



Courtship behaviour and display-site sharing appears conditional on body size in a lekking bat

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Leks are aggregations of sexually displaying males visited by receptive females and characterized by intense male–male competition to attract mates. Success in lekking species is often contingent upon male display output and/or lek attendance, with energetically costly displays functioning as an honest indicator of male quality. Furthermore, display spaces are vigorously defended by territorial males, and territory characteristics are often linked to male phenotype. Here we describe the courtship and territorial behaviour of lekking lesser short-tailed bats, *Mystacina tuberculata*, and both behaviours appear to be conditional on body size. During the breeding season, lekking males occupy and defend small tree hollows and sing for long periods of the night to attract females. Although some males sing alone, others form ‘timeshare’ singing roosts, where multiple males visit sequentially to sing each night. In our study, solitary males were significantly smaller than timeshare males and individually had both higher song outputs and higher roost occupancy rates, although timeshare roosts had higher overall occupancy rates. There appeared to be no fitness difference between the two male groups, and while one timeshare roost contained relatively closely related individuals (which roost settlement simulations indicate was not a chance event), four did not. We discuss factors that may promote timeshare formation, including competition for access to desired roosts and potential by-product mutualisms. Courtship and sexual selection in bats is largely undescribed, and thus our study provides a useful description of behaviour in a little-studied taxon.

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Body size affects many aspects of an organism's biology (Peters, 1986), and these effects can be sex specific. It has been well documented that male size influences performance, including competition (Arnott & Elwood, 2009), hunting ability (Hakkarainen et al., 1996) and female preference (e.g. Hakkarainen et al., 1996; Ryan & Wagner, 1987). Competition between males for access to females is a powerful selective force that has resulted in the evolution of multiple tactics for the attraction and retention of mates (e.g. exaggerated weaponry; Painting, Probert, Townsend, & Holwell, 2015; energetically expensive courtship displays; Murai & Backwell, 2006), while also promoting the evolution of alternative reproductive strategies that increase the mating opportunities of unfavoured males (Gross, 1996). Alternative strategies are often linked to some aspect of male phenotype, frequently associated

with a switchpoint or threshold in body size, with males of different size classes using the strategy that maximizes their fitness (Tomkins & Hazel, 2007; e.g. Painting & Holwell, 2014). Understanding how and why selection favours alternative strategies is an ongoing aim for behavioural ecologists (Gross, 1996).

Lek breeding is one of the rarest and most bizarre mating systems (Clutton-Brock, Deutsch, & Nefdt, 1993; Wiley, 1991), and lekking species have long been used as models for studying sexual selection in free-living animals (Höglund & Alatalo, 1995). Lekking males establish clustered, resource-free territories and collectively perform sexual displays for receptive females, while providing no parental care to their offspring. As such, female mate choice at leks is based solely upon honest male advertisements, and male display characteristics such as display frequency, display output and lek attendance are often positively correlated with reproductive success (Fiske, Rintamäki, & Karvonen, 1998; Höglund & Alatalo, 1995). Consistent female selection of one or a few males with the highest display output results in pronounced mating skews among lekking individuals (Bradbury, Vehrencamp, & Gibson, 1985; Mackenzie, Reynolds, Brown, & Sutherland, 1995). Reproductive skews favour

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the evolution of alternative reproductive tactics by males that would otherwise be at a competitive size disadvantage, such as sneakers who adopt female morphological traits to parasitize matings from males (Jukema & Piersma, 2006; Wikelski, Carbone, & Trillmich, 1996), and satellites who intercept females visiting attractive males (Gosling & Petrie, 1990).

Given the intense competition for access to females, display spaces are valuable commodities for males. As such, much interest has been paid to territoriality on leks, particularly with respect to their placement within the wider landscape (e.g. Toth, Dennis, Pattemore, & Parsons, 2015), processes that affect territory establishment (e.g. Kokko, Lindström, Alatalo, & Rintamäki, 1998), and correlations between territory location and mating success (e.g. Rintamäki, Höglund, Alatalo, & Lundberg, 2001). Territorial characteristics have also been linked to male phenotype. For example, in many species, males with centrally located territories are often older and heavier (e.g. Balmford, Albon, & Blakeman, 1992; Höglund & Lundberg, 1987; Tsuji & Sokolowski, 1992), and have higher testosterone levels (e.g. Alatalo, Höglund, Lundberg, Rintamäki, & Silverin, 1996). Lekking vertebrates possess territories that are often permanent, with males defending the same territories every day, even across years (Höglund & Alatalo, 1995). Males will even defend their territories year-round in species where competition for display space is high (Wiley, 1991). As such, outside of the few species where lekking males cooperate to attract mates (Krakauer, 2005; Loiselle, Blake, Durães, Ryder, & Tori, 2007; McDonald & Potts, 1994; Petrie, Krupa, & Burke, 1999), territory sharing has not been described.

The lesser short-tailed bat, *Mystacina tuberculata*, is a threatened species endemic to old-growth forests throughout New Zealand, and is one of only two lek-breeding bat species in the world described to date (Bradbury, 1977; Toth et al., 2015; Toth & Parsons, 2013). Moreover, some males appear to share their display sites (Toth et al., 2015). Male *M. tuberculata* occupy and defend small hollows in trees during the breeding season and sing almost continuously to attract passing females. These 'singing roosts' are aggregated around the large trees used by the population as day roosts, likely to maximize female encounter rates (Toth et al., 2015), and male songs are composed of several rapidly repeated monosyllabic elements that are largely audible to humans, but extend into the ultrasonic range (Toth, 2016). While singing roosts within the lek were previously believed to be used only by single males (i.e. 'solitary'), passive-integrated transponder (PIT) records recently revealed that some roosts were occupied by several males sequentially throughout the night (dubbed 'timeshares'; Toth et al., 2015). Furthermore, it is the same males returning to these roosts each night (although not overlapping temporally), and these males are mutually tolerated by each other (unlike sneakers, which are physically ejected from singing roosts by resident males; Toth et al., 2015). However, the mechanisms behind these arrangements are unknown.

The breeding behaviour of bats is chronically understudied due to their nocturnal habits, their ability to fly and use of inaccessible roosting sites (Behr & von Helversen, 2004). Thus, there is relatively little information on how sexual selection drives sexual traits and strategies in the taxon. *M. tuberculata* is an ideal species for studying sexual selection in Chiroptera because it uses a lek mating system, can be captured in large numbers for marking and males display from consistent locations that can be monitored remotely (Toth et al., 2015). In this study, we provide a description of the courtship behaviours of *M. tuberculata*, including an examination of shared singing roosts by largely unrelated lekking *M. tuberculata*. We quantify the characteristics and display behaviour of both solitary and timeshare males, including body size, display output and lek attendance patterns. Furthermore, we use microsatellite

analyses to infer male attractiveness and reproductive success, as well as relatedness estimates to investigate kinship between timeshare males.

METHODS

We studied a population of *M. tuberculata* in the Pureora Forest Park, New Zealand (38°26'S, 175°39'E) from November to April 2013–2014. As part of a larger study (Toth et al., 2015), 712 individuals in this population had been captured previously (either using mist nets or harp traps) and marked with PIT-tags for individual identification. After marking, individuals had their forearms measured with callipers as a proxy for body size. We used infrared video cameras in conjunction with automatic PIT-tag readers to monitor 12 singing roosts ($N = 6$ solitary, $N = 6$ timeshare) with 18 PIT-tagged resident males ($N = 6$ solitary, $N = 12$ timeshare; range 2–3 males/timeshare roost) for three nights each, to identify behavioural differences between the two roost types. Singing roosts were filmed as described previously (Toth et al., 2015). We used Miraclean MIV5870TA cameras with 950 nm infrared light-emitting diodes for illumination, with the video data recorded on Lawmate Eco digital video recorders (DVR) on to 32 GB Secure Digital memory cards. The cameras and DVRs were powered by 12-volt, 12-amp hour sealed lead acid batteries, and the DVRs and batteries were housed in Seahorse SE-520 waterproof cases. Lek attendance was calculated as the proportion of the night that a male spent within his singing roost, averaged across filming nights. Although roosts were filmed for three nights each, average lek attendance was only calculated for two nights for nine of the roosts, as cameras sometimes failed in the early mornings, and thus did not provide a full record of nightly activity. Finally, to compare potential differences in roost quality, we calculated the distance of each roost to the closest known communal roost (see Toth et al., 2015). Proximity to communal roosts may represent a desired quality for males, as the closer a singing roost is to a communal roost, the more likely commuting females will hear their songs. The capture and marking of individuals was approved by both the University of Auckland Animal Ethics Committee (permit AEC number 000920) and the New Zealand Department of Conservation (High Impact Research and Collection Permit WK-32184-RES).

We recorded the courtship vocalizations of 16 PIT-tagged males ($N = 6$ solitary, $N = 10$ timeshare) between 19 February and 5 April 2014 using a D980 bat detector (Pettersson Elektronik AB, Uppsala, Sweden) linked to a Sound Devices 722 digital recorder (Sound Devices, Reedsburg, WI, U.S.A.). Vocalizations were recorded at a sampling rate of 192 kHz with 24-bit precision. Recordings were made within 10 m of the roost tree and generally took place just after the male arrived at dusk (although in the case of timeshare roosts other resident males were recorded as they arrived). Males were recorded for 10 min of what was deemed to be continuous singing (i.e. vocalizing without significant pauses). The identities of recorded males were determined using a Biomark HPR Plus automatic PIT-tag reader (Biomark, Boise, ID, U.S.A.) mounted on the entrances of the singing roosts. For a complete breakdown of sampled bats, the information obtained from them and their roosts, see [Supplementary Material](#).

We used RavenPro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) to quantify male song output. Spectrograms were generated using a 1024-sample discrete Fourier transformation and a Hanning window with 95% overlap (frequency resolution 188 Hz, time resolution 2.67 ms). Because of the high vocal output by *M. tuberculata*, measurements were only made every other minute in each 10 min recording (i.e. first minute, third minute, fifth minute, etc.). In total, 25 701 syllables (i.e. discrete vocalizations uttered by males within singing bouts) were sampled. Song output was quantified as

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