Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird

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Recent studies of non-social animals have shown that sexually selected traits signal at least one measure of genetic quality: heterozygosity. To determine whether similar cues reveal group quality in more complex social systems, we examined the relationship between territory size, song structure and heterozygosity in the subdesert mesite (*Monias benschi*), a group-living bird endemic to Madagascar. Using nine polymorphic microsatellite loci, we found that heterozygosity predicted both the size of territories and the structure of songs used to defend them: more heterozygous groups had larger territories, and more heterozygous males used longer, lower-pitched trills in their songs. Heterozygosity was linked to territory size and song structure in males, but not in females, implying that these traits are sexually selected by female choice and/or male–male competition. To our knowledge, this study provides the first direct evidence in any animal that territory size is related to genetic diversity. We also found a positive association between seasonal reproductive success and heterozygosity, suggesting that this heritable characteristic is a reliable indicator of group quality and fitness. Given that heterozygosity predicts song structure in males, and can therefore be determined by listening to acoustic cues, we identify a mechanism by which social animals may assess rival groups, prospective partners and group mates, information of potential importance in guiding decisions related to conflict, breeding and dispersal.

Keywords: group living; heterozygosity; microsatellites; *Monias benschi*; song; territory size

1. INTRODUCTION

Decisions made by dispersing animals about where to settle and breed may have profound consequences for fitness. Individuals are therefore expected to exploit environmental and social cues containing reliable information about the quality of a prospective breeding site or mating partner. In social animals this decision-making process is complicated by the fact that survival and reproductive success within a group are strongly influenced by the combined ability of its members to defend resources, raise offspring and evade predation (see, for example, Stacey & Koenig 1990; Clutton-Brock 2003). Presumably, for each group encountered, dispersing individuals need to evaluate these attributes (i.e. group quality), as well as the likelihood of future breeding opportunities (i.e. group composition).

Theoretical and empirical studies in a wide variety of taxa (reviewed by Danchin *et al.* (2001)) have shown that cues provided by conspecifics are likely to be especially helpful in breeding patch decisions because conspecifics cannot afford to bias their performance. Such 'public information' may include cues relating to individual or communal performance (Part & Doligez 2003) or breeding success (Brown *et al.* 2001). In social animals, public information is predicted to be particularly valuable because dispersing individuals can observe many conspecifics simultaneously (Danchin *et al.* 2001). However, surprisingly little is known

about which cues are used, and what these cues reveal to a prospecting individual about the nature of a candidate group.

There is growing evidence that female birds may choose mating partners on the basis of genetic heterozygosity (Brown 1997; Foerster *et al.* 2003). Recent studies have also demonstrated that survival and fitness increase with heterozygosity (Keller & Waller 2002), and that females choosing extra-pair partners maximize heterozygosity in their offspring (Foerster *et al.* 2003). Further, it is known that heterozygosity in socially monogamous birds is revealed by sexually selected traits—including plumage ornamentation (Foerster *et al.* 2003) and song repertoire size (Marshall *et al.* 2003)—thus allowing females to gauge the genetic quality of potential mates.

Here, we ask whether group quality in social animals may also be signalled by sexually selected traits, and whether heterozygosity is a currency by which this quality can be measured. We investigate whether two sexually selected traits—territory size and song structure—correlate with (and hence reveal) heterozygosity in a population of the subdesert mesite (*Monias benschi*), a group-living bird endemic to the semi-arid forests of southwest Madagascar (Evans *et al.* 1996). Groups of subdesert mesites produce loud communal songs in a variety of contexts including joint defence of large permanent territories (Seddon 2002). Ownership and defence of these territories are likely to impose significant energetic and survival costs upon contributing individuals (Andersson 1994; Candolin & Voigt

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2001). Because the habitat of the subdesert mesite is homogeneous (Seddon 2001), variation in territory size probably reflects differences among groups in their ability to compete for and maintain large territories (Seddon *et al.* 2003). Two numerical measures—total group size and the number of males per group—are correlated with territory size in other social animals (Adams 2001). In the subdesert mesite, a weak positive relationship has been found between territory size and the number of males per group (Seddon *et al.* 2003). Therefore, controlling for the number of adult males, we investigate whether territory size is better predicted by the mean heterozygosity of male group members. Then, by examining mesite songs, we assess whether their primary advertising signal contains information about group and individual heterozygosity. Finally, we evaluate whether heterozygosity correlates with seasonal reproductive success, thereby providing a useful measure of group quality and fitness.

2. MATERIAL AND METHODS

(a) *Study species and population*

The subdesert mesite is a cooperatively breeding, terrestrial, gruiform bird belonging to a monotypic genus in the family Mesitornithidae (Evans *et al.* 1996). Breeding groups contain an average of three adult males and two adult females, all of which contribute to incubation, parental care and the defence of large, permanent, multipurpose territories (Seddon *et al.* 2003). Clutches contain 1–2 eggs and hatchlings are precocial (Evans *et al.* 1996). Social organization is very fluid: some groups comprise related individuals whereas others contain coalitions of unrelated birds; both sexes are essentially philopatric, but dispersal (or eviction) appears to be female-biased (Seddon *et al.* 2003; N. Seddon, unpublished data).

The species is restricted to a $3700\,km^2$ area of semi-arid coastal woodland and scrub in southwest Madagascar (Seddon *et al.* 2001), where its total population was recently estimated at 115 000 individuals (Tobias & Seddon 2002). We studied 23 unique groups of mesites (electronic Appendix A, table 2) during three field seasons (September–January, 1997–2000) at a study site in their natural range ($23°07'09''–04'57''$ S, $43°37'15''–37'30''$ E).

We caught birds in 18-m mist-nets, attached individual combinations of coloured plastic leg-rings, and took 0.2 ml blood samples and standard biometric measurements (Seddon 2001; Seddon *et al.* 2003). The body condition of trapped birds was calculated as the residual of mass on the cube of the first principal component derived from tarsus, bill and wing length ($R^2 = 0.50$, $p < 0.0001$, $n = 88$). Field observations revealed that group composition changed between seasons, and thus data were available for only a five-month study period per group. Moreover, because we studied the subdesert mesite for only 3 years, we were unable to measure individual fitness by estimating lifetime reproductive success. Instead, we estimated seasonal reproductive output as the number of young produced by a group that survived to at least three months of age (i.e. that developed adult plumage; Seddon 2001). The capture and blood sampling of mesites was conducted under official licence (granted by the Ministry of Water and Forests, Antananarivo).

(b) *Territory size*

A territory was defined as an exclusive, vigorously defended area within which a group performed routine activities, such as foraging, vocalizing, breeding and roosting. During daily focal watches we mapped the location of groups, treating each encounter (visual or audial) as a single registration (see Seddon *et al.* 2003 for group mapping details). Using Wildtrak v. 1.2 (Todd 1992), we drew minimum convex polygons (MCPs; Southwood 1966) of *ca.* 95% of all registrations gathered during a field season (Seddon *et al.* 2003). We estimated territory size for 17 groups with at least 70 registrations; using nine groups for which we collected 150 or more registrations in a season, we calculated that 70 registrations equated to 84.7 ± 2.6 s.e.m. of the final territory size.

(c) *Acoustic analyses*

Mesite groups produced communal songs involving between two and five birds singing simultaneously in contexts of sexual display and territorial communication (Seddon *et al.* 2002; Seddon & Tobias 2003). As all songs comprised alternating, invariable sex-specific syllables, it was not possible to measure repertoire size. Instead, we measured the basic overall structure of communal songs and the time-frequency characteristics of constituent syllables (Seddon 2002). We used a Sennheiser ME67 gun microphone and a WM-D6C Sony Walkman to record songs given by groups in natural situations throughout the day—from dawn (*ca.* 05.00) until dusk (*ca.* 19.00)—during which they sang at a fairly low and constant rate (Seddon 2002). Song data derive from 390 min of recordings containing a total of 437 songs by 23 unique groups. For each group, we calculated the mean hourly singing rate, and analysed each complete song recorded, using CANARY 1.2 (Charif *et al.* 1995) to calculate mean duration of songs, and mean number of syllables delivered per minute. A key component of sexual display in this species, and the commonest vocalization recorded, was a highly coordinated and stereotyped series of alternating male and female syllables produced by two individuals: the pair duet (Seddon *et al.* 2002). When at least one contributor to a pair duet had been genotyped, we analysed high-quality recordings of four syllables produced by both sexes, and generated sonagrams using a Kay Elemetrics Co. Digital Sonagraph DSP Model 5500 with a wide-band filter setting (300 Hz), a time resolution of 4 ms and a bandwidth of 0–8 kHz. The male syllable is a composite of two element types (a frequency-modulated element, or 'trill', immediately followed by 1–6 discrete 'tu' elements); the female syllable is a composite of 2–8 'tu' elements. Using on-screen cursors, we measured three simple characteristics (duration, maximum frequency and minimum frequency) of the male's 'trill' element and the second of the female's 'tu' elements. Four equivalent elements, each taken from different syllables, were sampled per individual and mean values were calculated. We restricted our analysis to the 'trill' element of the male syllable because the acoustic properties of male 'tu' elements were often masked by female syllables. Principal components analysis was used to reduce the three log-transformed variables into a single variable accounting for most of the variation in the original dataset (electronic Appendix B, table 3). Sonagrams of mesite vocalizations, together with definitions of all descriptive terms, are given elsewhere (Seddon 2002).

(d) *DNA analysis and estimates of genetic diversity*

The genetic characteristics of the nine microsatellite DNA loci used in this study are described in electronic Appendix C (table 4), and the laboratory procedures used to isolate and characterize them will be reported elsewhere (N. Seddon, unpublished data). Among 98 subdesert mesites sampled, a mean ($\pm$ s.d.) of 95.6 ± 4.1 individuals were typed per locus, whereas the mean number of loci typed per individual was 8.8 ± 0.5. Mean individual heterozygosity was 0.47 ± 0.13 (range of 0.13–0.78). Several studies have

Table 1. Regression models examining the effects of group heterozygosity (measured as SH and IR) on territory size and seasonal reproductive success, and the effects of individual heterozygosity on male and female song element structure.

(Significant relationships after sequential Bonferroni corrections are highlighted in bold. b is the unstandardized regression coefficient. Explained variance is the proportion of the total variance explained by the independent variable. Numbers beside independent variables refer to separate regression models examining the effect of each independent variable on the dependent variable. Confounding variables with $p < 0.1$ were removed from the final models. The relationship between song element structure and heterozygosity is quadratic.)

				full model			reduced model			
dependent variable	n		independent variables	b	t	p	F	d.f.	p	explained variance
territory size	15	(1a)	SH of group (incl. offspring)	0.97	3.68	0.003	19.3	1,13	**0.001**	0.60
			number of adult males	0.01	0.19	0.852				
		(1b)	SH of adults	0.76	2.61	0.023	10.2	1,13	**0.007**	0.44
			number of adult males	0.03	0.59	0.556				
		(2a)	IR of group (incl. offspring)	−1.19	−3.40	0.005	16.8	1,13	**0.001**	0.56
			number of adult males	0.01	0.14	0.895				
		(2b)	IR of adults	−0.88	−2.33	0.038	8.7	1,13	**0.011**	0.40
			number of adult males	0.00	0.47	0.645				
male song element structure	14	(1)	SH	—	—	—	6.4	1,11	**0.014**	0.54
		(2)	IR	—	—	—	5.9	1,11	**0.018**	0.52
female song element structure	10	(1)	SH	—	—	—	2.4	1,8	0.163	0.23
		(2)	IR	—	—	—	1.0	1,7	0.411	0.22
seasonal reproductive success	15	(1)	SH of adults	2.20	2.77	0.020	7.96	1,13	**0.014**	0.38
			territory size	−0.67	−1.27	0.235				
			body condition	0.00	−0.17	0.869				
		(2)	IR of adults	−2.33	−2.64	0.025	7.88	1,13	**0.015**	0.38
			territory size	−0.58	−1.09	0.301				
			body condition	0.00	−0.01	0.993				

proposed estimators that may improve on simple heterozygosity: these include: (i) mean d^2, a measure reflecting the evolutionary similarity of alleles (Coulson *et al.* 1998); (ii) standardized observed heterozygosity (SH), a form of heterozygosity that allows for incomplete genotyping (Coltman *et al.* 1999); and (iii) internal relatedness (IR), a measure that weights allele sharing by the frequencies of the alleles involved (Amos *et al.* 2001). Of these, both empirical and theoretical analyses indicate that mean d^2 is only likely to be informative under a very restricted set of circumstances (Hedrick *et al.* 2001). Applying these treatments to our data, we found that IR and SH were highly correlated ($r > 0.95$, $p < 0.0001$), whereas mean d^2-values were weakly correlated with the other two measures ($r = 0.42$–0.63, $p = 0.012$–0.131) and explained little of the variation in territory size, song structure or chick survival (data not shown). The heterozygosity of each study group was therefore calculated as the mean of the SH and IR values of its group members.

(e) *Statistical analyses*

SH and IR values were calculated for each individual, and averaged by sex and within group. Multiple linear regression models were then used to examine whether group heterozygosity could explain a significant proportion of the variance in territory size, song structure and seasonal reproductive success. When investigating the relationship between group heterozygosity and territory size, SH and IR were included as independent variables in separate multiple regression models. In the full regression model, number of adult males was also included as an independent variable (a weak positive correlation between territory size and this variable having been found in another study: Seddon *et al.* (2003)). However, this variable had no significant effect and was eliminated from the model (table 1). When assessing the relationship between group heterozygosity and seasonal reproductive success,

we included phenotypic quality (body condition, see § 2) and territory size in the full model, territory and parental quality being the main predictors of variation in the reproductive success of birds (Przybylo *et al.* 2001). To correct for deviations from normality and heteroscedasticity, data on territory size and song element structure were log-transformed before analyses, and data on seasonal reproductive success were square-root transformed. Independent variables used were not significantly correlated. We pooled data across seasons as there were no significant differences in population sex ratios, mean group sizes, territory sizes or song structure between seasons (Seddon 2001). Territory size effects were measured in 15 groups wherein all adult males were sampled; reproductive success effects were measured in the 15 groups with reliable data on offspring survival to three months; effects on song element structure were measured in 14 males from 10 groups, and by 10 females from eight groups. All analyses were conducted using SPSS v. 11.01. Sequential Bonferroni corrections were used to adjust the critical p-value to account for the number of tests conducted. All statistical tests are two-tailed.

3. RESULTS

(a) *Relationship between heterozygosity and territory size*

We found strong effects of group heterozygosity on territory size (figure 1), both including offspring (SH: $p = 0.001$; IR: $p = 0.001$), and excluding them (SH: $p = 0.007$; IR: $p = 0.011$). When we included mean adult male and female heterozygosity values in a multiple regression model we found that male heterozygosity had a significant effect on territory size (SH: $b = 0.405$, $t = 2.33$, $p = 0.042$; IR: $b = -0.493$, $t = -2.22$, $p = 0.053$, $n = 15$ groups). By contrast, female heterozygosity had no effect (SH: $b = 0.175 = t = 0.646 = p = 0.533$; IR: $b = -0.235$,
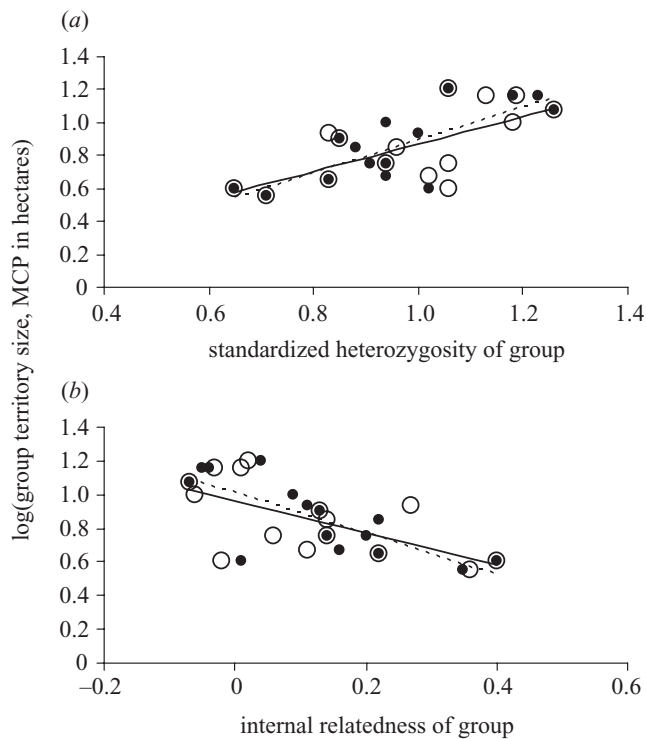
Figure 1. Relationship between territory size and two different measures of mean genetic diversity: (*a*) standardized heterozygosity; (*b*) internal relatedness. Filled circles denote values including offspring (with dashed trendlines), open circles denote values excluding offspring (with solid trendlines); $n = 15$ groups. (1 hectare $= 10^4 \, \text{m}^2$.)
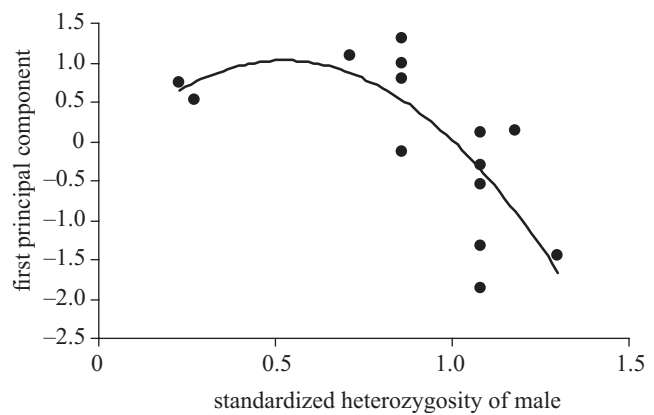

Figure 2. Relationship between standardized heterozygosity and the structure of male trills as defined by an axis of increasing trill frequency and decreasing trill duration, i.e. the first principal component (PC1; proportion of variance: 67.8%; eigenvalue: 2.71; factor loadings of acoustic properties of male trill: -0.760 (duration), 0.969 (maximum frequency), 0.707 (minimum frequency)); $n = 14$ males.

$t = -0.590 = p = 0.569$). We therefore removed female heterozygosity from the models and found a fairly strong effect of male heterozygosity on territory size (SH: $F_{1,13} = 7.28$, $p = 0.018 = R^2 = 0.36$; IR: $F_{1,13} = 7.12$, $p = 0.019 = R^2 = 0.35$).

(b) Relationship between heterozygosity and song structure

We found no significant relationship between SH and the mean hourly rate of singing ($R^2 = 0.08 = n = 8$ groups, n.s.). Nor did we find any significant relationships between group heterozygosity and the basic structure of communal songs (mean duration of songs: $R^2 = 0.08 = n = 8$ groups, n.s.; mean number of syllables per minute per song: $R^2 = 0.04 = n = 12$ groups, n.s.). However, we found that male (but not female) heterozygosity predicted song element structure, with more heterozygous males producing trills of longer duration and lower pitch (SH: $R^2 = 0.54$, $p = 0.014$; IR: $R^2 = 0.52 = p = 0.018$; table 1; figure 2).

(c) Relationship between heterozygosity and reproductive success

We found that the mean body condition of adult group members, and the territory size of the group, had no significant effect on seasonal reproductive success and we therefore dropped these measures from the model (table 1). In the final model, we found strong effects of heterozygosity on the number of surviving young (SH and IR: $R^2 = 0.38$, $p < 0.02$; table 1). When comparing the predictive power of adult male and female heterozygosity on offspring sur-

vival, we found that male but not female heterozygosity had a significant effect (e.g. adult male SH: $b = 1.07$, $t = 2.77$, $p = 0.020$; adult female SH: $b = 0.01$, $t = 0.01$, $p = 0.989$). Removing female values from the models we found that the mean SH and IR of adult males in a group explained 42% and 39% of the variance in offspring survival, respectively (SH: $F_{1,12} = 8.61$, $p = 0.013$; IR: $F_{1,12} = 7.75$, $p = 0.017$).

4. DISCUSSION

Our study examines the relationship between genetic heterozygosity (a surrogate measure of genetic quality) and traits associated with sexual selection and individual quality in a cooperatively breeding bird. We demonstrate a positive correlation between male genetic diversity and territory size, a link that has never been confirmed, to our knowledge, in any other species. In addition, we show that territory size and song structure correlate with male heterozygosity, and thus provide cues by which group genetic diversity could reliably be assessed by dispersing individuals. These findings are interesting for two reasons. First, they suggest that cues to group and individual heterozygosity in social animals may constitute a vital source of the 'public information' on which dispersing individuals base their settlement decisions. Second, they corroborate recent suggestions that sexually selected traits reveal individual, non-additive genetic variance, which has implications for 'good genes' models of sexual selection.

Correlations between male phenotypic quality and territory quality have been demonstrated in numerous species (Candolin & Voigt 2001). Similarly, recent studies reveal correlations between heterozygosity and measures of individual quality, such as freedom from disease and parasites (Acevedo-Whitehouse *et al.* 2003; Reid *et al.* 2003), enhanced reproductive success (Amos *et al.* 2001; Höglund *et al.* 2002; Foerster *et al.* 2003), and high likelihood of survival (Coltman *et al.* 1998). We found that heterozygosity is also strongly linked to an aspect of territory quality, namely size. This might be explained by the fact that heterozygosity is often related to an increase in metabolic efficiency (e.g. Mitton 1993), developmental stability and

resistance to disease (Aparicio *et al.* 2001), factors that probably allow heterozygous males or groups to afford the cost of defending larger territories with greater ease than their homozygous counterparts.

The finding that male (but not female) heterozygosity influences territory size implies that: (i) territory size is subject to sexual selection in the subdesert mesite, as is true for a wide range of other taxa (Andersson 1994); and (ii) males are largely responsible for territory defence, as in numerous other group-living species (including the pale-winged trumpeter *Psophia leucoptera*, another gruiform bird; Sherman 1996). Likewise, group reproductive success was predicted by heterozygosity in males, but not in females. This observation may partly reflect the fact that male mesites play a major role in chick defence by feigning injury to predators (Seddon 2001).

As a corollary of the foregoing, territory size seems likely to be associated with reproductive success. The fact that no correlation was detected could stem from limitations imposed by sample size or experimental design. It seems plausible, for instance, that our measure of reproductive success (number of offspring surviving for three months) fails to capture the true advantage of an extensive territory. For the duration of each breeding event, resources are relatively abundant and mesite territories contract to a core area, *ca.* 40–70% of their total size (measured over a minimum of five months; Seddon *et al.* 2003). However, group reproductive success is more likely to be related to total territory size over longer time-frames, especially during the dry season when food is scarce.

In the subdesert mesite, heterozygosity appears to reflect the combined ability of group members to defend resources, evade predation and raise offspring. In other words, it seems to constitute a reliable indicator of group quality to dispersing birds. Although few dispersal data were available, anecdotal observations supported the idea that dispersing birds selected groups on the basis of male heterozygosity. Only four genotyped individuals (one male and three females) settled in study groups of known heterozygosity. Out of these, the three females dispersed to groups with higher male heterozygosity than that of their natal group (mean SH of natal group versus new group: 0.91±0.11 versus 1.15±0.05 s.e.m.; mean IR of natal group versus new group: 0.09±0.09 versus −0.03±0.05 s.e.m.).

The positive relationship between group heterozygosity and seasonal reproductive success implies that individual fitness increases with heterozygosity in the subdesert mesite. This is more likely to be the case if: (i) more than two individuals per group produced young; or (ii) non-breeding group members accrued indirect fitness benefits through kinship with breeding birds. As such, it is worth reporting the results of a parallel molecular study that showed 3 out of 14 groups (21%) to be polygynandrous (i.e. reproduction was shared among two males and two females), and 5 out of 14 groups (36%) to be composed of closely related individuals (N. Seddon, unpublished data). We can therefore conclude that individual fitness almost certainly increases with heterozygosity in a large proportion of groups.

A key prediction of the 'good genes' model of sexual selection is that attributes of male traits advertise genetic quality (Andersson 1994). We have shown that the structure of trills given by male mesites during duets with females is strongly predicted by heterozygosity, which is itself correlated with seasonal reproductive success. Because trills are a key component of the sexual display of male mesites (Seddon *et al.* 2002), our findings parallel other recent work in which relationships have been shown between individual heterozygosity and sexually selected traits such as song repertoire size in sedge warblers *Acrocephalus schoenobaenus* (Marshall *et al.* 2003), and crown coloration in blue tits *Parus caeruleus* (Foerster *et al.* 2003). Our findings are also consistent with other studies showing that high-quality males with the greatest breeding success are those producing song syllables of greater duration and/or lower pitch (e.g. birds, Lampe & Espmark 1994; Martin-Vivaldi *et al.* 1999; anurans, Andersson 1994). Moreover, several studies have shown syllable duration (e.g. Welch *et al.* 1998) and pitch (e.g. Hoikkala *et al.* 1998) to be honest signals of male genetic quality. That these acoustic features should be honest indicators of quality is unsurprising given that long vocalizations impose high production costs (Welch *et al.* 1998), and pitch has been shown to reveal body size in numerous taxa (Andersson 1994), including a variety of passerine (Badyaev & Leaf 1997; Palacios & Tubaro 2000) and non-passerine birds (Tubaro & Mahler 1998; Bertelli & Tubaro 2002). In the subdesert mesite, we found a weak negative relationship between body condition and maximum trill frequency (Spearman rank correlation: $r = -0.55 = p = 0.062 = n = 12$ males), indicating that trill pitch may reliably indicate, not only heterozygosity, but also male phenotypic quality. The sensitivity of female birds to this type of subtle variation in the acoustic features of male songs has been demonstrated in numerous species (see, for example, Dabelsteen & Pedersen 1993; Vallet *et al.* 1998).

The extent to which molecular estimators of heterozygosity reflect genome-wide heterozygosity is unclear (Slate *et al.* 2004), but small samples of loci are expected to index overall heterozygosity if the population is inbred (Lynch & Walsh 1998). Inbreeding is likely to occur in the subdesert mesite because: (i) most individuals are philopatric (Seddon 2001); and (ii) mesites are poorly adapted for flight (Lowe 1924) and can therefore disperse over only very limited distances from their natal territory. If heterozygosity at microsatellite loci reflects genome-wide heterozygosity, then dispersing females choosing males in larger territories and with trills of lower pitch and longer duration would gain both more heterozygous group mates and more heterozygous potential fathers for their offspring. However, if the relationship between heterozygosity of the microsatellite markers we used and genome-wide heterozygosity is weak, our findings may have little to do with inbreeding and the link between male quality and heterozygosity would instead have probably arisen through heterosis at one or more specific loci (Hansson & Westerberg 2002). Interestingly, in this case, females that choose heterozygous mates will not maximize the heterozygosity of their offspring (e.g. in a two allele system, a heterozygous female will produce 50% heterozygous offspring whomever she mates with, whereas a homozygous female will produce maximum numbers of heterozygous offspring by choosing a complementary homozygous partner). Consequently, if male quality is enhanced by heterosis rather than outbreeding, it seems likely that females are selecting on male quality for direct short-term benefits (such as high territory

quality) rather than for 'good genes' to pass to their off-spring.

Irrespective of the genetic mechanisms underlying the relationships reported here, our findings corroborate the suggestion that sexually selected traits are linked to heterozygosity, rather than additive genetic variance (Brown 1997). This is important because it means that directional selection will have a negligible impact on the mean value or variance of a trait, and heritability will remain high. This might provide one resolution to the enduring debate among evolutionary biologists as to why sexually selected traits show high levels of additive genetic variance (Pomiankowski & Møller 1995) despite theoretical predictions to the contrary (Fisher 1930), although mathematical models are needed to investigate this possibility more thoroughly.

We have shown that dispersing subdesert mesites can learn something about the genetic quality of groups that they might want to join by listening to male songs, and that group and/or mate choice based on heterozygosity has important benefits, both in terms of territory quality and seasonal reproductive success, and should thus be favoured by selection. Given the ubiquity of male song as a signal in a wide range of social and non-social bird species, assessment of both group and male genetic diversity by means of acoustic cues may be a widespread phenomenon.

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