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Singing performance, frequency matching and courtship success of long-tailed manakins (*Chiroxiphia linearis*)

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Abstract We examined the relationship between song performance and courtship success in the lek-mating long-tailed manakin (*Chiroxiphia linearis*) of Costa Rica. Teams of male manakins form cooperative partnerships consisting of a dominant alpha male and a beta male partner with a variable number of subordinate affiliates. Each alpha and beta partnership performs a joint song virtually in unison, which attracts females to their lek arena. We quantified four aspects of song performance, including synchrony, degree of consistency in the alpha male's singing, degree of consistency in the beta male's singing, and degree of sound frequency matching between partners. When all four variables were included in a discriminant function analysis, average frequency matching alone was useful in discriminating between teams with high rates of visitation by females and those with low visitation rates. Only frequency matching was correlated with the rate at which females visited display lek arenas. We propose that the degree of frequency matching provides an unambiguous ideal against which dual-male courtship performance can be assessed. This aspect of song performance may provide information useful to females in assessing a potential mate's ability to form a cooperative, long-term partnership.

Key words Song · Manakin · Mate choice
Cooperation · Lek

Introduction

Intersexual selection can be a strong evolutionary force in driving the elaboration of courtship display, especially in lek species. A number of studies have shown that mating success correlates with the rate, duration or persistence of courtship display, suggesting that sexual selection influences the amount of display performed by males (Payne and Payne 1977; Gibson and Bradbury 1985; Andersson 1989). It has been more difficult to show a relationship between courtship success and the particular form a behavioral display takes, such as the strutting dances of grouse or the bows and postures of birds of paradise.

Bird song display behavior is especially suitable for studying sexual selection of display form because differences in song are easily described and measured. Because of this, the acoustic properties of song performance can be quantified and compared among individuals or populations. Despite this, attempts to uncover the effects of sexual selection on song performance have suffered from three limitations. First, few studies have identified aspects of song performance, other than amount, that contribute to courtship success. For example, it is often difficult to identify an unambiguous ideal upon which song performance converges. For morphological characters, fluctuating asymmetry can provide such an ideal (Watson and Thornhill 1994). Exceptions are studies suggesting that repertoire size and features of song reflecting geographic origin have been influenced by inter- and intrasexual selection (Catchpole 1986; Searcy and Andersson 1986; Searcy 1992). Second, in some studies, song performance has been defined in terms of its attractiveness to females, and cannot provide an independent test of the relationship between acoustic properties and courtship success (King and West 1983). Finally, most studies fail to perform the strongest test of sexual selection by demonstrating its effect on the variation in song performance among males of the same population.

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Instead, they attempt to show a role of sexual selection in generating interpopulation and interspecies differences in song (Payne 1983; Eastzer et al. 1985; Baker et al. 1987).

In our study of long-tailed manakins (*Chiroxiphia linearis*) we examined the relationship between song performance and courtship success. We avoided the above limitations by measuring four acoustic properties of manakin songs independently of female song preference. Furthermore, we tested whether courtship success of males within a population varied with these four measures of song performance.

The lek mating system of the long-tailed manakins is unusual in that males display cooperatively to attract females to display perch-zones (lek arenas) solely for the purpose of mating. Perch-zones are separated by 75–300 m, and each is occupied by a different alpha male who is dominant to other males in the lek. The alpha male displays most often with the beta male. Both of these top-ranking males have definitive plumage and are usually 8 years old or older. As many as 12 other males, including predefinitive males, may be affiliated with a given lek. The partnerships between alpha and beta males develop and become stable over a period of several years (McDonald 1989a). The partners perform a unison song that attracts females and a joint dance that precedes copulation (Trainer and McDonald 1993). With very rare exceptions all copulations are by alpha males. Alpha males from different perch-zones vary greatly in their success at attracting females and at obtaining copulations (McDonald 1989a, 1993b). We used the rate at which females visited perch-zones as a measure of courtship success. The relationships among visitation rate, copulation rate and characteristics of the dance display were examined elsewhere (McDonald 1989b).

The female attraction song is given by two males who sing nearly identical components almost in unison while perched 10–15 cm apart. The joint song onomatopoeically resembles the word “toledo”, with the first and last syllable sung at a flat F and the middle syllable rising to a flat A on the diatonic musical scale. The songs of some teams sound to the human ear more coordinated and harmonious than those of other teams. Harmonious songs sound like one bird singing, but have a noticeably full sound, easily distinguished from the rare solo songs. Non-harmonious songs sound dissonant, or out of tune, and sometimes sound poorly synchronized. Examination of sonagrams shows that in songs that sound harmonious to human ears, the frequencies of the two male’s components are well matched. Two measures of song performance, the degree of frequency matching and the degree to which the two males’ song contributions were synchronized, were designed to quantify the audible differences in song quality. Quality song performance probably depends not only on the ability to sing in a coordinated fashion, but on the ability to sing in a consistent

manner. Therefore, the remaining two measures of performance included the variability in the acoustic structure of the alpha male’s song contribution, and the variability in the beta male’s contribution. We tested the relationship between these four properties of song performance and female visitation rate using correlation and step-wise discriminant function analysis.

Methods

The study area, in Monteverde, Costa Rica (10° 18' N, 84° 48' W), is 80 ha of premontane tropical moist forest (Holdridge 1966) at an elevation of 1300 m. Female visitation at seven of the most active perch-zones was observed over 2 years. Recordings of the joint toledo songs were made at five of the perch-zones in the 1st year, and at two additional zones the 2nd year. At each perch-zone, both the alpha and the beta males were color banded, as well as many of the affiliate males. The sex and age of manakins were determined as described in McDonald (1989b, 1993b).

Perch-zones were compared on the basis of visitation rates per unit time because sample sizes varied. Observers conducted scheduled 2-h observations between 0600 and 1500 hours while sitting in blinds made from black plastic placed 8–12 m from display perches. From 9 to 19 scheduled observation periods were conducted at each of the seven perch-zones. During the scheduled observations, an observer recorded the number of females present on the perch during each 5-min block. These numbers were added over all observation periods to determine the total number of female visits to the perch-zone. The relative female visitation rate at a given perch-zone in a given year was calculated as follows: number of visits per observation period at that zone/total number of visits per observation period for all focal perch-zones during that year. In addition, to show how visitation changed over time, we calculated the number of visits per observation period at perch-zone Z over a period of 5 years.

Toledo songs of seven alpha-beta partnerships were recorded with a Sony WM D6C cassette recorder and a Sennheiser ME 80 directional microphone. Ten songs from each team were analyzed using a Kay Elemetrics Model 5500 Sonagraph with a grey scale printer. Singers were identified on the basis of their color bands. Occasionally during a bout of singing, one of the two males would give a small number of solitary toledos. By analyzing the frequency characteristics of these solitary toledos, we were able to identify the individual singer of each contribution to the toledo songs.

The two males of a team sing almost identical song contributions, each approximately 0.6 s in duration. The song contributions are sung nearly in unison, with one male commencing approximately 0.1 s after the first male begins. In sonagrams, each male’s contribution begins at about 1700 Hz and sweeps down to form a trough, then sweeps rapidly up to form an arch, and finally ends with an element at about 1450 Hz. The trough in a sonagram has two nodes of highest amplitude corresponding to two dips in frequency (Fig. 1a).

Our analysis of song structure was based on samples of ten unison songs from each team of males. For each male, we characterized his contribution to a toledo song by measuring four parameters: the minimum frequency reached in the first dip of the trough, the minimum frequency reached in the second dip of the trough, the maximum frequency reached in the arch, and the time interval between the onset of the song and the rapid frequency ascent (Fig. 1b). To determine the minimum or maximum sound frequency, the Sonagraph was set to display the narrowband (15 Hz) audiospectrogram and the power spectrum of a selected 0.10-s sample. The power spectrum where the minimum or maximum frequency occurred was displayed, and the frequency with the highest amplitude was noted. Frequency was measured with a minimum

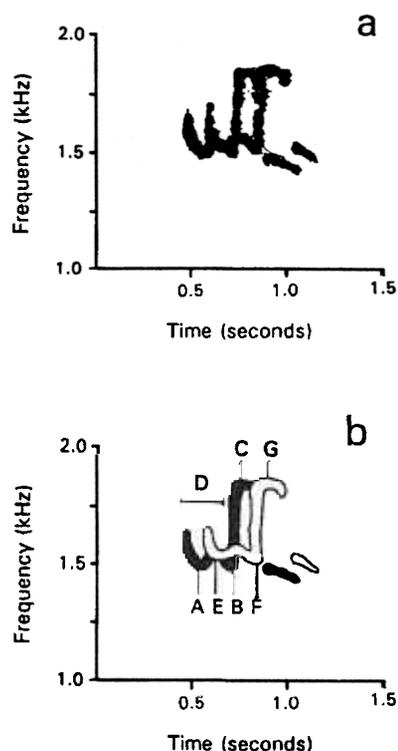


Fig. 1 a Audiospectrogram of a long-tailed manakin dual "toledo" song. b Drawing of the above spectrogram with the contribution of one male shown *solid*, and the other male shown *outlined*. Parameters *A*, *B*, *C*, and *D* were measured for each manakin male. *D* indicates the time interval between the onset and the ascending frequency sweep of a male's song contribution. *A*, *B*, and *C* indicate time points at which the sound frequencies were measured. These frequencies were compared to similar measurements at *E*, *F* and *G* of the partner's contribution to generate the index of frequency matching. The index of frequency matching in Hz = $200 - (|A - E| + |B - F| + |C - G|)$

resolution of 10 Hz and time was measured with a minimum resolution of 6.25 ms. These variables could be repeated reliably for many teams of males.

To quantify the audible differences in song quality, we devised an index of frequency matching. The index was calculated by taking the sum of the disparities between the two males' song contribution in the three minimum and maximum frequency variables. This sum was then subtracted from 200 so that the magnitude of the frequency matching index would increase in magnitude as the disparities in frequencies decreased. In addition, we measured three other variables of singing performance (Table 1). One of these, the time interval between the onsets of each contribution to the song, indicated the extent to which the partners' songs were synchronized. The other two variables measured the amount of variability in the singing of each partner, and indicated how consistently each male sang his contribution to the duet song. To estimate the amount of variability in the singing of each male, a multivariate measure of variance in the four song parameters was calculated for each male's sample of songs. The measure was calculated as the log of the determinant of the variance/covariance matrix of the four parameters (Sneath and Sokal 1973). To ensure that each parameter was weighted equally, the time interval measurements (ms) were multiplied by 10 so that they would have a magnitude similar to the frequency measurements (Hz).

The correlations among female visitation rate, average frequency matching index, average onset interval between song contributions (synchrony), song variance of alpha, and song variance of beta were

Table Variables of song performance in long-tailed manakins

Variable	Description
Index of frequency matching	Sum of the disparities between the alpha and beta males in 3 frequency parameters subtracted from 200
Onset interval (singing synchrony)	Time interval between the onsets of alpha and beta males' song contributions
Song variance of alpha male (inversely related to singing consistency)	Generalized variance in 4 parameters of alpha male's song contribution
Song variance of beta male	Generalized variance in 4 parameters of beta male's song contribution

tested using Pearson's coefficient, r . To determine which of the above variables best explained the variance among teams in the female visitation rate, we used a step-wise discriminant function. We divided the seven teams into two groups, one containing the teams with visitation rates above the mean ($\bar{x} = 0.82$), and one containing the teams with visitation below the mean. Because the song variables were not normally distributed, we used the rank values in the discriminant function analysis. This analysis revealed which variables or combinations of variables helped discriminate between teams with high or low visitation rates.

Results

Either male in a team could commence the duet song. In most of the teams, the alpha was the male that initiated nearly all of the duet songs. However, in two teams (A and Y), the alpha and beta males initiated songs about equally often. No significant difference existed between the song variance of alpha males ($\bar{x} = 19.39$; $SD = 2.59$) and that of the beta males ($\bar{x} = 19.17$; $SD = 2.51$).

There were no significant correlations among the four variables of singing performance (Table 2). When all four variables were included in a discriminant function analysis, average frequency matching alone was useful in discriminating between teams with high visitation rates and those with low visitation rates (step-wise discriminant function analysis; $F_{(1,5)} = 15.0$; $P = 0.012$) (Table 3). In addition, only average frequency matching was significantly correlated with visitation rate (Pearson's $r = 0.92$; $P = 0.003$) (Table 2).

After the 1st year of the study, the beta male at perch-zone Z disappeared and was replaced by the gamma male in subsequent years. This gave us the opportunity to observe the impact of a partner change on frequency matching and courtship success. Prior to the disappearance of the beta, team Z had the songs with the highest degree of frequency matching, highest visitation rate (Table 2), highest song rate, best dance, and highest copulation rate (McDonald 1989b). The replacement beta had an abnormal, incomplete

Table 2 Correlation (Pearson's coefficient, r) matrix among female visitation rate and four variables of song performance in long-tailed manakins

	Visitation rate		Average frequency matching		Average onset interval		Song variance α	
	r	P	r	P	r	P	r	P
Frequency matching	0.92	0.003						
Onset interval	-0.45	0.31	-0.53	0.22				
Song variance α	-0.59	0.17	-0.53	0.22	0.28	0.55		
Song variance β	-0.03	0.95	-0.30	0.95	0.38	0.40	-0.26	0.57

Table 3 Female visitation and song performance variables of long-tailed manakins. (+) designates visitation rates above the mean ($x = 0.82$); (-) designates visitation rates below the mean. The numbers in parentheses are ranks

Team	Visitation rate	Average frequency matching	Average onset interval	Song variance α	Song variance β
Z	2.00 (+)	174 (1)	0.110 (6)	18.3 (5)	16.8 (6)
Y	1.37 (+)	117 (2)	0.111 (5)	19.3 (4)	21.1 (3)
H	1.08 (+)	107 (3)	0.121 (3)	15.0 (7)	22.0 (2)
C	0.55 (-)	99 (4)	0.119 (4)	18.0 (6)	18.1 (4)
A	0.31 (-)	82 (6)	0.102 (7)	20.6 (3)	16.4 (7)
T	0.24 (-)	91 (5)	0.127 (2)	22.1 (2)	22.2 (1)
O	0.17 (-)	46 (7)	0.134 (1)	22.4 (1)	17.6 (5)

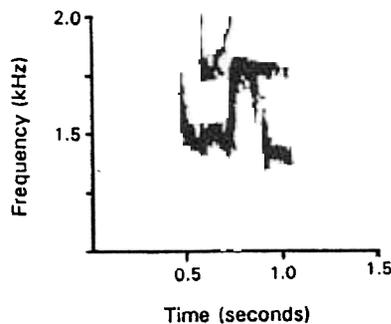


Fig. 2 Audiospectrogram of the song of team Z in 1986. The abnormal song contribution of the beta male occurs above approximately 1.75 kHz

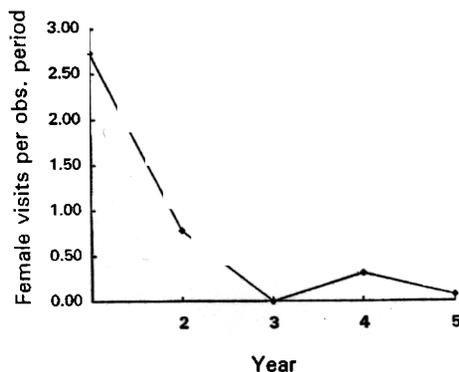


Fig. 3 Decline in female visitation at perch-zone Z after the replacement of the beta male in year 2

song, about 300 Hz higher in frequency than that of any other male sampled. Not only was the degree of frequency matching in the songs of the new team extremely low, songs were not as loud and were delivered from perches closer to the ground. Because the

abnormal song contribution of the new male did not contain the analogous elements necessary for comparison with his partner's contribution, an index of frequency matching could not be computed. Figure 2 shows the complete lack of frequency matching in the dual song. The number of visits per observation period declined dramatically during the new male's first season as beta, and continued to decline over the next few years (Fig. 3). Copulations per observation period fell from 0.41 in year 1 to 0 in succeeding years, after the new beta male took over.

Discussion

The measure of song performance that most directly accounted for the harmonious sound of well-coordinated manakin song was frequency matching. Songs with extremely poorly matched frequency not only sound dissonant to human ears, but sound unsynchronized as well. The apparent lack of synchrony was not due to unusually long intervals between the onsets of the two males' song contributions; onset intervals were similar in harmonious and unharmonious songs. Rather, the frequency mismatch renders the temporal offset between the two males' contributions more perceptible, making the song sound less synchronous. Likewise, the amount of variability in the singing of alpha and beta males was not related to the degree of frequency matching. All males in this sample were definitive (at least 4 years old) and sang quite consistently. Frequency matching appears to be the best measure of how harmonious and coordinated manakin songs sound to the human ear.

Teams of long-tailed manakins with songs that were well matched in terms of frequency attracted more

females. Neither the degree of synchrony nor the consistency with which team members sang was related to the ability to attract females. Although a significant relationship between visitation rate and frequency matching is suggestive, it is insufficient to allow us to conclude that well matched singing *per se* causes high visitation by females. Females may have been responding to other correlated behavioral cues. For example, teams of males that sang more persistently attracted more females (McDonald 1989b), and this may have been the primary basis for females' choice of perch-zone. Characteristics of the duet song, including amount of output, appear to be important in determining which perch-zones a female will visit. Once she arrives in the display area, characteristics of the dance, including a "butterfly" display, appear to determine whether or not she will choose to mate with the alpha male (McDonald 1989b). Nevertheless, our results suggest that females may have a preference for songs with a high degree of frequency matching.

Song quality in long-tailed manakins is a function of the behavior of two males. Mate choice based on a dual-male phenotype is an intriguing possibility, especially since one of the males does not mate. The success of the alpha male may depend on the ability of his partner to sing in a coordinated fashion. The effect of the non-mating partner on courtship success was illustrated the year that the beta partner disappeared from team Z, the most successful partnership in the study area. Visitation and copulation rates declined when the alpha male established a partnership with a male whose song was abnormal. The individual phenotype of the formerly extremely successful alpha male did not change, yet females ceased responding to his courtship. The change in the dual-male phenotype, therefore, is most likely to explain this decline in courtship success.

The above observations raise questions about the evolution of mate choice based on a dual-male phenotypic character. How does a dual-male character such as frequency matching help a female find or select a mate? We consider two possibilities, which are not mutually exclusive: frequency matched songs are more audible than unmatched songs, or frequency matching provides females with a criterion useful in assessing the quality of potential mates.

By matching sound frequencies, two males may produce a song with up to 2 times the intensity of that sung by a single male (a fourfold increase in intensity theoretically is possible if coherent sound waves are produced by two closely spaced sources; however, the distance between manakin singers, 10–15 cm, is too large for such near-field interference to occur). A dual song with twice the source intensity would be audible from a maximum of 1.41 times as far (sound intensity decreases in proportion with the square of the distance), and would be audible over twice the area. In reality, the additional distance a manakin song could

propagate would be less than this for two reasons. First, temporal overlap of matched frequencies is not perfect, so the intensity of a dual-male song is probably not doubled at the source. Second, sound intensity attenuates considerably in a dense forest (Wiley and Richards 1978), and this excess attenuation is linear with distance. Thus, the increased distance of audibility of a dual song would be somewhat less than the theoretical maximum of 1.41 times as far. Therefore, if female visitation preferences were based solely on audibility, a male with a partner might potentially attract more females than a solitary male, but the benefit is likely to be considerably less than a twofold increase in visitation. Solitary songs are rare, however, and our interest is in whether duet songs with close frequency matching may propagate further than poorly matched songs. It seems unlikely that a small difference in frequency matching would increase the area of audibility enough to impact the rate of female visitation, especially since temporal overlap of the two males' song contributions is imperfect in both well and poorly matched songs. It is more likely that active choice by females explains the higher visitation at perch-zones where well matched songs are heard.

Frequency matching may provide females with an unambiguous ideal against which dual-male performance can be judged. Like the morphological characters assessed under fluctuating asymmetry arguments (Watson and Thornhill 1994), frequency matching has a clear maximum of perfect matching. Thus, dual-male performances provide females with the opportunity for enhanced discrimination among potential mates. Furthermore, such performances may provide females with a criterion useful in assessing the quality of potential mates.

The expression of frequency matching may be related to the cooperative abilities of the participating males. The partnership between an alpha and beta male develops over several years. Young, predefinitive males initially participate in several partnerships, fluidly moving among perch-zones (McDonald 1989a). In this way, they become established in a dominance system in which status increases with age. As males grow older and their status relationships become better defined, they spend more time displaying at fewer perch-zones. The dominance hierarchy at a perch-zone appears to function as a queue of variously aged males awaiting opportunities to move into beta and alpha positions (McDonald 1993a). By the age of about 8 years, males tend to be established in stable, long-term partnerships as beta males. As long as these queues remain orderly, little overt aggression is observed. The orderliness of queues may be reinforced by female choice, since females seldom remain in a perch-zone while chasing among males occurs. Opportunities for males to move between queues, however, appears to be limited by aggression, particularly among the younger males (McDonald 1993a). We have some evidence to suggest

that frequency matching may be related to the duration of a partnership. First, frequency matching increases with age of the younger partner. Second, songs of established teams of males have better frequency matching than songs resulting from randomly combining the measurements of individual males' song portions to form artificial teams (J.M. Trainer and D.B. McDonald, unpublished work). Because partners are not genetically related (McDonald and Potts 1994), frequency matching is very unlikely to result from genetic similarity. These observations suggest that joint songs of established teams become better matched as the partnership develops.

Thus, females may be able to acquire information about the duration and stability of an alpha male's partnership from the degree of frequency matching in his joint songs. A male whose songs have a higher degree of frequency matching has demonstrated that he has survived eight or more years, acquired sufficient status to be a member of an established team, has the ability to perform highly coordinated courtship display, and exhibits the tolerance of other adult males necessary to form a stable partnership. To the extent that these qualities are heritable, females may benefit from choosing males with a high degree of frequency matching. Our studies of the long-tailed manakin help us understand how mate choice based on dual-male phenotype might have evolved.

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