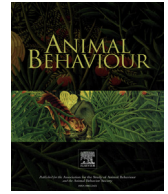




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## Special Issue: Breeding Aggregations

## The spatial dynamics of female choice in an exploded lek generate benefits of aggregation for experienced males

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The spatial distribution of prospective mates can dramatically affect the process and outcome of mate choice. In a variety of species, spacing between males influences the likelihood that females visit particular individuals or respond to competing signals. Discrimination by females is expected to be highest among neighbouring males, yet males of some species aggregate in ways that apparently facilitate such comparisons. To better understand the selective pressures affecting male aggregation, we investigated how spatial organization of male territories related to female mate sampling tactics and male mating success in the lance-tailed manakin, *Chiroxiphia lanceolata*. This species displays in a dispersed lek of alpha males, each of which usually has a subordinate beta partner that participates in displays but does not mate with females attracted by their cooperative courtship. We video-recorded courtship activity at display perches of 12 alpha–beta pairs for 42 days in 2013, and documented 478 visits by 82 banded females. We further quantified the relationship of aggregation with genetic mating success for 49 alphas displaying at georeferenced locations in 5 years. Males with close neighbouring alphas were visited by more females, but geographic centrality was unrelated to female visit frequency. Females moved shorter distances between consecutive courtship visits than expected at random, but only 20.5% of 73 females visiting males with video-monitored nearest neighbours visited both neighbouring alpha males. Effects of aggregation on annual genetic reproductive success were only evident after accounting for the stronger effects of alpha age and experience, and only experienced alphas benefited from having close neighbours. Selection for aggregation more likely influences social behaviour of older alphas than settlement decisions by younger males. Benefits of aggregation for experienced alphas mitigate declines in old age, and may generate selective pressure favouring the long-term social alliances that are a key characteristic of this mating system.

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Close aggregation of similar competitors is a widespread phenomenon. As such, understanding the selective factors that influence such aggregations has long been of interest in multiple fields of research, including human economics (Glaeser & Gottlieb, 2009; Hotelling, 1929), ecology (Clark et al., 2011) and animal behaviour (Bradbury, 1981). When mobile consumers assess the merits of relatively stationary products or service providers, spatial arrangement of competitors can profoundly affect the ultimate choices made (Jennions & Petrie, 1997; Simonson, 1999). Discrimination is expected to be highest when competitors are closely aggregated, as consumers can easily compare differences among nearby options (Chittka, Skorupski, & Raine, 2009; Murphy, 2012). It therefore seems that aggregation should mostly benefit the

highest-quality or most attractive competitors and so it is puzzling that inferior competitors would also aggregate.

In the field of animal behaviour, lek mating systems provide a prime example of aggregation of close competitors. Leks are spatial aggregations of males that perform courtship displays for females that visit the lek only to mate (Höglund & Alatalo, 1995). In 'classic' leks, such as those of Uganda kob, *Kobus kob* (Balmford, Albon, & Blakeman, 1992), greater sage grouse, *Centrocercus urophasianus* (Gibson & Bradbury, 1985), and white-bearded manakins, *Manacus manacus* (Lill, 1974), display areas contain no resources for females other than the males themselves, and aggregations may be so dense that males display only a few body lengths apart from each other. In other species, display areas that comprise the lek are more dispersed, and male display areas may contain food or nesting sites, but males do not defend those resources and females also have access to them away from male display territories (Alonso, Magaña, & Álvarez-Martínez, 2012). In all cases, lekking males provide no

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paternal care. Leks are typically characterized by extravagant male displays, and by extreme sexual selection as mating success among displaying males is highly skewed (Bradbury & Gibson, 1983; Gibson, Bradbury, & Vehrencamp, 1991; Lill, 1974; McDonald, 1989b). Leks, therefore, offer an ideal opportunity to investigate the causes and consequences of aggregation for competitors.

Given the apparent intense competition among neighbouring males, a long-standing question in the study of lek mating systems has been why competitors so often choose to display in close spatial proximity (Beehler & Foster, 1988). Sexual selection is at the root of the major hypotheses for the evolution of lekking aggregations, although other sources of selection (i.e. predator avoidance: Boyko, Gibson, & Lucas, 2004) are also known to play a role in lek dynamics. The three sexual selection hypotheses that have garnered the most attention are known as the hotspot (Bradbury & Gibson, 1983; Lill, 1976), hotshot (Beehler & Foster, 1988) and female preference hypotheses (Bradbury, 1981). The hotspot hypothesis predicts that males settle in areas of high female traffic, either because females are common in those areas or because of shared habitat preferences, resulting in dense clusters of males in areas where there are also many females (Bradbury & Gibson, 1983; Lill, 1976). The hotshot (or 'spatial spillover') hypothesis proposes that males cluster around highly successful competitors to intercept females en route to this preferred mate (Beehler & Foster, 1988; Foster, 1983). The female preference hypothesis proposes that females are more likely to visit male aggregations of certain sizes either because of decreased predation risk (Wittenberger, 1978) or improved ability to compare prospective mates (Bradbury, 1981). The benefits to females of larger aggregations are balanced by costs from increased male harassment, courtship disruptions (Trail, 1985b), or decreased efficiency of mate assessment if aggregations become too large (Alem, Clanet, Party, Dixsaut, & Greenfield, 2015). Each of these hypotheses generally predicts an increase in female visits (at least for some males on the lek) when males are spatially aggregated. This general prediction has been upheld in a variety of species, although other processes introduce variability in the outcomes of aggregation (Alatalo, Höglund, Lundberg, & Sutherland, 1992; Isvaran & Ponkshe, 2013). To understand the processes that generate sexual selection for aggregation, it is necessary to understand both the relationship between aggregation and female movements, and the effects of this aggregation on male reproductive success.

These major sexual selection-based hypotheses explaining why males aggregate in leks differ fundamentally in the proposed mechanisms by which aggregations generate increased visiting rates. They also vary in their predictions about who benefits from resultant differences in mating success (females, highly successful males and lesser competing males). The hotshot model predicts increased success of males that display near highly successful individuals. As such, the benefits of aggregation would accrue to the relatively unsuccessful individuals, with neutral or negative effects on the reproductive success of successful individuals around which they cluster (Widemo & Owens, 1995). In contrast, the female preference hypothesis predicts that, when preference is driven by increased ability to compare mates, relatively attractive males would experience increased success when aggregated. If females prefer larger aggregations for antipredator benefits, their behaviour would be driven by natural selection and the hypothesis makes no predictions about differences in sexually selected benefits for different types of males aggregating. The hotspot model predicts a correlated male and female response to habitat variation, but alone predicts no causal effect of aggregations on female behaviour and hence no differences in relative male success other than those generated by habitat-specific differences in female presence. In some lekking species, a male's centrality within the lek seems itself to increase

attractiveness to females (Fiske, Rintamaki, & Karvonen, 1998). However, potential direct effects of centrality are difficult to distinguish from hotshot effects, in which the relocation of unsuccessful males around successful competitors generates a correlation between centrality and success (Bradbury & Gibson, 1983). Additional hypotheses about lek evolution (i.e. indirect fitness: Höglund, 2003; black hole: Stillman, Cluttonbrock, & Sutherland, 1993; signal propagation: Lack, 1939) also predict increased female visits for more aggregated males but, like the hotspot hypothesis, do not make explicit predictions about which males within an aggregation should benefit from those visits. These hypotheses are nonexclusive, and recent work suggests that any single hypothesis is inadequate to explain decisions to aggregate. For example, in an elegant experimental comparison of key predictions from the hotshot, hotspot, female preference and black hole hypotheses, researchers showed support for each in the little bustard, *Tetrax tetrax* (Jiguet & Bretagnolle, 2006). Likewise, a theoretical modelling approach, validated with empirical data from the ruff, *Philomachus pugnax*, proposed that lek evolution was best explained by the combination of hotspot and hotshot effects (Widemo & Owens, 1995). Many factors influence male aggregation, and likely do so simultaneously.

Here we aimed to assess whether there is selection for aggregation in an exploded lek mating system and, further, to identify both the source and the consequences of this selective pressure. We investigated how the spatial dynamics of female movement shape the opportunities for selection to act on male aggregation in the lance-tailed manakin, *Chiroxiphia lanceolata*. Lance-tailed manakins are small passerine birds with an exploded lek mating system: males display in traditional locations, and are in auditory but not visual distance of (and presumably contact with) other displaying males. Male lance-tailed manakins form cooperative partnerships of dominant alpha and subordinate beta individuals, and work together to sing duet songs and perform two-male dance displays (DuVal, 2007b). Males do not normally exclude conspecifics from display areas unless they are actively courting a female, and so can be considered nonterritorial. However, each male display area is attended consistently by one alpha–beta pair, with a variable number of adult and subadult males that may move among display areas but do not display for females (DuVal, 2007c). With extremely rare exceptions, only alpha males copulate (DuVal & Kempnaers, 2008). Courtship displays are performed on low, horizontal sticks ('display perches') and comprise up to 11 different display elements (Vanderbilt, Kelley, & DuVal, 2015). Females move freely among male display sites and view multiple alpha–beta pairs during mate assessment, then raise their chicks outside of their mates' territories and with no male assistance.

To understand selection on male aggregation in this system, we first tested the main prediction of hypotheses about lek evolution: that more females visit spatially aggregated males. We asked whether males that were more centrally located or more clustered (closer to their nearest neighbouring alpha competitor, or 'nearest neighbour') received more visits from females, as detected by a video monitoring system. Second, we examined effects of male clustering on female movement, testing the prediction that individual females were disproportionately likely to visit close neighbours as they assessed males. Third, we investigated how increased female visits translated into male reproductive success to better determine which males benefited from the context of close aggregation among competitors. Finally, we explored preliminary hypotheses about the social mechanisms that could generate male aggregations. Together these analyses illustrate which individuals are most affected by selection for aggregation behaviour in this exploded lek mating system, and how that selective pressure could influence male behaviour, with implications for the cooperative social alliances of this species.

## METHODS

### *Study Site and General Field Methods*

The study was conducted in a population of lance-tailed manakins that has been monitored since 1999 on Isla Boca Brava, Republic of Panamá. Data addressed here were collected across 5 years, from 2009 to 2013. Each year, we captured birds using mist nets or as nestlings and colour-banded individuals with a unique combination of one numbered metal and three coloured plastic leg bands. As part of the long-term study, we observed all active display areas for a minimum of 10 one-hour observation sessions each year, during which we recorded the identity and behaviours of males and females present at the site. In each of these 5 years of the long-term study, there were 26–31 active male display areas, and we monitored 102–137 individual banded males and 90–121 individual banded females annually (ca. 3860 observation hours in 5 years). The majority of birds in our study population are banded and our netting efforts targeted unbanded individuals. In the years of this study, 22.1% of 456 captures of males and 33% of 416 captures of females or unknown sex green-plumaged birds were of unbanded individuals (2170 mist net hours of capture effort in 5 years; a mist net-hour is 12 m of net open for 1 h).

### *Definition of the Lek in *Chiroxiphia* Manakins*

A lek is defined as the spatial aggregation of displaying males (Höglund & Alatalo, 1995). Here we use the term 'lek' to describe the aggregation of alpha display areas that females may visit to view courtship displays; our study of 26–31 display areas represented an in-depth investigation of individual behaviour on one lek. However, in *Chiroxiphia* manakins, the lek includes several levels of spatial organization, which has led to variable definitions of 'lek' in the literature. These are (1) the cluster of males present at one display area, so that each lek includes only one potentially breeding male (Francisco, Gibbs, Galetti, Lunardi, & Galetti, 2007; Loiseau et al., 2007b; McDonald, 1989a), or (2) the aggregation of multiple display areas (also referred to as courts or perch zones) that are each attended by one dominant alpha male and his cooperative display partners (Foster, 1977). We argue that this second lek definition is most relevant for studies of mate choice and how female behaviour influences aggregation of breeding males for several reasons. First, in *Chiroxiphia* manakins, only alpha males perform solo displays for females that precede copulation, and the same alpha male performs all solo displays at any given display area. Therefore, females cannot choose among males at the same display area. Second, our behavioural observations, video and telemetry monitoring all indicate that individual females move among several display sites during mate search (DuVal & Kapoor, 2015), and sometimes visit several alphas in a matter of minutes. This suggests that females actively compare multiple alpha males among different display areas rather than making comparisons among males within a single display area. Finally, nonalpha adults attending display areas do not display in spatially distinct areas but instead interact extensively with the alpha and move throughout the attended area; it would not be possible to define a spatial location for those individuals other than the display perches on which they interact with the alpha male. We explicitly highlight the definition of the lek in *Chiroxiphia* as a point of semantic confusion that should be taken into consideration when assessing the literature on lekking behaviour of this genus.

### *Social Status*

We categorized males as alpha if they were the most commonly present male at an area and performed solo and alpha-specific

parts of the display (DuVal, 2007b, c). Other adult-plumage males were present in the population but did not enter into analyses here, as they did not display independently for females. Males were classified as betas if they were the alpha's most common duet song or courtship dance partner. Other adult males were often present at display areas although they did not hold alpha or beta status, nor engage in displays for females (DuVal, 2007c).

### *Spatial Relationships Among Displaying Males*

We recorded the GPS locations of male display perches annually using GARMIN eTrex Summit HC hand-held GPS units ( $\leq 6$  m accuracy). We converted these locations into a 'SpatialPointsDataFrame' using the R package 'sp' (Pebesma & Bivand, 2005) and then generated three measures of spatial relationships using the package 'rgeos' (Bivand & Rundel, 2016). These measures were centrality, distance to the nearest neighbour and distance to the nearest highly successful ('hotshot') male. When analyses contained data from multiple years, spatial relationships were calculated separately within each year. We calculated display area centrality by combining display perch GPS locations to generate a minimum convex polygon encompassing all male display perches in that year. We then calculated the distance, in metres, from the centroid of that irregular polygon to the main display perch of each male display area on the lek ('centrality'). This approach assumes that there is one lek centre, and so for comparison we also calculated centrality as the harmonic mean distance between a male's main display perch and those of all other alpha males active that year (following Gibson et al., 1991). These two measures of centrality (distance to study area centroid and harmonic mean of distances to other males) were highly correlated in the data set available for analysis of female visits (Spearman rank correlation:  $r_s = 0.89$ ,  $N = 12$ ,  $P < 0.0001$ ) and results were unchanged if calculated using the harmonic mean of distances as the measure of centrality. Because we expected the geographical arrangement of sites to affect female movements, we present the first centrality measure here. We calculated nearest-neighbour distance as the distance, in metres, between the major display perch of each alpha's site and that of the nearest display site active in the same year. Finally, to calculate distance to the nearest highly successful ('hotshot') male, we first defined only one most successful hotshot in each year, but found significant multicollinearity among all spatial variables (model variance inflation factor  $> 3$ ), precluding analysis. Because there were commonly several males with similarly high numbers of mates in a given year, we instead identified the minimum number of males required to account for 50% of all genetically detected matings and classified these males as hotshots. When we identified a threshold that led to different categorization of males with equivalent reproductive success, we classified all those males as hotshots. This approach identified two to seven hotshots each year. We then calculated the distance in metres for each male to the nearest hotshot male. In analyses including hotshot measures, the hotshots themselves were excluded, as distance to these males was necessarily zero.

### *Female Visits*

To quantify how spatial aggregation of males affected female visits, we calculated the number of unique banded females that observed courtship displays at each of 12 video-monitored display sites during 22 February – 5 April 2013. We used Canon Vixia HF M500 cameras, powered by 12 V batteries, allowing a maximum of 9.5 recording hours at each site each day. Recordings started between 0700 and 0800 hours each morning. One pair of males sometimes displayed for females on multiple display perches and,

in such cases, the camera monitored the most commonly used perch. To detect any changes in display perch use within the focal display area, we conducted in-person observation sessions for 1 h, three times per week, at video-monitored sites. An additional 19 display areas were active during the month of monitoring but not video-monitored due to equipment and time limitations. Those males were, therefore, excluded from analyses of female visits but, nevertheless, entered into analyses of spatial effects on genetic reproductive success.

Because we know females frequently revisit the same male over time (DuVal & Kapoor, 2015), we restricted analyses to visits by colour-banded, fully identified females. Sometimes females observed a male for repeated, consecutive displays over a short period. We treated the initial visit and all repeat visits within a 1 h period by the same female as a single visiting event, as we did not consider these repeat visits to be independent visiting decisions. Although visits by unbanded females were excluded from all analyses, our data seem to be a reasonable representation of mate choice dynamics in this population as a whole because visits by unbanded females represented only 26% of 618 total visits recorded, and this value approximated the proportion of unbanded females in the population as estimated from capture records (see above). Furthermore, the number of visits by unbanded females was correlated with the number of visits by banded females at the same sites (Spearman rank correlation:  $r_s = 0.60$ ,  $N = 12$  video-monitored sites,  $P = 0.037$ ).

#### Reproductive Success

To assess how spatial relationships influenced reproduction, we quantified male reproductive success as the number of unique mates, as determined by genetic paternity. We used number of females, rather than number of chicks sired because, while females reinitiate detailed mate searches each year (DuVal & Kapoor, 2015), they often return to mate with the same male in multiple nesting attempts within a year and within-year mate decisions are likely not independent (DuVal, 2013b). We genotyped chicks, mothers and candidate sires at 20 variable microsatellite loci, and assigned paternity by maximum likelihood in Cervus 3.0 (Kalinowski, Taper, & Marshall, 2007). To assign a male as the sire of a chick, we required confidence of 95% or higher and no more than one genotypic mismatch with the most likely candidate male. We considered all adult-plumage males as candidate sires. Paternity assignment methods are described in detail elsewhere (DuVal & Kempnaers, 2008). In these five study years, this approach identified a sire for 86% of 726 genotyped chicks sampled, with 91–164 chicks from 43–73 unique females assigned paternity each year. When we could not identify the female attending the nest, but were still able to assign the chick to a sire (DuVal & Kempnaers, 2008), we conservatively considered all chicks with unidentified mothers to represent one unique genetic mate. Number of assigned chicks was highly correlated with number of genetic mates (Spearman rank correlation:  $r_s = 0.98$ ,  $N = 129$  male-years,  $P < 0.0001$ ); repeating analyses with number of chicks as the response variable did not change our conclusions qualitatively.

#### Male Age and Experience

Male age and alpha experience are important predictors of alpha annual reproductive success in this population (DuVal, 2012a) and so here we considered not only direct relationships of spatial relationships with siring success, but also how known effects of age and experience may be modified by spatial relationships among competing alpha males. We knew the exact age of 37 alpha males monitored in 2009–2013 from capturing that male in one of the

three distinct predefinitive plumages of this species (DuVal, 2005), or from having banded that male in the nest (age range 4th – 15th year after hatching). An additional 13 alphas first captured as adult-plumaged birds were assigned a minimum age given time elapsed since the year of their first capture (age range  $\geq 5$ th – 16th year after hatching). Year as alpha was defined as the male's current year of experience in the alpha role, determined by having identified the male as nonalpha in years before he became alpha. The males in this sample ranged from year 1–10 of alpha status during the 5 years analysed.

#### Statistical Analyses

We conducted three major analyses to understand how male aggregation relates to mate attraction and success. The first two analyses used data from the single year of video monitoring to investigate how male spatial relationships correlate with female visits and movements among display areas. The third investigated the relationship of spatial measures to realized reproductive success, using a more extensive 5-year analysis of genetic siring data. This combined approach aims to place the more limited information on female movements in the context of male reproductive success, developing an understanding of how spatial arrangement of males relates to both the process and outcomes of mate choice.

#### Effects of spatial relationships on mate attraction

We performed analyses investigating the relationship of alpha male spatial aggregation with female visits using generalized linear models in R v.3.4.1 (R Core Team, 2017). Our response variable was number of unique colour-banded females recorded visiting a male, and because our responses are counts, we modelled error using a Poisson distribution with a log link function. We assessed effects of two measures of aggregation on female visits (centrality and nearest-neighbour distance). We were unable to independently assess a third spatial effect (distance to hotshot male) on female visits because, in the year video monitoring was conducted to calculate female visits, there were two hotshot males that both occupied relatively central territories and had relatively close neighbours (Spearman rank correlation: centrality and hotshot distance:  $r_s = 0.67$ ,  $N = 10$  non-hotshot alphas,  $P = 0.04$ ; nearest-neighbour distance and hotshot distance:  $r_s = 0.69$ ,  $P = 0.03$ ). Considering effects of only distance to the nearest competing alpha and centrality allowed inclusion of all monitored males (i.e. the hotshot male could be included in the analysis) and these variables were uncorrelated with each other ( $r_s = 0.30$ ,  $N = 12$  alphas,  $P = 0.34$ ). We included monitoring effort (hours of video recording at that display perch) as a fixed effect to account for slight variation in recording time due to occasional battery failure at some sites. We log transformed all aggregation variables, and all explanatory variables were scaled by subtracting the mean and dividing by the standard deviation to improve model convergence and facilitate comparisons between effect sizes of different predictors (Schielzeth, 2010). From the full model, we generated a reduced model of spatial effects on female visits using backwards elimination by likelihood ratio testing. We tested for overdispersion using the R package 'AER' (Kleiber & Zeileis, 2008) and found that the final model was slightly but not significantly overdispersed: the dispersion parameter, estimated as null deviance divided by model degrees of freedom, was 6.8 ( $\alpha = 1.20$ ,  $z = 1.14$ ,  $P = 0.13$ ). Repeating the analysis using a negative binomial model produced qualitatively similar results.

#### Female movements among alpha display sites

To assess how movements by individual females generated differences in relative visits among males and, specifically, whether females tended to view multiple close neighbours, we calculated



the distance travelled by each female between consecutive visits to male display perches (using video-detected visits). We then used a Kolmogorov–Smirnov test to compare the distribution of these distances with a null distribution created by randomly drawing the same number of distances from all possible distances that she could have flown. Because we were interested in whether individual females disproportionately visited close males, we limited the analysis to movements of 44 females that were detected on video visiting more than one male, and limited our random distances to those that were less than or equal to the maximum distance actually observed (567 m).

#### *Spatial relationships and male reproductive success*

To address whether genetic siring success was influenced by the spatial relationships among adjacent alphas that influenced female visits, we used an information-theoretic approach to assess relative support for models with and without spatial information (Anderson & Burnham, 2002; Burnham & Anderson, 2002) in R package 'lme4' (Bates, Maechler, Bolker, & Walker, 2015). The data set included genetic siring success for all alpha males on the study site in 5 years, and in this larger data set, correlations between both centrality and nearest-neighbour distance with hotshot distance were lower, thereby enabling us to consider all three spatial metrics at once. We compared support for models representing five major biological hypotheses explaining variation in number of unique genetic mates: (1) age and experience effects only (model 1, Table 2; DuVal, 2012b); (2) age and experience with additive effects of spatial relationships (models 2–8, Table 2); (3) spatial effects only (models 9–15, Table 2); (4) age and experience with interactive effects of spatial relationships (models 16–19, Table 2); and (5) two reference models: an intercept-only model that included only the random effects and a model comprising only a fixed effect of sampling success (models 20–21, Table 2). All models included random effects of alpha identity (to control for repeated measures of individuals over time) and (with the exception of the intercept-only model) a fixed effect of number of chicks for which paternity was assigned that year ('sampling success', in order to control for differences in sampling among years). Precise model parameterization is reported in Table 2. We assessed multicollinearity by calculating the variance inflation factor (VIF) for the global model and found VIF <3, indicative of no significant multicollinearity among predictors (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). This analysis used all display sites active on the study area in each year to calculate nearest-neighbour distance, but then excluded records with missing data for any of the variables of interest to allow model comparisons (11 of 141 yearly male-site records excluded). Because distance to the nearest highly successful hotshot male was, by definition, 0 for the hotshot individuals, these

males were excluded from the analysis in the year they were identified as hotshots (15 male-site records excluded, which included all records for two males). As before, we log transformed all aggregation variables, and all continuous explanatory variables were scaled by subtracting the mean and dividing by the standard deviation. Quadratic terms were included using orthogonal polynomials. All models were generalized linear mixed models with Poisson error distributions and log link functions. We assessed goodness of fit for each model by examining distribution of model residuals and Q–Q plots. We tested for overdispersion by calculating the ratio of the sum of squared Pearson residuals to the residual degrees of freedom, and found no evidence that models were significantly overdispersed (all overdispersion parameters less than 1.1,  $P > 0.29$ ). We inferred strong support for a particular model when Akaike's information criterion for small samples (AICc) value was at least 2 AICc units less than the next-best model (Burnham & Anderson, 2002). To obtain final parameter estimates, we model-averaged models with equivalent support using the R package 'MuMIN' (Barton, 2014).

It is possible that processes such as spatial spillover of reproductive success lead to covariance of success among nearby males (positive or negative). For example, if females are more likely to visit certain areas of the lek for copulations, we would predict positive correlations of success among neighbours. In contrast, if females that compare close males tend to prefer one over the other, we would predict that an increase in success of one male comes at a cost to success of his neighbours, and hence there would be negative correlations of neighbour success. To investigate how alpha males' genetic reproductive success was related to success of their nearest neighbours, we ran a glmm with Poisson error distribution and log link function, including random effects of year and alpha male identity. We used nearest neighbour's number of genetic mates as the response variable, number of genetic mates assigned to the focal male as the predictor, and included scaled sampling success as a fixed effect in the model to control for yearly sampling success. Because distance values were repeated for both neighbouring individuals when males were each other's nearest neighbours, we randomly selected only one male from each such pair to include in the model.

Based on results from these analyses, we hypothesized that males with more years of alpha experience may benefit from displaying near less experienced alphas (as female comparisons would favour the more experienced males). Experienced alphas could be expected to have inexperienced neighbours even if males are randomly distributed in space, with respect to experience, because the nearest neighbour of an experienced male will almost always be a less experienced male. However, it is also plausible that clusters of similarly aged alpha males may persist over time as males sometimes retain high social status for many years: the longest observed alpha tenure to date has lasted 11 years (E. H. DuVal, personal observations). It is also possible that well-established alphas may actively recruit young and inexperienced neighbours, as has been suggested in some colonially nesting birds (Morton, Forman, & Braun, 1990). To test whether experienced males were more likely than expected to display next to inexperienced neighbours, we compared the relative experience of neighbours in our data to a null model where males were randomly distributed among display site locations. To quantify the relationship between neighbours' experience levels, we used a linear mixed effects model with relative alpha experience of the neighbour as the response and the focal male's years of alpha experience as the predictor, including random effects of focal male identity (ID) and neighbour ID to account for repeated measures of both focal males across years and nearest neighbours within a year (for males that were nearest neighbours of multiple individuals). We did this for 10 000 randomized data sets that we created by randomly shuffling males

**Table 1**  
Distance to the nearest neighbouring alpha was the best spatial predictor of the number of females that visited a male

	Variable	Estimate	SE	z value	P
Full model	Intercept	2.50	0.09	28.69	<0.0001
	Effort	0.15	0.10	1.55	0.12
	log (Centrality)	0.03	0.10	0.28	0.78
	<b>log(Nearest neighbour)</b>	<b>-0.46</b>	<b>0.08</b>	<b>-5.83</b>	<b>&lt;0.0001</b>
Reduced model	Intercept	2.50	0.09	28.89	<0.0001
	<b>log(Nearest neighbour)</b>	<b>-0.50</b>	<b>0.08</b>	<b>-6.52</b>	<b>&lt;0.0001</b>

Full and reduced models are shown for tests of the relationship of number of females visiting, with two measures of male spatial relationships on the lek: centrality and distance to the nearest neighbouring alpha male. Explanatory variables were log transformed and scaled to improve model fit, and significant predictors of female visits are shown in bold. Analyses were generalized linear models run with a Poisson distribution in R v.3.3.3, with the reduced model generated from backwards elimination by likelihood ratio testing ( $N = 12$  video-monitored display areas in 2013). Estimates are presented here on the transformed scale, and backtransformed in Fig. 1.

**Table 2**  
AICc comparisons of models explaining male genetic reproductive success revealed support for a model with interactive effects of proximity to the nearest neighbour and experience in the alpha role, in addition to previously identified effects of age and experience on success

ID	Model parameters	–logLik	k	AICc	Delta AICc	w <sub>i</sub>
<b>17</b>	<b>Age + Age<sup>2</sup> + Exp * logNN + sampling</b>	<b>–165.21</b>	<b>8</b>	<b>347.86</b>	<b>0</b>	<b>0.37</b>
<b>1</b>	<b>Age + Age<sup>2</sup> + Exp + sampling</b>	<b>–167.96</b>	<b>6</b>	<b>348.74</b>	<b>0.88</b>	<b>0.24</b>
4	Age + Age <sup>2</sup> + Exp + sampling + logCent	–167.81	7	350.73	2.87	0.09
3	Age + Age <sup>2</sup> + Exp + sampling + logNN	–167.95	7	351	3.15	0.08
5	Age + Age <sup>2</sup> + Exp + sampling + logHS	–167.96	7	351.02	3.17	0.08
8	Age + Age <sup>2</sup> + Exp + sampling + logHS + logCent	–167.78	8	353.01	5.15	0.03
6	Age + Age <sup>2</sup> + Exp + sampling + logNN + logCent	–167.79	8	353.03	5.17	0.03
19	Age + Age <sup>2</sup> + Exp * logCent + sampling	–167.8	8	353.04	5.18	0.03
18	Age + Age <sup>2</sup> + Exp * logHS + sampling	–167.88	8	353.19	5.34	0.03
7	Age + Age <sup>2</sup> + Exp + sampling + logNN + logHS	–167.95	8	353.33	5.48	0.02
2	Age + Age <sup>2</sup> + Exp + sampling + logNN + logHS + logCent	–167.78	9	355.37	7.52	0.01
16	Age + Age <sup>2</sup> + Exp * logNN + Exp * logCent + Exp * logHS + sampling (global model)	–164.38	12	356.02	8.16	0.01
20	Sampling	–181.51	3	369.24	21.39	0
10	Sampling + logNN	–181.41	4	371.2	23.35	0
12	Sampling + logHS	–181.51	4	371.4	23.54	0
11	Sampling + logCent	–181.51	4	371.4	23.54	0
15	Sampling + logNN + logCent	–181.38	5	373.34	25.48	0
13	Sampling + logNN + logHS	–181.40	5	373.38	25.52	0
14	Sampling + logHS + logCent	–181.51	5	373.6	25.74	0
9	Sampling + logNN + logHS + logCent	–181.37	6	375.57	27.71	0
21	Intercept	–186	2	376.12	28.27	0

Models in bold are those with substantial support (within 2 AICc points of the best-supported model). All models were generalized linear mixed models with Poisson distributions, log link functions and a random effect of alpha male identity. Model fits were checked by examining the distribution of model residuals and Q–Q plots of sample versus theoretical quantiles. VIF was <3 for all models, indicating no problems with multicollinearity. Data were 109 yearly observations on 47 different alpha males in 5 years. Fixed effects considered were alpha male age (Age; *n*th year since hatching), the quadratic term for age (Age<sup>2</sup>), years of experience as an alpha (Exp), log of the distance in metres to the nearest neighbouring alpha's main display perch (logNN), log of the distance in metres to the geographic centre of the lek (logCent), log of the distance in metres to the nearest highly successful male (logHS) and annual sampling success (sampling; number of chicks for which paternity was genetically determined that year). All variables were scaled to improve model diagnostics. Relative support for each model in the tested set is reported as AICc weights (w<sub>i</sub>).

among sites within years, thereby generating a distribution of expected relationships between a male's experience level and his nearest neighbour's experience level. We then calculated a two-tailed *P* value for the observed relationship as two times the proportion of randomized observations that were more extreme than the observed value.

We investigated whether alphas benefited from favourable comparisons with close and relatively inexperienced neighbours by testing the specific prediction that, in this case, genetic reproductive success should be related to the interaction of proximity and difference in experience with their nearest neighbours. This analysis used a glmm with Poisson error distribution and log link function, and included a random effect alpha male identity.

Means are reported ± 1 SD. All analyses were performed in R 3.4.1 (R Core Team, 2017).

#### Ethical Note

This study incorporated permanent individual marking of free-living birds using leg bands to identify interacting individuals from a distance and over time, blood sampling of adults and chicks for paternity analyses, and behavioural observations conducted at display sites. Marked and sampled birds in the study population are monitored for their lifetimes, and we have observed unhindered display, reproduction and longevity following these manipulations that indicate that the birds are not adversely affected. All procedures employed here were approved by the Animal Care and Use Committee of Florida State University (IACUC protocols 0718, 1101, 1407 and 1706). Local research permits were granted by Autoridad Nacional del Ambiente, Republica de Panamá.

## RESULTS

Video monitoring recorded 478 visits by 82 unique females at the major dance perch of 12 display areas. We detected more than

one visit by 70 females, and 44 females visited more than one monitored male. We recorded copulations for 49 females (range 0–24 copulations per female in the monitored time period), and six of these females copulated with two different alpha males.

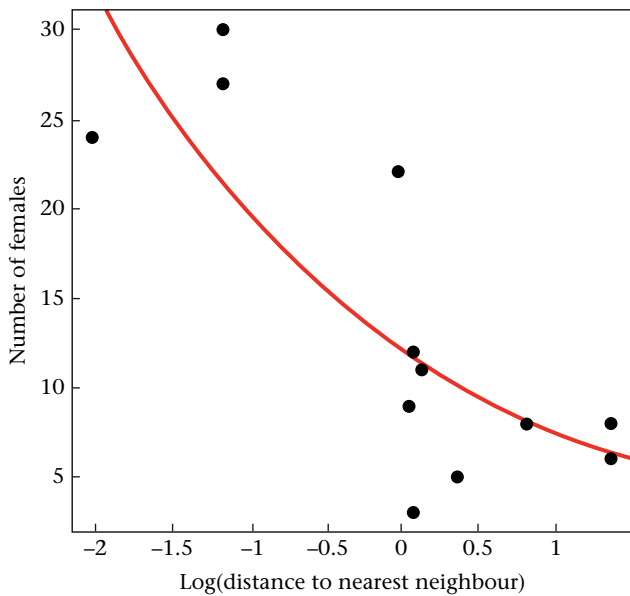
#### Effects of Spatial Aggregation on Mate Attraction

Alphas that displayed at sites closer to other alpha males were visited by more females (Table 1, Fig. 1). In contrast, geographic centrality was unrelated to the number of females visiting a male (Table 1).

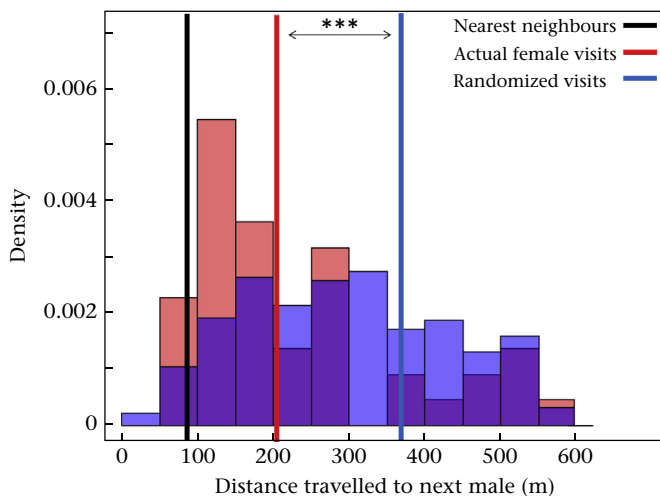
#### Female Movements Among Male Display Sites

The majority of second visits were returns to the male that a female had most recently visited, and 50 of 82 females revisited the same male two or more times (range 2–11 distinct visits). When they moved among sites, females made significantly shorter movements between consecutive visits than expected at random (Kolmogorov–Smirnov test:  $D = 0.29$ ,  $P = 0.001$ ; range 22–567 m between consecutive recorded visits), although the average movement between actual consecutive visits ( $204 \pm 169$  m for 122 recorded distances between consecutive visits) was more than twice that of the average distance between nearest neighbouring alphas ( $86 \pm 48$  m,  $N = 30$  display areas in 2013; Fig. 2). Together these data suggest a spatial signature to the search behaviour of individual females within our study site, but that most females did not directly compare nearest neighbouring alphas in consecutive visits.

Simultaneous video at four pairs of nearest neighbouring sites created the opportunity to detect whether individual females visited both nearest neighbouring alphas at any point in their recorded mate search. Only 20.5% of 73 females that visited at least one of these males also visited his nearest neighbour. At two of the paired display sites (77 and 149 m apart), none of the 23 total



**Figure 1.** Relation between nearest-neighbour distance and number of visiting females. Visits were those detected during just over 1 month of video monitoring at 12 male display sites. Data were restricted to visits by colour-banded and, therefore, uniquely identifiable females. Points show raw data, and the red line shows fit of the reduced model (Table 1).



**Figure 2.** Measured distances between nearest neighbours (solid black line) and actual female movement distances among consecutively viewed males (red bars; mean shown by the solid red line) in relation to hypothetical movements among male sites in randomized spatial locations (blue bars; mean shown by blue line). Purple regions indicate overlap between distributions of real (red) and hypothetical (blue) movement distances. \*\*\* $P = 0.001$  (Kolmogorov–Smirnov test). Data were 122 recorded distances between consecutive visits to different males, compared to the distribution of all possible distances generated by randomly drawing 10 000 possible female movements.

visiting females also visited the nearest neighbour. The other two pairs of sites had visiting females that viewed both alphas. At one pair of sites (with neighbouring alphas 76 m apart), six of nine total females visited both nearest neighbours. At the other, 11 of 46 total females viewed both nearest neighbours (with 16 only viewing one alpha, and 19 only viewing the other; neighbouring alphas were 41 m apart). While we cannot completely exclude the possibility that some visits occurred before cameras were deployed or late in the afternoon after recording had ended, these observations further indicate that females do not strictly – or even commonly – visit both males in nearest-neighbour associations.

### Spatial Relationships and Male Reproductive Success

The best model for predicting the number of genetic mates included both the previously identified effects of age (including its quadratic term) and years of alpha experience on male success, and an interaction between male experience and nearest-neighbour distance (Tables 2, 3). This interaction indicated that only males with more years of alpha experience benefited from having a close nearest neighbour (Fig. 3). When models of reproductive success did not include age and experience, we found no evidence that male aggregation was related to reproductive success.

When we tested the hypothesis that spatial spillover of reproductive success led to covariance of success among nearby males, we found that alpha males' genetic reproductive success was not correlated with the success of their nearest neighbours (gmm, estimate of focal male number of genetic mates as a predictor of neighbour's genetic mates:  $-0.03 \pm 0.04$ ,  $z = -0.94$ ,  $N = 89$  observations on 41 alphas in 5 years,  $P = 0.35$ ).

We hypothesized that males with more years of alpha experience may benefit from favourable comparisons with nearby younger and/or less experienced males, perhaps performed through more distant evaluation than the visits to display perches detected with video monitoring. Such a situation could create a selective pressure for well-established alphas to disproportionately tolerate or even recruit young and inexperienced neighbours. Older and more experienced males did have relatively young and inexperienced neighbours (gmm, estimate of the effect of alpha experience on the experience difference between neighbours:  $0.99 \pm 0.06$ ;  $t = 17.43$ ,  $N = 125$  observations of 49 focal males with 44 neighbours,  $P < 0.0001$ ). However, this relationship was not significantly different from that produced by a model where males were, in fact, randomly distributed among perches (two-tailed  $P = 0.51$  for experience, two-tailed  $P = 0.87$  for age, for actual versus randomized slopes). If experienced alphas benefit from favourable comparisons with close and relatively inexperienced neighbours, reproductive success should correlate with an interaction of neighbour proximity and experience difference between nearest neighbours. This was not the case (gmm, estimate of the interaction between distance and difference in experience between nearest neighbours:  $-0.02 \pm 0.02$ ,  $z = -1.05$ ,  $P = 0.29$ ).

### DISCUSSION

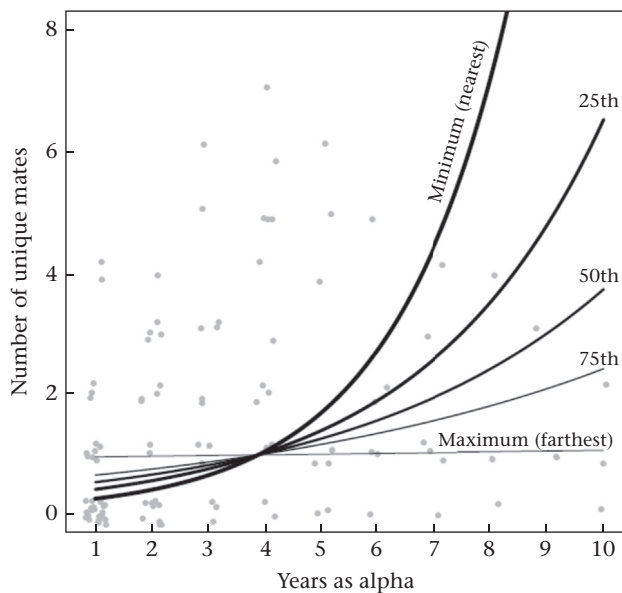
Alpha male lance-tailed manakins with closer neighbouring alphas experienced higher rates of female visits on this exploded lek. However, only males with many years in the alpha role had higher genetic reproductive success when they were close to other males. Although experienced males did have relatively inexperienced neighbours, this effect was not stronger than expected through random male settlement and we found no strong evidence that females directly compared males through visits to pairs of nearest neighbouring alphas. Together our results suggest that female mate search is not spatially restricted to the scale of male aggregation tested in this study, and potential selection on male aggregation from female choice is weak for most males. However, small benefits of aggregation for experienced males may be relevant for understanding long-term social dynamics in this species.

Sexual selection for male aggregation is a key component of the majority of hypotheses about why males display in leks (Bradbury & Gibson, 1983). Our results support the widespread prediction that aggregation enhances mate attraction in lek mating systems (Bradbury & Gibson, 1983; Isvaran & Pongshe, 2013). Interestingly, this was the case even though our study species displays in dispersed leks, and so males might not be expected to benefit from aggregations in the same way as those of species that lek in tight

**Table 3**  
Model-averaged coefficients and their 95% confidence intervals revealed support for an effect on male siring success of the interaction between alpha experience and distance to the nearest neighbouring alpha

Parameter	Est.	SE	z value	Upper 95% CI	Lower 95% CI	P
Intercept	0.12	0.13	0.91	−.014	0.39	0.16
Age	−1.90	2.09	0.90	−6.04	2.24	0.37
<b>Age<sup>2</sup></b>	<b>−5.35</b>	<b>1.24</b>	<b>4.26</b>	<b>−7.82</b>	<b>−2.89</b>	<b>&lt;0.0001</b>
<b>Experience as alpha</b>	<b>0.57</b>	<b>0.18</b>	<b>3.06</b>	<b>0.20</b>	<b>0.94</b>	<b>0.002</b>
Log (Nearest-neighbour distance)	0.06	0.10	0.58	−0.14	0.27	0.57
<b>Sampling success this year</b>	<b>0.29</b>	<b>0.08</b>	<b>3.53</b>	<b>0.13</b>	<b>0.46</b>	<b>0.0004</b>
<b>(Experience as alpha)*(Nearest-neighbour distance)</b>	<b>−0.25</b>	<b>0.10</b>	<b>2.31</b>	<b>−0.46</b>	<b>−0.04</b>	<b>0.02</b>

Experienced males with close neighbouring alphas sired chicks with more females than expected given their age and years of alpha experience. Averaged models are those that differed by <2 AICc points. All explanatory variables were scaled to improve model diagnostics, and the model was a generalized linear mixed model with Poisson error distribution and log link function. Estimates presented here are on the transformed scale, while effects plotted in Fig. 3 show backtransformed values. Parameters that were significant predictors of siring success are shown in bold.



**Figure 3.** Relation between reproductive success (number of unique mates), experience (years as alpha) and nearest-neighbour distance. Effects plotted here are the partial effect of the interaction of nearest-neighbour distance with alpha experience, derived from the model-averaged generalized linear mixed model with Poisson distribution and random effect of male identity, for an alpha male in his 13th year after hatching. Lines indicate the predicted effect for different distances to the nearest neighbouring alpha, with increased line weight indicating closer nearest-neighbour distances. Lines from thickest to thinnest correspond to values of the minimum, 25th quantile, 50th quantile, 75th quantile and maximum values of reproductive success from 47 alpha males in 5 years. The full model is shown in Table 3. Points show raw data, jittered to visualize overlapping points. A plot demonstrating effects across varied alpha ages is provided in the Appendix (Fig. A1).

aggregations. We found no support for an influence of geographic centrality on the number of visiting females, a factor that has been suggested as important in lekking species (Wiley & Poston, 1996), but which has received limited empirical support (Sæther et al., 2005). However we were unable to assess effects on visits of displaying near highly successful males, as in the year of video monitoring the two ‘hotshot’ individuals were both geographically central and had many close neighbours. This is perhaps unsurprising, as it has been pointed out before that leks may form when males cluster more tightly around highly successful individuals, which would result in correlations in these spatial variables (Bradbury & Gibson, 1983).

We investigated how females moved among available males to better understand the mechanisms by which male aggregation may be related to female choice. We found that the increased female visits to clustered males resulted not from individual females visiting

several males in a cluster, but instead from independent visits of many different females to the same general area. A relatively small proportion of females that visited one male of a video-monitored nearest-neighbour pair also visited his neighbour. Our video system specifically detected females that perched on a small area of one stick to observe intense male courtship displays, and so our measures of increased visits reflect mating-relevant behaviour rather than passive female traffic through an area (but see discussion of possible hotspot effects below). It is likely that early stages of mate assessment leading to these decisions to visit a display perch use longer-range cues, such as duet songs or broad-ranging pip-flight displays not quantified here (DuVal, 2007b). When female lance-tailed manakins did visit specific males to view displays, they did not necessarily view all males in the area. Spatial aggregation alone was insufficient to explain male reproductive success, and this makes sense given the intense mate search behaviour that has been recorded for this species; mate search movements in lance-tailed manakins take place over broad spatial scales and females often view the same males many times before mating (DuVal & Kapoor, 2015).

Although alpha males with closer neighbours received more female visits, we only detected fitness benefits for those males that had both many years of alpha experience and close neighbours. Experience-specific correlations of neighbour proximity and siring success suggest that the context in which females view males may affect final mate choice decisions. Contextual effects on choice have been studied most extensively in humans, for which empirical work shows that the comparison set (‘product assortment’) can influence choices made (Chernev, 2012; Simonson, 1999), and similar effects were recently demonstrated in tungara frogs, *Engystomops pustulosus* (Lea & Ryan, 2015). In particular, choices of a moderate-quality option increase when it is presented alongside low-quality options, whereas the outcomes for high-quality options are relatively unaffected (Simonson & Tversky, 1992). In contrast, choices of high-quality options are maximized by marketing them in isolation (Nowlis & Simonson, 1997). Similar processes may be at work in the context of aggregations of displaying lance-tailed manakins, as the males that experienced fitness gains in the context of aggregations were those moderately attractive males that had many years of alpha experience but were also older than the apparent optimum (DuVal, 2012b). Only males in adult plumage display as alphas, and males do not have adult plumage until their fourth year after hatching (DuVal, 2005); e.g. a male with 8 years of experience as alpha must at least be in his 12th year after hatching). Benefits associated with clustering therefore mitigate senescence of reproductive success in highly experienced males rather than elevate their success to the level of highly successful males in the population, as highly successful males tend to be younger. Understanding the processes by which females arrive at a mate choice will be a key part of understanding the mechanisms by which aggregation might affect male fitness.



Experienced males had inexperienced neighbours, which creates the potential for these spatial effects on reproductive success to come from favourable comparisons with nearby inferior competitors. Although average alpha tenure of lance-tailed manakins lasts only a few years (DuVal, 2013a), these birds can be very long-lived and some males retain their alpha status for more than a decade. However, in contrast to the preferential recruitment of inexperienced neighbouring males by older male purple martins, *Progne subis* (Morton et al., 1990), we found that the difference in experience levels between neighbouring alpha manakins was no greater than expected from random male settlement. We therefore found no evidence for an active process of recruitment of inexperienced neighbours by experienced alphas.

Although we found that aggregated and highly experienced males had higher reproductive success than predicted given their age and experience, this does not imply that aggregation is the specific trait being chosen by females. Such a pattern could also be generated by alpha traits that lead to both success with females and increased tolerance of close neighbouring males. For example, highly aggressive males may repel competing alphas, but also be less attractive to females, as has been reported in little bustards (Jiguet & Bretagnolle, 2006). Hotspot effects may also generate such a pattern, if males are more closely aggregated in areas of favourable habitat that are also frequented by females, and increased encounter rates disproportionately benefit experienced males. A test in three species of manakins revealed that leks tended to occur in areas of relatively high fruit abundance (Ryder, Blake, & Loiseau, 2006), although a separate examination of co-occurrence for species with similar habitat requirements did not support the hotspot predictions (Loiseau et al., 2007a). Aggregation could play a more direct role if, for example, areas with many displaying alphas (and therefore many displaying alpha–beta pairs) broadcast more duet calls that initially attract females to the area (the signal propagation hypothesis: Lack, 1939).

The relationships identified here have several interesting implications for understanding the unusual cooperative display behaviour of lance-tailed manakins. When aggregation increases fitness, even to a minor extent, selection may operate on behavioural mechanisms to increase aggregation. Selection favouring aggregation by experienced alpha males could refine complex social interactions and provide reasons for alpha males to tolerate nearby conspecifics. In *Chiroxiphia* manakins, the primary benefit to cooperating as a beta helper seems to be an increased likelihood of attaining an alpha position (DuVal, 2007a; McDonald & Potts, 1994). Betas are generally younger than their alpha partners, and can inherit their alphas' display sites if the alpha dies, or 'bud' off from their alpha's territory while their alpha is still alive. Long-term alliances may affect settlement decisions when betas become alphas, allowing experienced alphas to accrue close neighbours with which they have an established dominance relationship. If this is the case, benefits of aggregation for highly experienced males may in part explain why alpha males have beta partners. Social context has long been known to play a role in settlement decisions of lekking males (Wiley, 1991), and can also influence reproductive success. For example, age-related social dominance in the great bustard, *Otis tarda*, correlates with decreased aggressive interactions during the breeding season (Magaña, Alonso, & Palacín, 2011). The process by which lekking males establish display sites represents an interesting avenue for further study.

Here we have investigated whether male aggregation is under current sexual selection, but other sources of selection may also influence male settlement decisions. For example, male aggregation may also be influenced by predation risk (Boyko et al., 2004; Bradbury & Gibson, 1983). Reduced predator vigilance during display (Cowles & Gibson, 2015) could be offset by increased

likelihood of predator detection or reduced individual risk in a group of conspecifics (Delm, 1990). Resource abundance on and near leks has generally been considered through the lens of sexual selection, as it could influence female visits (Jiguet, Jaulin, & Arroyo, 2002), but male aggregation could be influenced by survival benefits to males if males displaying in areas of high resource abundance benefit directly from access to those resources. Such patterns are suggested by foraging behaviour near leks of white-bearded manakins (Cestari & Pizo, 2013).

Much work on lekking species has focused on why males aggregate, but the dispersed nature of the exploded lek in *Chiroxiphia* manakins also raises the question of why males do not aggregate more closely. In the absence of forces selecting for greater dispersion among competitors, economic theory predicts close aggregation in space as the default arrangement of competitors (Hotelling, 1929). Factors selecting for increased dispersion of competitors, as well as those that lead to aggregation are, therefore, of interest for explaining the evolution of lekking behaviour. Courtship disruption represents the most plausible cost to close spatial aggregation in this system, as disruptions during courtship displays can decrease male mating success (Lanctot, Weatherhead, Kempnaers, & Scribner, 1998; Saether, Fiske, & Kalas, 1999; Trail, 1985a). A multispecies comparison supported the prediction that there are fewer courtship disruptions on exploded leks, in which male display territories are further apart (Thery, 1992).

Our results have several implications for the understanding of lek evolution. Although aggregated males received more female visits, we found that independent mate choice based on male characteristics (here, age and experience) had a stronger effect than the short-range comparative context that results from the spatial clustering of males. Spatial effects were only evident after taking relationships with age and experience into account. This means that, as reported for greater sage grouse, factors relating to mate attraction were distinct from those relating to active choice (Gibson, 1996). In summary, we have shown that males experience sexual selection for aggregation only when they have held alpha tenure for many years. Male lance-tailed manakins generally remain at a specific display territory for the duration of their alpha tenure (DuVal, 2013b), and so this suggests that sexual selection for male aggregation is more likely to influence behaviour of well-established alphas rather than settlement decisions of younger males.

## Acknowledgments

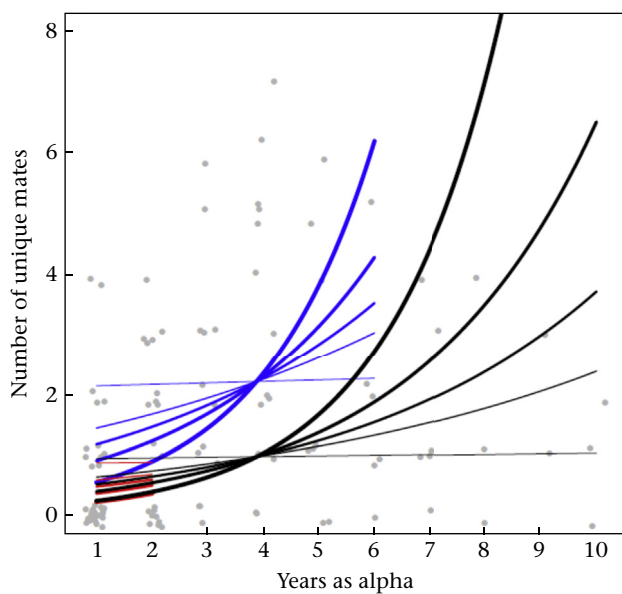
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## Appendix



**Figure A1.** Plotting predicted mating success across the realized age range of alpha males demonstrates that experienced alphas fertilized more females when they displayed relatively close to their nearest neighbours. Lines indicate the predicted effect for different distances to the nearest neighbouring alpha, with increased line weight indicating closer nearest-neighbour distances. Lines from thickest to thinnest correspond to values of the minimum, 25th quantile, 50th quantile, 75th quantile and maximum values of nearest-neighbour distance recorded in our data, as in Fig. 3. This effect was in concert with previously identified effects of age (including its quadratic effect, indicating decreased siring success for very young and very old alphas) and alpha experience (years in the alpha role) on male reproduction. Effects plotted here are the partial effect of the interaction of nearest-neighbour distance with alpha experience, derived from the model-averaged generalized linear mixed model with Poisson distribution and random effect of male identity. Red lines are model-predicted values for an alpha male in his 5th year after hatching, blue lines are values for alphas in their 9th year after hatching (the mean age of alphas in our sample) and black lines are for alphas in their 13th year after hatching. Alpha males of average age (9th year after hatching) experienced slight decreases in reproductive success when they had close nearest neighbours early in their alpha tenure. Because males do not hold alpha status until after they attain adult plumage (4th year after hatching), all combinations of male age and years as alpha were not possible. Curves were therefore truncated to only illustrate biologically possible relationships of age and experience. Data were 109 observations of reproductive success from 47 alpha males in 5 years. The full model is shown in Table 3. Points show raw data, jittered to visualize overlapping points.