Behavioral Ecology
The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2015), 26(1), 65–74. doi:10.1093/beheco/aru137

Original Article

Telemetric and video assessment of female response to male vocal performance in a lek-mating manakin

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Received 8 April 2014; revised 7 July 2014; accepted 7 July 2014; Advance Access publication 9 September 2014.

Sexual signals play an important role in mate attraction. In this study, we explore male vocal behavior and female mate attraction in long-tailed manakins, tropical lekking birds where males perform cooperative displays to attract females, and males provide only gametes to choosy females. We monitored female visitation at 37 sites using two techniques: video recordings and automated radiotelemetry. Simultaneously, we used digital recorders to sample male vocal behavior, quantifying vocal output as well as frequency matching and temporal synchrony in male–male duets. We compared male vocal performance to the rate at which females visited male display sites. Video data revealed that both male vocal output and the temporal synchrony of male–male duets were positively related to female visitation, matching our expectations. Telemetry data, in contrast, revealed no such relationship. Our results suggest that telemetry data may yield biased estimates of patterns of female choice, because the tracked females may not adequately represent the pool of potential female visitors to leks. We also demonstrate that male vocal behavior and female visitation vary, in concert, with time of day, peaking in the early morning, with a pronounced drop in the mid-day heat. We compare these results with those of another study, of the same species, in a montane environment with cooler daytime temperatures.

Key words: ***Chiroxiphia linearis*, duet, female mating behavior, frequency matching, lek, long-tailed manakin, mate attraction, male vocal behavior, temporal synchrony.**

INTRODUCTION

Animal acoustic signals play a vital role in mate attraction (Bradbury and Vehrencamp 2011). Female red deer (*Cervus elaphus*), for example, prefer males with deeper roars (Charlton et al. 2007); female Túngara frogs (*Engystomops pustulosus*) prefer males with more complex calls (Rand and Ryan 1981); and female greater sac-winged bats (*Saccopteryx bilineata*) prefer males with complex vocal repertoires (Davidson and Wilkinson 2004). Birds produce the most complex and well-studied acoustic signals in the animal kingdom, and males often use elaborate acoustic signals to attract choosy females (reviewed in Catchpole and Slater 2008).

Lekking species can serve as an ideal study system for studying female mate choice because males provide only gametes (Balmford 1991; Höglund and Alatalo 1995), males may mate with multiple females, and females may choose freely between males (Höglund and Alatalo 1995). By studying the relationship between male acoustic traits and female preferences for those traits in lekking animals, we can focus on how male traits may influence female mate choice in the absence of the potentially confounding variables imposed by social mates and extrapair mates (Balmford 1991). This approach has proven fruitful in prior investigations of neotropical manakins (e.g., Durães et al. 2009; Barske et al. 2011), a group of lekking birds where males produce complex and coordinated vocal signals and other mate attraction signals.

Long-tailed manakins (*Chiroxiphia linearis*) are neotropical lekking birds with an unusual mating system (Foster 1977). Pairs of unrelated males form long-term partnerships for the purposes of attracting mates (McDonald and Potts 1994). Together, males produce highly coordinated vocal duets to attract females to their display area (McDonald 1989; Lukianchuk and Doucet 2014). If they attract a female, males perform a complex dance on a low horizontal display perch while producing short-range vocalizations (McDonald 1989; Lukianchuk and Doucet 2014). If the female is receptive, the older, dominant male will mate with her, and she will then lay one or two eggs and rear the young on her own (Foster 1977). The subordinate male gains no immediate direct benefits from his relationship with the dominant male, but receives delayed fitness benefits if he inherits the display area from the dominant

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partner (McDonald 1989; McDonald and Potts 1994). Long-tailed manakins have a large repertoire of at least 13 unique vocalizations (see the full description in Trainer and McDonald 1993). Their male–male duets—onomatopoetically named *toledos*—are the most common vocalization, and are understood to play an important role in attracting females to male display areas (Trainer and McDonald 1995; Maynard et al. 2012). *Toledo* duets are frequency-modulated calls produced by a pair of males in near-perfect synchrony, such that they sound like a vocalization from a single individual (Figure 1a; Trainer and McDonald 1995).

Previous research on long-tailed manakins in the premontane tropical moist forests of Monteverde, Costa Rica, revealed that male *toledo* rate correlates positively with female visitation (McDonald 1989). Females in this study population were influenced not only by the total output of vocalizations but also the quality of those vocalizations; the level of frequency matching between the two contributions of a *toledo* duet was also positively correlated with female visitation (Trainer and McDonald 1995). Trainer and McDonald and their colleagues (Trainer and McDonald 1995; Trainer et al. 2002) theorized that duets with a high degree of frequency matching could indicate to a female that the males involved had achieved frequency matching over the course of a long partnership, potentially indicating longevity. Support for this idea came from the observation that males who had been partners for longer periods of time had duets that were more closely matched in terms of frequency (Trainer et al. 2002).

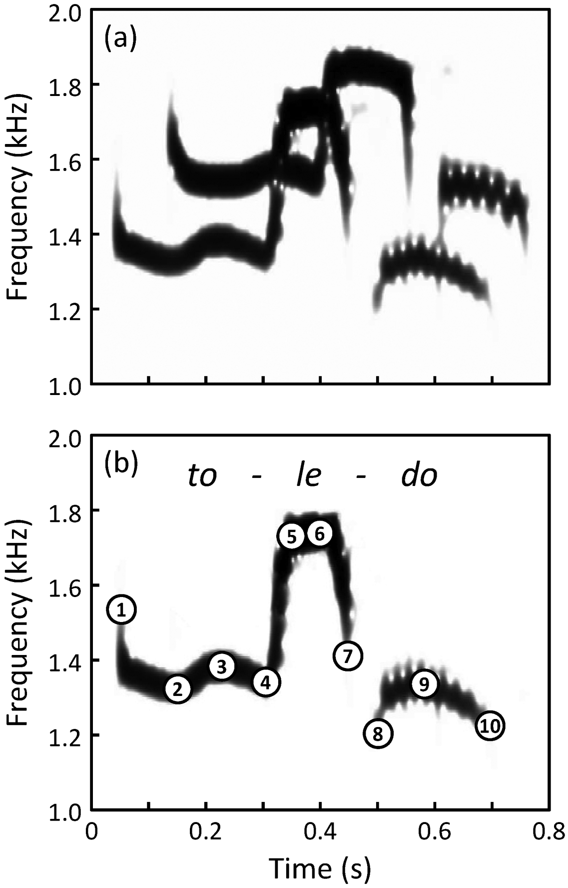

Figure 1

(a) Sound spectrogram of a coordinated *toledo* duet produced by two male long-tailed manakins recorded with an automated digital recorder in Costa Rica. (b) A modified sound spectrogram where we removed the vocalization of one of the two males for display purposes. For this male's vocalization, we show the 10 points we measured to calculate time and frequency coordination: (1) the start of the male's *toledo* call, (2) the nadir of the first dip following the start of the call, (3) the apex of the first rise, (4) the nadir of the second dip, (5) the point at the apex of the first major rise, (6) halfway between the point at the apex of the rise and the end of the first element of the *toledo*, (7) the end of the first element of the *toledo*, (8) the beginning of the second element of the *toledo*, (9) halfway between the beginning and end of the second element, and (10) the end of the second element. Phonetically, within the *toledo* call, these measures correspond to: *to* (1–4), *le* (5–7), and *do* (8–10). All 10 measurements were collected for each of the two males' calls in each duet.

Another unusual feature of the long-tailed manakin mating system, documented in prior studies, is that male duet output remains relatively constant over the course of the day (Trainer and McDonald 1993; McDonald 2010). This pattern differs markedly from that of several other species of manakin that show pronounced morning and afternoon peaks in output (e.g. Snow 1962; Bradbury et al. 1986), and many other birds that are known to show significant diel variation in vocal output (e.g., Slagsvold 1977; Staicer et al. 1996). Female visitation to display areas also remains relatively constant throughout the day, with visits by females roughly corresponding to male vocal output (McDonald 2010). The fact that male vocal output and female lek visitation seem to show parallel patterns of diel variation provides further support for the idea that these behaviors are linked. Previous research on long-tailed manakins was conducted in premontane moist forests, where the temperature is not as hot as in other parts of the species' range, such as the lowland Neotropical dry forests at our study site. Studying circadian variation in male vocal behavior and female mate searching behavior in the more extreme environment of the Neotropical dry forest offers the opportunity to better understand the range of diel variation in mating activities in tropical ecosystems.

In the current study, we investigate the relationship between male vocal behavior and female visitation behavior in long-tailed manakins. We used three field technologies that allowed us to comprehensively sample male vocal behavior and female lek visitation behavior over thousands of hours: automated digital recorders used to sample male vocal behavior, and digital video cameras and an automated radiotelemetry system used to track female lek visitation. Our study focuses on three main objectives. First, we explore whether the output of male *toledo* duets correlates with female visitation to male display areas. Second, we evaluate whether the temporal coordination and frequency matching in the males' contribution to the *toledo* duet corresponds with female visitation. Third, we describe the patterns of diel variation in male vocal behavior and female visitation. For all three of these objectives, we compare the results from our study population in Costa Rica's lowland Neotropical dry forests to previously published results from a long-term study population of this species in Costa Rica's premontane moist forests to evaluate whether climatic patterns might shape any differences between these populations. Our approach also allows us to directly compare the use of video recordings versus an automated telemetry system for tracking female lek visitation behavior.

METHODS

General field methods

We conducted this study in 2011 in Sector Santa Rosa of the Guanacaste Conservation Area in Guanacaste Province, Costa Rica (10°53′N, 85°46′W). The Guanacaste Conservation Area is the world's largest remaining stand of Neotropical dry forest and is home to a color-banded population of long-tailed manakins that has been studied since 2003 by S.M.D. and her research team (Doucet et al. 2007). To address the question of how male vocal behavior influences female visitation, we studied $n = 37$ male leks. Each lek consists of a display area with an associated alpha male, a beta male, and several subordinate males. Every lek contained a primary display perch, and many also contained one or more secondary display perches. At each lek, we quantified male vocal output using autonomous digital recorders (Mennill et al. 2012a), and we quantified female visitation behavior using two techniques: digital video recordings and data from a custom-made automated radiotelemetry system (Mennill et al. 2012b).

Male vocal behavior

We deployed autonomous digital recorders within male leks, approximately 3–10 m from the primary display perch in each lek. We used Wildlife Acoustics Song Meter SM-2 digital recorders with built-in omnidirectional microphones (details in Mennill et al. 2012a). Recordings were collected with 22 050 kHz sampling frequency, 16-bit accuracy in WAVE format. We deployed recorders in the early morning (0500–0700h) and allowed them to continue to record for 1–3 days.

In the laboratory, we visualized spectrograms of the recordings using Syrinx-PC sound analysis software (J. Burt, Seattle, WA) and used the time and frequency cursors to annotate all *toledo* duets. Between 4 April 2011 and 9 May 2011, we annotated 2378 daylight hours of recordings at 37 different leks (64.3 ± 4.4 h of daylight recordings per lek; average ± SE). To control for variation in the number of hours recorded at each lek, we converted the vocal output into rates (number of vocalizations per hour for each lek). In total, we annotated 168 262 *toledo* duets (4,548 ± 741 per lek; average ± SE).

For our analyses of diel variation, we calculated the output of four additional vocalizations in addition to *toledo* duets: *teeamoo* calls (solo calls produced by an alpha male, believed to attract his beta male partner), *owng* calls (solo calls produced by a male, believed to indicate the presence of a prospecting female), bouts of dance song (duet vocalizations produced while males perform visual displays), and *buzz-weent* calls (a call produced by males late in courtship, before performing silent visual displays; Trainer and McDonald 1995). For analysis of diel variation in these vocalizations, we focused on a sample of recordings collected between April 3 and May 9 (24.4 ± 0.6 h of daylight recordings per lek; average ± SE), including two additional leks ($n = 39$) which we had excluded from our analyses of female visitation as the leks were located far from the core population. In total, we annotated 14 486 additional vocalizations (371.4 ± 42.5 additional vocalizations per lek per day; average ± SE).

Duet quality

In addition to *toledo* duet output, previous research has suggested that the degree of frequency matching between the two males' contributions to the *toledo* duet may be important in female mate attraction (Trainer and McDonald 1995; Trainer et al. 2002). Meanwhile, research on the duets of other species also suggests that the degree of temporal synchronization may reflect the quality of the singers (Hall 2004). To quantify the level of both frequency matching and temporal synchrony, we followed a modified version of the methods outlined by Trainer and McDonald (1995). For each of the 37 leks, we selected 10 separate bouts of duetting with a high signal-to-noise ratio (based on visual assessment of spectrograms in Syrinx-PC). A bout was defined as a series of at least 10 *toledo* duets with no silent gaps exceeding 10 s. Within each bout, we used a random number generator (Microsoft Excel, 2007) to randomly select one duet. We restricted our sampling to duets that did not start or end a bout (i.e., the first and last duets were never selected; our observations suggest that the first and last duet in a bout were sometimes broadcast as solos, indicating that one of the two males may be unmotivated to contribute to the first or last duet within a bout). In some cases, we did not have high-quality recordings of 10 separate bouts; in these cases, we selected another random duet from within one of the previously measured bouts. We restricted our analyses of duet synchronization to the early portion of our field study (i.e., April 2 to May 17) so that we compared males at a similar stage in the breeding season.

We used AviSoft SASLab Pro to view spectrograms of the 10 high-quality *toledos* for each pair of males (fast Fourier transformation length: 512, frame size: 100%, overlap: 93.75%). We adjusted the cutoff frequencies with a high pass of 1.00 kHz and a low pass of 2.00 kHz. We used AviSoft's "magic reticule cursor" to trace the frequency of maximum amplitude of each male's duet contribution, setting the cursor's threshold to −50 dB with a snap distance of 82 Hz. We took 10 measurements at specific stereotyped points for each of the two males' duet contributions, to collect 20 measurements per duet (details in Figure 1b). We calculated the absolute difference between the two males for each of these 10 time and frequency values. We then calculated the average absolute difference between the 10 frequency and time values across each duet and used these two time and frequency difference values as our measures of frequency matching and temporal synchrony. Larger differences between the two contributions to a duet produce a larger score; therefore, these two measures can be thought of as being measures of frequency mismatch and temporal asynchrony, where higher scores indicate that the two males' duet components are dissimilar. This analysis is an extension of a comparable technique used by Trainer and McDonald (1995); that study, which pre-dates automated parameter measurements of digital sound spectrograms, relied on four comparison points between the vocalizations of the two duetting males, rather than 10. In addition to our 10-point measurement approach, we also used Trainer and McDonald's (1995) four-point approach, so that we could compare the two approaches directly. We found that the same pattern reported in the Results held true regardless of what approach was used (correlation between 4-point scores and 10-point scores; frequency match: $r^2 = 0.80$, $P < 0.0001$; temporal synchrony: $r^2 = 0.40$ $P < 0.0001$); we therefore chose to report the 10-point approach because it provided a more comprehensive measurement of synchrony and frequency matching for each duet.

Female visitation

We located the low horizontal branches where males regularly display for females (herein referred to as "display perches") by listening for the *nyanyownh* vocalization that males produce when displaying (Trainer and McDonald 1993). We confirmed that the perch was being used by adult males to display for females through visual observation.

Our first technique for quantifying female visitation was video monitoring of male display perches. We used digital video cameras (Sony Handycam HDR-XR101 and DCR-SR20) to record from 0600 to 1100 h. Video cameras were set back from the male display perches so they could record the entire area where females might land; the resulting resolution did not allow us to distinguish between banded and unbanded females in the videos. Visits were considered to be from unique females when multiple females could be seen concurrently within the frame, or when more than 60 s elapsed between the time that a female was within frame. We collected 425 h of video data at 37 long-tailed manakin leks (11.5 ± 0.7 h per lek) between April and mid-June 2011.

Our second technique for quantifying female visitation was direct tracking of females using a custom-built automated telemetry system called "Encounternet" (Mennill et al. 2012b). We captured females using mist nets in the area immediately adjacent to the leks and banded them with an aluminum leg band and a unique combination of colored leg bands. We outfitted 50 females with a digital radiotag (tags were attached with a figure-eight leg harness, as described in Mennill et al. 2012b) that pulsed with an individually distinctive signature every 4 s. We attached radio receiver stations to branches above male display perches at each of the 37 leks, to monitor females as they came within range. We evaluated all female encounters where the female remained in range of the receiver station for at least 12 s (equivalent to three consecutive pulses from the female's radiotag; see Mennill et al. 2012b for details of a ground-truthing experiment). This allowed us to eliminate cases where females may have flown near the receiver station, but not remained in the area to assess males. We excluded all detections where the female was detected near the perch at the end of the day and at the beginning of the subsequent day; we interpreted these instances as cases where females slept near male leks (Mennill et al. 2012b). We ran the automated telemetry system between 13 April 2011 and 16 May 2011, and collected over 16 000 h of monitoring at the 37 lek sites (i.e., near-continuous monitoring at each site except for short battery changes).

Temperature

We used the temperature recorders in the Song Meters (a surface mount thermistor accurate to within 2 degrees C; Wildlife Acoustics, personal communication) to log the temperature over the course of the day. Two Song Meters logged the temperature every 5 min throughout the recording period (13 April to 16 May), and we calculated the average hourly temperature between 0530 and 1830 h.

Statistical analyses

The automated telemetry system generated six measurements of female visitation to male display perches: number of female visits on the perch and near the perch (defined as 5–30 m from the perch; see Mennill et al. 2012b for details), average length of female visit on the perch and near the perch (in minutes), and number of unique females detected on the perch and near the perch. All six variables were correlated (average ± SE correlation: 0.57 ± 0.06), so we summarized these six measurements with principal components analysis. This analysis generated a single principal component with an eigenvalue greater than one (eigenvalue = 4.0). This principal component explained 67.0% of the variation in the original variables, with positive loading from all six variables (average ± SE eigenvector: 0.40 ± 0.05) and strong correlation with all six variables (average ± SE correlation: 0.65 ± 0.04). Therefore, high values of this principal components score indicate leks with many females visiting the perch and the area near the perch, long visits by females to the perch and near the perch, and more unique females on and near the perch.

We also tested to see whether our measure of female visitation as measured through our telemetry system was correlated with our measure of female visitation as measured with our video monitoring system. We ran these analyses for both our entire dataset and a subset of the 10 most-visited leks.

We ran analyses with three independent variables: male *toledo* output, frequency matching in males' *toledo* duets, and temporal synchrony in males' *toledo* duets. We ran each analysis twice, first using female visitation from the video data (number of female visits per hour) as the dependent variable, and then using female visitation from the automated telemetry data (the telemetry principal component score) as the dependent variable.

Female visitation data were non-normal and could not be transformed to achieve normality; we used nonparametric statistics to analyze these data. Given that we tested for a relationship between each aspect of male vocal behavior and female visitation twice, once with our video data and once with telemetry data, we corrected for multiple comparisons by lowering our significance threshold to $\alpha = 0.025$. All tests are two-tailed, and all values are presented as means ± SE.

To examine patterns of diel variation in male vocal behavior, we analyzed vocal output at 37 leks based on 194 separate recording events; first, we calculated an average output for each hour for each lek, and then we calculated an average across all leks so that each site contributed equally to the overall average. To facilitate comparisons with previous research by McDonald (2010) in a Monteverde premontane population, we calculated hourly output between the hours of 0530 and 1830 h. To assess the pattern of diel variation in female visitation, we used telemetry data on female visits to male display perches (video data were collected only in the morning, and therefore, could not be used to calculate diel variation). We report variation in both female visits on the perch (indicative of females assessing male displays at close range) and female visits near the perch (indicative of females sitting 5–30 m from the male display perch; see Mennill et al. 2012b). We converted these data to proportions, where we divided the total number of visits made to a single perch in each hour by the total number of visits made over the course of the study. This facilitated comparisons to previously published results by McDonald (2010).

RESULTS

Male vocal behavior and mate attraction

We compared 2378 h of acoustic recordings of male long-tailed manakins at 37 unique leks (64.3 ± 4.4 h per display area) to 425 h of video data on female visitation (11.5 ± 0.7 h per lek). On the basis of video data, male *toledo* output showed a strong positive correlation with female visitation (Figure 2a; Spearman's rank correlation: $\rho = 0.42$, $P = 0.009$, $n = 37$ leks). Frequency matching in male–male duets did not show a relationship with female visitation (Figure 2b; $\rho = 0.06$, $P = 0.73$). However, temporal synchrony in male–male duets showed a positive correlation with female visitation (Figure 2c; $\rho = -0.38$, $P = 0.02$).

We also compared the acoustic recordings of males to more than 16,000 h of automated telemetry monitoring of female visitation. In contrast to the video data, the telemetry data showed no association between male long-tailed manakin *toledo* output and female visitation behavior (Figure 3a; Spearman's Rank correlation: $\rho = -0.03$, $P = 0.84$, $n = 37$ leks). Frequency matching showed a trend in the same direction as assessed by telemetry, but was not

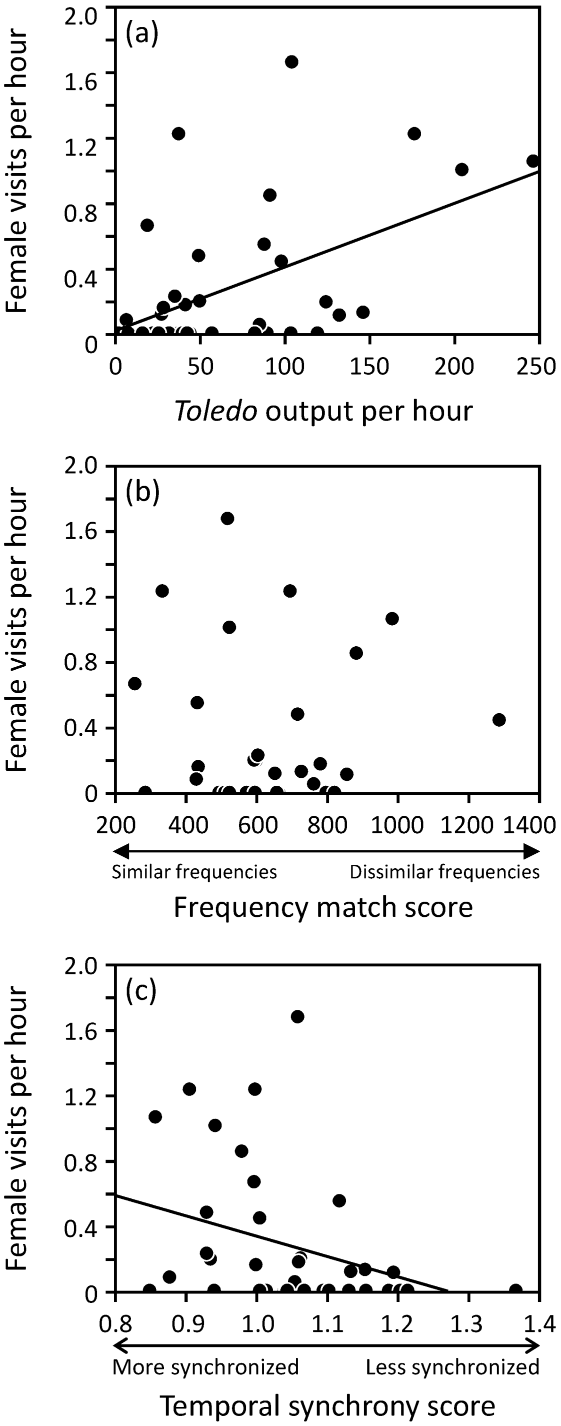

Figure 2

The vocal behavior of male long-tailed manakins was correlated with female visitation to male lek sites, as assessed by video recordings at male display perches. (a) Female visitations to male display perches increased significantly with male *toledo* duet output. (b) Female visitation showed no significant relationship with the frequency matching between the two males' contributions to their *toledo* duet. (c) Female visitation showed a significant relationship with the temporal synchrony in the males' contributions to their *toledo* duet, where males producing more synchronized duets received more female visits. Bivariate plots of male vocal behavior versus female visitation are shown with lines of best fit; the statistics discussed in the body of the article are nonparametric correlations.

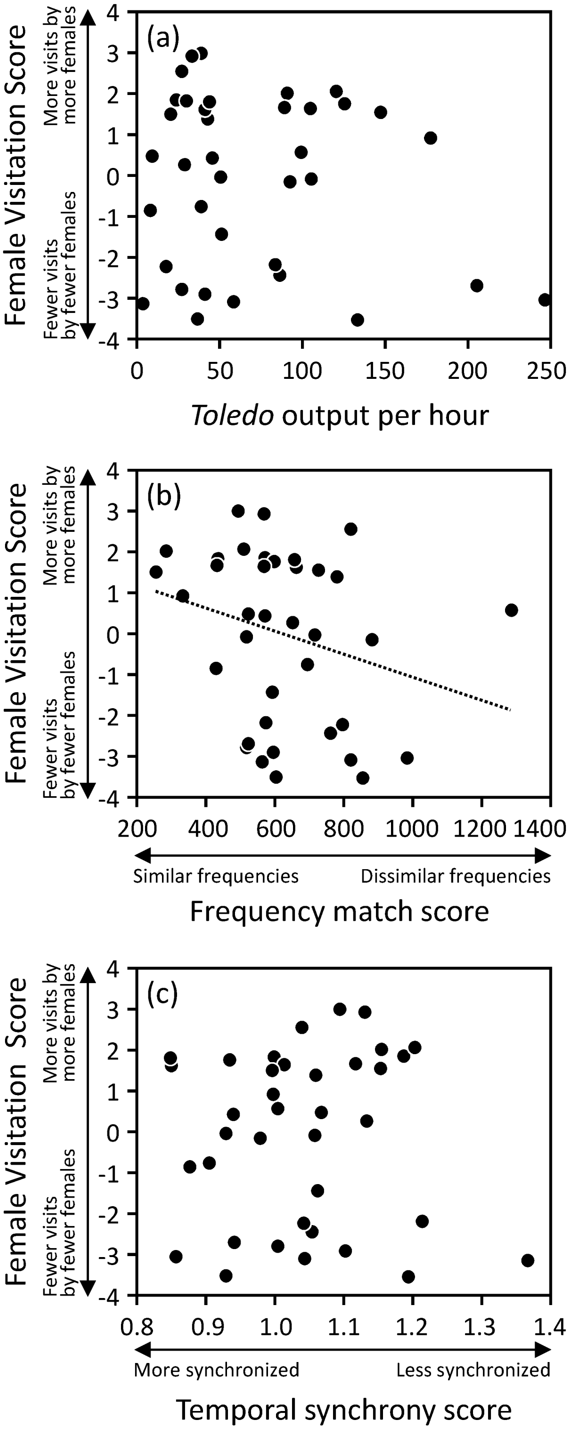

Figure 3

The vocal behavior of male long-tailed manakins showed no relationship with female visitation to lek sites when assessed by an automated telemetry system. (a) Female visitations to male display perches showed no relationship with male *toledo* duet output. (b) Female visitation showed a nonsignificant trend with the frequency matching between the two males' contributions to their *toledo* duet, where males with duets that were more matched in terms of frequency received more female visits. (c) Female visitation showed no relationship with the temporal synchrony in the males' contributions to their *toledo* duet. Bivariate plots of male vocal behavior versus female visitation are shown with lines of best fit; the statistics discussed in the body of the article are nonparametric correlations.

significant after correction for multiple comparisons (Figure 3c; ρ = −0.37, P = 0.05). Temporal synchrony in male duets showed no relationship with female visitation as assessed by telemetry (Figure 3b; ρ = 0.10, P = 0.57).

Correlation between measures of female visitation

Our measure of female visitation as measured through automated radiotelemetry was not correlated with our measure of female visitation as measured through video monitoring; this was true whether we compared across all leks (ρ = −0.22, P = 0.20, n = 37 leks), or whether we restricted our analyses to only the 10 most-visited leks (ρ = −0.45, P = 0.19, n = 10 leks).

Diel variation in male vocal behavior and female visitation

Analysis of diel variation in vocal output revealed pronounced differences with time of day. *Toledo* duets showed a peak in the morning (0630–0830 h) and then declined to lower levels around mid-day, before increasing to a second peak in the mid-afternoon (1430–1530 h; Figure 4a). Female visitation to male display perches also showed substantial diel variation, with the highest levels in the morning (0630–0930 h) decreasing to lower levels after 0930 h and slowly declining as the day progressed (Figure 4b). Female visitation to the area near the display perch (>5.0 m) showed a similar pattern that was slightly less demarcated (Figure 4c).

The temperature profile in our Neotropical dry forest study site increased from a low of 22°C in the early morning to highs of approximately 33°C between 1130 and 1330 h, and then slowly decreased to lower temperatures at sunset (Figure 4d). The temperature peak near mid-day coincided with declines in both male vocal behavior and female visitation behavior (Figure 4).

We also quantified diel variation in other aspects of male vocal display that are associated with mating. The *teeamoo* call showed a unique pattern in comparison to all of the other vocalizations we studied, increasing in frequency throughout the day to a peak at 1430–1530 h (Figure 4e). This vocalization is produced by the alpha male at each lek and is understood to stimulate the beta male to begin performing mate attraction duets (Trainer and McDonald 1995). The *owng* call—a vocalization produced by males near the display perch when a female is detected in the immediate vicinity—showed a similar pattern to the output of *toledos* with a peak in the morning, followed by a steep decline during mid-day, with a second smaller peak during the mid-afternoon (Figure 4f). Bouts of dance song—vocalizations produced while males perform visual displays before females—also showed a similar pattern, although in this case, the calling peak in the afternoon was small in comparison to the morning peak (Figure 4g). The *buzz-weent* call—which is usually given by alpha males to initiate a solo display by the alpha, which can sometimes lead to copulation—showed its highest level in the early morning (0630–0730 h) and then declined to lower levels throughout the remainder of the day (Figure 4h).

DISCUSSION

In lekking long-tailed manakins, digital recordings of male vocalizations and video recordings of female visitation reveal significant associations between male duet output and female lek visitation as well as between temporal synchrony in male duets and female lek visitation. Surprisingly, our parallel comparisons of male vocalizations and automated telemetry data on female visitation did not show the same pattern; the automated telemetry analyses revealed no relationship between male vocal behavior and female visitation. We also quantified diel variation in male vocal behavior and female visitation and found that both showed high activity levels in the morning and low levels in the intense mid-day heat at our Neotropical dry forest study site, with a second smaller peak in many behaviors later in the afternoon. We explore each of these results below and contrast our findings to previous studies of long-tailed manakins living in a different habitat.

A positive association between male vocal output and female mate attraction is well known in previous studies of many different taxa, including frogs (Ryan 1988), deer (McComb 1991), crickets (Hedrick 1986), and sage grouse (Patricelli and Krakauer 2010). Using video recordings at 37 long-tailed manakin lek sites to quantify female visitation, our data match this widespread pattern. Male long-tailed manakins with high duet output had higher levels of female visitation to their lek sites. Male vocal output may serve as an honest indicator of male quality, where the highest quality males are capable of sustained, physically demanding, vocal performances, and these may attract females (Ballentine 2009). In our study population, males produce *toledo* duets at high rates—one pair produced 883 duets in a single hour, whereas the highest daily *toledo* output was 3857 duets—and females may be attracted to males with high vocal output as a component of assessing male quality.

Previous investigations have revealed associations between male display behavior and female visitation behavior in other species of manakins. Female golden-collared manakins (*Manacus vitellinus*) choose males that display more intensely (Barske et al. 2011), and female blue-crowned manakins (*Lepidothrix coronata*) selectively mate with high-displaying males within leks (Durães et al. 2009). These examples lend support to the conclusion of a meta-analysis which showed that display frequency was positively correlated with mating success across at least 20 lekking species (Fiske et al. 1998). In other species of manakin, however, studies have revealed no obvious female preference for more intense or numerous displays. For example, male display rate and male mating success are not related in white-bearded manakins (*Manacus manacus*; Shorey 2002), and male display-flights and male mating success are not related in round-tailed manakins (*Ceratopipra chloromeros*; Tello 2001). One key difference with our study is that the *toledo* duets of long-tailed manakins serve strictly as advertisement calls and are therefore largely independent of the presence of females; males switch from *toledo* duets to other display behaviors once females are present at the lek. In many of the aforementioned studies, males perform the displays in the presence of females, and the presence of females may incite males to increase display rates. Further work across the family Pipridae, and other lekking animals, will help to clarify the extent to which male display activity and mate attraction are related.

We found that male long-tailed manakins whose duets show high temporal synchronization (i.e., more precise overlap) are visited by more females. Prior investigations have linked specific acoustic properties of male sexual signals and female mate attraction, including male repertoire size (Searcy 1984, Davidson and Wilkinson 2004), vocal pitch (Charlton et al. 2007), and call complexity (Rand and Ryan 1981). Male–male duets present an additional mechanism whereby vocalizations may indicate male quality, because they rely on coordination between two individuals. Temporal synchronization may be an indicator of male–male partnership length in our study population, just as frequency-synchronization seems to serve

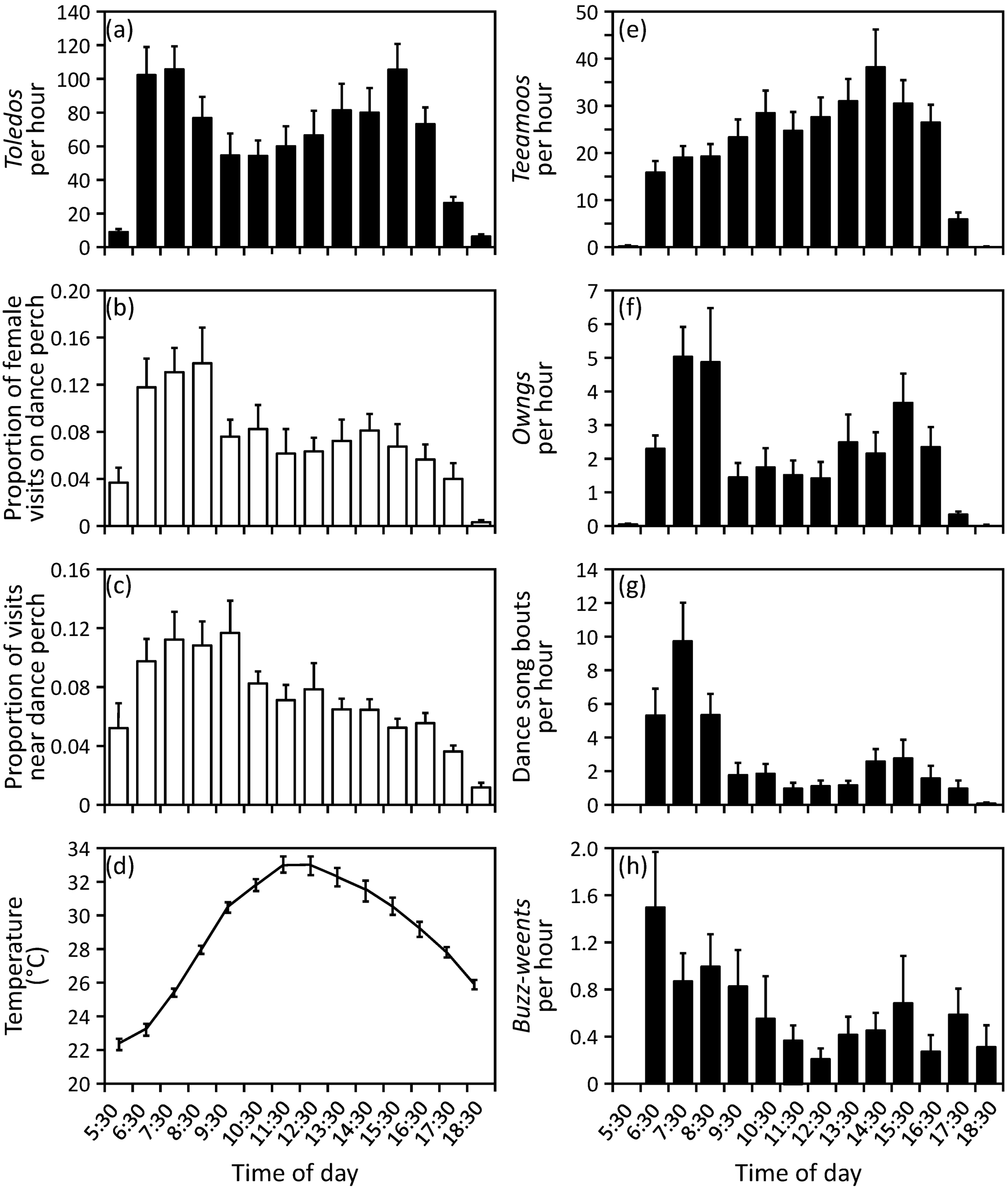

Figure 4

Diel variation in the vocal behavior of male long-tailed manakins (black bars) and the visitation behavior of female long-tailed manakins (white bars) as well as ambient temperature. Patterns of diel variation for five male vocalizations are shown: (a) male *toledo* duets understood to function in mate attraction; (e) male *teeamoo* calls, produced by the alpha male to attract his beta male partner; (f) male *owng* calls, understood to indicate that a female has arrived near the lek; (g) male dance song bouts, produced by pairs of males while they dance for females on their display perch; and (h) male *buzz-weent* calls, which are produced by alpha males before copulation. The pattern of female visitation is shown for both (b) female visits on male dance perches, and (c) female visits near male dance perches (5–30 m from male dance perch). (h) Temperature showed marked variation over the course of the day.

as an indicator or partnership length in a different study population of long-tailed manakins (Trainer and McDonald 1995, Trainer et al. 2002). By preferring males with improved temporal synchrony in their vocal duets, females may focus on older males with established partnerships. The good genes models of sexual selection suggests that male longevity should be an important target of selection (Kokko 1998), and this may be especially important in long-lived species, where age may be a critical predictor of lifetime reproductive success. Accordingly, longevity and lekking effort have been shown to relate to lifetime success in lekking Black Grouse (*Tetrao tetrix*; Kokko et al. 1999). In long-tailed manakins, males undergo a 4-year delay in plumage maturation before attaining definitive adult plumage in their fifth year (Doucet et al. 2007). Furthermore, males do not typically achieve beta status until at least 8 years of age, and alpha status until 10–12 years (McDonald 1989). Because only alpha males copulate with females (McDonald and Potts 1994), most males must survive until 10 years of age before even having an opportunity to copulate with a female, a remarkable example of longevity for a small passerine bird (Linstedt and Calder 1981). Long-term studies may be able to address whether vocal output and duet synchronization relate to partnership length, longevity, and lifetime reproductive success in long-tailed manakins.

In contrast to the video data on female visitation, our automated telemetry data revealed no association between male vocal behavior and female visitation. The two measurements that showed strong relationships in the video dataset (male vocal output, and time synchrony in male–male duets) showed no relationship in the telemetry data, whereas our remaining measurement of male vocal quality (male frequency matching) revealed a nonsignificant tendency for males who produced more frequency-matched duets to attract more female visits. Our telemetry data did not correlate with our measure of female visitation as measured through video monitoring. This was true whether we looked across all leks, or only the 10 most-visited leks.

Why did these two parallel techniques for assessing female visitation yield contradictory findings? We examined several possibilities. First, we considered the possibility that our principal component of female visitation as measured through the radiotag data might differ too much from the measurement of female visitation obtained through video analysis; the principal component scores were composite variables of six measurements of female visitation, including female visits to areas as far as 30 m from male display perches, whereas the video data yielded a single measurement of the number of unique females to each male display perch. Therefore, we re-ran our analyses of the telemetry data using only the number of unique female visits to the display perch (see Mennill et al. 2012b for details). We also considered the possibility that females visiting in the morning when we collected video recordings (between 0600 and 1100 h) may have been exhibiting different behavior than females that arrived later in the day when only the telemetry devices were operating. Therefore, we also restricted the analysis of our telemetry data to the number of female visits between 0600 and 1100 h. In each of these additional analyses, we found no statistically significant association between the number of visiting females and male vocal behavior (even before correcting for multiple comparisons), suggesting that differences in methodology were not responsible for the two different patterns we report here.

Alternatively, it is conceivable that the radiotags may have altered the behavior of the females we monitored with telemetry. Our observations of the behavior of the tagged females suggest that this was not the case: we detected radiotagged females moving around the study site for more than a week after tagging (7.5 ± 0.8 days; range 1–24; after that point, we suspect that the short-life batteries on the tags died), and we detected tagged females visiting multiple male display perches (average 4.02 ± 0.42; Ward 2012; Mennill et al. 2012b), often separated by significant distances. Future analyses will focus on female search strategies in this dataset. In addition to these tracking data, we found the active nests of two of the tagged females, and in neither case did the tag seem to impinge on their nesting behavior (Mennill et al. 2012b). These separate lines of evidence indicate that radiotagged females were exhibiting normal activities, suggesting that they did not alter their mate search strategies as a result of the tags. Yet, we cannot exclude the possibility that the presence of the radiotags changed the behavior of females in some way that we did not detect.

A third alternative, and the one we think is a likely explanation for our contradictory results, is that our telemetry technique may have sampled a nonrepresentative subset of the females within our study population. We captured females for radiotagging by placing mist nets around male display perches. Over the course of the field season, we moved the mist nets around to each of the different lek sites, in an effort to sample females who were interested in males across the population. In so doing, we may have biased the subset of females that we measured with the automated telemetry system; the females captured in mist nets at unpopular or low-quality leks may have had different preferences from the females captured in mist nets at popular or high-quality leks. Alternatively, females captured at leks on the periphery of our population may not have had the rest of our leks in their mate-searching zone. By attempting to spread our capture effort across the population, we may have inadvertently oversampled females with preferences that differed from the population average. Our video recorders, in contrast, were set up near male lek sites and were capable of recording the visits of any female in the study population, and therefore, we expect that the females sampled with video recorders provide an unbiased assessment of the preferences of females.

Our analyses of diel variation in male vocal behavior and female visitation behavior revealed that activity levels varied substantially throughout the day, and that female visitation behavior closely tracked male vocalization behavior. Manakins exhibited a roughly bimodal distribution in terms of vocal output and female visitation, with a pronounced peak of activity early in the day, a substantial decrease in activity at mid-day, and a smaller secondary peak of activity in the afternoon. One vocalization that differed from this pattern however was the *teeamoo* call, which increased in frequency over the course of the day. This rise in *teeamoos* might be associated with the decline in *toledos* that corresponds with the hottest part of the day. This increase in *teeamoo* calls may represent the alpha male, who has more to gain from continued effort in difficult conditions, attempting to attract his beta partner to initiate more duets.

The pattern of diel variation in male vocal behavior and female visitation in our lowland dry forest study population in sector Santa Rosa showed a striking difference from the pattern observed in a premontane moist forest population in Monteverde, Costa Rica: manakins in Monteverde exhibited a relatively constant pattern of vocal output and female visitation throughout the day (McDonald 2010). It is well known that temperature can strongly influence metabolic demand, and it seems likely that both males and females should adjust their energetically demanding activities to avoid times of the day when thermoregulation might be more challenging (Kendeigh 1969). This could explain the different patterns of diel variation in female visitation and male vocal behavior between Santa Rosa and Monteverde. The cooler temperatures of Monteverde may be more conducive to energetically demanding displays by males, and mate searching by females, throughout the day, giving rise to the relatively constant levels of vocal output and lek visitation observed in this population (McDonald 2010). Conversely, the high afternoon temperatures seen in Santa Rosa may severely limit animal activity, both in terms of male display behavior and female mate searching behavior. Our experience at the study site suggests that many animals reduce their activities at mid-day (Mennill and Vehrencamp 2005; Baldo and Mennill 2011; Koloff and Mennill 2013); the forest becomes quiet, and we have observed the unusual behavior of birds panting with drooped wings. In a lowland evergreen forest in eastern Ecuador, six species of manakins were observed to exhibit varied patterns of diel variation (Durães et al. 2011), suggesting that daily rhythms vary both between habitats and between species.

Significance and future work

Our work helps to highlight some of the similarities and differences that can exist between nearby populations. Many studies of female preferences for male traits focus on only a single population (Dugatkin 2001). This can result in spurious conclusions when those results are applied to a species as a whole, or even to other populations. This is because different populations can experience substantially different environmental conditions and evolutionary pressures, which can interact with one another resulting in unique female preferences between populations (Møller 1995; Dugatkin 2001; Dunn et al. 2008). It is not uncommon for patterns observed in one population to differ in other populations (Dunn et al. 2008). The differences between our lowland dry forest population of long-tailed manakins and the previously studied premontane moist forest population may provide an additional example of this pattern, where females in Santa Rosa seem to use temporal synchrony as a selection criteria, and females in Monteverde focus on frequency matching. These population differences enhance our understanding of natural and sexual selection and lay the groundwork for future experiments and comparative studies.

Our study represents the first field test of the new Encounternet automated telemetry technology (also see Mennill et al. 2012b). The use of automated radio receivers allowed us to monitor birds at 37 different sites over extended time periods and monitor the movement behavior of females in a way that would not have been possible otherwise. However, the conflicting results between our telemetry data and our video data highlight the importance of considering potential insidious effects when subsampling a population in a radiotelemetry study. Future radiotelemetry studies should carefully consider the circumstances that lead to the individuals being captured, and the ways that subsampling might influence the results. If we had not simultaneously sampled the display sites with video recorders, we might have erroneously concluded that vocal behavior does not have a significant effect on female visitation within our population.

One of the most interesting directions for future research lies in closely examining the search strategies of females. Encounternet provides a unique type of data that bird researchers have not previously had access to—specific information on the movement patterns of females in a wild population. By examining these data, we can improve our understanding of what strategy females use when mate searching, what criteria they use, and how the process unfolds.

FUNDING

This research was funded by Paul A. Stewart Awards from the Wilson Ornithological Society, Frank M. Chapman Memorial Awards from the American Museum of Natural History, and Student Research Grants from the Animal Behavior Society to D.F.M. and K.A.W.; a Grant-In-Aid of Research from Sigma Xi and a Research Grant from the American Ornithologists' Union to K.A.W.; and by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation (CFI), the Government of Ontario, and the University of Windsor to S.M.D. and D.J.M.

We are deeply thankful to J. Burt for his collaborative assistance with the Encounternet automated telemetry system. We thank the staff of Sector Santa Rosa of the Guanacaste Conservation Area for logistical support, especially R. Blanco. We thank K. Lukianchuk for field assistance. We thank N. Al-Farra, M. Battiston, S. Dundas, C. Girgenti, M. Watson, and S. Wonsch for assistance analyzing recordings.

Handling editor: Bob Wong

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