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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.

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 & Kempenaers, 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.

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