The development of coordinated singing in cooperatively displaying long-tailed manakins

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Long-tailed manakins (*Chiroxiphia linearis*) have a puzzling social system in which teams of two males display cooperatively in dispersed lek arenas, but only the alpha partner mates with visiting females. One benefit of performing as a nonmating partner might be to gain experience as an "apprentice" to improve the performance of the complex duet song and joint dance. We examined the relationship between the age of singers and two measures of singing performance: song variability and sound frequency matching. Singing performance improved with age; variability in four song characteristics of males less than 3 years old was greater than that in their older partners, and frequency matching increased with the age of the younger partner. Randomization tests of song samples from seven well-established teams showed that males did not track the song-to-song variation in their partners' singing. Another randomization test showed that frequency matching by these teams was higher than that of randomly paired partners. We considered three alternative hypotheses for the congruent songs: (1) short-term accommodation to the partner's song; (2) active choice of partners with similar intrinsic frequencies; and (3) long-term development of congruent song through either practice or song copying. Our results and evidence from long-term monitoring of banded birds best support the hypothesis that frequency matching develops over several years during the complex and protracted process of partner formation. Nonmating males may benefit from increasing their competence at display, eventually enjoying increased mating success when they inherit display sites from older males. *Key words:* age, *Chiroxiphia,* cooperation, learning, lek, manakin, Pipridae, sexual selection, song, suboscine, vocal development. *[Behav Ecol 13:65–69 (2002)]*

Long-tailed manakins (*Chiroxiphia linearis)* have an unusual cooperative courtship display in which two males perform a song and dance in dispersed lek arenas (Bradbury, 1981) that we call "perch-zones," visited by lone females or females in small groups (Foster, 1977, 1985). Each lek contingent (defined as the males associated with a perch-zone) comprises a linear dominance hierarchy of three to 15 males of varying ages. The two top-ranking males (alpha and beta) perform the great majority of the duet song and dance courtship displays. Only alpha males mate with visiting females, while the subordinate, beta partners may spend as much as 4 to 10 years in the supporting role, waiting for the opportunity to move up in rank and become potential copulators (McDonald, 1993a). To understand this puzzling example of cooperation, we need to know how the beta male benefits from the partnership. McDonald and Potts (1994) ruled out an indirect inclusive fitness benefit by showing that relatedness among display partners is not higher than the ambient level in the population. Foster (1981) suggested that one of the direct, though delayed, benefits of performing as a beta male might be to gain experience as an "apprentice" to improve the performance of the complex duet song and joint dance. Subsequent studies showed that females tended to visit and mate with males that are highly competent performers of the song and dance displays (McDonald, 1989b; Trainer and McDonald, 1995). Therefore, the potential exists for beta males to increase their eventual reproductive success by "apprenticing," providing that their display performance improves during their tenure as a noncopulating partner. Until now, we lacked information on the development of the manakin courtship display.

Courtship display in long-tailed manakins is hierarchical, with duet song acting as a long-range attractant for visitation, and dual-male dance acting to induce females that have chosen to visit a perch to remain for copulations. Only one team of males displays in a given perch-zone at any one time (McDonald, 1989a). In unison, two males (usually the alpha and beta) perform the duet song display (phonetically resembling the word toledo) (Figure 1), which advertises their presence and attracts females to visit the perch-zone (Trainer and McDonald, 1993). As soon as a female arrives in the vicinity of a display perch, the males begin to perform a joint, backwards leapfrog dance. Copulations occur only after one or more lengthy bouts of dancing (McDonald, 1989b). Hence, singing plays an important role in the first, long-range step of mate choice: selecting which perch-zone to visit. Our previous work showed that teams of males whose individual toledo components were well matched in sound frequency received more visits from females (Trainer and McDonald, 1995).

Acquisition of social status involves plumage sequences and interactions among males that develop over a period of as much as 10 years. Three distinct predefinitive plumages precede the definitive plumage, acquired at 4 years of age. McDonald (1993a) provided evidence that the predefinitive plumages function as honest status signals directed at other young males in queuing for dominance rank in lek contingents. Predefinitive and young definitive males interact with members of two to six different lek contingents simultaneously, traveling among perch-zones to interact with various partners at each. The number of lek contingents with which a male associates decreases as his status increases. Eventually, some males work their way up to the alpha and beta positions, comprising the principal display team. By the time a male reaches beta status at approximately 7 years of age, he usually interacts at no more than two perch-zones. Males attain alpha
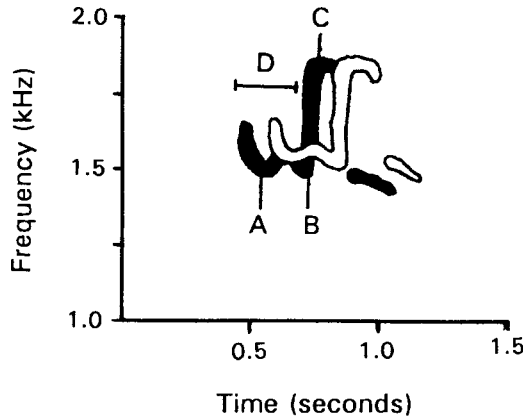
Figure 1
Four variables illustrated in these sonograms were measured for each male's contribution to the dual toledo song of the long-tailed manakin. The contribution of one male is shown solid, and the other male shown outlined. A and B are minimum frequencies, C is a maximum frequency and D is a time interval.

status at approximately 10 years of age, and almost always interact and display at only one perch-zone. Thus, alpha-beta partnerships take many years to consolidate, gradually becoming more stable as advancing males display with fewer and fewer partners. New opportunities arise when higher-ranking males disappear, which occurs at the rate of nine to 23% per year for definitive males. Because of the high survival rates of top-ranking males, only approximately 8% of first-year males will actually become alpha males with the potential of copulating (McDonald, 1989a). Thus, lek contingents are fluid, with memberships (especially at the lower ranks) changing from year to year, and the network of social interactions is arguably as complex as that found in any non-human society.

The long and complex route to acquisition of social status in lek contingents entails deferring breeding for 6 to 10 years (McDonald, 1993a; McDonald and Potts, 1994). Young males have almost no chance of breeding, since females appear not to be attracted to songs in which a male in predefinitive plumage participates, and rarely to watch dances involving predefinitive males. Even after a male attains definitive plumage, females will mate only with the older, dominant alpha. Deferring reproduction for such a long period of time would select for long-term behavioral strategies that increase a male's personal reproductive success, the benefits of which do not accrue until at least 6 years of age (McDonald, 1993a; McDonald and Potts, 1994).

The development of display competence may be a long-term strategy of great potential importance for reproductive success in male long-tailed manakins. Singing competence in this species is unique because it involves an unusual dual phenotype in which frequency matching is dependent on the performance of two individuals. Well-executed performance of the song confers a more immediate benefit on the alpha male, which has a chance to mate with females attracted to the dual song. Nevertheless, beta males tend to inherit the alpha position when the older males disappears, and females exhibit site fidelity, continuing to visit favorite perch-zones even after a change in alpha male (McDonald and Potts, 1994). Thus, beta males also benefit, albeit in the long run, from performing frequency matched songs with their partners. The development of singing competence may be a consequence of prolonged partnership formation that benefits males over the long term.

Here we investigate development of the singing display used to attract females to perches where the dance display and cop-

ulation occur. We quantify singing competence using two parameters. First, we estimate the singing consistency of each male from the generalized variance in four song variables describing his contribution. We consider males with less variability in their singing to be more competent singers. Second, we develop an index of frequency matching (IFM) as the congruence between partners in the frequencies of three song elements. We use this quantitative information to test whether frequency matching and singing consistency improve with age. In addition, we determine whether the songs of established alpha-beta teams of definitive males are more congruent than expected by chance.

We test three alternative hypotheses for the high congruence of songs by partners in well-established teams: (1) a short-term accommodation hypothesis under which partners "track" each other's song contributions during each round of singing; (2) an active choice of partner hypothesis, whereby males gravitate toward other males with similar intrinsic frequencies as preferred singing partners; and (3) a long-term developmental hypothesis, under which partners converge on congruent song by practice or song copying.

METHODS

The study area, in Monteverde, Costa Rica ($10°$ $18'$ N, $84°$ $48'$ W), is 80 ha of premontane tropical moist forest at an elevation of 1300 m. We recorded toledo songs as teams of two males sang in the subcanopy, usually at a distance of 8 to 10 m. Duetting males perch 10 to 15 cm apart, making it easier to age both partners, and in many cases to identify them individually by their color bands. Using a database of age-specific information for color-banded birds, we aged males using the plumage sequences described in McDonald (1993a). Each of 14 males in seven teams of definitive males that formed the crux of the recording effort was color-banded—we will call these the "focal" teams. The partnership patterns, singing, courting, and mating behavior of these focal teams were well documented (McDonald, 1989a,b, 1993a,b; McDonald and Potts, 1994; Trainer and McDonald, 1995). The focal teams received nearly all of the copulations and most of the visits by females over the 2 years of the present study. In addition, we recorded 15 partner combinations that contained a banded or unbanded definitive male and an unbanded predefinitive male. The 15 predefinitive males in these combinations were evenly divided among three age classes (1, 2, and 3 years old). Each individual male is represented in only one of the 22 partner combinations described above.

For each team we analyzed 10 consecutive songs from a single song bout recorded during June or July of the breeding season. We tested whether a consecutive sample was representative of a team's singing over these months by comparing the consecutive sample at perch-zone Z with a temporal sample of the same team over several days. Due to the difficulty of obtaining song samples in which the color-bands of both males were identified during a recording session, this was the only pair of focal males for which repeated samples existed. The frequency characteristics of 10 consecutive songs at perch-zone Z did not differ significantly from a sample of seven songs by the same team, each recorded on a different day between 12 June and 3 July (MANOVA; Wilks's Lambda = 0.54; $F_{(6,10)} = 1.42$; $p = .30$). Visual inspection of sonagrams of two teams recorded on two or three different days showed their songs also varied little over time. We assumed, therefore, that samples of consecutive songs were representative of the rather stereotyped singing throughout the duration of the breeding season.

We recorded songs with a Sony WM D6C cassette recorder and a Sennheiser ME 80 directional microphone, and ana-

lyzed them using a Kay Elemetrics Model 5500 Sonagraph with a gray scale printer. The two males of a team sing almost identical song contributions of approximately 0.6 s duration, with one male commencing approximately 0.1 s after the first male begins (Figure 1). We were able to identify the singer of each contribution to the toledo songs based on slight differences in the frequency characteristics of partners' contributions. Additionally, one of the two males would sometimes give a small number of solitary toledos, allowing us to verify that male's contribution to the duet songs.

We used the techniques developed by Trainer and McDonald (1995) to measure songs quantitatively. In sonagrams, each male's contribution appears roughly J-shaped (Figure 1). For each male, we measured the minimum frequencies occurring at two nodes of high amplitude in the bottom of the J (A and B of Figure 1), the maximum frequency at the top of the J (C of Figure 1), and the time interval between the onset of the song and the stem of the J (D of Figure 1). To determine how consistently each male sang his contribution to the duet song, we calculated the generalized variance in the above four song parameters for a sample of 10 songs from each male. This multivariate measure was the log of the determinant of the variance/covariance matrix of the four parameters (Sneath and Sokal, 1973). To give each parameter approximately equivalent weight, we multiplied the time interval measurements (ms) by 10 so that their magnitude would be comparable to those of the frequency measurements (Hz). Using a two-way ANOVA of age class and partner status, we compared the generalized variance in the song parameters of males of different ages.

For each song we measured an index of frequency matching (IFM). We calculated the IFM by taking the sum of the disparities between the two males' song contribution in the three minimum and maximum frequency variables. We then subtracted this sum from 200, so that the magnitude of the IFM would increase as the disparities in frequencies decreased. Using a repeated-measures, one-way ANOVA with teams nested within age class, we compared the IFM among plumage classes to see if it increased with the age of the younger partner.

Short-term accommodation

We performed randomization tests to determine whether alpha and beta males in the focal teams tracked one another's songs (Manly, 1997; Smith et al., 1990). The song contributions of each partner in a team showed slight variation from one song to the next. If partners tracked one another, then their song contributions should have varied together. Therefore, the frequency matching in the observed sample of 10 songs was expected to be higher than that in artificial samples containing rearranged duet songs. For example, an alpha male's contribution to the first song might be compared to the beta male's contribution to the fifth song in an artificial sample. For each of seven focal teams, we used an Ada program on a PC to generate 999 random permutations of rearranged songs and calculated the mean IFM for these artificial samples. We compared the mean IFM of the actual sample to the distribution of the randomly generated mean IFMs. The significance level is equal to the number of artificial samples with a mean IFM equal to or greater than the mean IFM of the actual sample, divided by 1000 (the number of random samples plus the actual sample; Manly, 1997).

Nonrandom frequency matching by partners

We tested the hypothesis that the IFM of the focal teams was higher than expected by chance by performing a randomi-
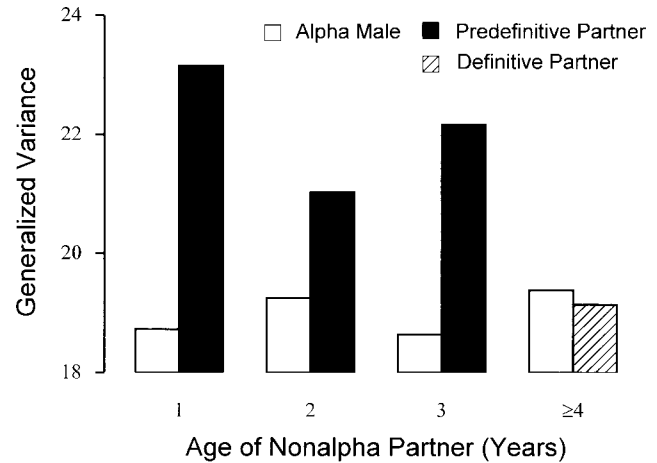

Figure 2
Singing consistency of each long-tailed manakin male was measured using the generalized variance in four song variables. The song contributions of alpha males were less variable, hence more consistent, than those of their predefinitive plumaged partners (ANOVA, $F = 6.93$, $p = .012$). There were five teams in age classes 1, 2, and 3, and seven teams in age class 4.

zation test. We generated randomly formed assemblages, each containing seven artificial teams. We formed artificial teams by repairing alpha males with non-partner beta males. We calculated an IFM for each artificial team using the means of the three song variables in the samples for each male in a team. The assemblages were random permutations of the artificially paired teams. We generated 999 random permutations, and calculated the mean IFM for each permuted assemblage of seven artificial teams. We performed a significance test by comparing the mean IFM of the seven focal teams with the distribution of mean IFMs of the random assemblages. The significance level is equal to the number of mean IFMs that are equal to or greater than the observed IFM divided by 1000 (the number of random assemblages plus the one focal assemblage; Manly, 1997).

RESULTS

The song contributions of predefinitive, non-alpha partners were significantly more variable than those of their definitive, alpha partners (two-way ANOVA; $F = 6.93$; $p = .012$; Figure 2). However, the differences in variability among predefinitive males of different age classes were not significant ($F = 0.88$; $p = .462$). We consider more variable singing to indicate less competent performance.

ANOVA showed that the IFM differed significantly among four age classes to which the non-alpha partner belonged, and increased with the age of the predefinitive partner (one-way ANOVA; $F = 103.10$; $p = .0001$; Figure 3). The differences among teams of males within age classes were also significant ($F = 39.14$; $p = .00001$). Tukey's Studentized Range Test revealed that all comparisons were significant at the .05 level.

We found no evidence that members of a team track one another's songs. The mean IFMs of the seven focal teams' 10 field-recorded songs could not be distinguished from those in randomized samples of rearranged songs. The p-values for the comparisons between the seven focal teams' observed simultaneous samples versus randomly matched non-simultaneous samples were .49, .08, .56, .21, .91, .14, and .67.

The randomization test showed that frequency matching by the seven focal teams was significantly higher than that of the artificially constructed, random assemblages. The mean IFM
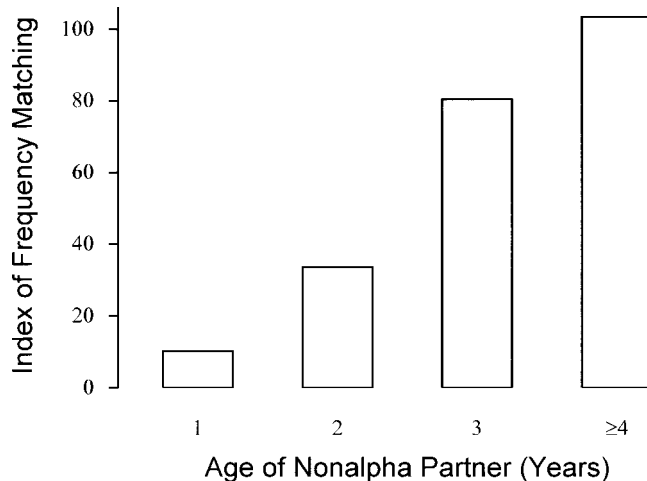
Figure 3
The average index of frequency matching increased with age of the
nonalpha partner in the team. All differences among age classes
were significant (ANOVA, $F = 103.10$, $p = .0001$; Tukey's
Studentized Range Test, $p \leq .05$). There were five teams in age
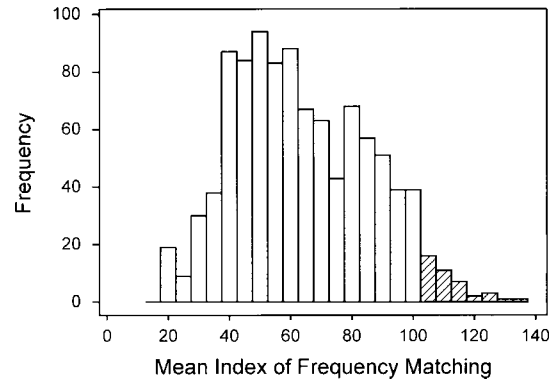classes 1, 2, and 3, and seven teams in age class 4.

Figure 4
The songs of established teams of definitive males were more
congruent than expected by chance. Out of 999 artificial
assemblages, each containing seven randomly paired teams, only 33
(shown hatched) had a mean index of frequency matching greater
than that of the focal teams.

of the seven focal teams was greater than all but 33 of the
values in the distribution of IFMs for the 999 artificial assem-
blages ($p = .033$; Figure 4).

DISCUSSION

Our results clearly demonstrate (1) that singing competence,
including consistent singing and frequency matching, in-
creased as a function of the age of the subordinate partner
and (2) that frequency matching by established teams was
greater than the random expectation. Because frequency-
matched songs attract more females (Trainer and McDonald,
1995), any process that improves frequency matching would
enhance the mating success of males. We consider three al-
ternative hypotheses that could account for our results on
change in performance with age, and the increased congru-
ence of partnerships: short-term accommodation between
singing partners, active choice of partners with similar intrin-
sic frequencies, and long-term development of frequency
matching.

Short-term accommodation hypothesis

We found no evidence that congruence in partners' songs
results from males making short-term accommodations to
their partners' songs, adjusting the sound frequencies as they
sing. If this were true, then partners would be expected to
track subtle variation in one another's songs, matching the
frequencies of each song. That did not occur. The randomi-
zation tests showed that song contributions that actually co-
occurred were no more similar than randomly paired, non-
simultaneous contributions. Observations of color-banded
males provide further counter-evidence. Under the short-term
accommodation hypothesis, males would also be expected to
change the frequency characteristics of their songs when sing-
ing with different partners. A color-banded alpha male sang
with two different partners at the same perch on the same
day. Inspection of sonograms and comparisons of frequency
measurements showed that the alpha male did not alter his
song contribution to match the frequencies of the two differ-
ent partners. Similarly, a color-banded beta male sang with two
different alpha males at different perch-zones one week apart,

but did not alter his song contribution. Long-tailed manakin
males do not, therefore, appear to make short-term accom-
modations to produce congruence with partners' songs.

Active choice of partners hypothesis

Another possible cause of congruence in songs would be
males choosing partners with songs similar to their own.
McDonald's (1989a, 1993a) observations, however, suggest
that social history and patterns of male mortality in different
lek contingents are the most important determinants of which
partners end up together. Rather than commit to a single
partner early on, males interact with many partners in several
different lek contingents, narrowing the range of partners
and lek contingents over a period of several years. This should
allow them to advance in the most opportune queue when a
higher-ranking male unpredictably disappears. Such a long,
fluid process of establishing an alpha–beta partnership is un-
likely to result in partnerships between males based primarily
on active choice of those with intrinsically similar song fre-
quencies.

Long-term developmental hypothesis

The final alternative is a long-term developmental hypothesis,
under which males gradually accommodate to their partners'
frequencies. Consistent with this hypothesis is our observation
that predefinitive males gained competence at dual singing as
they aged; variability in song structure decreased and fre-
quency matching increased with age in predefinitive males.
   In addition, we found that the song contributions of defin-
itive members of established teams were congruent; that is,
they were more similar to each other than expected, given
the song variation in the population. Under the developmen-
tal hypothesis, congruence may develop over time as males
spend time singing together. Males may make long-term ad-
justments to more closely match their partners' songs. It
seems most likely that the younger, beta male would match
the alpha, but alphas matching betas and mutual convergence
of songs would also produce congruence in partners' songs.
If congruence develops over time, then frequency matching
in a new team should increase over the years as the partner-
ship develops. Again, this is supported by our observations
that singing variability decreased with age and that frequency
matching of teams increased with the age of the predefinitive
partner.

Frequency matching could develop in long-tailed manakins either by imitation of adult males early in life or by practice, over time, as partners tune their song contributions to one another. The long tenure of subordinate males as non-copulators would provide ample opportunity to perfect song through practice. Direct observations of vocal development in color-banded long-tailed manakins are needed to discover how songs are initially acquired and how and at what ages they may become modified with practice as partnerships develop.

Whereas vocal learning is widespread and well documented in the songbirds (Kroodsma, 1988; Kroodsma and Baylis, 1982), its occurrence has only recently been suggested in the closely related taxon, the suboscines, which include manakins. Kroodsma (unpublished data) has found perhaps the best evidence of vocal learning in a suboscine, the three-wattled bellbird, *Procnias tricarunculata*. Several young males in a contact zone between two song dialects have been observed singing both dialect variants. In addition, bellbird songs appear to change over time, similarly to many songbirds that exhibit vocal learning. These observations contrast with earlier studies of three species of flycatchers, the suboscines most closely related to manakins, which showed that normal songs develop in socially isolated young flycatcher males without imitation of a taped model song (Kroodsma, 1984, 1989). Further studies of the relatively poorly known suboscines may reveal other examples of song learning.

Our long-term developmental hypothesis has implications for understanding the selective advantages that maintain the unusual system of cooperation in long-tailed manakins. Present success of the alpha partner is dependent on the cooperation, since females will mate only after observing one or more prolonged dual dance displays, and they avoid perch-zones where overt aggression among males occurs in the presence of females (McDonald, 1993a). Whereas the benefits of cooperative display to the copulating male are clear and present, the benefits to his partner are not.

While ruling out indirect benefits, McDonald and Potts (1994) found evidence for three direct benefits of cooperative display to the subordinate males: an older beta male may rarely copulate when the alpha male is absent temporarily, subordinate males may eventually succeed to alpha status, and females usually remain faithful to a perch-zone after alpha male turnover. Our results provide support for a fourth benefit: subordinate males increase their competence at display while they help to attract mates for their older partners. Since well-performed displays increase the success of the partnership at attracting females to the dance perch and stimulating females to mate, the beta male whose singing improves with time should eventually enjoy increased mating success when he inherits the perch-zone and its suite of site-faithful females.

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