PAIR FORMATION AND COPULATION BEHAVIOR IN LEAST FLYCATCHER CLUSTERS[1]

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Abstract. Least Flycatcher *Empidonax minimus* pairs form dense clusters of territories on the breeding grounds. We describe pair formation and copulation behavior (both within- and extra-pair) in Least Flycatcher clusters. Pair formation involved a complex behavioral sequence of trill vocalizations and visual display. Within-pair copulations were five times more likely to achieve cloacal contact than were extra-pair copulations. Least Flycatchers exhibited an overall within-pair mating effort of 2.0 ± 0.5 events pair^{-1} hr^{-1} compared to an extra-pair mating effort of 1.8 ± 0.3 events pair^{-1} hr^{-1}. Within- and extra-pair mating behavior by focal birds were distinctly different with respect to rate, conspicuousness, duration, aggression intensity, and pre-copulatory display. The rate of territory incursions for extra-pair copulations was high. We discuss copulation behavior in the context of male and female mating tactics, and highlight the disparity in our knowledge of mating behavior in other members of this genus.

Key words: copulation, Empidonax minimus, *extra-pair copulation, Least Flycatcher, within-pair copulation.*

INTRODUCTION

In recent years there has been growing interest in the behavior of avian pairs (Black 1996) and in the prevalence and evolutionary consequences of extra-pair copulations (EPCs) in socially monogamous birds (Westneat et al. 1987, Birkhead and Møller 1992). We describe pairing and copulation behavior in the Least Flycatcher (*Empidonax minimus*), a socially monogamous, migratory suboscine. Least Flycatchers form tight clusters (2–29 pairs per cluster) on the breeding grounds, behavior that has been reported previously (Sherry and Holmes 1985, Briskie 1994, Perry 1998). Clusters are discrete aggregations of small, all-purpose territories (ca. 15 m diameter) with contiguous boundaries, separated by adjacent unoccupied habitat. Clustering behavior is uncommon among passerines, and pair formation and copulation behavior within Least Flycatcher clusters has not been described previously.

Least Flycatchers are small (10 g), open-cup nesting birds that breed throughout Canada and the United States from early May to late July (Briskie 1994). Sexes are monomorphic. Females build nests alone, but biparental care is common. Double-brooding is rare. Males sing upon arrival at the breeding grounds and estab-

lish territories using song, threat display, and aggressive chasing. We document pair formation and maintenance, and compare within-pair copulation (WPC) and EPC behavior. Least Flycatcher clusters offer a fascinating system for examining mating behavior because territory proximity facilitates observation of copulation behavior. Understanding how Least Flycatchers interact is fundamental to evaluating settlement patterns, mechanisms of cluster formation, and the mating tactics adopted by males and females.

METHODS

STUDY AREA AND GENERAL METHODS

We studied Least Flycatchers from 1997–2000 at Queen's University Biological Station (44°34′N, 76°19′W), a 2,200-ha research facility located 50 km north of Kingston, Ontario, Canada. This area is predominantly mixed-hardwood deciduous forest comprised of sugar maple (*Acer saccharum*), hop-hornbeam (*Ostrya virginiana*), and white birch (*Betula papyrifera*). We mapped the location of territories by monitoring males daily early in the breeding season, noting border disputes, relative positions of male counter-singing, and using song playback. We mist netted and banded arriving individuals using Canadian Wildlife Service and colored leg bands. We banded 12 adults in 1997, 33 in 1998, 34 in 1999, and 19 in 2000. Birds were sexed in the field using differences in behavior, vocal-

TABLE 1. Song performance of Least Flycatcher males for whom before and after pairing data are available ($n = 1$ male in 1997, 2 males in 1998, and 7 males in 1999). Values are mean $\pm$ SE. Three males sang for the entire watch (i.e., a single 60-min song bout) without pausing in 1999.

Song measure	Unpaired	Paired	t_9	P
Song sum (songs hr^{-1})	$1,339.3 \pm 254.1$	191.6 ± 100.4	3.7	0.005
Song rate (songs min^{-1})	24.4 ± 3.9	5.0 ± 1.9	3.8	0.004
Time spent singing (min hr^{-1})	50.5 ± 3.4	22.2 ± 6.6	3.6	0.006
No. song bouts (hr^{-1})	3.9 ± 0.7	5.1 ± 0.1	-1.0	0.34
Mean bout length (min)	25 ± 7.7	3.3 ± 0.8	2.7	0.02

izations, flattened wing chord length, and presence of a brood patch found only in females.

BEHAVIORAL OBSERVATIONS

Behavioral data are based upon 1997–1999 only. Daily visits enabled confirmation of territory residency and pairing status of all singing males. Paired males were those with a female occupying their territory over successive days and who subsequently nested with that female. Female detection was based on conspicuous *whit* vocalizations (Briskie 1994). We were unable to capture all adults, but most of our behavioral data were based on marked individuals. We only included behavioral watches from first nesting attempts to control for possible variation in copulation behavior associated with re-nesting.

Observations of pair behavior were based on 10 pairs and began prior to female arrival to encompass the entire pairing process. We recorded timing of pair initiation, time required for pair formation (determined behaviorally, see below), and behavioral interactions. We also noted pair maintenance behaviors such as nest site selection, incubation feeding, and mate guarding. In 1997 and 1998, we quantified mate guarding as the number of times per hour a fertile female changed location and was followed within 5 m by her mate.

We quantified copulation behavior based on 1-hr focal watches of 51 breeding pairs, as well as anecdotal observations totaling over 4,000 hr. Watches were performed daily during three morning time intervals (06:00–08:00, 08:00–10:00, and 10:00–12:00). We controlled for possible time of day effects (see below). Pairs were observed for a total of 2–4 hr (mean 2.5 $\pm$ 0.1 hr) on different days during the fertile period, except for one pair that was observed for 5 hr, over a 10–11 day period (including approximately 5 days for nest-building). At the end of this sampling period, most females had begun

incubation. Fertile period was defined as the time from nest initiation until laying of the penultimate egg (clutch size $= 4$). Observations for each pair were distributed throughout the fertile period to avoid potential problems of behavioral changes during the fertile period. We recorded the number of successful and unsuccessful WPCs and EPCs, the identity of individuals involved whenever possible, copulation rate (copulations pair^{-1} hr^{-1}), the estimated duration of copulations and incursions onto focal territories (sec), and incursion rate (incursions pair^{-1} hr^{-1}). We also quantified excursions off territory by focal males or females. Incursions were defined as intrusions onto a focal territory (where the male approached the female for EPC) that were interrupted by the resident male prior to attempted mounting. Successful copulations were those achieving cloacal contact (and presumably insemination), and were readily differentiated from unsuccessful copulations. We defined unsuccessful WPCs as copulation attempts by males where the female rejected the mounting attempt by her mate; unsuccessful EPCs were cases where intruding males approached a nonmate female and initiated physical contact with her but were interrupted by the resident male prior to cloacal contact. Estimated timing of copulations was based on the beginning and ending of cloacal contact. During focal watches we also recorded song sum (total number of songs hr^{-1}), song rate (songs min^{-1}), time spent singing (min hr^{-1}), number of song bouts (hr^{-1}), and mean bout length (min) to quantify song performance for males before and after pairing ($n = 10$ males total; see Table 1 for further details). Song bouts were periods of singing separated by periods of silence lasting at least 1 min.

Within-pair copulation rate (including successful and unsuccessful copulations) was used as an estimate of within-pair mating effort

(pair^{-1} hr^{-1}) and compared to extra-pair mating effort (pair^{-1} hr^{-1}) for all pairs included in this study in two ways. First, we used EPC rate (including successful and unsuccessful copulations) as a parameter comparable to within-pair mating effort. We then included incursion rate in our estimate of extra-pair mating effort, to obtain a representative measure of the frequency of extra-pair mating, based on the assumption that the principal purpose of incursions is obtaining EPCs. We are confident that males making incursions were seeking EPCs for four reasons: (1) unpaired males experienced fewer incursions onto their territories than paired males, (2) incursions always involved male-male competition over females, (3) intruders always approached the female, as opposed to the male, and (4) intruders were never seen foraging while on neighboring territories.

STATISTICAL ANALYSES

Pseudoreplication was limited because pairs did not reunite in subsequent seasons. We recognize that multiple copulation events for a given pair within a single season are not independent events, but we included all copulations for an overall representation of mating behavior. We compared male song performance before and after pairing using two-tailed paired t-tests. We used a chi-square test to compare the number of successful versus unsuccessful WPCs and EPCs. Nonparametric tests were used to analyze year and time of day effects and to compare incursion rates onto territories of paired versus unpaired males. We consider differences significant at $P < 0.05$ and descriptive statistics are expressed as mean ± SE.

RESULTS

PAIR FORMATION

Pairs formed quickly as birds arrived at the breeding grounds in early May. Pair formation behavior was only seen when females first arrived on territory, and involved paired, coordinated movements often accompanied by quiet trills from both sexes. Males stopped singing during pair formation. To facilitate description, we have divided pair formation into two phases.

Phase one. Pair formation begins with a male and female moving to within 1 m of each other on the same tree branch. The male commences 180° perch-orientation changes beside the female (behavior that is subsequently imitated by

the female), or the pair may begin with synchronized perch changes for up to 5–8 min. Next, the female either remains with the male or flies off his territory. If the female leaves the territory, the male resumes singing at a rate typical of unpaired males (see below). However, if the female is receptive to courtship, the pair continues with a more elaborate social display.

Phase two. Male and female make several reciprocal short hops or flights toward each other until the pair is side by side trilling quietly. The female may begin silent flights around the territory in concert with the male for 1–3 min before landing in the same area of initial contact. The male then resumes perch changing but accompanies this behavior with wing flutter display, whereby the male assumes a crouch posture with his body leaning slightly horizontal and flutters his wings while puffing out his chest, raising his head, and trilling softly. At this point, the female either stays beside the male and slowly raises and lowers her tail (approximately 30% of females), or the pair flies elsewhere within the territory and forages together, maintaining close proximity (i.e., within 5–10 m) (approximately 70% of females). Pair formation (including phases one and two) lasted 15–20 min, during which time WPCs were never observed. Of the 51 paired males observed, none were found to be subsequently unpaired within a season except in one case in 1999 where the female died. This widowed male did not attract another mate that season. We found no instances of within-season mate desertion or divorce. No pairs reunited the following year based on two banded male returns.

PAIR MAINTENANCE

Once pairs formed, we noted several changes in pair behavior. For example, male song performance decreased significantly post-pairing (Table 1) as found by Lavers (1998). Pairs were maintained by copulation, reciprocal whit "contact" calls, and joint silent flights throughout the territory. Paired males combined whit calls with singing, whereas unpaired males almost always only sang. Paired males and females chose nest sites and foraged together, as well as cooperated in nest and territory defense. All females began nest-building within 2 days of pairing. We never observed courtship feeding during pairing; however, males provisioned their mates during incubation (based on observations of five pairs) in

response to whit begging calls given by females. The rate at which males immediately followed their mates' movements was 0.5 ± 0.2 times hr^{-1} ($n = 22$ observations) in 1997 and 1.5 ± 0.3 ($n = 48$ observations) in 1998.

OCCURRENCE OF COPULATIONS

Frequency. The number of successful WPCs showed significant year effects due to one pair in 1999 that copulated at an unusually high rate (7 to 9 WPCs $pair^{-1}$ hr^{-1}). Year effects were nonsignificant after this pair was excluded from analyses. Male incursions were significantly less frequent in 1999, but other EPC behaviors showed no year effects. Similarly, we found no overall time of day effects in copulation behavior (all $H_2 < 5.43$, all $P > 0.07$). Consequently, we pooled data across years for analyses presented below unless otherwise indicated.

We observed 224 WPCs during focal watches, 43 (19.2%) of which appeared successful. The mean rate of successful and unsuccessful WPCs was 0.3 ± 0.1 $pair^{-1}$ hr^{-1} and 1.7 ± 0.5 $pair^{-1}$ hr^{-1}, respectively, with an overall within-pair mating effort of 2.0 ± 0.5 events $pair^{-1}$ hr^{-1}. The highest observed rate of WPC attempts by males was 23 hr^{-1}. We also witnessed 52 EPCs, 2 (3.8%) of which appeared successful. The mean rate of successful and unsuccessful EPCs was 0.03 ± 0.03 $pair^{-1}$ hr^{-1} and 0.5 ± 0.1 $pair^{-1}$ hr^{-1}, respectively. The overall extra-pair mating effort was 0.5 ± 0.1 events $pair^{-1}$ hr^{-1} excluding incursions, and 1.8 ± 0.3 events $pair^{-1}$ hr^{-1} including incursions. We recorded 135 incursions onto focal territories by neighbors (mean 1.3 ± 0.3 $pair^{-1}$ hr^{-1}) and 26 excursions by individual pair members (mean 0.2 ± 0.1 $pair^{-1}$ hr^{-1}). Thirty additional WPC and 86 EPC attempts were observed outside of focal watches. Successful WPCs lasted approximately 4 sec and always appeared to involve a single cloacal contact, except one copulation that lasted 20 sec with three cloacal contacts; successful EPCs lasted 1–2 sec. Approximately 19% of WPCs were successful, compared to 4% of EPCs; WPCs were therefore almost five times more likely to achieve cloacal contact than were EPCs ($\chi^2_1 = 7.3$, $P < 0.01$). Unpaired males experienced significantly lower incursion rates (number incursions hr^{-1}) than paired males in 1997 (paired [$n = 19$]: 1.3 ± 0.3 vs. unpaired [$n = 3$]: 0.4 ± 0.2; $Z = -1.8$, $P = 0.04$). This same pattern approached significance in 1998 (paired [$n = 20$]: 1.9 ± 0.4 vs. unpaired [$n = 1$]: 0.5 ± 0.3; $Z = -1.7$, $P = 0.07$) but not in 1999 (paired [$n = 12$]: 0.6 ± 0.2 vs. unpaired [$n = 7$]: 0.4 ± 0.2; $Z = -0.8$, $P = 0.30$).

Female copulation behavior. Females initiated 18/43 successful WPCs (41.9%). Seven of 135 incursions onto focal territories (that did not necessarily result in EPCs) were by neighboring females; in two of these instances the female was chased back onto her territory by her social mate, whereupon he copulated with her. Focal females solicited EPCs from neighboring males by either advertising to neighbors while on territory ($n = 19$ observations involving 11 females), or by foraying off territory (6/26 excursions [23%] were by females). Females advertised for EPCs while on territory by whitting quietly and wing fluttering toward extra-pair males near territory boundaries. Two of these observations involved an individual female who successfully obtained an EPC on two different occasions from the same neighboring male. Remaining female solicitations did not result in an EPC because the resident male either chased his mate or the neighboring male away from the boundary ($n = 15$ observations), or landed between his own mate and the neighboring male and gave "alarm" whits (Briskie 1994) ($n = 2$ observations). Mean female excursion rate was 0.1 ± 0.07 excursions hr^{-1}. We could not determine whether these furtive female excursions resulted in EPCs.

FORM OF COPULATIONS

Within-pair. Within-pair copulations were highly conspicuous. On average, males initiated 70% of WPC attempts (41% of which were preceded by pre-copulatory display). In about 30% of attempted mountings, the sex of the initiating bird could not be determined with confidence, however, it is probable that approximately two-thirds of these "unknowns" were males (based on the above percentages). Pre-copulatory display involved the initiating bird approaching his/her mate, perching beside them, and slowly raising and lowering their tail while wing fluttering and quietly trilling. Approximately 50% of male WPC attempts that were not preceded by pre-copulatory display appeared forced; rejected copulation attempts involved chasing and rapid alarm whits given by the female. Alternatively, females sometimes resisted by flying away (and not being pursued by their mates), perch chang-

ing, or by lowering their tail. WPCs were always observed on territory, often near the nest. Within-pair copulations also occurred in mid-flight, with one bird directly on top of the other making cloacal contact ($n = 4$ pairs).

Extra-pair. Extra-pair copulation attempts were predominantly by immediate neighbors within a cluster, although some individuals crossed several territories at once ($n = 10$ observations). When intruders were intercepted by the resident male, EPC attempts escalated into highly aggressive fighting and chasing (resident female followed by intruding and resident male, respectively) accompanied by alarm whits and bill snapping.

DISCUSSION

We observed over 500 copulation events and found that Least Flycatchers copulate frequently and adopt a mixed reproductive strategy whereby individuals pursue copulations with social and extra-pair mates. However, copulations differed in their behavioral characteristics. Within-pair copulations were conspicuous, longer than EPCs, relatively non-aggressive, and frequently were preceded by pre-copulatory display. In contrast, EPCs were covert, brief, highly aggressive, and only involved pre-copulatory display when initiated by females. Other studies that have examined copulation behavior include Cattle Egrets *Bubulcus ibis* (Fujioka and Yamagishi 1981), Little Blue Heron *Florida caerulea* (Werschkul 1982), Indigo Buntings *Passerina cyanea* (Westneat 1987), and Red-billed Gulls *Larus novaehollandiae* (Mills 1994), and report similar behavioral differences as those found in this study. For example, in Cattle Egrets, WPCs often involve male display prior to mounting, and are longer in duration and less aggressive than EPCs. The higher success rate of WPCs versus EPCs in Least Flycatchers also was consistent with these studies. Although we are confident that incursions by males were for the pursuit of EPCs, we cannot rule out the possibility that males could have been attempting to expand their territory or attract additional social mates (Briskie and Sealy 1987).

Least Flycatcher pairs formed quickly following a stereotyped sequence of coordinated interactions. Coordinated nest-site selection, also reported in Nero (1959), presumably functions in pair maintenance and also could enhance nesting success. Least Flycatchers only attempted WPCs

once pairs formed, suggesting that copulation is, at least in part, a means of pair maintenance rather than pair formation. Alternatively, this finding could imply some degree of female choice of copulation partner. We are currently investigating possible cues females may use in social and genetic mate choice.

Limited research has been conducted on pair and copulation behavior in other members of this genus, thereby restricting comparisons among *Empidonax* flycatchers. However, variation does exist in nest-site selection. Buff-breasted Flycatchers *Empidonax fulvifrons* choose nest sites together (Bowers and Dunning 1994), whereas female Acadian Flycatchers *Empidonax virescens* (Mumford 1964) and Hammond's Flycatchers *Empidonax hammondii* (Sedgwick 1994) choose nest sites alone. Although our data show pairs choose nest sites together, de Kiriline (1948) found one female Least Flycatcher selecting a nest site in the absence of her mate. Data on copulation behavior in this genus are limited. We found only one other study reporting two WPCs in Buff-breasted Flycatchers (Bowers and Dunning 1994). To our knowledge, our study is the first to compare within- and extra-pair copulation behavior in *Empidonax* flycatchers. Reports of aggressive interactions involving multi-bird chases, displays, fights, and mate guarding suggest extra-pair mating may be common in this genus.

LEAST FLYCATCHER MATING TACTICS

Least Flycatchers demonstrate considerable propensity for seeking copulations with extra-pair partners. Our data corroborate earlier studies reporting that males may use vocal cues to attract non-mates (Davis 1959), and that incursions are common during female fertility (Hobson and Sealy 1985). Our observations suggest that female Least Flycatchers use multiple mating tactics in pursuing extra-pair mates. Females either foray off territory for EPCs, or solicit EPCs while on territory using whit vocalizations and visual display. Neudorf et al. (1998) have shown similar evidence for multiple mating strategies in female Hooded Warblers *Wilsonia citrina.* Whether females are inciting male-male competition to appraise males (Montgomerie and Thornhill 1989) or are advertising fertility status to neighbors (Neudorf et al. 1998) is unclear. We are currently investigating the extent to which females may behaviorally influence copulation

success. How Least Flycatcher mating behavior in clusters may be linked to settlement patterns, cluster configuration, and social and genetic mate choice remain to be determined.

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