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Female Mate Fidelity in a Lek Mating System and Its Implications for the Evolution of Cooperative Lekking Behavior

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ABSTRACT: The extent and importance of female mate fidelity in polygynous mating systems are poorly known. Fidelity may contribute to high variance in male reproductive success when it favors attractive mates or may stabilize social interactions if females are faithful to mating sites rather than males. Using 12 years of data on genetic mate choice in the cooperatively lekking lance-tailed manakin (*Chiroxiphia lanceolata*), I investigated the frequency of fidelity within and between years, whether females were faithful to individual males or to mating sites across years, and whether fidelity favored attractive males. Mate fidelity occurred in 41.7% of 120 between-year comparisons and was observed for 41.1% of 73 individual females that had the opportunity to mate faithfully. Females were not more likely to mate at prior mating sites when previous mates were replaced. Faithful females mated with the same male in up to four consecutive years but were not disproportionately faithful to attractive partners. Mating history influences current mate choice, and fidelity in this lekking system apparently represents active mate choice by females but little consensus in mate choices among faithful females. This study underscores the prevalence of mate fidelity in polygynous mating systems and emphasizes the need to consider the larger context of lifetime reproductive behavior when interpreting patterns of female choice.

Keywords: reneating, mate choice, cooperation, satin bowerbird, monogamy.

Introduction

In species with long reproductive life spans, females often have the opportunity to choose among the same candidate males across consecutive breeding seasons, and it is not uncommon for mated pairs to remain together for multiple years (Bried et al. 2003; Jeschke and Kokko 2008). Inter-season mate fidelity in monogamous mating systems is an important reproductive strategy that may maximize repro-

ductive success by increasing the coordination of parental care, ensuring access to familiar breeding sites, or reducing mate search costs (Choudhury 1995; Cezilly et al. 2000; Bried et al. 2003). In contrast, the extent and importance of female mate fidelity in mating systems characterized by non-resource-based polygyny remains poorly known (Amos et al. 1995; Rossiter et al. 2005). Lek mating is an extreme type of polygyny, in which males court females at aggregated display sites and provide no paternal care to the resulting offspring (Bradbury 1981; Höglund and Alatalo 1995). Female mate or mating site fidelity may be particularly influential in lek polygyny, as mate choice by females in lek mating systems is relatively unconstrained by mate guarding or coercion and females choose among males that display in reliable locations, often for several consecutive years (Höglund and Alatalo 1995). However, both the frequency of female mate fidelity in lek mating systems and its influence on variation in male reproductive strategies and lifetime reproductive success remain unclear. In this article I present 12 years of longitudinal data on mate choice by females in the lance-tailed manakin (*Chiroxiphia lanceolata*) to evaluate the extent and importance of female mate fidelity in this lek mating system and to assess the relative importance of fidelity to mates versus mating sites.

Though few studies have tested for mate fidelity across years in lek mating systems, the limited evidence available suggests that fidelity may be common. Female fidelity to a particular lek is widespread: female great bustards (*Otis tarda*) return to the same lek of males across several years (Alonso et al. 2000), as do greater sage-grouse (*Centrocercus urophasianus*; Gibson et al. 1991), great snipe (*Gallinago media*; Sæther et al. 2005), and long-tailed manakins (*Chiroxiphia linearis*; McDonald and Potts 1994), though in many cases it is unknown whether observed females also attended other leks during mate choice. More specifically, fidelity to individual males across breeding seasons has been reported in a number of lekking species

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(table 1). However, fidelity to individual males can be difficult to distinguish from fidelity to the sites that males occupy. Female mating site fidelity is a proposed mechanism that provides incentives for young and low-ranking males to perform displays though their immediate chances of reproduction are low (Gibson 1992; McDonald and Potts 1994). Female fidelity to particular display sites is hypothesized to be a stabilizing force in male interactions at those sites, and more general fidelity to groups of display areas on the lek could select for lekking behavior as a whole (Beehler and Foster 1988; Foster 1981). Furthermore, fidelity to mating sites may be an important contributing factor to observed variation in male mating success, particularly in combination with mate choice copying (Gibson et al. 1991).

Few studies have assessed whether females remain faithful to mating sites when their preferred mate is replaced, and the limited empirical evidence has produced conflicting results. Female long-tailed manakins and Uganda kob

(*Kobus kob thomasi*) remain faithful to mating sites even when the males that attend them change (Balmford et al. 1992; McDonald and Potts 1994). In contrast, female satin bowerbirds (*Ptilonorhynchus violaceus*) do not mate with males replacing their mates from previous years at traditional bower sites. This lack of site fidelity suggests that satin bowerbirds base mate choice on individual male characteristics rather than display site information (Uy et al. 2001). Similarly, female great snipe tend to mate at new sites when their prior mates are no longer present and prefer mates from previous years even when those males switch territory locations (Sæther et al. 2005). Distinguishing mate fidelity from site fidelity requires longitudinal data on female choice that span the reproductive tenures of multiple males on a lek.

The degree to which female fidelity determines male reproductive success may have a strong influence on male reproductive strategies. Strong reproductive skew among lekking males is a common feature of lek mating systems

Table 1: Occurrence of between-year mate fidelity in polygynous mating systems

Species (scientific name)	Between-year mate fidelity (% [N])	Within-year mate fidelity (% [N])	Social mating system	Reference
Black grouse (<i>Tetrao tetrix</i>)	100 (5) ^a		Classic lek	Rintamaki et al. 1995
Great snipe (<i>Gallinago media</i>)	71.4 (28) ^a		Classic lek	Sæther et al. 2005
Cock-of-the-rock (<i>Rupicola rupicola</i>)	33 (40) ^a		Classic lek	Trail and Adams 1989
Lance-tailed manakin (<i>Chiroxiphia lanceolata</i>)	41.7 (120) ^b	67.4 (46) ^b	Exploded lek	This study
White-bearded manakin (<i>Manacus manacus</i>)	...	68.8 (32) ^a	Classic lek	Lill 1974
Golden-headed manakin (<i>Pipra erythrocephala</i>)	...	62.5 (24) ^a	Classic lek	Lill 1976
Wire-tailed manakin (<i>Pipra filicauda</i>)	50 (4) ^b	50 (6) ^b	Exploded lek	Ryder et al. 2009
Lawes' parotia (<i>Parotia lawesii</i>)	80 (5) ^a		Exploded lek	Pruett-Jones and Pruett-Jones 1990
Satin bowerbird (<i>Ptilonorhynchus violaceus</i>)	42 (36) ^b		Non-resource-based polygyny (approximates an exploded lek)	Uy et al. 2000
Gray seal (<i>Halichoerus grypus</i>)	30 (87) ^c		Harem polygyny	Amos et al. 1995
Greater horseshoe bat (<i>Rhinolophus ferrumequinum</i>)	56.8 (51) ^d		Non-resource-based polygyny	Rossiter et al. 2005

Note: This table includes only studies that provided information on the proportion of females that mated with previous partners between and within breeding seasons, given that the prior mate was available for mating when the second choice event occurred. Comparison types, noted as superscripts following sample sizes (*n*), were (a) observed copulations when prior mate still alive, (b) genetic paternity of nests when prior mate still alive, (c) genotyped pairs of offspring from the same female identified genetically as full siblings, and (d) individual females for which genetic paternity indicated fidelity in at least 2 years (unknown whether prior mate was alive). Work quantifying within-season fidelity from observed copulations in the white-bearded manakin did not report the relative timing of observations and so may reflect repeated copulations for the same clutch rather than distinct nesting efforts (Lill 1974). Exploded leks are those in which male display territories are dispersed in available habitat and are often in auditory but not visual contact. Classic leks are composed of clustered male display areas. These are specific forms of non-resource-based polygyny, which includes a range of mating systems in which females do not depend on males for nest sites or food resources, and male and female activities are often spatially segregated. In harem polygyny, unlike other mating systems listed, males often forcibly control female movements and mating behavior. Results from Amos et al. (1995) are included here as they suggested male control in systems with harem polygyny may be more limited than previously thought.

(Höglund and Alatalo 1995). If successful males recruit proportionately more faithful females, much of reproductive skew observed among males on the lek may result from “conservative” female mating behavior rather than direct discrimination among male phenotypes (Beehler and Foster 1988). In combination with initial differences in male attractiveness, female mate fidelity is a potentially important force that could result in a small number of highly successful males on the lek, around which other males cluster (Beehler and Foster 1988). Female satin bowerbirds, whose mating system approximates a lek with dispersed male display sites, are more likely to be faithful to more attractive males (i.e., those with high mating success), but this effect has not been demonstrated in other species (Uy et al. 2000). A combination of strong consensus in female mate choices within years and female site fidelity could also influence male reproductive strategies, as suggested by the rapid reoccupancy of vacated territories of highly successful male sage grouse (Gibson 1992). Arguably, returning females are likely to employ different search strategies or choice criteria than females assessing males for the first time, which could influence the performance or effectiveness of male displays. Despite the theoretical importance of fidelity in generating or reinforcing reproductive skew among males, it remains unclear whether faithful females prefer more attractive males.

The choice to be faithful to a previous mate may also incorporate an assessment of mate quality if females are more likely to return to a prior mate when that pairing previously produced viable offspring (Beehler and Foster 1988). Sensitivity to breeding success may reflect the need for effective partner contributions to offspring care, which is irrelevant in lek mating systems as males do not care for young. However, it could also result from factors independent of offspring care such as fertility or genetic compatibility of partners. In many monogamous species that exhibit mate fidelity, partners are more likely to separate following the nest failure or low nesting productivity (Choudhury 1995). Additionally, in some species, fidelity to a mate may result in increased success of the subsequent nest effort, perhaps through decreased energy spent in mate search and courtship (Cezilly et al. 2000). While nesting success influences divorce in several monogamous species (Lindén 1991; Catlin et al. 2005), this hypothesis has not been tested in lekking taxa.

Chiroxiphia manakins offer an excellent opportunity to investigate female mate fidelity in a lek mating system. Manakins are small passerine birds known for their elaborate courtship displays performed at traditional display sites (Sick 1967; Prum 1994). Manakins of the genus *Chiroxiphia* perform displays in cooperative multimale groups (Snow 1971; Foster 1977, 1981; DuVal 2007c). These birds have an exploded lek mating system, in which male display

areas are dispersed in available habitat and are in auditory but not visual contact (DuVal 2007b). Though males are not strictly territorial and many males may be regularly present within each display area, displays for females are performed only by the dominant “alpha” individual and his close affiliates. In most *Chiroxiphia*, the alpha forms a long-term partnership with one subordinate “beta” male, defined as an individual that cooperates in performing two-male duet song and dance displays for females but, with rare exceptions, does not copulate during beta tenure (McDonald 1989; DuVal 2007a, 2007c). Female site fidelity has been proposed as a critical aspect of this mating system. Female long-tailed manakins are apparently site-faithful in mating behavior, providing a delayed direct benefit from cooperation for beta males: betas frequently inherit the display site where they served as subordinates, and mate with females returning to that site (McDonald and Potts 1994). *Chiroxiphia* manakins may live to be older than 14 years, and highly successful males may hold alpha status for more six or more consecutive years (DuVal 2012), providing ample opportunity for mate fidelity to occur.

To investigate the frequency and influence of mate fidelity across breeding seasons in a lek mating system, I examined patterns of genetic mate choice by individual females sampled repeatedly across twelve consecutive years in a population of cooperatively lekking lance-tailed manakins (*Chiroxiphia lanceolata*). Beta male inheritance of display sites in this species is not as frequent as reported in the long-tailed manakin, but betas nevertheless sometimes inherit the display sites where they serve as helpers, and so female fidelity to mating sites may provide an important delayed direct benefit for beta helpers (DuVal 2007a). Substantial mate fidelity would suggest that female mate choice behavior is modified by females’ previous experience with a set of males, and that female choice of male traits must be evaluated in the context of lifetime or at least long-term reproductive behavior. The goals of this research were to characterize the extent of female mate fidelity in the lek mating system of the lance-tailed manakin, to determine whether females are faithful to males or to mating sites, and to test the hypothesis that females are more likely to be faithful to attractive males.

Methods

Study System

Lance-tailed manakins are small (ca. 15.5–22 g) passerine birds in the Neotropical family Pipridae. Like most manakins, males and females are distinguished by strikingly different plumages: adult males have black body and flight feathers, a blue back, and a red crest, while females are olive green (DuVal 2005). Males form cooperative partnerships

of one alpha and usually one beta male to perform elaborate duet song and dance displays for females at traditional display sites (DuVal 2007c). Songs consist of overlapping calls repeated by two males, perched ~10 cm apart in a tall tree (DuVal 2007b). When a female enters the area, males fly to a low display perch, which is a smooth bent sapling or vine approximately 50 cm high. Courtship displays contain up to 11 different display elements, including slow butterfly-like flights around the display perch and a “backwards leap-frog” display in which two males leap over one another in close proximity to a female on the display perch (DuVal 2007b). If the female is receptive, the beta male leaves the immediate area and the alpha continues a solo display that includes slow flights, swoops, and bounces before copulation. At a given display area, the alpha is the most commonly present individual and the only male to perform solo displays for females, while the beta is that male’s most common duet partner and performs two-male components of courtship displays with the alpha (DuVal 2007c). Individual male alliances may last for up to 6 years, with no reversal of alpha or beta status within a pair (DuVal 2007c). With extremely rare exceptions, only alpha males mate with females that a pair attracts (DuVal 2007a; DuVal and Kempenaers 2008). Females fly among display areas and may observe the displays of many alpha-beta pairs before choosing a mate. After mating, females raise their offspring without male assistance.

Study Site and General Field Methods

The study was conducted on Isla Boca Brava, Chiriquí Province, Panama, in the years 2000–2011. The study site is a 46-ha area of secondary-growth dry tropical forest, described in detail elsewhere (DuVal 2007b). Lance-tailed manakins were captured on this site using mist nets, and individuals were marked with a unique combination of one numbered aluminum and three colored plastic leg bands. All captured individuals were genetically sampled by collecting approximately 20 μ L of blood from the brachial wing vein and storing this in an ambient-temperature lysis buffer for later analysis (Longmire et al. 1988).

In each year of the study, male status was identified by behavioral observations of color-marked individuals at traditional display areas. Observation sessions were 2- or 1-h periods of continuous monitoring during which observers recorded all occurrences of male duet songs, dance displays, and courtship dances performed for females. These observations were used to quantify display behavior of males at each display area and thereby define male social status using the criteria outlined above and described in detail elsewhere (DuVal 2007c).

Male reproductive success was quantified as offspring sired. Nests were located via regular visual inspection of understory vegetation or by observing female nesting be-

havior. Nests were monitored every other day until chicks hatched, and blood samples for use in paternity analyses were collected from chicks on or before the third day after hatching. Due to high levels of natural nest predation, one egg of most two-egg clutches discovered since 2010 was incubated in a Lyons Turn-X tabletop incubator (Lyon Technologies, Los Angeles) to ensure a genetic sample. The source nest was monitored every other day, and incubated eggs for which the nest was depredated before hatching were sacrificed for a genetic sample (Tori et al. 2006). When the egg in the source nest survived to hatch, incubator-hatched nestlings were returned to their nests and raised naturally. Monitoring continued until nests failed or fledged, and chicks were color-banded on day 12 after hatching. The female attending the nest was assigned as the mother of the chicks in that nest, and verified genetically. Genetic maternity always coincided with nest attendance, and there were no mixed maternity clutches. Nest fate was recorded as “failed” when nest contents disappeared before 15 days after hatching or more direct evidence of predation was observed, or “fledged” when chicks survived to at least 16 days after hatching and their disappearance from the nest coincided with feather development appropriate for flight.

Paternity Analyses

Details of the genetic paternity analyses used in this study are provided in DuVal and Kempenaers (2008), including polymerase chain reaction conditions, primers used, and detailed assignment criteria. In short, genomic DNA was extracted from blood or tissue samples and amplified at 20 variable microsatellite loci with a combined second-parent nonexclusion probability of 0.00001. All adult males alive in each year of the study were considered as candidate sires. Paternity assignments were conducted by year in CERVUS 3.0 (Kalinowski et al. 2007), using analysis parameters as described in detail elsewhere (DuVal and Kempenaers 2008). Of 1,087 offspring genotyped in 2000–2011, fathers were assigned with for 975 individuals (89.7%). Male “attractiveness” was quantified as siring rank, which was a male’s relative success in number of assigned chicks sired (i.e., the male that sired the most assigned offspring was given a rank of “1”).

Classifying Female Mate Choices

Mate choice was determined in at least two consecutive breeding seasons for 90 unique females (sampled in 2–8 years). This sample includes 309 nests representing 263 female-years, and 44 female-years in which two ($N = 42$ females) or three ($N = 2$ females) nests were sampled from the same female in the same year.

Mate choices by females were classified as faithful if their chicks were sired by the same male in two consecutive years, and unfaithful if their chicks were sired by a different male in the second of two consecutive years while the original sire was still alive in the study population. Data for each nest in this data set included the identity of the female's prior mate, whether the female mated faithfully, the location of the current and prior mate's display area, whether the female mated with her current male in the subsequent year, and whether the prior mate was alive if a mate switch occurred. For females that nested more than once in the same year, fidelity was assessed by comparing her last detected nest in the first year with her first detected nest in the following year. When the two chicks of a brood were sired by different males (27 of 309 nests in this sample), the mate choice was classified as "faithful" if at least one of the chicks was sired by a previous mate. Of nests with multiple paternity, 7 of 22 showed evidence of partial fidelity between years (i.e., when mate choice was assessed in nests sampled in the year before or after the focal nest with multiple paternity) and 3 of 5 showed evidence of partial fidelity within years. Chicks from "faithful matings" were defined as offspring whose mothers had produced previous broods sired by that chick's father.

Mating site was identified as the sire's regularly attended display areas, and consecutive mate choices were classified as occurring at the same or a different display area as that occupied by the female's prior mate. Males that sire chicks (i.e., alpha-status individuals) are usually found within a defined display area (ca. 50 m in diameter) throughout the breeding season and commonly display on the same perch or set of perches for several years at a time (DuVal 2007*b*). Observation sessions were performed at discrete display areas, and males' consistent presence in such areas is one of the major factors that identified them as alpha individuals (DuVal 2007*c*). It is therefore unlikely that females copulated with these males in locations other than their usual display area.

Statistical Analyses

If females are faithful to mating sites but not to individual males, the presence of prior mates should not influence whether females mated at the same or different display areas. To test this prediction, I first compared the occurrence of site fidelity when the prior mate was alive with that in cases when he was gone from the study population using a generalized linear mixed model with a binomial distribution (logit link) and maternal identity as a random effect.

Some females may remate at prior breeding sites by chance, particularly given that the number of mating females in the study population exceeds the number of mating sites available each year. Two randomization tests

therefore assessed whether the observed occurrence of site fidelity differed from that expected at random in the study population. In each year of the study, an average of 29 ± 6 active display sites were identified at which females observed courtship displays. However, a maximum of 27 distinct alphas were assigned as sires in any given year, and so simulations assessed choice from among 27 potential mates. Consecutive choices of mating site when the prior mate was alive were recorded for 120 between-year comparisons, and site choices when the prior mate was gone were recorded in 39 comparisons. To assess situations in which prior mates were alive in the study population, the first test simulated two consecutive mate choices by 120 females from 27 display sites and assessed the proportion of chosen sites that were the same between mate choice events. The second test simulated choice by 39 females from the same number of sites and again assessed the proportion of simulated females that chose the same site in both choice events. To account for the nonnormal distribution of mating success in the study population, mating sites in the randomization tests were randomly drawn from an empirical distribution reflecting the average annual siring success of males by rank. This distribution was calculated using the average proportion of assigned chicks sired by males in rank order of annual siring success, multiplied by 100 and rounded to the nearest integer, and the hypothetical male of each success rank was entered into the randomization matrix that number of times. For example, the top male in each year sired on average 15.6% of sampled chicks, and so the matrix from which females randomly sampled mating sites included "site 1" 16 times. Simulations were repeated 10,000 times, and the two-tailed significance level of observed data was determined as two times the proportion of simulated cases that were more extreme than the observed value. Randomization tests were implemented as a macro in Microsoft Excel.

If female decisions regarding mate fidelity are influenced by nesting success, females should be more likely to switch mates following nest failure. On the other hand, fidelity could influence nest success if females that mate faithfully reduce energy or time expenditure during mate choice and thereby increase their chances of fledging chicks. To examine the relationship between female mate fidelity and nest fate, I used generalized linear mixed models with a binomial distribution (logit link) and maternal identity as a random factor, and conducted separate analyses within years and between years.

The hypothesis that attractive males achieve disproportionate success through fidelity predicts a positive relationship between overall success and the proportion of a male's success due to fidelity. To examine whether fidelity favored attractive mates (males that were successful in siring chicks with many females), I tested for a relationship between

annual rank in siring success of individual males and whether females remained faithful to that male in the following year using a generalized linear mixed model (GLMM) with binomial distribution and independent random effects of male and female identity. A second set of models tested for a relationship between a male's siring success and the proportion of his chicks sired through faithful matings, separately assessing information on annual siring success and total siring success (chicks summed across all years of monitoring). Analysis of fidelity in relation to total siring success was conducted using a generalized linear model (GLM) with binomial distribution, and fidelity in relation annual success was analyzed in a GLMM with binomial distribution and male identity as a random effect. Finally, I considered the relationship between the proportion of a male's mates that mated faithfully and the number of unique females mating with a given male in all years of the study using a Spearman's rank correlation. Qualitatively similar results were obtained when analyses were restricted to 52 males for which lifetime reproductive success was known (i.e., both the beginning and end of alpha tenure were observed), but only 12 of these males with measured lifetime success experienced any mate fidelity. Analysis of lifetime success excluded several males with long breeding tenures that held alpha status at the start of the study, and so only results from the analysis of cumulative success are reported here.

Generalized linear mixed models were run in "lmer," package lme4, and generalized linear models were run in "glm," package MASS in the program R 2.13.1 (R Development Core Team 2011). Parameter estimates are reported ± 1 SE.

Results

Frequency of Female Mate Fidelity on the Lek

Faithful females had chicks sired by the same male in 2–4 distinct years (2.33 ± 0.62 , mean \pm SD years with the same male). Between breeding seasons, females mated faithfully in 41.7% of 120 comparisons in which the previous mate was present in both years. Of 73 individual females for which mate choice was detected in two consecutive years and their initial mate was alive in both years, 41.1% mated faithfully at least once. Fidelity was more common within than between breeding seasons. Females mated with the same male in 67.4% of 46 cases in which more than one nest was sampled in the same year, representing mate choice of 38 individual females (two-tailed Fisher's exact test, $P = .003$).

Fidelity to Males versus Mating Sites

Females were faithful to individual males rather than to display areas. Females were significantly more likely to return to mate at the given display area when their prior mate was still alive than when that male had disappeared (GLMM: intercept -1.89 ± 0.49 , $z = -3.86$, $P < .001$; male alive 1.22 ± 0.53 , $z = 2.32$, $P = .02$; 159 observations on 90 females; fig. 1). The observed level of between-year mate fidelity when the prior mate was alive was significantly more than expected by chance (37.5% site fidelity observed in 120 comparisons when the prior mate was alive, randomization test: $P < .0001$). When previous mates died, females were no more likely to mate with the successor at their prior mate's display area than with a randomly chosen alpha from the study area (15.4% site fidelity observed in 39 comparisons when prior mate was gone: randomization test, $P = .11$). Further evidence that females were faithful to individual males rather than display sites came from two cases in which females mated with the same male in two consecutive years despite significant changes in his display location. In the first instance, the male moved 156 m, and in the second, he moved 97 m between consecutive breeding seasons, and in both cases other breeding males occupied their prior display sites.

In this study population, beta males do not necessarily inherit the display areas where they formerly cooperated and so lack of female fidelity to mating sites may instead

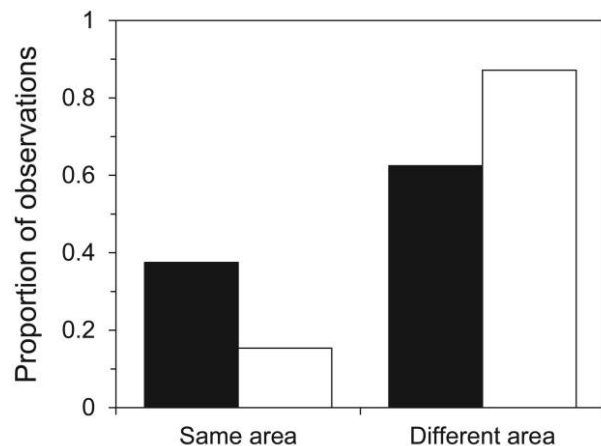


Figure 1: The occurrence of site fidelity between breeding seasons varied depending on whether the prior mate was alive (black bars; $N = 120$ comparisons) or gone from the study population (open bars; $N = 39$ comparisons). When a female's prior mate was gone, she was not more likely than expected by chance to mate with that male's replacement at his prior display site (randomization test, $P = .11$; "Results"). Females were therefore faithful to individual males but not to mating sites.

reflect fidelity to betas with whose alphas they copulated in previous years. However, in 12 cases where females mated with a male that was in his first year as alpha and had previously been a beta, that male was the former beta partner of her mate in the prior year only four times, and in all four instances that beta had assumed alpha status at his prior display site.

Nest Fate and Mate Fidelity

Females were not more likely to switch mates between breeding seasons following failed nest attempts (GLMM: intercept -0.94 ± 0.37 , $z = -2.53$, $P = .01$; nest fate 0.51 ± 0.46 , $z = 1.10$, $P = .27$; 103 observations on 66 females). While the majority of repeated nesting events within breeding seasons represented reneating after nest failure, 15 females reneated after an early nest fledged chicks. Success of early nests was unrelated to subsequent mate fidelity within breeding seasons (GLMM: intercept 1.05 ± 0.43 , $z = 2.42$, $P = .02$; nest fate -0.71 ± 0.72 , $z = -0.99$, $P = .32$; 46 observations on 38 females). Finally, females were not more likely to have successful nests following faithful mating decisions: mate fidelity was unrelated to the fate of the resulting nests (GLMM: intercept 0.13 ± 0.25 , $z = 0.5$, $P = .61$; fidelity 0.31 ± 0.40 , $z = 0.79$, $P = .43$; 108 observations on 71 females between years when prior mates were alive).

Do Attractive Males Recruit More Faithful Females?

Female mate fidelity may be an important component of male reproductive success if females are more likely to mate repeatedly with relatively attractive (successful) males in the population. Of 54 individual males that sired chicks in at least 2 years of the study, 48.1% sired chicks with faithful females. Females were not more likely to remain faithful to attractive mates: fidelity was unrelated to male siring rank (GLMM, with random effects of male and female identity: intercept -0.12 ± 0.33 , $z = -0.36$, $P = .72$; male rank -0.04 ± 0.04 , $z = -1.00$, $P = .32$; $N = 111$ observations of 68 females that mated with 39 males that were alive in the following breeding season).

Males with low siring success also sired few or no chicks from faithful matings, and so the total number of offspring sired was positively related to the proportion of chicks sired as the result of mate fidelity (GLM: intercept -2.32 ± 0.16 , $z = -14.21$, $P < .001$; total offspring sired 0.02 ± 0.005 , $z = 3.34$, $P < .001$; $N = 110$ individual males siring any chicks; fig. 2). However, contrary to the prediction that highly successful males have disproportionate success from fidelity, the proportion of chicks from faithful matings was unrelated to total number of offspring sired when analyses were restricted to only those males

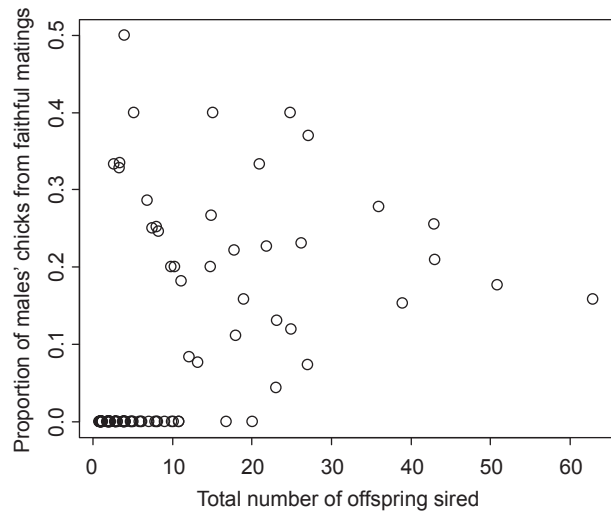


Figure 2: The proportion of offspring sired through faithful matings was unrelated to the total number of offspring sired for males that sired any chicks with faithful females.

with at least one chick from a faithful mating (GLM: intercept -1.40 ± 0.19 , $z = -7.40$, $P < .001$; total offspring sired -0.01 ± 0.01 , $z = 0.93$, $P = .35$; fig. 2). Similarly, among males with any mate fidelity, the proportion of females that were faithful to a male was negatively correlated with the overall number of unique females that mated with that male during this study ($r_s = -0.64$, $P < .001$, $N = 35$ males). Furthermore, males' annual proportion of chicks sired through faithful matings was negatively related to number of chicks sired that year (GLMM, with random effect of male identity, 62 observations on 35 males that sired any chicks through fidelity: intercept -0.69 ± 0.21 , $z = -3.32$, $P < .001$; total chicks sired that year -0.05 ± 0.02 , $z = -2.37$, $P = .02$).

Discussion

The occurrence of female mate fidelity across breeding seasons in the lance-tailed manakin indicates that female experience and breeding history are important components of mate choice. Observed female mate fidelity represented active choice of individual males, as females were faithful to males and not mating sites. Importantly, this evidence rejects one of the key hypotheses regarding the adaptive benefits of display for nonbreeding cooperators on the lek (McDonald and Potts 1994); helpers do not apparently inherit the attentions of site-faithful females. Mate fidelity benefited both relatively successful and unsuccessful males and therefore was not the main source of elevated reproductive success experienced by some males in the population. Because the attention of faithful

females was shared among many of the males mating in multiple years, chicks from faithful matings were proportionately more important in determining lifetime reproductive success for less successful males.

Given that female mating site fidelity is one of the key factors suggested to stabilize cooperative alliances in similar species (Foster 1981; McDonald and Potts 1994), it is somewhat surprising that female lance-tailed manakins were not site faithful in mate choice behavior. Subordinate betas in the congeneric long-tailed manakin tend to inherit their alpha partners' display sites and benefit from cooperation via site fidelity of females. In that species, observational data indicated that females return to mate at particular display sites even when males that they mated with previously have been replaced: 10 of 16 females returning to a prior mating site copulated with a replacement male, not their prior mate (McDonald and Potts 1994). In contrast to the long-tailed manakin, beta male lance-tailed manakins in this study population cooperate in courtship displays but do not reliably inherit alpha status at the display areas where they cooperate (DuVal 2007a). A lack of female site fidelity may provide little incentive for beta males to establish themselves at their prior display sites. Alternately, the lack of site fidelity reported here could be explained if females are faithful to males that they observed previously as beta helpers, despite changes in that male's display location. However, the few cases in which females did mate with the previous beta partner of her mate from the prior year all occurred in situations when the beta had inherited the prior male's display area, excluding this possibility. As reported for a few cases in this study, female great snipe returned to mate with the same male in multiple years, even when he changed mating sites (Sæther et al. 2005). Similarly, mate fidelity was not an artifact of site fidelity in greater horseshoe bats (Rossiter et al. 2005).

The prevalence of mate fidelity in a range of species highlights the need to assess its influence on the relative mating success of males, and inferences drawn from female mate choice behavior. Levels of interyear mate fidelity observed in the lance-tailed manakin were remarkably similar to those reported in several polygynous mating systems (table 1). Though sample size in many of these studies is small, this growing body of literature suggests between-year mate fidelity is a common feature of polygyny in long-lived animals. The occurrence of mate fidelity has even been reported in American alligators (*Alligator mississippiensis*), for which 7 of 10 females with multiyear mating records mated with the same male in multiple breeding seasons (Lance et al. 2009). Studies of mate choice frequently aim to quantify the strength of selection on male phenotypes. Importantly, when mate choice is in part determined by processes such as fidelity and mate choice copying, variance in male mating

success will not necessarily reflect current selection on specific male traits (Gibson et al. 1991). These female-driven processes therefore complicate the interpretation of observed male mating success.

Fidelity could be an important force in generating variance in reproductive success among males if females are disproportionately faithful to relatively successful males. However, relatively attractive males in this study did not recruit a disproportionate number of faithful females, and female lance-tailed manakins were not more likely to remain faithful to more attractive males (those with high relative siring success in a given year). These results are in contrast to findings in the satin bowerbird that indicated females were more likely to remain faithful to attractive males between years (Uy et al. 2000). The high levels of siring success achieved by some males in the lance-tailed manakin study population therefore resulted from mating with many different females, not from repeated matings with a few faithful individuals. Female fidelity to both highly successful and relatively unsuccessful males between years could result from varied individual mating preferences, preferences persisting from previous stages of a male's reproductive tenure (i.e., for formerly attractive males), or differences in the pools of males assessed by different females. Such variation could also result if time or energy saved by mating with a particular male (e.g., one close to a female's nesting or foraging sites) outweigh the benefits of extensive sampling to identify attractive males.

If long-lived, faithful females are plentiful in the population and male reproductive opportunities are scarce, attracting a faithful female early in a male's reproductive tenure could greatly increase his lifetime reproductive success. Previous work in this study system has shown that the combination of alpha age and tenure are important factors that influence reproductive success (DuVal 2012). While the relative contribution of female mate fidelity to annual patterns of success may well change over a male's life, the current fidelity data include relatively few sires for which both age and year of alpha tenure are known. Longitudinal effects of fidelity remain an interesting area for future research.

The reasons that some females are faithful and others change mates between nesting episodes remain unclear. Mate fidelity in other systems has been hypothesized to improve coordination of parental care or ensure access to familiar or successful nesting sites, and unsuccessful nesting attempts in monogamous systems are often followed by divorce (Choudhury 1995; Cezilly et al. 2000). In this lek mating system, however, males provide no care and nest sites are outside male display areas, and as expected from this separation of mate choice and nesting behavior female lance-tailed manakins were no more likely to switch mates following nest failure. Faithful females could also decrease

energy expenditure during mate search, though manakins were no more likely to fledge chicks following a faithful mating choice, suggesting that energy saved through fidelity does not translate into greater reproductive success. Energetic benefits may also be realized through increased female survival or earlier nesting, which could allow more chances for re-nesting following nest failure, possibilities not addressed in this study. Costs of mate sampling in non-resource-based mating systems rarely have been quantified, but were substantial in harem-mating pronghorn (*Antilocapra americana*; Byers et al. 2005) and lekking Galápagos marine iguanas (*Amblyrhynchus cristatus*; Vitousek et al. 2007). Considerably lower costs were estimated for lekking sage grouse (Gibson and Bachman 1992). Decreasing time spent in mate search may be more important than decreasing energetic expenditure, as female manakins typically have large home ranges encompassing multiple male territories (Hansbauer et al. 2008; They 1992).

Potential nonenergetic benefits of mate fidelity include inbreeding avoidance, reduced risk of parasitism, or reduced harassment by males. A recent study of female black grouse (*Tetrao tetrix*) showed that females mating faithfully experienced lower coefficients of kinship to their mates than females that switched mates. This effect was found only among older females that, late in life, may be mating at leks that include their adult male offspring. Mate fidelity therefore may serve as a mechanism of avoiding inbreeding in this highly polygynous mating system (Soulsbury et al. 2012). Faithful females could also benefit from decreased risk of diseases or parasites transmitted through direct contact with males, though female lance-tailed manakins were as likely to remain faithful to highly successful males that had many other sexual partners as they were to males with few partners, so such a benefit may be limited in this system. Faithful bowerbirds visit fewer males, likely decreasing their risk of forced copulation (Uy et al. 2000), but no evidence of forced copulation has been recorded in 12 years of observation in the lance-tailed manakin study population.

Further understanding of how females move among potential mates will be required to understand the behavioral mechanisms that generate patterns of mate fidelity. For example, females may first return to prior mates or prior mating sites before initiating a broader mate search, suggesting that prior mating decisions influence the current process of choice even when females are not faithful. Alternately, females may search broadly and arrive at the same choice in successive years. Results reported here indicate that the presence of prior mates influences current mate choice, and so expressed patterns of mate preference should be considered in light of information on females' mating history. Widespread occurrence of mate fidelity may complicate inferences about female preferences for

male traits, particularly given that searching females likely vary in mate search experience.

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