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Female mate choice across spatial scales: influence of lek and male attributes on mating success of blue-crowned manakins

Renata Durães*, Bette A. Loiselle, Patricia G. Parker and John G. Blake

Department of Biology and Whitney R. Harris World Ecology Center, University of Missouri-St Louis,
One University Boulevard, St Louis, MO 63121, USA

Lekking males compete for females within and among leks, yet female choice is expected to work differently at each of these spatial scales. We used paternity analyses to examine how lek versus male attributes influence mate choice in the blue-crowned manakin *Lepidothrix coronata*. We tested the hypotheses that females prefer (i) to mate at larger leks where a larger number of potential mates can be assessed, (ii) to mate with unrelated or highly heterozygous males expected to produce high-quality offspring, (iii) to mate with males that display at higher rates, and that (iv) display honestly reflects male genetic quality. Our results show that (i) males at larger leks are not more likely to sire young, although females nesting close to small leks travel further to reach larger leks, (ii) siring males are not less related to females or more heterozygous than expected, (iii) within a lek, high-display males are more likely to sire young, and (iv) both male heterozygosity and display rate increased with lek size, and as a result display does not reliably reflect male genetic quality across leks. We suggest that female mate choice in this species is probably driven by a Fisherian process rather than adaptive genetic benefits.

Keywords: display rate; Fisherian sexual selection; genetic benefits; lek size; *Lepidothrix coronata*; male quality

1. INTRODUCTION

Leks are male aggregations that females visit to assess potential mates and copulate, without receiving any critical resources from males other than gametes (Bradbury 1981). Mate choice in lekking species is primarily female driven and often leads to skewed male mating success within leks (Mackenzie *et al.* 1995). Mating skew among leks has also been observed and is probably due to female mating biases related to lek size (Lank & Smith 1992; Höglund *et al.* 1993; Jiguet & Bretagnolle 2006). Males therefore compete for females both within and among leks, but the process of female mate choice is likely to be influenced by different factors across spatial scales (Gibson 1996). For example, males at large leks may enjoy higher rates of female visitation due to active female preference or passive attraction; however, they also face stronger competition and actual copulation success will depend on their competitive abilities relative to other lek mates (Hernandez *et al.* 1999). As a result, both lek and male attributes may contribute to mating patterns, but there have been few attempts to investigate female mate choice at the among- and within-lek scales simultaneously.

Non-random mating patterns in the apparent absence of direct material benefits have been taken as an indication that female choice among lek breeders is primarily driven by indirect (genetic) benefits. The expectation is that females mating with high-quality males receive indirect benefits in the form of increased viability for their progeny, either through the transmission of 'good genes' or by maximizing offspring genetic variability (i.e. heterozygosity). Females from both lekking and non-lekking species were shown to present consistent preferences for certain male phenotypic traits (e.g. Doucet & Montgomerie 2003), and evidence that preferred males produce offspring that is more viable (Petrie 1994; Welch *et al.* 1998) suggests that such traits are in fact indicators of male quality. While the adaptive value of particular 'good' genes is likely to be strongly environment-dependent (Zhou *et al.* 2008), high heterozygosity is generally beneficial to individuals and has been associated with increased fitness across a wide range of species, including in wild and non-isolated populations (Brown 1997; Coltman & Slate 2003). Females can effectively increase heterozygosity in offspring by choosing mates that are genetically dissimilar (Suter *et al.* 2007) or highly heterozygous themselves (Hoffman *et al.* 2007). While in the first case the 'best mate' should vary among females and consistent mating biases are not expected, in the second case female preferences could lead to mating skew without erosion of genetic diversity in the population, a potential solution for the 'lek paradox' (Kirkpatrick & Ryan 1991).

A non-adaptationist alternative is that female preferences are arbitrary in relation to male quality but yield indirect benefits through increased attractiveness in sons (Fisherian model of sexual selection, Fisher 1958; Lande 1981). Fisherian models have now received some

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*Author and address for correspondence: Center for Tropical Research, University of California-Los Angeles, La Kretz Hall, Suite 300, Box 951496, Los Angeles, CA 90095-1496, USA (rduraes@ucla.edu).

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important empirical support in lekking (Jones *et al.* 1998) and non-lekking species (Wedell & Tregenza 1999; Head *et al.* 2005) and were proposed to be the main mechanism of sexual selection acting in the predominantly lek-breeding clade of manakin birds (Pipridae; Prum 1997).

Indirect benefits through increased viability or attractiveness are not mutually exclusive and can add up to outweigh direct costs of female choice (Head *et al.* 2005). Yet, it is perhaps ironic that the most compelling evidence for indirect benefits comes from studies on extra-pair copulatory behaviour in socially monogamous species (e.g. Houtman 1992; Fossøy *et al.* 2007; Suter *et al.* 2007). In lekking or other socially promiscuous species, genetic benefits of mate choice are expected to prevail but have been supported by less than a handful of studies (Alatalo *et al.* 1991; Petrie 1994; Jones *et al.* 1998).

In this study, we employed molecular analyses of paternity to investigate patterns of female mate choice in a Neotropical frugivorous bird at two different spatial scales, among and within leks. At the among-lek scale, we test the hypothesis that females prefer to mate at large leks. This can occur, for example, because large leks passively attract more females, or because females actively prefer large leks where they can assess more males within a visit. If the ratio of females to males is higher at large leks, then males at these leks should be more likely to sire young (Bradbury 1981). Alternatively, if females are not selective in relation to where they mate, a reasonable null hypothesis is that they mate at the lek nearest to their nest. Within leks, we ask whether female mating patterns can be explained by the gain of indirect benefits. Specifically, we ask whether females prefer mates that can maximize heterozygosity in offspring, which are either individuals less related to them than expected by chance or highly heterozygous themselves. In addition, we investigate the potential role of vocal display rates as a correlate of male mating success and as an indicator of male heterozygosity. Sustained display rate can be energetically challenging (Vehrencamp *et al.* 1989; Höglund *et al.* 1992; Hunt *et al.* 2004) and it is a typical correlate of mating success among lekking males (Fiske *et al.* 1998), making this behavioural trait a good candidate as an honest signal of male quality that can be readily assessed by females. We thus tested the hypothesis that males within a given lek presenting more vigorous vocal displays are more likely to sire young, and that vocalization rate is correlated with male heterozygosity.

2. MATERIAL AND METHODS

(a) *Study site and study species*

We studied blue-crowned manakins (*Lepidothrix coronata*) at Tiputini Biodiversity Station (0°38′ S, 76°08′ W, 190–270 m above sea level), eastern Ecuador. Data were collected at two 100 ha (approx. 1×1 km) permanent study plots (Harpia and Puma plots) established approximately 1.5 km apart at the nearest edges (Blake & Loiselle 2008). Males exhibit delayed plumage maturation: juveniles (less than 1 year old) have a green, female-like plumage, subadults (2 years old) have an intermediate, predefinitive plumage and only in their third year do males fully acquire adult plumage (Ryder & Durães 2005). Adult and subadult males, but not juveniles, display solitarily or at leks with up to seven contiguous individual territories, each approximately 1000 m^2 in area (Durães *et al.* 2007), which females were seen visiting always alone. For simplicity, we refer to both solitary and group display sites as ‘leks’.

(b) *General field methods*

Fieldwork was conducted during the breeding seasons (November–April) of 2001–2006; we refer to a season by the year of the last sampled month (e.g. the season of November 2005–April 2006 is referred as ‘2006’). Birds were captured with ground-level mist nets operated on one day in January and one day in March at 96 fixed locations on each plot (Blake & Loiselle 2008). Additional nets were operated as necessary to target territorial males and nesting females. A total of 435 post-fledging individuals were banded and sampled for blood. Leks were located and mapped each year by searching systematically for displaying males within and around the plots. Territory boundaries were mapped by the location of song perches and were assigned to the same lek when males were within auditory contact or interactions among neighbours were observed. Leks are very traditional in location across years, despite relatively high male turnover at territories (Durães *et al.* 2008). Each year, territorial males were resighted and new males were banded. Vocalization rates were estimated during behavioural observations conducted at a subset of leks in Harpia plot in 2005 and 2006. Each year, 25–32 males in 10–11 leks were observed during multiple observation sessions. Individual vocalization rates are presented as mean number of calls per minute. Vocalization rates were constant throughout the season (correlations between vocalization and date, $n=3$–8 observation sessions/male each year; 23 out of 28 comparisons in 2005 and 21 out of 22 comparisons in 2006 had $p>0.09$; three significantly positive and three negative correlations). Nineteen individuals were observed in both years, and vocalization rates were correlated between years ($r=0.73, p<0.001$); we thus averaged rates between years to avoid pseudo-replication; analyses yielded similar results if rates were not averaged (see the electronic supplementary material for details on behavioural analyses). We systematically searched for nests in 2004–2006, and sampled offspring for genetic material. We attempted to search the entire area of each plot at least once a month, but due to logistic limitations, Harpia was more efficiently searched than Puma; because of sample size issues, some of the analyses were limited to nests in Harpia from 2005 to 2006.

(c) *Molecular analyses*

Paternity of offspring, male heterozygosity and genetic similarity between males and nesting females were established with six microsatellite loci. Nests were assigned to the attending female, when known, and paternity was assigned using a maximum-likelihood approach with CERVUS v. 3.0.3 (Kalinowski *et al.* 2007; see the electronic supplementary material for details on molecular and paternity analyses). Confidence levels were estimated with 10 000 simulations; assignments were accepted if made at the 95 per cent level of confidence whether the mother was known or not, or at the 80 per cent level if the mother was known and the trio (mother–offspring–father) received 95 per cent of confidence. Lekking males were classified binarily as siring or non-siring individuals within a given year. Despite our intensive nest searches, it is always possible that some males were incorrectly classified as non-siring; to reduce bias when comparing classes of males in relation to vocalization rates and heterozygosity, we limited our comparisons to males in leks located in well-sampled areas of Harpia. For this reason, sample sizes differ slightly between some analyses. Maximum-likelihood estimates of genetic relatedness between nesting females and their mates were estimated in ML-RELATE (Kalinowski *et al.* 2006). Heterozygosity was estimated with two multilocus indices that carry potentially different and relevant information about the population inbreeding history: mean d^2 uses the difference in length of alleles as an indication of the time since coalescence, and should reflect inbreeding due to longer term processes in the population's past history (Coulson *et al.* 1998); H_s measures the proportion of heterozygous loci, corrected for incomplete genotyping, and should reflect genetic diversity due to more recent events, e.g. parental inbreeding (Coltman *et al.* 1999).

(d) *Choosing a lek: distances to mate and lek size*

Territory and lek boundaries and nests were displayed as shapefiles in ARCGIS v. 9.1 (ESRI, Redlands, CA). The (minimum) distance travelled by females in order to mate was measured as the distance between each nest and the territory centroid or nearest lek edge of the siring male. To test whether females mate at the nearest lek, we compared the distance between each nest and the edge of the nearest lek to the distance to the edge of the actual sire's lek with a paired *t*-test. To test whether females prefer to mate at larger leks, we drew individuals at random and with replacement from the pool of territorial males present in a plot in a given year, in a number similar to the paternity assignments done for that year, and computed the mean size of the leks to which those males belonged. We repeated this 1000 times and computed the one-tailed probability that the mean lek size of siring males was larger than expected by chance. To avoid pseudoreplication owing to the fact that siblings in almost all nests were sired by the same male (see §3), in this analysis we considered each nest as a single assignment, except when multiple paternity was observed. Owing to sample size limitations, this analysis was restricted to Harpia, 2005–2006.

(e) *Choosing a male: relatedness between mates, male heterozygosity and vocalization rate*

To test whether females are less related to their mates than expected by chance, we used permutations in which we paired each female nesting in Harpia in 2005 or 2006 with a randomly chosen male among those holding territories in that plot that year, and recorded the relatedness between them. We repeated this 1000 times and computed the one-tailed probability that the average relatedness observed between mates was lower than expected. Vocalization rates and heterozygosity levels were compared between siring and non-siring males with *t*-tests. Parametric or non-parametric bivariate correlations and multiple linear regressions were used to investigate how heterozygosity or lek size was related to vocalization rates.

Analyses were conducted in SPSS 15.0.0 (SPSS Inc., Chicago, IL). Variables violating normality or heteroscedasticity assumptions were transformed when possible, otherwise non-parametric tests were adopted. Unless stated, values are means ± 1 s.e.

3. RESULTS

(a) *Paternity analyses*

Paternity was assigned to 56 young in 37 broods (clutch size = one to two eggs). Among 20 two-egg broods for which both offspring were assigned a father, only one indicated mixed paternity. Paternity was assigned to a total of 24 males, all known to hold lek territories with two exceptions: the first was captured at a lek where he did not hold a stable territory but could have intercepted copulations from other territorial males, while the second sired young at two nests at the outer edge of Harpia and could hold a territory in an undetected lek outside the plot. All siring males were adults or subadults; no juvenile males sired young. Most males (63%) sired a single brood, with a maximum of three broods sired by a single male (figure 1). Most of the siring males (83%) were in Harpia, the best sampled plot, and represented approximately 50 per cent of the territorial males presented in a given year in that plot (average of 40 territories yr^{-1}, Durães *et al.* 2008).

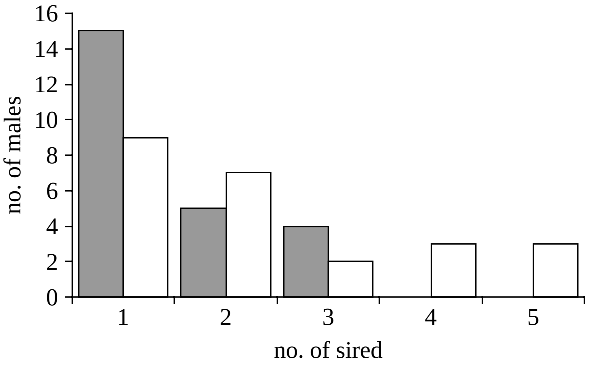

Figure 1. The number of broods (filled bars) or young (open bars) with paternity assigned to each of 24 blue-crowned manakin males between 2004 and 2006.

(b) *Choosing a lek: distances to mate and lek size*

Females mated at leks significantly further than the one nearest to their nest (distance to the closest edge of the nearest lek: 101 ± 9.6 m; to the closest edge of sire's lek: 208 ± 21.0 m; paired *t*-test $t_{29} = -4.79$, $p < 0.001$). In fact, in only 33 per cent of the cases ($n = 10$) did females mate at the nearest lek (figure 2). The average distance between a nest and the territory centre of the siring male was 265 ± 19.7 m (range: 94–592 m, $n = 30$). Assuming that a circle with 265 m radius is representative of the average area of influence of females around their nests, mating females are expected to come into contact with 8.5 ± 0.5 males in 3.1 ± 0.1 leks.

Males in leks of all sizes sired young, including solitary males. Siring males did not belong to leks larger than expected by chance in Harpia in 2005 (observed lek size of sires: 3.6 ± 0.4; expected lek size: 3.7 ± 0.3, $p = 0.41$) or 2006 (observed: 3.9 ± 0.6; expected: 4.2 ± 0.6; $p = 0.32$). Other lines of evidence suggest, however, that females travel further to larger leks when nesting close to small leks. First, comparing females mating at the nearest lek versus females mating elsewhere, we observed that the latter females were nesting close to smaller leks, although the difference was non-significant (size of the nearest lek when females mated at that lek: 3.5 ± 0.4 males, $n = 10$; when they mated elsewhere: 2.7 ± 0.4, $n = 20$; Mann–Whitney $U = 66.50$, $p = 0.13$; figure 2). More importantly, for the subset of females that did travel beyond the nearest lek to mate ($n = 20$), the nearest lek was significantly smaller (2.7 ± 0.4 males) than the lek where they actually mated (3.9 ± 0.4 males, paired *t*-test, $t_{19} = 2.40$, $p = 0.03$).

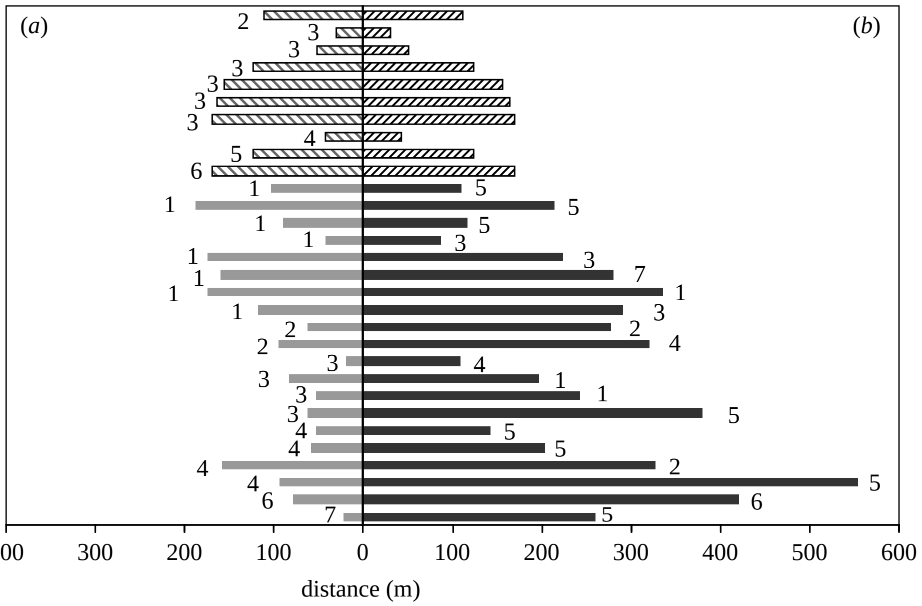

Figure 2. Distance between nests and (*a*) the closest edge of the nearest lek (in grey) or (*b*) the lek to which the siring male belongs (in black); each row represents a nest; hatched bars represent cases in which the nesting female mated at the nearest lek ($n=10$), solid bars represent cases in which the nesting female mated at a lek located further than the nearest one ($n=20$); the numbers associated with bars indicate the size of the lek (i.e. the number of territorial males).

(c) *Choosing a male: relatedness between mates*

Mates that were genetically more similar produced less heterozygous offspring, although the relationship was significant for H_s ($r=-0.37$, $p=0.01$, $n=48$) but not for mean d^2 ($r=-0.12$, $p=0.42$), supporting the idea that H_s is a more direct measure of parental inbreeding. Females nesting in Harpia were not less related to their mates than expected (2005: observed relatedness, 0.072 ± 0.052, $n=7$ pairs; expected, 0.049 ± 0.030, $p=0.80$; 2006: observed, 0.062 ± 0.034, $n=11$ pairs; expected, 0.041 ± 0.024, $p=0.82$), suggesting that females cannot discriminate or do not select mates based exclusively on relatedness. As a word of caution, however, a retrospective power analysis (Thomas 1997) indicated that these sample sizes would require a minimum absolute difference of 0.19 (in 2005) or 0.10 (in 2006) between observed and expected relatedness values for a departure from random to be detected with 75 per cent of confidence.

(d) *Choosing a male: male heterozygosity and vocalization rate*

We examined the potential role of vocalization rates as indicator of male heterozygosity, a measure of genetic quality, and found that mean d^2 (ln transformed for normality) was correlated with vocalization rate ($r=0.37$, $p=0.03$, $n=35$), but H_s was not ($r_s=-0.14$, $p=0.41$). In addition, an effect of lek size was observed, as males at larger leks had higher mean d^2 (ln transformed, $r=0.38$, $p=0.02$, figure 3*a*) and higher call rates ($r=0.51$, $p=0.001$; figure 3*b*), but not higher H_s ($r_s=0.005$, $p=0.98$). We used a multiple regression model to evaluate the independent effects of lek size and mean d^2 heterozygosity on vocalization rates. The model explained a significant proportion of the total variance ($r^2_{adj}=0.20$, $F_{2,34}=5.232$, $p=0.01$), but vocalization rate was primarily attributable to lek size ($\beta=0.363$, $p=0.04$), and not to mean d^2 ($p=0.18$). In summary, these results show that males increase vocal display according to lek size; that males at larger leks tend to have higher mean d^2 heterozygosity, although not higher H_s; and that, after controlling for lek size, vocalization rates no longer reflect mean d^2 heterozygosity.

Next, we examined the influence of vocalization rates and heterozygosity on male mating success. Males siring or not siring young did not differ in vocalization rates (siring males: 7.9 ± 1.3, $n=10$; non-siring males: 7.5 ± 0.6 calls min^{-1}, $n=21$; $t_{29}=-0.39$, $p=0.70$) or heterozygosity (ln mean d^2: 4.91 ± 0.33 versus 5.11 ± 0.18, $t_{29}=0.57$, $p=0.57$; H_s: 0.90 ± 0.04 versus 0.96 ± 0.04, $t_{29}=0.88$, $p=0.39$). In addition, contrary to our expectations, heterozygosity of the siring male did not predict offspring heterozygosity (H_s: $r=0.09$, $p=0.53$, $n=49$; mean d^2: $r=0.18$, $p=0.22$).

Because both vocalization rates and mean d^2 values increased with lek size, we used the residuals of each of these variables on lek size to compare siring and non-siring males within leks. Size of some leks changed slightly between years and because it is possible that males adjust their display accordingly (but not heterozygosity), for regressions involving vocalization rates we did not average data between years. Siring males vocalized more than non-siring males at leks of a given size (siring males: 1.61 ± 0.75; non-siring males: -0.59 ± 0.55, $t_{31}=-2.27$, $p=0.03$; figure 3*b*), but still did not differ in mean d^2 ($t_{29}=0.40$, $p=0.69$). These results suggests that, although males at leks of all sizes (including solitary males) may sire young, within a given lek, males that invest more in display are more likely to sire young. Owing to the effect of lek size on vocalization rates, however, this does not translate in siring males being necessarily more heterozygous.

4. DISCUSSION

Female mate choice is an important mechanism of sexual selection that in lekking systems can lead to remarkable levels of mating skew among males (Mackenzie *et al.* 1995). Aggregation of males, unusual in other mating systems, implies that they compete for females at two

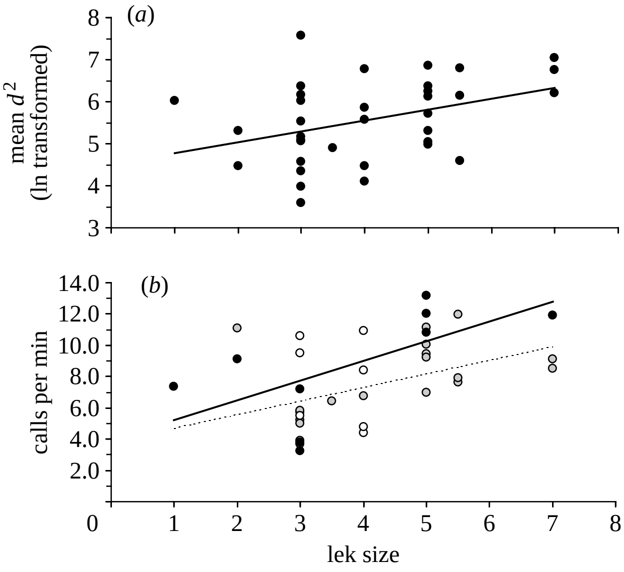

Figure 3. Relationship between (*a*) lek size (as the number of male territories) and individual mean d^2 heterozygosity (ln transformed) and between (*b*) lek size and vocalization rates among blue-crowned manakin males. In (*b*), tendency lines are fitted separately for males that sired young (black circles, solid line) and males that did not sire young (grey circles, hatched line); open circles represent males for which no information is available on reproductive success.

distinct spatial scales, among and within leks. Mate choice in lekking systems is often investigated in relation to phenotypic correlates of mating success (manakin examples: Trainer & McDonald 1995; Shorey 2002; Stein & Uy 2006), which are probably more important at the within-lek scale, or attributes of lek structure, such as size (e.g. Lank & Smith 1992; Höglund *et al.* 1993; Jiguet & Bretagnolle 2006), probably more important at the among-lek scale, but this study is among the first attempts to integrate these two levels of analysis. We investigated female mate choice in blue-crowned manakins among and within leks and tested multiple hypotheses based on the idea that mate choice in this species is driven by the gain of adaptive indirect benefits. We expected that, when choosing among leks, females prefer to mate at the larger ones where mate assessment is maximized, and when choosing among males within a lek, females prefer those that are able to produce more heterozygous offspring, those that display more and those whose vocal display honestly reflects male heterozygosity, a measure of genetic quality. By refuting most of these hypotheses, we gained important insights into mate choice processes in this lekking bird.

Females frequently mated at leks located further than the one nearest to their nests and, in fact, often travelled considerably beyond their usual home ranges to mate. Female blue-crowned manakins have small home ranges (4 ha on average) that usually encompass a single lek or no leks at all (Durães *et al.* 2007), and it is likely that females travel further to encounter and more effectively assess potential mates. A female travelling within a 265 m radius around her nest (i.e. the average distance from a nest to the sire's territory) would encounter on average eight to nine males in three leks; this is indirect evidence that females may visit multiple leks before mating. Contrary to our expectations, however, there were no mating biases towards larger leks within the population at large, although females nesting close to small leks tended to travel further and mate at larger leks. These observations are consistent with a 'best-of-*n*' model (Real 1990), in which females examine *n* potential mates before mating, rather than to a female preference model that benefits males at large leks.

Lekking systems are ideal to investigate indirect benefits because little or no influence of direct benefits is expected on female choice. Yet, empirical support for indirect benefits in lekking species is scarce (but see Alatalo *et al.* 1991; Petrie 1994; Jones *et al.* 1998). We investigated two mechanisms by which females can increase the genetic variability of offspring through mate choice, but found no strong evidence for either. First, nesting females were not less related to their mates than expected. Second, siring males were not more heterozygous than non-siring males, and in fact heterozygosity was not correlated between males and their offspring. We did confirm our prediction that females prefer males that within a given lek display more vigorously, and a correlation between vocalization rates and mean d^2 heterozygosity at first suggested that females cue on display to infer male genetic quality. However, display rates were strongly affected by lek size, and as a result do not reliably reflect male heterozygosity across leks; for example, a male in a seven-male lek vocalizes on average 30 per cent more than one with similar heterozygosity in a four-male lek.

This relationship between vocalization rates and lek size may be due to behavioural plasticity or differential recruitment according to male quality, with different implications for sexual selection. Changes in behaviour can be caused by social facilitation, if males stimulate each other during display (Brooke *et al.* 2000), or if increased competition at larger leks cause males to invest more in display (Greenfield 1994). This would imply that individual display is determined primarily by the social environment and mate choice based on display rates would not have adaptive value. Differential recruitment, alternatively, implies that high-quality males are inherently able to display more vigorously than low-quality ones, and that males recruit into leks of different sizes according to their competitive abilities (Sutherland 1996; Hernandez *et al.* 1999). In this case, display could honestly signal male quality and female choice based on display would be adaptive.

These two possibilities are not completely mutually exclusive, and we found evidence that a combination of both may act in blue-crowned manakins. On one hand, lek size explained a significant proportion of the vocalization variance, while our measure of genetic quality (heterozygosity) did not. On the other hand, the fact that only the most vigorous males within a lek succeed in copulating suggests that males are constrained to some extent by how much they can increase investment in display. This is further supported by the fact that individual vocalization rates were consistent across years and throughout the breeding season, and that males in larger leks tended to be more heterozygous, suggesting that males recruit into leks according to their perceived competitive abilities and then adjust their display rates according to that of their lek mates. The implication of these results is that vocalization rates are likely to be informative about male heterozygosity only for the subset of females mating at large leks, where they would find sets of males that are both more heterozygous and whose vocalization rates more honestly reflects this heterozygosity. This underscores the fact that flexible behavioural traits may carry reliable information about the signaller in some contexts, but not in others.

In general, however, our findings show that mate choices of blue-crowned manakin females are relatively arbitrary with respect to lek size, heterozygosity, travel distance, and, across leks, also for display rate. Although this study does not rule out the possibility that non-resource-based direct benefits, such as parasite avoidance and fertilization assurance, are being overlooked (e.g. Reynolds & Gross 1990), it does refute multiple hypotheses for adaptive indirect benefits. As such, our observations are consistent with a Fisherian model of female preference (Fisher 1958, Lande 1981), which has been championed by Prum (1997) as the main mechanism of sexual selection acting upon lekking manakins. Vocal display attributes are often sexually selected (Fiske *et al.* 1998) and may be heritable (Houtman 1992; Zhou *et al.* 2008), and thus females mating with preferred high-display males may enhance offspring fitness by other means than increased viability, such as by the transmission of genes conferring attractiveness in sons. In our study, females seem to sample a set of *n* males and mate with those that display more vigorously. As long as display is not completely shaped by the social environment but also influenced by the male's intrinsic competitive abilities—as indeed suggested by our data—female preferences that are arbitrary in relation to adaptive traits (such as heterozygosity) can lead to fitness benefits in the form of increased mating success in offspring.

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