

Patterns of dawn singing by Buff-breasted Flycatchers

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Received 14 June 2007; accepted 1 September 2007

ABSTRACT. Many passerine species exhibit a “dawn chorus”—a bout of intense singing activity before or at dawn, but our understanding of this phenomenon is poor. Tyrant flycatchers (Tyrannidae) exhibit pronounced daily bouts of dawn singing. I documented this behavior in several populations of Buff-breasted Flycatchers (*Empidonax fulvifrons*) in Arizona, tape recording > 30,000 songs of 23 individuals during dawn singing. Individual males sang a dawn bout each morning, even during breeding phases when daytime song was almost completely absent. Dawn bouts began 5–10 min before local civil twilight and continued for 25–30 min. Each male possessed two song types delivered at high rates during dawn singing (four times the rate during sustained daytime singing). Song rate varied significantly over the course of dawn bouts, increasing to 55 songs / min at mid-bout, then declining to the end of the bout. Type 2 songs comprised about 30% of songs during dawn singing, and decreased significantly in proportion during the final 10 min of the bout. Songs of the two types were delivered in a nonrandom fashion. Males sang at locations near territory boundaries and pairs of neighbors engaged in counter-singing from the same locations each morning. A number of dawn singing bouts ended with attempted or successful copulations. These observations are consistent with the social dynamics hypothesis for the functional significance of dawn singing in this species.

SINOPSIS. Patrones en el canto matinal de *Empidonax fulvifrons*

Varias especies de Passeriformes se caracterizan por hacer un “canto matinal”, cual es evento intensivo de cantos antes de o al amanecer. Sin embargo, nuestro conocimiento sobre este comportamiento es pobre. Miembros de la familia Tyrannidae se caracterizan por hacer cantos matinales pronunciadas y a diario. He documentado este comportamiento en varias poblaciones de *Empidonax fulvifrons* en Arizona mediante grabaciones de > 30,000 cantos de 23 individuos cuales hacían cantos matinales. Los machos cantaban el canto matinal diariamente, inclusive durante las fases de la época reproductiva cuando los cantos hechos durante el día eran casi ausentes. Cantos matinales comenzaban desde 5–10 min antes del crepúsculo y continuaban por 25–30 min. Cada macho poseía dos tipos de canto matinal, caracterizados por altas tasas de canto (cuatro veces más rápidos que las tasas de canto realizados durante el día). La tasa del canto variaba significativamente durante los eventos de cantos matinales, incrementando hasta 55 cantos/min en el medio del evento, y después reduciéndose hasta el fin del evento de cantos. Cantos del Tipo 2 representaban aproximadamente el 30% de los cantos matinales y disminuyeron significativamente en proporción durante los últimos 10 min del evento. Los dos tipos de cantos no fueron pronunciados al azar. Los machos cantaban en sitios cerca de los límites de sus territorios y parejas que eran vecinas se encontraban cantando una a la otra desde los mismos sitios cada mañana. Algunos de los cantos matinales terminaron con intentos de copulación o con copulaciones exitosas. Estas observaciones son consistentes con la hipótesis de la dinámica social en cuanto a la importancia funcional de los cantos matinales en esta especie.

Key words: Buff-breasted Flycatcher, dawn singing, *Empidonax fulvifrons*, song function, subsong

Dawn singing is characteristic of many passerine species (Staicer et al. 1996). Individual males exhibit bursts of intense singing activity lasting 20–60 min, usually in the dawn twilight. These bouts are followed by a period of relative silence; males may or may not resume singing at lower intensity during daytime activities. The functional significance of this phenomenon has been the subject of much speculation (reviewed by Staicer et al. 1996), but relatively little empirical study. There are theoretical arguments explaining why dawn singing may be favored

by conditions for sound transmission (Hewood and Fabrick 1979, Brown and Handford 2003) or energetic considerations (McNamara et al. 1987, Hutchinson et al. 1993, Hutchinson 2002). However, these latter arguments focus on explanations of when this phenomenon should occur rather than on the function of the singing per se.

Various hypotheses suggesting how dawn singing influences the fitness of individuals have been proposed, but few have been examined specifically and existing empirical evidence is inconsistent with others (Staicer et al. 1996). Several factors contribute to our poor understanding of dawn singing. Detailed studies of

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dawn singing by known individuals, whose behavior and reproductive success can be tracked, are required to answer many of the outstanding questions. The small number of recent studies of this type (Ballentine et al. 2003, Liu 2004, Poesel et al. 2004, Burt and Vehrencamp 2005, Liu and Kroodsma 2007) indicate that dawn singing differs from daytime singing in many aspects, and suggests that the two types of singing may have different functions.

The large literature on bird song is biased heavily toward studies of oscine passerines (Order Passeriformes, Suborder Passeri). Information on patterns of song variation within and among species of suboscine passerines (Suborder Tyranni), and how this variation is used in their singing behavior, is particularly important because the mechanism of song development differs between these subfamilies. While some aspect of learning is involved in song development of all oscine species, the limited information available suggests that suboscines may require no imitative learning or auditory feedback for development of normal songs (Kroodsma 1996).

The majority of studies of song in suboscine birds have dealt with tyrannid flycatchers (Tyrannidae), the only suboscine group distributed widely in North America. Dawn singing is especially pronounced in tyrannid flycatchers (Craig 1943, Smith 1966, 1970). As part of a broader study of song variation and singing

behavior in the genus *Empidonax*, I documented dawn singing in several populations of Buff-breasted Flycatchers (*Empidonax fulvifrons*) in southeastern Arizona in 1999. Dawn singing in this species is typical of patterns demonstrated by other members of the family. However, this species is of particular interest because of limited knowledge of its biology and its limited distribution in the United States (Bowers and Dunning 1994).

Each male Buff-breasted Flycatcher sings two similar, but distinctive, song types (Fig. 1) during dawn singing, and also during intense daytime singing (e.g., prior to pair formation). These song types are poorly described in the literature and were not distinguished in the most recent account of the life history of this species (Bowers and Dunning 1994). Although the songs of different individuals are extremely similar in form, and cannot be distinguished by ear, they are individually distinctive and can be discriminated with statistical analyses (Lein, in press).

METHODS

I recorded dawn singing of 23 male Buff-breasted Flycatchers at seven sites in two isolated mountain ranges in southeastern Arizona between 7 June and 25 June 1999. Recording localities in the Chiricahua Mountains (number of individuals in parentheses) included Cave

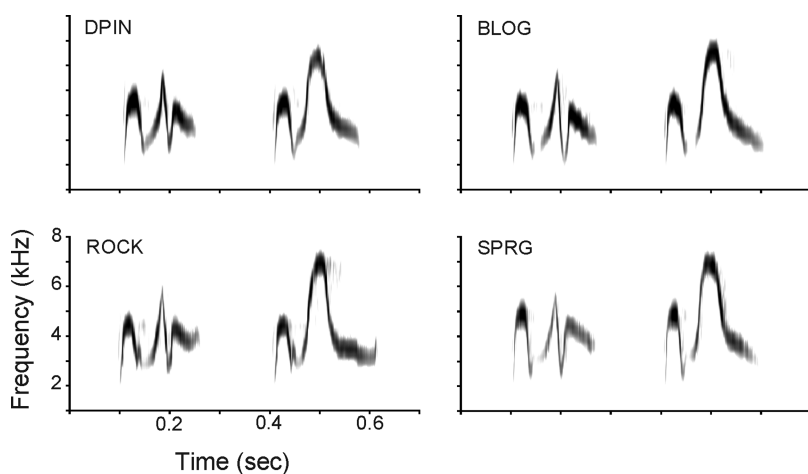


Fig. 1. Audiospectrograms of songs of four male Buff-breasted Flycatchers. Each panel shows a Type 1 song and a Type 2 song of one individual. Males in the left column were from sites in the Chiricahua Mountains; those in the right column were from the Huachuca Mountains.

Creek (3), Pinery Canyon (2), Rucker Canyon (6), and West Turkey Creek (2). Localities in the Huachuca Mountains included Carr Canyon (3), Garden Canyon (1), and Sawmill Canyon (6). Males at West Turkey Creek and Sawmill Canyon were color-marked and were recorded on multiple dates whereas individuals at other sites were recorded only on one or two dates. Buff-breasted Flycatchers occupied open woodlands dominated by pines (*Pinus* spp.), live oaks (*Quercus* spp.) and alligator juniper (*Juniperus deppeana*). Although they arrived on breeding territories in mid-April and paired immediately, nesting did not begin until late May. Pairs were followed daily for periods of 2–3 h to determine territory locations and stage in the breeding cycle. During the period of recording most pairs were involved in nest building or egg laying (often following repeated destruction of nests by predators).

Recordings were made between 04:36 and 05:18 (MST) using a Sony TCD-D10 ProII DAT recorder and a Telinga ProII parabolic microphone, or a Sony TC-D5 ProII cassette recorder and an Audio-Tech AT815a “shotgun” microphone. Recording started each day with the first song of preselected individuals. Because of time constraints, complete dawn bouts of individuals were not recorded. Rather, my field assistant and I switched to recording a second, or even a third, individual after recordings of 5 min or more had been obtained. Recording continued each morning until the last male in the area had ended his dawn bout. Consequently, beginning and ending times for dawn singing are calculated for birds in the local population being sampled on that date, and not for individual males.

Because the frequency and rate of daytime singing decreases precipitously following pair formation, I obtained only six recordings of sustained daytime singing for comparison with dawn singing. Four recordings were made of male DPIN prior to pairing, and two were made of male WEST, who was apparently unmated at the time of recording in mid-June.

Recordings were acquired as digital files using RTS Version 2.0 bioacoustical analysis software (Beeman 1996) at a sample rate of 20000 Hz and 16-bit amplitude resolution. Digitization was done using a Gateway Pentium P5–166 desktop computer with a DT 2821 High Speed Single Analog and Digital I/O board. Analog

input from tape recorders was band-pass filtered during acquisition using a Krohn-Hite Model 3550 filter to prevent aliasing and to eliminate background noise outside the frequency range of interest.

I made 70 recordings of dawn singing of 23 males with a total duration of 626 min, and including 30,727 individual songs. Identification of song types and measurement of timing was done in an automated fashion by a custom program written in the command language of SIGNAL Version 3.1 bioacoustical analysis software (Beeman 1999). Each sound file was processed with the Event Detector module of SIGNAL to detect sounds with the general time and frequency characteristics of Buff-breasted Flycatcher songs. Detected “events” were compared to sound files of both song types of the subject individual using spectrographic cross-correlation to eliminate spurious events ($r < 0.5$) and to identify song types (maximum r value in comparison with known examples). The identity of each detected song, and the time of onset, was recorded in an output file. The accuracy of this procedure was confirmed by comparisons with audiospectrograms of a sample of recordings, and all sections of recordings with excessive background noise were reviewed manually. The number of songs missed or misclassified was $\ll 1\%$. Such an error rate would have no meaningful influence on the conclusions.

For analyses of song rates and proportional use of song types during dawn singing, I selected recordings of continuous singing from a single date for each male. Only individuals with ≥ 10 min of recording were included. The sample consisted of 332 min of recordings of 18 males with a total of 16,622 songs (mean \pm SD = 18.4 ± 6.4 min and 923.4 ± 325.5 songs per individual). Rates of song delivery and proportional use of the two song types were calculated for each minute of each recording. I eliminated partial intervals < 30 s in duration at the end of recordings ($N = 11$) and intervals with less than 20 songs ($N = 5$). The latter were intervals during sporadic singing at the beginning of dawn singing, or intervals when the subject was disturbed or changed perches and stopped singing briefly. I used PROC MIXED in SAS Version 9.1 (SAS Institute 2004) to fit general linear models to changes in song rate and proportions of the two song types across the predawn singing period. To control for autocorrelation

of song rates of individual males across time, I used a repeated measures design with a first-order autoregressive model for the variance-covariance structure (Littell et al. 2006) with male identity as a categorical factor. The technique of Kenward and Roger (1997) was used to adjust the degrees of freedom to account for the autocorrelation of responses for individual males, which can result in fractional degrees of freedom. The fit of different models was evaluated using the Akaike Information Criterion. Date was included as a covariate in initial analyses but was dropped from the final models because it did not contribute significantly to the fit. Normality of residuals was checked using probability plots. I applied an arcsin transformation to proportions of song types prior to analysis.

Because the time of sunrise varies seasonally at a given location, and varies between locations on a given date, I adjusted all times relative to the time of Civil Twilight at each recording location on each date. All times are given as offsets from the time of local Civil Twilight (ca. 28 min before local sunrise), as determined from tables from the U.S. Naval Observatory (<http://aa.usno.navy.mil/>).

Sequencing of song types was examined in single recordings from eight individual males. These were selected because they were long recordings (mean \pm SD = 20.2 \pm 3.6 min) made during the peak of dawn singing and contained large numbers of songs (1076.3 \pm 196.1 songs). Four individuals were from the Chiricahua Mountains and four were from the Huachuca Mountains. A FORTRAN program processed the output files generated by the Event Detector procedure described above, determining song dyads (pairs of preceding—following songs) of the four possible types (1-1, 1-2, 2-1, and 2-2) and calculating the time intervals for dyads (time from the start of the first song to the start of the second song). The combined recordings included a total of 8602 song dyads. I arbitrarily eliminated all dyads with intervals $>$ 2.0 s from analyses. Such long intervals usually represented breaks in singing resulting from disturbances, perch shifts, and so forth. This eliminated 681 dyads (7.9%) from the analysis. However, analyses not reported here demonstrate that exclusion of such dyads, or use of an exclusion threshold slightly shorter than 2.0 s, had no impact on the patterns demonstrated.

I conducted chi-squared tests of contingency tables for each male to test the null hypothesis that songs were used in a random sequence, as determined by their relative frequencies. I also used a chi-squared test to determine whether the frequencies of different dyad types varied among the eight males, using a Monte Carlo estimate of the *P*-value because 25% of the cells had expected counts of $<$ 5. Time intervals between dyads of different song types were compared with ANOVAs followed by Bonferroni pairwise comparisons of means.

Statistical analyses used SAS 9.1.3 software (SAS Institute 2004). I report mean values \pm 1 SD unless otherwise indicated.

RESULTS

Behavior during dawn singing. During dawn singing, males used relatively low perches (estimated heights of 3 – 5 m), often in the center of a dense tree, usually a juniper. This was in marked contrast to perches used during sustained daytime singing that were usually in the open and often near the top of the canopy. Because it was almost completely dark when dawn singing began, I was unable to determine whether males sang from their overnight roost sites or moved to these positions prior to beginning to sing. Males frequently gave “pit” call notes prior to beginning to sing, and singing was often sporadic for the first several minutes of the dawn song bout.

Males recorded on multiple dates used the same small region of their territory for dawn singing on each occasion. This was often near an edge of a territory, and frequently in a part of their territory that was rarely used during daytime activities. Pairs of neighboring males used locations close to the common boundary of their territories, and seemed to interact vocally during dawn singing, often exchanging songs in alternation for extended periods.

Most dawn song bouts ended when the male stopped singing and flew away from the site, sometimes beginning to forage. On five occasions, however, the bout ended when the singing male was approached by another bird, presumably a female, and an apparent copulation attempt occurred. Because of poor light conditions, it was impossible to determine the identity of the second bird, or whether the copulation attempts were successful. In four of the five cases,

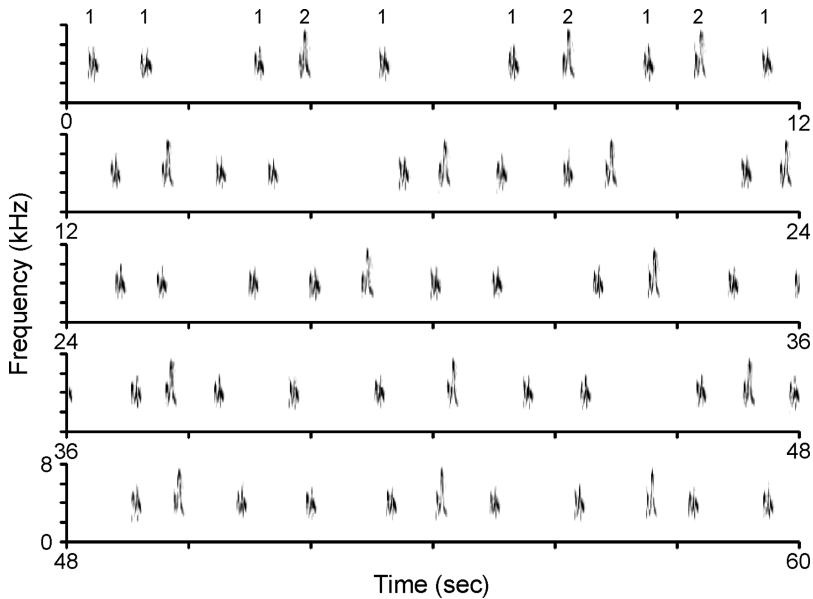


Fig. 2. Audiospectrogram of a 60-s segment of dawn singing by a male Buff-breasted Flycatcher. Each panel continues from the panel immediately above. Song types are identified by number in the top panel.

the second bird gave a trilling vocalization and was observed in a precopulatory posture with raised tail and quivering wings. In all cases, the male appeared to land momentarily on top of the second bird.

Song rates and proportions of song types. Dawn singing began at approximately local Civil Twilight (median for 16 dates = 3 min after CT; range = -9 to 6 min) and continued for almost 30 min (median = 27.5 min; range = 21–37 min). Males sang continuously at very high rates during dawn bouts (Fig. 2). Rates measured from recordings with a minimum length of 5 min (45 of 70 recordings) averaged 48.1 ± 9.5 songs/min (range = 23.8–67.1 songs/min). For comparison, rates measured from 6 recordings of unpaired males singing strongly during the day averaged 12.8 ± 4.8 songs/min (range = 7.7–19.6 songs/min). The minimum rate recorded during dawn bouts was greater than the maximum rate observed during daytime singing.

Although the data were gathered for a number of different males on various dates, a temporal pattern of variation in rates of song delivery during dawn bouts is apparent (Fig. 3). Males increased their song rate during the first 15–20 min of dawn singing, then slowed toward the end of the bout. A quadratic relationship of song rate to time relative to Civil Twilight ($y = 49.74$

$+ 1.12x - 0.058x^2$) provided a significant fit to the data ($F_{1,47.9} = 32.7$, $P < 0.0001$ for linear term; $F_{1,46.2} = 59.2$, $P < 0.0001$ for quadratic term). Male identity had a significant effect in the model ($F_{17,25.2} = 3.2$, $P = 0.003$).

There was a change in proportional use of the two song types over the course of dawn singing. During most of the bout, about 30% of songs given were Type 2. However, the proportion of Type 2 songs decreased to <20% toward the end

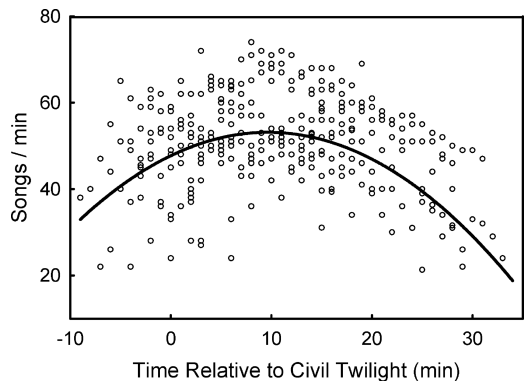


Fig. 3. Song rates during dawn song bouts in relation to time of Civil Twilight. The line is a nonlinear regression fitted to the data.

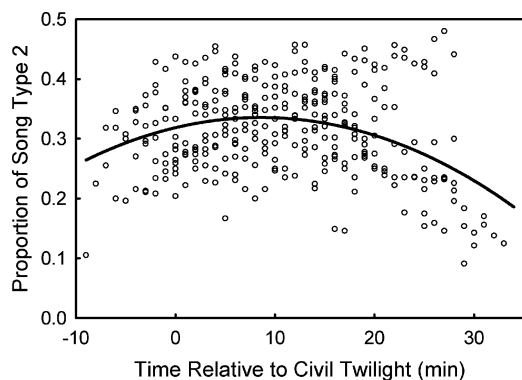


Fig. 4. Proportional use of Type 2 songs during dawn song bouts in relation to time of Civil Twilight. The line is a nonlinear regression fitted to the data.

of the bout (Fig. 4). A quadratic relationship of transformed proportion of Type 2 songs to time relative to Civil Twilight ($y = 0.324 + 0.00413x - 0.00024x^2$) provided a significant fit to the data ($F_{1,83.8} = 44.6$, $P < 0.0001$ for the linear term; $F_{1,82.4} = 105.6$, $P < 0.0001$ for the quadratic term). Male identity had a significant effect in the model ($F_{17,66.7} = 60.1$, $P < 0.0001$).

Sequencing of song types. The pattern of song delivery during dawn singing was decidedly nonrandom. Songs are delivered in groups of 1–5 songs. These groups are separated by pauses longer than those within groups (Fig. 2). In addition, the sequencing of songs (Table 1) differed significantly from that expected if song types were given at random. Two-by-two contingency tables for transitions between preceding and following song types differed significantly from random expectations for all eight individuals (all

$\chi^2_{1} \geq 48.2$, all $P < 0.001$). The frequency of different dyad types varied significantly among individuals ($\chi^2_{21} = 528.3$, $P < 0.001$). The most noticeable departure from random sequencing was the almost complete absence of 2–2 song dyads. Only six of 7921 transitions were of this type, whereas random sequencing of songs would predict 719 2-2 song dyads in this sample. Although all of these were sung by a single male (GULL, Table 1), several males not included in the sample also used 2-2 dyads at very low frequencies. Transitions between songs of different song types (1-2 and 2-1 dyads) were more frequent than expected by chance while 1-1 dyads, although the most common type, were also less frequent than expected by chance.

Patterning of song delivery is also apparent in the timing of songs. Song intervals varied significantly among different dyad types, both for individual males (all $F \geq 107.0$, all $P < 0.001$) and for the eight males combined ($F = 982.6$, $P < 0.001$). In the combined sample, Bonferroni comparisons showed that the mean interval for 1-2 dyads (0.71 ± 0.21 s, $N = 2489$) was significantly shorter than those for both 1-1 (1.12 ± 0.42 s, $N = 3150$) and 2-1 dyads (1.07 ± 0.39 s, $N = 2276$), whereas that for 1-1 dyads was significantly longer than that between 2-1 dyads. All eight individual males had mean intervals between 1-2 dyads that were significantly shorter than those between 1-1 or 2-1 dyads, whereas only six had mean intervals for 1-1 dyads that were significantly longer than those for 2-1 dyads. The mean interval for the 2-2 dyads sung by a single male was very short (0.59 ± 0.06 s, $N = 6$).

Table 1. Frequencies of transitions between different song types in dawn singing of eight male Buff-breasted Flycatchers. Only pairs of songs separated by intervals of ≤ 2.0 s are included.

Male	Number of transitions	Frequency of transitions between songs:			
		1-1	1-2	2-1	2-2
CATT	965	0.376	0.317	0.308	0
EAST	1051	0.437	0.285	0.278	0
GATE	751	0.595	0.210	0.194	0
GULL	1024	0.264	0.388	0.343	0.006
REDR	878	0.282	0.383	0.335	0
SNAG	847	0.443	0.290	0.267	0
SPRG	1061	0.243	0.404	0.353	0
UPIC	1344	0.543	0.236	0.221	0
TOTAL	7921	0.398	0.314	0.287	0.001

DISCUSSION

The most noticeable feature of dawn singing bouts of Buff-breasted Flycatchers was the extremely high rate of song delivery. The mean rate was approximately four times that observed during sustained daytime singing, suggesting that dawn singing differs functionally from daytime singing. Apparently, males sing at a maximal rate during dawn bouts, but may be unable to sustain very high rates during the entire bout, as evidenced by the eventual decrease in song rates (Fig. 3). This decrease in song rate was accompanied by a decrease in the proportion of Type 2 songs (Fig. 4). High song rates are characteristic of dawn singing in many birds (Staicer et al. 1996), including other species of *Empidonax* (Stehelin 2005, pers. obs.) and other tyrannid flycatchers (Craig 1943, Smith 1966, 1969, Smith and Smith 1996).

In spite of possessing a repertoire of only two song types, Buff-breasted Flycatchers demonstrate marked patterning in their singing behavior. Songs were given in groups of 1-5, although single songs were invariably Type 1. Type 1 songs may precede or follow songs of either type, but Type 2 songs were given almost exclusively as parts of 1-2 dyads, with very short intervals separating the two songs. Dyads consisting of two Type 2 songs were extremely rare. Similar patterns of nonrandom sequencing of multiple song types are found in other *Empidonax* species (Sedgwick 1975, pers. obs., Johnson 1980) and other tyrannid flycatchers (Craig 1943, Smith 1969, Smith and Smith 1996).

Intense bouts of dawn singing occurred long after pair formation in Buff-breasted Flycatchers, and probably throughout the breeding season. In contrast, daytime singing was reduced to occasional and sporadic occurrence after pairing, with low rates of song production and an almost complete absence of Type 2 songs. Similar changes have been noted for other species as well (Staicer et al. 1996, Liu 2004) and suggest that dawn singing does not serve primarily for territorial establishment or mate attraction.

Male Buff-breasted Flycatchers clearly are interacting with their territorial neighbors during dawn singing. Pairs of neighboring males selected dawn singing locations close to, and on opposite sides of, their shared territorial boundary and appeared to use these sites con-

sistently throughout the season. They engaged in "song duels," counter-singing at high rates for extended periods. These behaviors have also been reported for Dusky Flycatchers (*Empidonax oberholseri*; M. R. Lein and T. E. Stehelin, unpubl. data) and Acadian Flycatchers (*E. virescens*; Wiley 2005). Regular use of dawn singing sites at or near territorial boundaries has been noted for a variety of species (Willis 1960, Lemon et al. 1987, Staicer 1989, Nelson and Croner 1991, Liu and Kroodsmma 2007). Direct vocal interaction between pairs of neighbors during dawn singing also has been recorded for a range of species (Smith 1966, Staicer 1989, Spector 1991, Dabelsteen 1992, Liu and Kroodsmma 2007).

Overall, these observations are consistent with the social dynamics hypothesis for the functional significance of dawn singing (Staicer et al. 1996), which suggests that this behavior functions in the maintenance and adjustment of social relationships among neighboring males. Neighbors seem to be engaged in "song duels" during their interactions. Songs are delivered at extremely high rates, and often in alternation for extended periods. The observation that dawn singing bouts ended on a number of occasions with what were apparently attempted or successful copulations is suggestive. Smith (1966, 1970) reported similar cases where male tyrannid flycatchers were approached by females at the end of dawn singing with subsequent attempted or successful copulations. Despite many hours of observations of mated pairs during the nest building and laying stages of the breeding cycle, I observed no copulation attempts during daylight hours. Bowers and Dunning (1994) observed two daytime copulations by Buff-breasted Flycatchers during nest-site selection, and reported that a female gave a pre-copulatory display, including crouching and vocalization at the selected nest site, and that a male flew in and copulated. However, I believe that they misinterpreted their observations. On numerous occasions, I observed pairs of Buff-breasted Flycatchers "prospecting" for nest sites. Females frequently flew into a crotch or other appropriate site, raised their tails, quivered their wings, and gave trilling vocalizations. However, marked males also were observed to perform the same display in nest sites, and members of a pair sometimes alternated in displaying at the same nest site. On occasion, one member of the pair

would fly to the prospective nest site before the other had left and land on top of the displaying individual. However, both males and females exhibited this behavior, and I believe that this is what was interpreted incorrectly as copulations by Bowers and Dunning (1994).

Although the dynamics of dawn singing may be determined primarily by interactions between males, songs may not necessarily be directed solely or primarily to other males (Kroodsma et al. 1989). The continuation of dawn singing long after territorial establishment and pairing suggests that its primary function does not lie in either of these areas. I suggest that dawn singing in Buff-breasted Flycatchers may be shaped by sexual selection. The ability to maintain sustained and regular song production at an extremely high rate may be an indication of male quality, and males may be competing with neighbors for opportunities to mate with receptive females, either their own mates or those of neighboring males (Slagsvold et al. 1994). A similar function for dawn singing has been suggested previously for several species. Male Black-capped Chickadees (*Poecile atricapillus*) with high dominance ranks in winter flocks began dawn singing earlier and sang longer and at higher rates than did low-ranking flockmates (Otter et al. 1997). Female Blue Tits (*Parus major*) mated to males that exhibited high song performance times, high versatility, and low "drift" in performance time, started to lay earlier and had larger clutches (Poesel et al. 2001). Amrhein et al. (2004) suggest that nonterritorial male Nightingales (*Luscinia megarhynchos*) may use the dawn chorus to assess singing residents and that dawn singing may therefore play a role in territorial maintenance. However, this would not preclude the possibility that females simultaneously could use dawn singing to assess males as possible partners for extra-pair copulations. Additional observations or experiments, and a genetic analysis of paternity patterns in a population of Buff-breasted Flycatchers, would be required to test this hypothesis.

ACKNOWLEDGMENTS

V. Haines provided outstanding assistance in the field and made many of the recordings used in the analyses. S. Russell, J. and V. Austin, and S. Stone provided valuable advice or logistical support for the field work. T. Stehelin acquired the digital sound files from tape recordings and prepared much of the raw data for analyses. L. Harder

provided essential advice on statistical procedures. The comments of four anonymous reviewers improved the manuscript considerably. Capture and marking of birds was done under authorization of a federal banding permit from the Bird Banding Laboratory of the U.S. Geological Survey and following a protocol approved by the Life and Environmental Sciences Animal Care Committee of the University of Calgary. Field work was conducted under permits from the USDA, Coronado National Forest and the United States Army, Fort Huachuca Military Reservation. This research was supported by a grant from the Natural Sciences and Engineering Research Council of Canada.

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