, 2006), which allowed us to incorporate key aspects of their ecology into the model. We focus on the inbreeding coefficient f , which represents the probability that two homologous alleles in a diploid individual are identical by descent (Falconer & Mackay, 1996). We use our model to first estimate the expected heritability of the nonadditive genetic benefit (low f) in the Mandarte Island population. Such heritability would provide a genetic benefit to females that prefer to mate with males with more complex songs (Reid *et al.*, 2004; Reid, 2007). Second, we were interested in determining whether or not the heritability of f in the Mandarte population was driven by immigration – i.e. immigrants are relatively outbred ($f \approx 0$) and themselves largely unrelated to the rest of the Mandarte breeding population (Reid *et al.*, 2006). Finally, we were interested in determining if a mating preference for song complexity could contribute to the maintenance of genetic diversity in the population.

Materials and methods

Our model was coded using the C++ programming language. It focuses on the effect of mate choice on the inbreeding coefficient f ; f can range from 0 (outbred, no homologues are identical by descent) to 1 (inbred, all homologues are identical by descent). The inbreeding coefficient was based on 100 loci, but similar results were found when we instead examined 500 or 1000 loci (data available from the authors). Each generation, novel genetic variation was introduced by mutations that followed the infinite allele model with a rate of μ mutations per locus. Thus, each mutation gave rise to a unique allele and any two equivalent alleles were identical by descent. As such, the inbreeding coefficient f for each individual could be calculated as the proportion of loci that are homozygous (i.e. identical by descent). The locus mutation rate was set at $\mu = 1.0 \times 10^{-2}$, so that the population f at mutation–migration–drift–selection equilibrium was equal to the empirically determined value of 0.05 (Reid, 2007). This mutation rate is at the upper end of those estimated for higher eukaryotes (e.g. assuming a genome size of 10^4 genes and a point mutation rate of 0.1–100 mutations per genome per generation; Drake *et al.*, 1998) and suggests that the population may not be in equilibrium.

We assumed a mean breeding population of 35 pairs with a range of 30–40 pairs; this range encompasses a majority of the recorded breeding population sizes (Smith *et al.*, 2006). We incorporated a male-biased sex ratio of 1.2 : 1, which meant that 20% of the males did not pair with a female in any given season (Smith *et al.*, 2006). Each generation, females select social mates based on song complexity (repertoire size; Reid *et al.*, 2004). To determine the strength of the preference and ultimately its effect of male f we took the product of the correlation

coefficients associated with the relationships between the probability a male mates and his song repertoire size ($r_1 = 0.37$ reported in Reid *et al.*, 2004) and between song repertoire size and male f ($r_2 = -0.49$ reported in Reid *et al.*, 2005): $r_{\text{pref}} = 0.37 \times -0.49 = -0.18$. The r_{pref} thus represents that correlation between male f and the probability that a male mates. The calculation assumes that females do not directly assess male f through, for example genetic or pedigree data, but instead rely on an indicator trait (i.e. song repertoire size) to indirectly assess male f . We found that the equation Probability of Mating = $1 - f$ accurately captured the empirically estimated preference strength [exact test: model $r_{\text{pref}} = -0.24 \pm 0.10$ (SD), $P = 0.30$ for comparison with -0.18].

We also incorporated nonrandom mating whereby outbred females tend to pair with outbred males (Reid *et al.*, 2006). To do this, we ranked females in our simulation based on their f and had females select their social mate in the order from most outbred to most inbred. This approach effectively captured the weak correlation reported by Reid *et al.* (2006) between an individual's f and the deviation between the observed kinship between mates and that expected by chance (i.e. given random mating). Extra-pair matings were incorporated at a mean rate of 28% (O'Connor *et al.*, 2006) and females were assumed to select extra-pair mates based on the same f -dependent preference function they used to select social mates.

Each female generated two clutches with a mean of four offspring per clutch and females survived to reproduce in two seasons (Arcese *et al.*, 2002). We did not incorporate matings between overlapping generations including mother and son or grandson, or father and daughter or granddaughter as such matings are rare (Smith *et al.*, 2006). Natural selection via inbreeding depression was incorporated by introducing f -dependent mortality on the offspring according to the equation Survivorship Probability₁ = $1 - 1.24f$ (Smith *et al.*, 2006, p. 119).

Immigration was incorporated using a second, outbred population with rates that averaged one male (range 0–2) and two females (range 0–4) per generation (i.e. per 2 years; Smith *et al.*, 2006, p. 55). The second population had analogous parameters to the Mandarte population except for a larger population size ($N = 1000$ breeding pairs with mean population $f < 0.005$, and $f \approx 0$ for offspring of crosses between immigrants and resident Mandarte individuals; analogous results were found when population sizes of 500 or 2000 pairs were considered). Because these males are relatively outbred compared with resident males in our simulated Mandarte population, by definition immigrant males had a mating advantage as modelled by the f -dependent female preference (see above).

A total of 200 replicate populations were generated and each 'evolved' for 2000 generations at which point a mutation–drift–selection equilibrium for both heritability

and f was achieved. The initial population (first generation) was seeded with a mixture of related and unrelated individuals such that the mean population f was 0.05 (however, equivalent results were found when the initial population was seeded with all unrelated individuals). The heritability of f was calculated in each population using mid-parent–offspring regression (Falconer and Mackay, 1996). We also generated an additional 200 populations that had the same parameters as outlined above, but either utilized a random mating algorithm (i.e. no female preference for male f) or excluded immigration. We compared the mean population f from the original model and the model incorporating random mating and used the difference in the values to estimate the effect on inbreeding depression that would result if females did not exert a mating preference. This analysis was accomplished using two different f -dependent survivorship function. The first function was the inbreeding depression observed in typical years (see above) and the second function was based on severe weather years. This latter function was derived from the data plotted in fig. 2 of Keller *et al.* (1994); we fit a weighted logistic regression to the data, which provided the equation:

$$\text{Survivorship Probability}_2 = \frac{1}{1 + e^{33.1f - 0.49}}$$

Results and discussion

Our dynamic model revealed that the inbreeding coefficient f should be heritable in the song sparrow population found on Mandarte Island. Specifically, using mid-parent–offspring regression we estimated that the heritability will be 0.18 ± 0.08 (SD), which was significantly greater than zero ($P = 0.005$ for comparison with $h^2 = 0$; based on the exact probability from the 200 simulated populations). Our model thereby corroborates empirical data from Reid *et al.* (2006) that revealed a positive correlation between parent and offspring f , and found that the correlation was stronger than expected under random mating. Thus, females that mate with males with more complex songs and hence lower inbreeding coefficients (Reid *et al.*, 2004) secure a non-additive genetic benefit for their offspring – their offspring are themselves less inbred.

Why is there a correlation between sire and offspring f ? Reid (2007) argued that the correlation may be driven by immigrants; immigrants are outbred (low f) and unrelated to most of the breeding population. Thus, the offspring of immigrants are themselves outbred. Our model indicated a positive relationship between male f and males' mean relatedness to the female breeding population [$r = 0.33 \pm 0.18$ (SD), $P = 0.025$, $n = 200$; Figs 1 and 2], and the correlation coefficient of 0.33 was well within those estimated from a 15-year sample of the

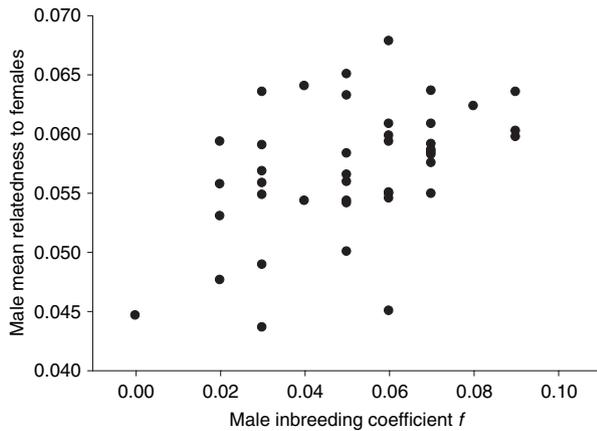


Fig. 1 The correlation between male inbreeding coefficient f and his mean relatedness to breeding females in a simulated population of song sparrows (*Melospiza melodia*). The data represent one of the 200 populations analysed and show the positive relationship between the two variables ($r = 0.46$, $P = 0.002$, $n = 42$). The mean correlation across the 200 populations was 0.33 ± 0.18 (SD) (see text).

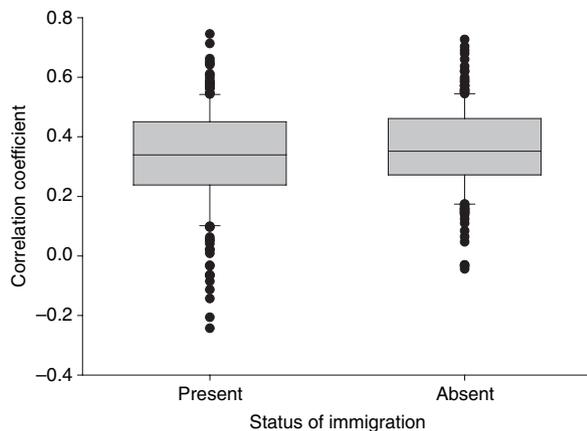


Fig. 2 The effect of the presence or absence of immigration on the correlation coefficient between male f and males' mean relatedness to the female breeding population in simulated populations of song sparrows (*Melospiza melodia*). Box plots denote 25, 50 and 75 percentiles, whiskers denote the 10 and 90 percentiles and filled circles denote data outside the 10–90 percentile range. The plots are based on 200 replicate populations.

Mandarte Island population ($r = 0.13$ – 0.82 reported in Reid *et al.*, 2006). However, this relationship and the heritability of f were independent of immigration. A simulation that excluded immigration revealed that there was still a positive relationship between male f and males' mean relatedness to the female breeding population [$r = 0.36 \pm 0.14$ (SD), $P = 0.01$, $n = 200$; Fig. 2] and f remained heritable [0.17 ± 0.06 (SD), $P = 0.005$, $n = 200$]. Interestingly, across our simulated populations,

there was a strong positive correlation between the heritability of f and the correlation coefficient between male f and males' mean relatedness to breeding females for both models including and excluding immigration ($r > 0.63$, $P < 0.001$, $n = 200$). In the absence of immigration, the mean population inbreeding coefficient did increase dramatically to 0.19 ± 0.01 (SD) ($P < 0.001$ for comparison with 0.05). Nevertheless, immigration is in itself not driving the correlation between an individual's f and its mean relatedness to the population or the heritability of f .

Instead, focusing on the more general case of heterozygosity, Lehmann *et al.* (2007) argued that inheritance of the nonadditive effect occurs in populations characterized by biased mutation rates. The biased mutation rate ensures that homozygous individuals fixed for alternative alleles are not equally frequent in the population. Consequently, females that mate with heterozygous males produce an average of 50% heterozygous offspring, whereas females that instead mate randomly produce fewer than 50% heterozygous offspring. As such, heterozygosity effectively becomes 'heritable'. We have previously shown that genetic drift can similarly lead to the necessary deviations in the frequencies of alternative homozygous genotypes in populations (Neff & Pitcher 2008). Because the influence of genetic drift is inversely related to population size, the correlation between parent and offspring heterozygosity is the highest in small populations. Thus, it may be genetic drift and not immigration that is the key driving force underlying the correlation between sire and offspring f in the song sparrows.

Our model also allowed us to determine the population inbreeding coefficient in the Mandarte Island population should females instead mate randomly with respect to song repertoire and male f . Replacing the preference function with a random mating function, we found that the population f increased by 12% from $f = 0.050 \pm 0.006$ (SD) to $f = 0.056 \pm 0.006$ (SD) ($t_{398} = 8.1$; $P < 0.001$; Fig. 3). Furthermore, the inbreeding coefficient remained heritable at 0.17 ± 0.06 (SD) ($P = 0.005$, $n = 200$), which is consistent with the models of Reid *et al.* (2006) that showed that the heritability was an intrinsic property of the population even under an assumption of random mating. Based on estimates of inbreeding depression on Mandarte Island, we calculated that the 12% increase in f would increase mortality due to inbreeding depression by about 1% in typical years and 15% during severe years. Equivalently, females expressing the preference would obtain a fitness benefit of between 1% and 15% relative to females that mate randomly. Consequently, provided exercising the preference does not come with an associated fitness cost greater than about 1%, there should be positive selection for the evolution of the preference. Furthermore, because the preference reduces inbreeding depression, it could decrease the possibility of local population extinction.

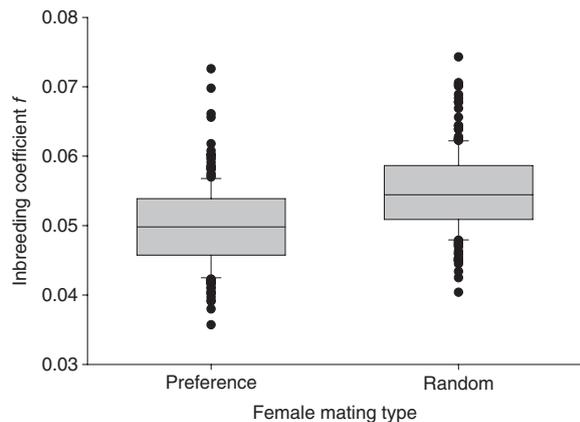


Fig. 3 The effect of female mating type on the population inbreeding coefficient f in simulated populations of song sparrows (*Melospiza melodia*). Without a preference for males with more complex songs the population f would increase by 12% from 0.050 to 0.056 and would reduce population viability via increased mortality from inbreeding depression of between 1% and 15% per generation. Box plots denote 25, 50 and 75 percentiles, whiskers denote the 10 and 90 percentiles and filled circles denote data outside the 10–90 percentile range. The plots are based on 200 replicate populations.

It is interesting that Reid *et al.* (2006) found that inbred individuals paired with more closely related mates than expected based on random mating. This pattern should exasperate inbreeding depression and may thus appear surprising. It is conceivable that inbreeding depression reduces the ability to recognize kin in inbred individuals (Szulkin & Sheldon, 2006). Alternatively, it is possible that inbreeding depression constrains mate choice. Indeed, outbred males should be more attractive to females because they have more complex courtship songs (Reid *et al.*, 2004). Outbred males may similarly reject relatively inbred females as social mates. Given the social pair bond that forms around raising offspring and the only marginally skewed sex ratio in the Mandarte population, inbred individuals may have little choice but to pair with mates that are themselves inbred and close relatives. For example, we were able to capture the weak positive correlation between an individual's f and its relatedness to its mate by allowing relatively outbred females to select their social mates prior to inbred females. Regardless, the pattern could lead to an overestimation of the magnitude of inbreeding depression because inbred offspring also have inbred parents (Szulkin & Sheldon, 2006).

Finally, our model assumes that fitness and male trait expression (song repertoire size) are governed by overdominance genetic effects. The genetic mechanisms underlying inbreeding depression and trait expression in song sparrows are currently unknown, and it is possible that additive genetic effects instead explain the f -dependent relationships. Indeed, previous research focusing on model systems that are maintained in

laboratories such as *Drosophila* have instead argued that overdominance effects on fitness are not likely to be important, but that deleterious mutations probably play a major role in causing inbreeding depression (e.g. Charlesworth & Charlesworth, 1999). By contrast, studies on other species have revealed a strong nonadditive genetic effect on components of fitness (reviewed in Neff & Pitcher, 2005). For example, Wedekind *et al.* (2001) estimated in a fish that nonadditive genetic effects account for 19% of the variation in early egg mortality, whereas additive effects were considerably weaker. Similarly, Wilkinson *et al.* (2006) uncovered overdominance effects on female fecundity in a fly, and several studies have revealed overdominance effects at the immune loci of the major histocompatibility complex (e.g. Worley *et al.*, 2006). Thus, it is unclear as to the relative importance of additive vs. nonadditive genetic effects on fitness and the expression of sexually selected traits in natural populations.

Conclusions

Our dynamic model corroborates empirical data published on Mandarte Island song sparrows showing that the inbreeding coefficient f is inherited from parent to offspring. Although immigration reduced mean population f , it is not required for f to be heritable. The heritability of f may instead be dependent on genetic drift and an emergent positive correlation between an individual's f and its mean relatedness to the population as a whole. We also show that mate choice for nonadditive genetic benefits mediated through directional selection on song repertoire size contributes to the maintenance of genetic diversity in the population. These findings may be widely applicable to small populations and particularly to populations that are threatened or endangered. Maintaining sexual selection in such populations may be important in ensuring their viability.

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