

Are least flycatcher (*Empidonax minimus*) clusters hidden leks?

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We use the natural propensity for least flycatchers (*Empidonax minimus*) to form dense territorial clusters to test the hidden lek hypothesis as an explanation for clustering behavior. The hidden lek hypothesis proposes that socially monogamous males can cluster their all-purpose territories owing to female pursuit of extrapair copulations, analogous to females seeking promiscuous copulations at leks. We define a hidden lek as a cluster of all-purpose territories that resembles a classical lek but whose characteristics are less overt because of larger territory sizes, a pair bond between the territorial male and female, and biparental care. We tested four predictions: (1) clustered males should be preferred by females as social mates; (2) late-arriving males in clusters should settle next to early-arriving males; (3) males near central males should pair before peripheral males; and (4) spatial position (centrality) should explain much of the variation in male social and genetic mating success. Females preferred to pair with clustered males. In clusters, compared with peripheral males, central males arrived earlier, were heavier and in better body condition, and had higher pairing success. Microsatellite profiling from 1999 and 2000 revealed that some extrapair paternity was more common in peripheral nests, but we did not detect a skew in genetic mating success favoring central males. We conclude that least flycatcher breeding clusters resemble hidden leks in some predicted ways, but our data are insufficient to conclude that female mating behavior promotes clustering. We discuss alternative hypotheses for clustering and additional possible ways to test the hidden lek hypothesis in this species. This is the first test of the hidden lek hypothesis in a socially monogamous, all-purpose territorial bird. *Key words*: centrality, cluster, *Empidonax minimus*, hidden lek hypothesis, mate choice, paternity, sexual selection. [*Behav Ecol*]

Territorial clustering occurs in insects (Muller, 1998), fish (Itzkowitz, 1978), reptiles (Stamps, 1988), primates (for review, see Treves, 2000), and birds (for review, see Danchin and Wagner, 1997; Muller et al., 1997; Stamps, 1994). Explanations for clustering have been based mostly on natural selection. In birds, studies have traditionally invoked hypotheses that are related to heterogeneous resource distribution (e.g., food or nest sites; material resources hypothesis; Keister and Slatkin, 1974), reducing nest predation (predation hypothesis; Turner and Pitcher, 1986), increasing foraging success (information center hypothesis; Wittenberger and Hunt, 1985), or excluding heterospecifics (competitive exclusion hypothesis; Getty, 1981). In the past, clustering in birds has meant the aggregation of nesting territories in colonies. Our examination of clustering is in the context of socially monogamous birds that defend all-purpose territories (where copulation, nesting, and feeding co-occur). Clustering has been found in many species, including willow flycatchers (*Empidonax traillii*, Walkinshaw, 1966), willow warblers (*Phylloscopus trochilus*, Tiainen et al., 1983), Kirtland's warblers (*Dendroica kirtlandii*, Morse, 1989), lazuli buntings (*Passerina amoena*, Greene et al., 1996) song sparrows (*Melospiza melodia*, Nice, 1937), blue-black grassquits (*Volatinia jacarina*, Almeida and Macedo, 2001), and dusky bush-tanagers (*Chlorospingus semifuscus*, Bohórquez and Stiles, 2002). However, natural selection may not explain clustering in these species. Here, we test a hypothesis for clustering based on sexual selection.

The hidden lek hypothesis (Wagner, 1998) is a novel explanation for the clustering of all-purpose territories derived from lek mating system theory. Classical leks are assemblies of males that females visit for copulation. Most habitat surrounding the lek remains unoccupied, albeit apparently suitable for

settlement (Westcott, 1993). The sex ratio is male-biased and aggression among males can be intense owing to competition for females. Mating success is often skewed toward central "hotshot" males, such as in black grouse (*Tetrao tetrix*, Alatalo et al., 1996), sharp-tailed grouse (*Pedioecetes phasianellus*, Rippin and Boag, 1974), and bullfrogs (*Rana catesbaiana*, Emlen, 1976). Lekking males do not provide parental care (for review, see Höglund and Alatalo, 1995). The hidden lek hypothesis proposes that the mechanisms producing leks can also produce clusters of all-purpose territories. Just as males at a lek cluster display territories for promiscuous copulations, socially monogamous males can cluster all-purpose territories in response to female pursuit of extrapair copulations (copulations outside the pair bond; EPCs) in species where females engage in extrapair matings (Petrie and Kempnaers, 1998; Stutchbury and Neudorf, 1998).

The hidden lek hypothesis can operate through two models of lek evolution: the female preference model (Bradbury, 1981) or the hotshot model (Beehler and Foster, 1988). In the female preference model, females prefer clustered males in order to facilitate mate appraisal, thereby reducing time and energy costs associated with mate choice (Shelly, 2001). Solitary males are generally avoided, effectively reducing per capita mating success for these males (Westcott, 1997). In the hotshot model, females are attracted to central males. Females around the hotshot subsequently attract additional males to the cluster. Hotshot males are preferred as extrapair mates over other males in a cluster because of their superior attractiveness (Höglund and Alatalo, 1995). As a result, hotshots secure paternity in their own nests and gain extrapair fertilizations (EPFs) in neighboring males' nests. Cuckolded males in the cluster risk paternity loss to the hotshot male, but obtaining some copulations is better than none.

We define a hidden lek as a cluster of all-purpose territories that resembles a classical lek but with characteristics that are

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less overt because of larger territory sizes, a pair bond between the territorial male and female, and biparental care. If mechanisms that form leks can influence the spatial distribution of all-purpose territorial birds, then three critical lines of evidence should be supported. First, males in clusters should be preferred as social mates. Second, females should pursue EPCs, although males may also seek EPCs. Third, extrapair paternity patterns should indicate a skew in male realized reproductive success (RRS) favoring central males, analogous to observed skews at leks. Skews in RRS could be produced by females seeking genetic benefits from central males (Hamilton, 1990; for review, see Boag and Ratcliffe, 2000). The hidden lek hypothesis is compatible with other explanations for clustering, such as reduced nest predation.

We examine the extent to which the hidden lek hypothesis can explain clustering in least flycatchers. In this species, most males establish small, all-purpose territories (mean \pm SE = 0.14 \pm 0.01 ha, n = 101) with contiguous boundaries in unusually dense clusters, whereas apparently suitable adjacent habitat remains unoccupied (Tarof and Ratcliffe, 2004). Clustering is ubiquitous across their breeding range (Davis, 1959; MacQueen, 1950; Perry, 1998; Sherry and Holmes, 1985), although in at least some populations approximately 10% of males are solitary (Tarof, 2001). This conspicuous and consistent clustering provides neighbors with an exceptional degree of access to one another. Sherry and Holmes (1985) examined possible discontinuities in vegetation characteristics as an explanation for clustering in least flycatchers. They concluded that clustering was most likely related to "sociality" rather than habitat, establishing the framework for testing the hidden lek hypothesis as one possible explanation for this behavior.

We tested four predictions. If females prefer clustered males as social mates then (1) clustered males should have higher pairing success than solitary males. To test this prediction, we compared pairing success of clustered and solitary males. We also compared arrival dates, morphology, body condition, and age. For clustered birds, we predicted that (2) late-arriving males would settle next to early-arriving males, and that (3) males near central males would pair before peripheral males. If central males are hotshots, we predicted that (4) spatial position should explain most variation in male social and genetic mating success. The present study is the first test of the hidden lek hypothesis in a socially monogamous, all-purpose territorial bird.

METHODS

Study area and species

We studied least flycatchers at the Queen's University Biological Station (QUBS) near Kingston, Ontario, Canada, from May–July 1997–2000 (44°34' N, 76°19' W). QUBS is a 2200-ha research facility comprising primarily sugar maple (*Acer saccharum*), ironwood (*Ostrya virginiana*), and white ash (*Fraxinus americana*) forests. Clusters ranged in size from two to 30 territories each (mean \pm SE = 7.4 \pm 1.44 territories, n = 21 clusters), occurred at densities of up to 11 territories/ha, and were ephemeral among years. We defined clusters as aggregations of two or more territorial males with contiguous boundaries in the same forest and separated from other conspecifics. Distance between clusters averaged 1244.6 \pm 200.8 m (range = 345.8–2402 m). We defined solitary males as birds with no conspecific neighbors for at least 200 m. The average distance between a territorial solitary male and the next nearest male was 693.1 \pm 108.2 m (range = 312.4–2139 m). We could detect a singing male up to 200 m away. Females build the nest, incubate eggs, and brood nestlings, but both sexes choose the nest site and feed offspring. Four of 98 (4%)

adults returned during this study. One female (but not the male) occupied the same solitary territory in 1999 and 2000. One male returned to the same territory in a cluster in 1999 and 2000; two males returned to different clusters in 1999 than where they were caught the previous year. Therefore, our population was composed almost exclusively of new birds each year. One nestling banded in 1998 returned as a second-year (SY) male to a different cluster in 1999.

We found nests by monitoring nest building females to and from the nest site. Nests (n = 112 first nests and 24 re-nests) were found during building or egg laying. Construction of compact, open cup nests took approximately 5 days, after which females laid one egg per day for 4 days (clutch size = 3.87 \pm 0.06, n = 38 nests). We checked accessible nests (nests under 12 m high; 60% of first nests and 35% of re-nests) every 2–3 days by using an extendible mirror pole to monitor first-egg dates and nest status. For remaining nests we estimated first-egg dates by subtracting 3 days from incubation onset. The fertile period for a given female was the time from nest initiation until laying of the penultimate egg (approximately 8 days). Females copulated throughout this period. We assumed females were not fertile during incubation and brooding.

Field methods

Arrival dates and pairing success

We monitored arrival and settlement for 150 males and 116 females (including four polygynous males with two females each) occupying territories in 21 clusters (six in 1997, three in 1998, five in 1999, and seven in 2000). We also monitored 32 males and eight females occupying solitary territories (including two polygynous males with two females each). Arrival date was recorded as the day a male was first seen establishing a territory (May 1 = day 1). Males arriving overnight were recorded as having arrived the next day. To remove year effects for males in clusters, we performed an ANOVA of arrival date with year as a factor ($F_{3,132} = 21.79$, $p < .0001$) and used residuals in subsequent analyses (Lozano et al., 1996). Male pairing status was based on pair bond formation behavior (Tarof and Ratcliffe, 2000). Pairing date was the day we first observed a territorial male with a female that later copulated and nested with that male. Females were detected by their conspicuous whit calls (Briskie, 1994). We used pairing success (mated or unmated) and pairing date as measures of social mating success (Thusius et al., 2001).

Morphometrics and age

We caught males either by using a playback and decoy between two mist nets or by erecting multiple nets at territory boundaries; females were caught by using the latter technique. A few adults were caught later in the season by using mist nets elevated up to 10 m into the forest canopy. We marked 98 adults with a Canadian Wildlife Service aluminum band and a unique color combination. The sex of all caught adults was confirmed by using molecular markers (Griffiths et al., 1998). Nestlings surviving to at least 7 days of age were marked with an aluminum band on the right leg (n = 16 from five first nests, n = 4 from one re-nest).

We aged adults (SY or after-second year [ASY]) by using rectrix shape (Pyle, 1997) and measured body mass (to nearest 0.1 g), tarsus length, and flattened wing length (to nearest 0.1 mm). Male body mass was negatively related to capture date ($r^2 = .15$, $n = 51$, $p = .005$) so we used residuals to control for variation in mass owing to capture date (Thusius et al., 2001). We removed one outlier by using Cook's D influence test (Sokal and Rohlf, 1995).

We estimated male body condition by using residuals from a regression of residual body mass (corrected for date) on

tarsus length. Male body mass, body condition, and wing length did not differ among years (all $p > .15$). Tarsus length was shorter in 1997 than in other years ($F_{3,54} = 3.37$, $p = .03$). Because tarsus length was the only male morphological trait that varied across years and because variation was restricted to one year, morphometric data were pooled across years.

Mating behavior and song output

We quantified mating behavior and male song output during 1-h focal watches for 51 pairs in clusters from 1997–1999 while females were fertile and in their first nesting attempt. We recorded 10 mating behaviors and four song behaviors (for complete details, see Tarof and Ratcliff, 2000). Pairs were observed for 2–4 h (2.5 ± 0.1 h) during early, mid, and late morning (0600–0800, 0800–1000, and 1000–1200 h, respectively) before and after pairing. We defined within-pair mating activity (per pair per hour) as the number of successful and attempted within-pair copulations (WPCs); extrapair mating activity was the number of successful and attempted EPCs plus the number of incursions onto a focal territory by a neighboring male or female. These variables provided estimates of overall mating activity. We defined excursions (per pair per hour) as the number of extraterritorial forays by a focal male or female. Song output in least flycatchers decreases dramatically after pairing (Tarof and Ratcliff, 2000), so we analyzed pre- and postpair song separately.

Territory mapping

In late June, we obtained Universal Transverse Mercator coordinates (datum NAD 83 Canada, zone 18 north) for territory boundaries in clusters ($n = 101$ territories for 10/21 clusters in total) by using a Trimble single-antenna global positioning system (GPS) unit attached to a TSC1 data logger with real-time correction. This system allowed mapping of territories to within 1-m accuracy during the peak period of breeding activity. All clusters were mapped identically. We used AutoCad Map 2000, version 4.0, and Arcview 3.2a for Windows 95/98 to generate cluster maps. We smoothed boundaries by using “heads-up digitizing” without changing territory position or orientation. We also mapped territories for five solitary males.

We calculated three measures of centrality for territories with known boundaries: (1) the linear distance (in meters) from the geometric center of a territory to the cluster center, (2) the number of adjacent neighbors, and (3) the proportion of the territory perimeter shared with neighbors (Högglund and Alatalo, 1995). We defined a male as central if neighbors completely surrounded his territory or if more than 50% of his boundary was shared. Peripheral males were located along the edge of a cluster, with less than 50% of their boundary shared. Territory size did not increase with distance from cluster center ($r_s = -.07$, $n = 86$, $p = .54$), as might be expected owing to reduced pressure from fewer neighbors toward the cluster edge. Therefore, we were confident in including both centrality and territory size as independent variables in multiple regressions. The proportion of the territory perimeter shared and the number of adjacent territories were correlated with each other ($r_s = .86$, $n = 98$, $p < .0001$).

Microsatellite methods

We used microsatellites to determine rates of extrapair paternity and assign parentage to young for nests sampled in 1998–2000 (Tarof et al., 2001). Five to 50 ml blood samples were collected by brachial venipuncture from 98 adults and stored at 4°C in 1 ml lysis buffer (Seutin et al., 1991). We collected 83 eggs from 22 nests in five clusters (two in 1998 and 1999, one in 2000) because of high natural rates of nest

predation (up to 70%; Tarof, 2001). In three additional nests, nestlings survived to at least 7 days of age, so blood samples were used in DNA extractions ($n = 25$ nests in total; Tarof et al., 2001). In 1998, we collected eggs on day 5 of incubation (date range = May 29–June 21); in 1999 and 2000 we collected eggs upon clutch completion (May 23–June 7 and May 21–June 7 respectively) and incubated embryos for 5 days in a Hova-Bator incubator. Embryos were frozen in 1 ml of $1 \times$ TNE₂ buffer before DNA extraction (Seutin et al., 1991). Females began to re-nest within 3 days of nest loss owing to egg collection, similar to females whose nests were lost owing to natural predation. We were confident egg collection did not trigger changes in cluster location among years because the persistence of manipulated and unmanipulated clusters was similar and adult return rates were low.

We report paternity data based on the social parents of 23 families in five clusters (five families in 1998, eight in 1999, and 10 in 2000), as many neighboring adults as possible, and two solitary families sampled in 1999 (56 adults and 89 young in total). For each nest, both social parents and offspring were sampled except for one nest in 1999 and two nests in 2000 in which the attending female was not caught. One of the 10 families sampled in 2000 included a polygynous male with two females. One of the solitary breeding males also had two females nesting on his territory, but we only obtained paternity data from the primary nest because three of the four nestlings from the secondary nest fledged on the day of sampling. We assumed that nests of different females in the same cluster were independent (Westneat and Gray, 1998). Paternity data were based on a new adult population each year, and adults were unrelated (Tarof et al., 2001). No clusters were sampled completely. Only two solitary families were sampled because so few solitary males paired and adults were difficult to capture.

We determined the number of extrapair young (EPY) in nests and assigned parentage to offspring based on polymerase chain reaction amplification of four polymorphic microsatellite loci (Tarof et al., 2001). Genotypes were scored independently by S.A.T. and M.M.K. for accuracy. We then used paternity inference software CERVUS 2.0 for Windows 95/98 (Marshall et al., 1998; Slate et al., 2000) as an aid for exclusions and assignments. The software was used first to identify potential EPY in nests of breeding pairs; the genotypes of suspected EPY were then checked manually against the genotypes of their parents to confirm their EP status, based on criteria described below. CERVUS was then used to identify candidates for true sires of these EPY. By using genotype data, CERVUS calculates allele frequencies, deviations from Hardy-Weinberg equilibrium, polymorphic information content, null allele frequencies, and exclusion probabilities. A likelihood ratio approach is used to determine parentage of offspring from the pool of candidate sires by evaluating all offspring–sire genotype combinations (maternal genotype known). Computer simulations based on population allele frequencies generate 95% confidence limits for assignments. In conjunction with the high resolving power of microsatellites, CERVUS is an accurate and reliable detector of paternity (Pemberton et al., 1999; Richardson et al., 2001; Slate et al., 2000).

We included the putative male (social father) and all other males sampled each year (as opposed to only the males in a cluster) as candidate sires of offspring to avoid making assumptions about how far birds might travel for EPCs. We set parentage criteria so that the “most likely” and “second most likely” sires were identified for each offspring sampled. We set simulation parameters as follows: 10,000 cycles (default); 75% of candidate sires sampled (population-based); 97.1% of loci typed (from population allele frequencies); and 1% genotyping error rate (default). Increasing the number of

Table 1
PCA of measures of morphology ($n = 41$), song output before ($n = 31$) and after ($n = 50$) pairing, and degree of centrality ($n = 86$) for territorial paired male least flycatchers in clusters

Variable	Principal component		
	1 (PC1 \times)	2	3
Morphology index (PC1$_m$)			
Mass (g)	0.5890	-0.4468	0.6734
Tarsus (mm)	0.5444	0.8352	0.0779
Wing (mm)	0.5973	-0.3207	-0.7351
Eigenvalue	1.178	0.925	0.897
Cumulative variance explained (%)	39.26	70.11	100.00
Song index (pre-pair) (PC1$_{pre}$)			
Sum (number/h)	0.5379	0.0241	-0.2447
Time (/h)	0.4894	0.3011	0.2573
Rate (no./min)	0.4996	0.1256	-0.5832
Number bouts (/h)	-0.1053	0.9028	0.2175
Bout length (min)	0.4587	-0.2791	0.6975
Eigenvalue	3.273	1.137	0.385
Cumulative variance explained (%)	65.47	88.21	95.91
Song index (post-pair) (PC1$_{post}$)			
Sum (number/h)	0.4907	-0.3041	0.1217
Time (/h)	0.4897	0.2411	-0.3578
Rate (no./min)	0.4607	-0.2766	0.6879
Number bouts (/h)	0.2731	0.8643	0.2580
Bout length (min)	0.4824	-0.1606	-0.5635
Eigenvalue	3.589	0.941	0.318
Cumulative variance explained (%)	71.79	90.61	96.97
Centrality index (PC1$_c$)			
Distance to center (m)	-0.5262	0.8488	0.0506
Number adjacent territories	0.5977	0.4116	-0.6880
Proportion territory perimeter shared ^a	0.6049	0.3318	0.7239
Eigenvalue	2.386	0.470	0.143
Cumulative variance explained (%)	79.55	95.22	100.00

The first PC axis (PC1 \times) was used as a male quality index for each of these four sets of variables (see Methods).

^a Arcsine transformed.

cycles did not affect results. Of the 89 offspring, 77 (87%) were genotyped at all four loci. Nine offspring (10%) were genotyped at three loci. Three offspring (3%) were genotyped at two loci. Following the method of Johnsen et al. (2000), offspring were defined as within-pair young (WPY) if they showed a complete match at all loci genotyped with the social parents ($n = 51$ offspring), or had one paternal mismatch ($n = 8$ offspring) but a low probability of chance inclusion for the social male after excluding the mismatched locus (0.0014 ± 0.0018 SD, median = 0.00045; i.e., remaining matches were highly confirmatory because the chance of another male besides the social male conferring them was low). EPY were offspring who mismatched the social male at two or more loci ($n = 30$ offspring). Of the 30 EPY, 24 (80%) matched the most likely candidate sire completely. Two EPY mismatched the most likely candidate sire at one locus and were left unassigned. Four remaining EPY could not be assigned extrapair sires with confidence because they mismatched both the most likely and second most likely candidate males at several loci (see Figure 2). Unassigned offspring were likely sired by unsampled males. We defined RRS as the total offspring sired

by a male in his own nest plus EPY detected in other nests (Gibbs et al., 1990). The total probability of exclusion with both social parents known was 0.997. For EPY, we determined the probability of alleles matching the candidate extrapair male by chance alone based on nonexclusion probabilities calculated by CERVUS. Nonexclusion probability (1 - exclusion probability) was the chance of not excluding a single candidate male that is not related to the offspring. The mean (\pm SD) of these probabilities with both social parents known was 0.016 ± 0.041 ($n = 22$, median = 0.0007); the overall average was $.017 \pm 0.036$ ($n = 30$, median = 0.006).

Statistical methods

We tested for normality and homogeneity of variance and used transformations where necessary. For multiple comparisons, we applied sequential Bonferroni corrections to reduce type I error (Rice, 1989). Tests were two-tailed. Means were expressed with SEs unless otherwise indicated. We analyzed each cluster in each year separately before pooling to check for possible cluster or year effects (pooled results presented wherever possible). We used categorical designations of male position when comparing mean arrival and pairing dates in clusters. Analyses were performed by using JMP 4.02 for Macintosh unless otherwise indicated.

To examine the number of EPY in each nest in relation to year and male traits while controlling for variation in clutch size, we used generalized linear models (GLMs) with binomial errors and logit links (McCullagh and Nelder, 1983) using GLMstat for Macintosh. This analysis used the number of EPY in each nest as the response variable and clutch size as the binomial error term. To test for a random distribution of EPY in nests, we used a chi-square analysis in which the expected number of nests with zero, one, two, or three to four EPY was calculated from 1000 randomizations per nest by using Resampling Stats.

To examine the relative effects of the estimates of male quality used in this study on mating success (morphology, body condition, song output, territory size, and centrality), we used principal component analysis (PCA) and multiple regression. We used PCAs to combine multiple measures of male morphology, song output before and after pairing, and centrality into quality indices as estimated by principal component (PC) scores. The first PC axis (PC1 \times) explained 39.3%, 65.5%, 71.8%, and 79.6% of the variation in male morphology (PC1 $_m$), song output before (PC1 $_{pre}$) and after (PC1 $_{post}$) pairing, and centrality (PC1 $_c$) (Table 1). Next, we used these indices (PC1 $_m$, PC1 $_c$, territory size, and body condition) in multiple regressions to examine how well they explained variation in arrival date, pairing date, extrapair mating activity, and RRS. Song output was analyzed separately because this variable reduced the number of individuals that we could otherwise include in multiple regressions by up to one third.

To aid in the interpretation of nonsignificant results from multiple regressions, we generated confidence intervals around effect sizes (regression slope, b ; Colgrave and Ruxton, 2003; Thompson, 2002). For each predictor in regression models, we calculated confidence intervals around b using the formula $b \pm [(t_{n-2, 1-\alpha/2})(Sb)]$, where Sb is the regression standard error (Kleinbaum et al., 1998).

RESULTS

Clustered versus solitary males

Most males settled in clusters; about 10% of males were solitary (Tarof, 2001). Clustered males (87.2%, 245/281) were more successful at gaining a social mate compared with solitary males (22.7%, 10/44; $\chi^2_1 = 76.36$, $p < .0001$). The

Table 2
Comparison of clustered versus solitary male least flycatchers

Variable	Settlement Status		Test	<i>p</i>
	Clustered (<i>n</i>)	Solitary (<i>n</i>)		
Arrival date	May 11 ± 0.66 (132)	May 11 ± 1.15 (43)	<i>t</i> = 0.59	.56
Body mass (g)	10.46 ± 0.10 (47)	10.17 ± 0.27 (5)	<i>z</i> = -0.96	.34
Tarsus (mm)	18.89 ± 0.10 (46)	18.84 ± 0.27 (5)	<i>z</i> = 0.02	.99
Wing (mm)	64.97 ± 0.32 (46)	65 ± 1.04 (5)	<i>z</i> = 0.48	.63
Body condition ^a	0.55 ± 0.01 (46)	0.54 ± 0.01 (5)	<i>z</i> = -0.23	.82
Age ^b	60% (27/45)	20% (1/5)	$\chi^2 = 3.02$.08
Territory size ^c (ha)	0.14 ± 0.01 (89)	0.29 ± 0.06 ha (5)	<i>z</i> = 2.59	.01

Values are mean ± SE, and *n* = number of males. Most comparisons were tested by using either unpaired *t* tests or Wilcoxon sign rank tests (*z* scores corrected for ties). Male age was compared using a chi-square test.

^a Residuals from regression of residual body mass (corrected for date) on tarsus length.

^b Proportion of ASY males out of the total sampled.

^c Territory size for clustered males similar across years ($F_{3,89} = 0.47$, *p* = .70).

overlapping distribution of arrival dates for clustered versus solitary males indicated that this low probability of pairing for solitary males was not due to the late arrival of these males (Tarof, 2001). Females had the opportunity to pair with solitary males but did not do so. We found no differences between clustered and solitary males in arrival date, morphology, or body condition; the territories of clustered males were significantly smaller than those for solitary males (Table 2). Clustered males tended to be older than were solitary males, although this pattern was not statistically significant.

Patterns of male arrival in clusters

Males arrived approximately six days before (May 11 ± 0.51, *n* = 220 males) females (May 17 ± 0.79, *n* = 89 females; $F_{1,309} = 43.92$, *p* < .0001). Males in a cluster often settled at the same time in “groups” of up to six birds and competed aggressively by using visual displays (chasing, crest raising) and song. Male-male interactions often escalated into physical confrontations up to 60 s in duration (aggression not quantified formally). Before pairing, males sang 1255.4 ± 96.7 songs/h (*n* = 15, range = 0–2406 songs/h). Song output for clustered males that remained unpaired averaged 1509 ± 213.4 songs/h (*n* = 7, range = 0–2951 songs/h).

Early arriving males were heavier ($r_s = -.38$, *n* = 37, *p* = .02) and in better body condition ($r_s = -.36$, *n* = 36, *p* = .04) than were males that arrived late in the season. Arrival date was also correlated with centrality, as estimated by $PC1_c$ scores (Figure 1a). Therefore, early arriving males at clusters were not only heavier and in better body condition than were late-arriving males but also occupied central territories. Arrival date also correlated with distance to cluster center ($r_s = .32$, *n* = 80, *p* = .004), suggesting that later-arriving males at clusters settled next to central males. Male arrival date was not correlated with tarsus length, wing length, or $PC1_m$ (*n* = 36, all *p* > .05). Mean arrival dates were similar for ASY (*n* = 23) and SY (*n* = 16) males (*p* > .05). Arrival date was not correlated with territory size (*n* = 74) or song output before (*n* = 28) or after (*n* = 43) pairing (all *p* > .05), nor was song output before (*n* = 26) or after (*n* = 41) pairing correlated with $PC1_c$ (all *p* > .05). When we analyzed $PC1_m$, $PC1_c$, territory size, and body condition in a multiple regression, males first to arrive at clusters settled closer to the center and were in better body condition (Table 3). In a categorical comparison (controlled for year), central males (May 11 ± 1.1, *n* = 47) arrived earlier than did peripheral males (May 13 ± 0.88, *n* = 63; unpaired $t_{108} = -2.47$, *p* = .02).

Patterns of male pairing success in clusters

Male pairing date was correlated with $PC1_c$ (Figure 1b). Pairing date also correlated with distance to cluster center ($r_s = .29$, *n* = 67, *p* = .02), suggesting that males tended to pair in a sequential fashion toward the periphery of clusters. Pairing date was not correlated with individual measures of male morphology, $PC1_m$, or body condition (all *p* > .05), nor did average pairing date differ between ASY and SY males (*p* > .05). Pairing date was not correlated with male song output before or after pairing or with territory size (all *p* > .05). In a multiple regression, $PC1_c$ was the only predictor of pairing date (Table 3). There was no relationship between the proportion of males that paired in a cluster and cluster size ($r_s = .08$, *n* = 15 clusters, *p* = .78). In categorical comparisons (controlled for year), more central males (94%, 126/134) paired relative to peripheral males (81%, 118/146; $\chi^2_1 = 11.52$, *p* = .0007). Average time to pairing was also lower for central males (5.32 ± 0.71 days, *n* = 37) than peripheral males (7.72 ± 0.69 days, *n* = 39; unpaired $t_{74} = -2.41$, *p* = .02).

Mating behavior

We recorded 224 WPC and 52 EPC events. Within-pair mating activity averaged 2.0 ± 0.5 events/pair/h; extrapair mating activity averaged 1.8 ± 0.3 events/pair/h. Although mating behavior was often brief and obscured by vegetation, several lines of evidence supported the notion that female least flycatchers may seek EPCs. Eleven of 51 paired females appeared to solicit EPCs from neighboring males during the fertile period by advertising to males while on territory (*n* = 19 observations in total). Advertisement was of the general form of females whiff calling quietly and wing fluttering at or near territory boundaries in view of potential extrapair males. In at least two of these 19 cases, the neighboring male copulated with the female. Extraterritorial foray rates averaged .2 ± 0.1 forays/pair/h (*n* = 26). Twenty-three percent (six of 26) of these forays were female-initiated, but we could not determine whether they resulted in EPCs. Incursions onto focal territories averaged 1.3 ± 0.3 incursions/pair/h (*n* = 135); 5% (seven of 135) were by neighboring females. In 15% (eight of 52) of EPC attempts by intruding males involving different females, the females did not appear to avoid male mounting. Two females seemed to accept cloacal contact by raising their tail before mounting by the extrapair male. Remaining EPC attempts were too brief for interpretation (see Tarof and Ratcliffe, 2000).

We tested the prediction that territories closest to the center of clusters would experience greater extrapair mating

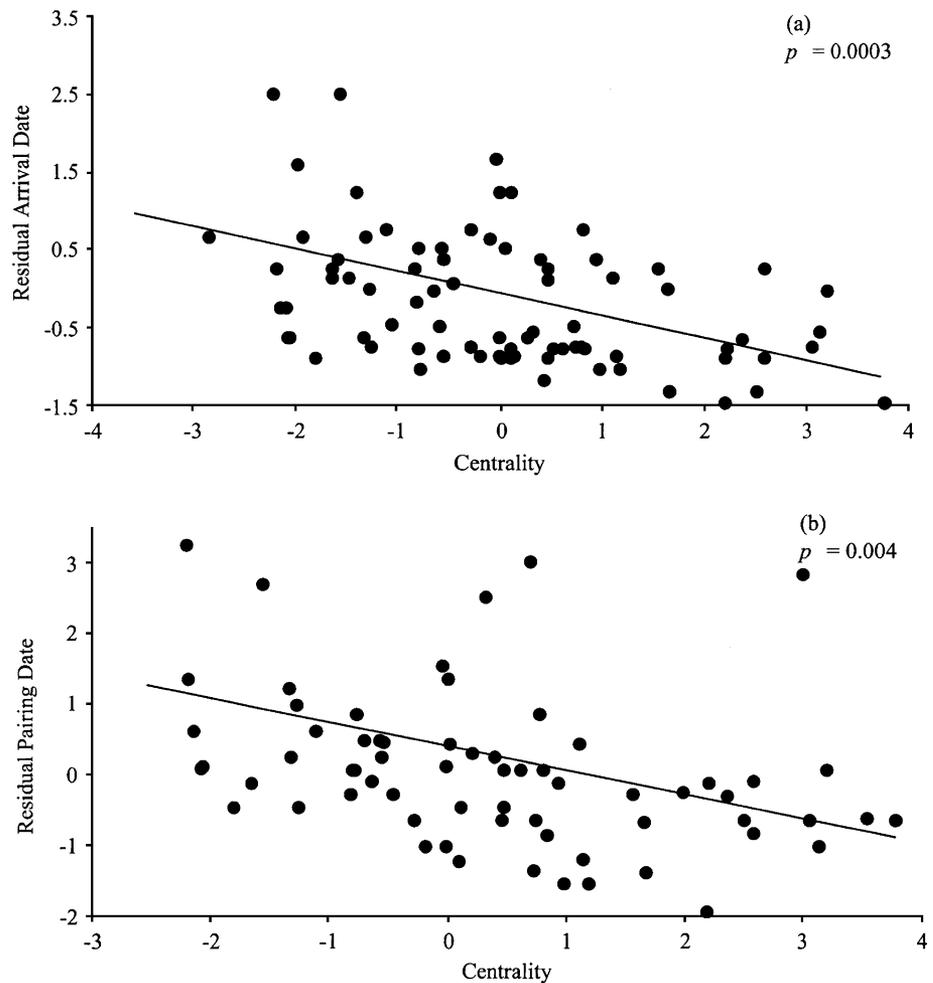


Figure 1

Centrality versus (a) arrival date and (b) pairing date for territorial male least flycatchers of known pairing status in clusters. Residual arrival date and pairing date were used to control for year effects. Large positive residuals correspond with late May. Centrality was estimated using PC_1 scores (see Methods). Regression lines are included to show trends, but analyses were based on correlations. Centrality correlated with arrival date ($r_s = -.42$, $n = 80$, $p = .0003$) and pairing date ($r_s = -.35$, $n = 67$, $p = .004$).

activity based on the idea that females not paired with central males should seek EPCs from them. Extrapair mating activity was not correlated with PC_{1c} ($p > .05$). Extrapair mating activity was also unrelated to PC_{1m} , body condition, and territory size (all $p > .05$) and did not differ for ASY or SY males ($p > .05$). Extrapair mating activity was most explained by PC_{1c} (but not significantly so), but sample sizes may have been insufficient to detect a significant difference (Table 3). This pattern was not owing to having more neighbors as potential intruders because there was no relationship between extrapair mating activity and the number of neighbors in a cluster ($r_s = .26$, $n = 40$, $p = .11$). Within-pair mating activity, incursion rates, and extraterritorial forays did not correlate with PC_{1c} ($n = 40$), PC_{1m} ($n = 21$), territory size ($n = 40$), or body condition ($n = 21$) (all $p > .05$), nor did these behaviors differ between ASY and SY males ($p > .05$). We did not observe EPCs on the territories of solitary pairs.

Patterns of extrapair paternity

Extrapair copulations resulted in EPFs (Figures 2 and 3). We assigned paternity to 93% (83/89) of offspring (81 from clusters and eight from solitary nests) based on candidate males sampled. We excluded two nests from analyses. One nest in the 2000 cluster was excluded because the social male was not sampled (male B in Figure 3). The secondary nest of the polygynous male in this same cluster (based on relative male attendance at each nest) contained three of three EPY; comparing this nest with those of nonpolygynous males could have biased results (male G in Figure 3).

In clusters, EPFs resulted in 39% (30/78) EPY in 62% (13/21) of nests (Table 4). Nine nests (43%) contained mixed paternity, eight nests (38%) had no EPY, and four nests (19%) contained only EPY. Eight extrapair males were adjacent neighbors; six other males sired EPY up to three territories away in the same cluster. Two extrapair males were territory owners in neighboring clusters separated by approximately 400 m of unoccupied forest. Four nests contained multiple extrapair sires (Figures 2 and 3). Two males sired EPY in two and three nests, respectively (see below). We had no evidence for conspecific brood parasitism. The number of EPY in nests did not differ among years (GLM: change in deviance = 1.88, $df = 2$, $p = .39$). EPY were not distributed randomly among nests ($\chi^2_3 = 16$, $p = .001$); there were more nests than expected with either no EPY or three or more EPY. The two solitary nests contained no EPY.

We found no convincing evidence for a skew in male RRS favoring central males. In GLM analyses, we examined the relationship between genetic mating success and male traits in three ways. First, we examined the number of EPY in nests (response variable) versus male traits as separate predictors while correcting for clutch size. In this analysis ($n = 21$ nests), the number of EPY was related positively to male pairing date ($z = 2.58$, $p = .01$), PC_{1m} ($z = 2.83$, $p = .01$), body condition ($z = 2.32$, $p = .02$), and negatively to PC_{1c} ($z = -1.94$, $p = .05$), but not with arrival date ($z = 1.44$, $p = .15$). These relationships involving male morphology and body condition were driven largely by one or two large, central males whose nests contained EPY. When we repeated this analysis including all predictors in a single model, pairing date remained the only

Table 3
Multiple regressions of arrival date, pairing date ($n = 32$), extrapair mating activity ($n = 17$), and RRS ($n = 20$) for territorial male least flycatchers of known pairing status in clusters

Response	Predictors	b (lower, upper)	F	p	t^a
Arrival date	PCI _m	-0.01 (-0.32, .30)	.006	.94	2.04
	PCI _c	-0.22 (-0.40, -0.04)	6.44	.02	
	Territory size	-0.07 (-0.231, .17)	3.24	.08	
	Condition	-0.30 (-0.60, -0.004)	4.56	.04	
$r^2 = .37, F_{31} = 4.05, p = .01$					
Pairing date	PCI _m	-0.12 (-0.59, 0.35)	.34	.57	2.04
	PCI _c	-0.29 (-0.55, -0.03)	5.26	.03	
	Territory size	-0.38 (-2.53, 1.77)	.13	.72	
	Condition	-0.15 (-0.63, 0.33)	.37	.55	
$r^2 = .23, F_{31} = 2.06, p = .11$					
Extrapair mating activity ^b	PCI _m	-0.09 (-0.50, 0.32)	.23	.64	2.131
	PCI _c	0.17 (-0.02, 0.36)	3.26	.09	
	Territory size	-0.26 (-0.211, 1.59)	.09	.77	
	Condition	-0.29 (-0.73, 0.15)	1.97	.19	
$r^2 = .32, F_{16} = 1.44, p = .28$					
Realized reproductive success ^c	PCI _m	-01.2 (-02.65, 0.25)	3.22	.09	2.101
	PCI _c	-0.3 (-01.06, 0.46)	.44	.52	
	Territory size	1.6 (-4.02, 7.22)	.24	.63	
	Condition	0.28 (-1.16, 1.72)	.18	.67	
$r^2 = .26, F_{19} = 1.34, p = .30$					

Predictors of male quality were based on morphology (PCI_m) and centrality (PCI_c) indices calculated from principal component analyses (see Methods), territory size (log transformed), and body condition. Condition was based on residuals from a regression of residual body mass (corrected for date) on tarsus length. Determination of confidence based on calculation of confidence intervals around regression slope, b (lower, upper) (see Methods).

^a Student's t value; based on $t_{n-2, 1-a/2}$.

^b EPC attempts and incursions onto a focal territory.

^c Total number of offspring sired (WPY plus EPY).

predictor of the number of EPY in nests ($z = 2.50, p = .01$). In a multiple regression, we found no predictors of RRS, but confidence in the sample sizes for this analysis was low (Table 3). There was no relationship between extrapair paternity and male age ($G_1 = 2.11, p = .15$). The only result suggesting

higher RRS for central males was from a categorical comparison of the presence/absence of EPY; extrapair paternity was more common in peripheral nests (82%, nine of 11 nests) than in central nests (30%, three of 10 nests; $G_1 = 6.03, p = .01$).

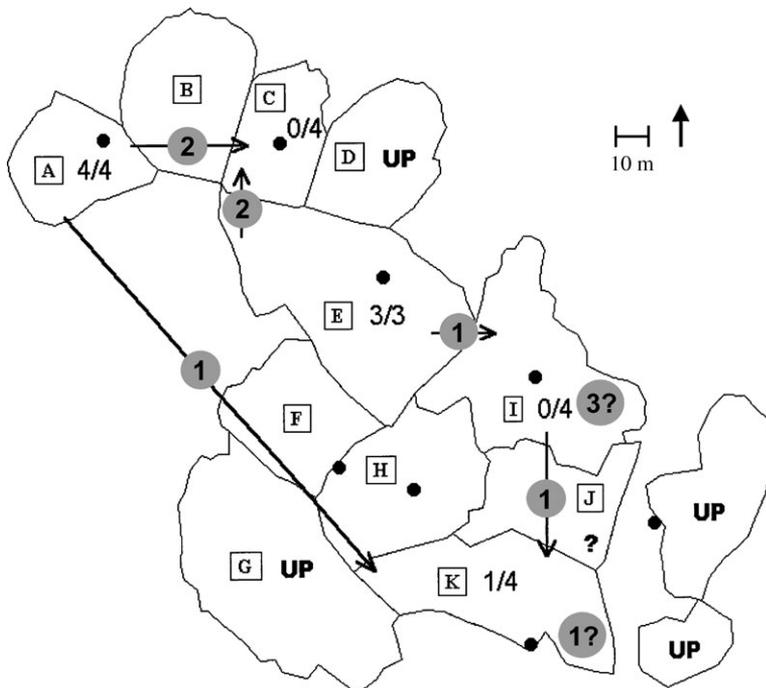


Figure 2
 Paternity map of the 1999 least flycatcher cluster sampled at Skycroft property, QUBS. Territories are labeled with letters. Unpaired males are shown as UP; male J's pairing date was unknown as shown by a question mark. Fractions are the number of within-pair to total young per nest. Arrows identify extrapair sires, without implying which sex forayed off territory, the distance, or route traveled for EPFs. Grey circles at arrow midpoints indicate the number of EPY. Grey circles enclosing a number and question mark in a territory denote unassigned EPY in that nest. Positions of first nests are given by black circles and are from GPS data.

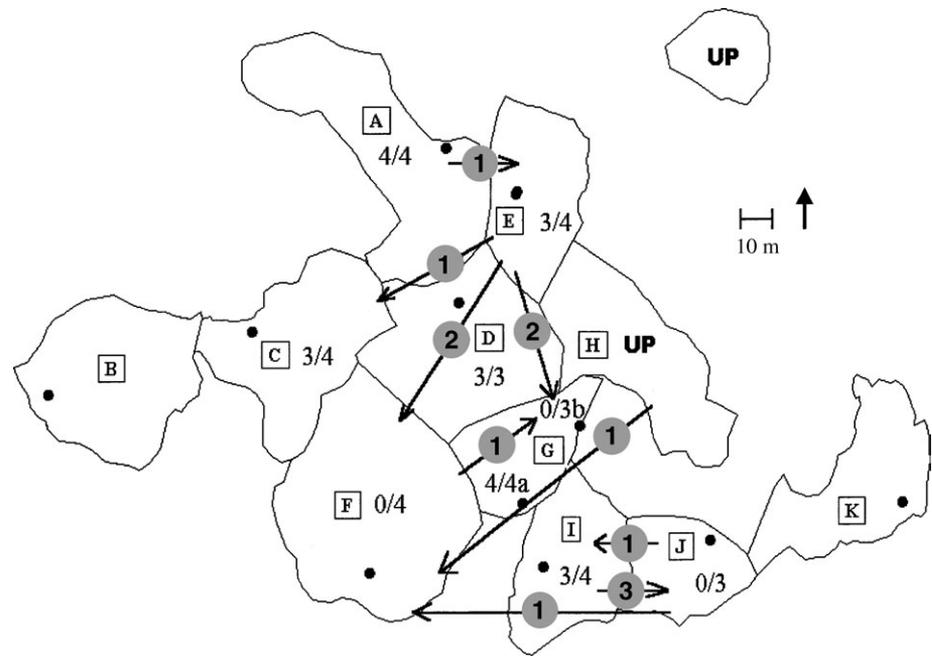


Figure 3

Paternity map of the 2000 least flycatcher cluster sampled at Campground property, QUBS. Symbols explained in Figure 2. Male G was polygynous; his secondary nest was excluded from analysis.

In the cluster sampled in 1999, male E sired three offspring in his own nest plus three additional EPY in two neighboring nests (six offspring total) (Figure 2). This male was also among the first to arrive and pair. We never observed females foraging off territory to visit this male, but the female on territory C gave copulation solicitation displays (whit calls and wing fluttering) at the border between these two territories on at least two occasions. The male with the highest RRS occupied a peripheral territory (male A). In the cluster sampled in 2000, there was no genetic evidence for a hotshot male (Figure 3). In another 1999 cluster (data not shown), two central males secured paternity in their own nests and sired EPY in a peripheral nest. The two clusters from 1998 were sampled insufficiently to draw conclusions.

DISCUSSION

Are least flycatcher clusters hidden leks?

Least flycatcher clusters in our population resembled hidden leks in some, but not all, of the ways predicted. Most males formed dense aggregates of small, all-purpose territories with contiguous boundaries. In these clusters, males sang at high rates presumably to establish territories and attract females, behavior analogous to lekking male courtship display (Höglund and Alatalo, 1995). Prolific song may also attract

additional males to clusters (Morton et al., 1990; Widemo and Owens, 1995). We predicted that clustered males would have higher pairing success compared with that of males settling solitary (prediction 1). Consistent with this prediction, clustered males were more likely to gain a social mate than were solitary males. We found no differences between clustered and solitary males in arrival date, morphology, or body condition, but clustered males tended to be older than were solitary males. We also predicted late-arriving males in clusters would settle next to early-arriving males (prediction 2), and birds near central males would pair before more peripheral males (prediction 3). Arrival and pairing date were correlated with distance to cluster center in bivariate and multivariate analyses. Central males were also heavier and in superior body condition compared with peripheral males. Finally, we predicted that central males would have high social and genetic mating success (prediction 4). Central males were preferred as social mates, but we found no genetic evidence for hotshot males. Although extrapair paternity was more common in peripheral nests, we found no skew in extrapair mating activity or RRS in favor of central males. Keeping in mind that no cluster was sampled completely, this last finding indicates that at least some peripheral males gained EPFs.

Alternative hypotheses for clustering

Alternative hypotheses for clustering are plausible and should be considered. Birds might cluster to take advantage of heterogeneous resources (Keister and Slatkin, 1974), to reduce nest predation (Turner and Pitcher, 1986), or to exclude other species with similar resource requirements (Getty, 1981). If so, then the first two predictions that we tested (female preference for clustered males, late-arriving males settling next to early-arriving males in clusters) could equally be derived from these alternative hypotheses. The third prediction of an association between pairing success and centrality could also stem from these hypotheses, providing their possible effects could be shown to operate at the scale of less than the size of a single cluster.

We have tested the material resources hypothesis in several ways (Tarof and Ratcliffe, 2004). We compared tree species composition plus 11 forest stand structure parameters inside

Table 4

Extrapair paternity from 21 nests in five least flycatcher clusters expressed as the proportion of offspring resulting from EPFs, and the proportion of nests that contained at least one EPY

Year	No. of clusters ^a	Proportion extrapair paternity	
		Offspring	Nests
1998	2 (3/9, 2/30)	32% (6/19)	80% (4/5)
1999	2 (3/5, 5/9)	48% (14/29)	50% (4/8)
2000	1 (8/11)	33% (10/30)	63% (5/8)
Overall	—	39% (30/78)	62% (13/21)

The number of clusters sampled each year is also indicated.

^a Number of territories sampled of the total in cluster.

versus outside five least flycatcher clusters in 1997 and three clusters in 1998 by using univariate and multivariate analyses. Next, we compared forest stand structure for three of these clusters with each of two other forests known to be unoccupied by least flycatchers since at least 1996. Finally, we compared forest stand structure for five sampled solitary least flycatcher territories with those inside two clusters. Vegetation characteristics could not account for clustering. We also compared arthropod biomass inside versus outside two clusters sampled in 1999 and found no differences. That clusters in our population were ephemeral (20/21 clusters formed in different locations among years) further suggests that clustered settlement was not a response to habitat features. To test the idea that least flycatchers might cluster to reduce nest predation, we examined the relationship between predation rates and both territory position in clusters and cluster size. Predation rates were not related with territory position or cluster size. Predation rates were also similar for clustered and solitary breeding pairs (Tarof and Ratcliffe, 2004).

Other least flycatcher studies have tested the material resources hypothesis (Perry, 1998; Sherry and Holmes, 1985). In these earlier studies, and in the current study, results did not support this hypothesis. However, interpretation must be made with caution. The degree of similarity or difference of vegetation characteristics (or arthropod abundance) inside versus outside clusters will depend on the spatial scale at which resources are measured. In addition, least flycatchers in our population might be cueing in on resources that we did not measure (e.g., topography, water proximity). Our ability to test the predation hypothesis was limited because we collected eggs from 22 nests in five clusters for paternity analyses. Anecdotal observations of cooperative nest defense against blue jays involving several neighboring least flycatcher pairs suggest that clustering may indeed be linked to reduced nest predation. We have not tested the competitive exclusion hypothesis, but playback experiments imply that competitively dominant least flycatchers may be able to exclude American redstarts (*Setophaga ruticilla*) from settling in areas where food resources overlap on the breeding grounds (Martin et al., 1996). In our population, American redstart territories rarely overlapped with least flycatcher clusters. In summary, we cannot rule out the possibility that potential benefits of clustering may be related to reduced nest predation and/or resource monopolization.

It is also possible that clustering could be explained by the social mate choice hypothesis, which predicts males should cluster to improve social mate attraction (Allee, 1951; Darling, 1952). If sexual selection favors male aggregation because it facilitates social mate choice (Real, 1990), then settling in a cluster will be expected to be an adaptive male strategy. This may be especially important in birds in which female choice is constrained temporally because of a compressed breeding season (Veen et al., 2001) or in which male parental care is important (for review, see Gowaty, 1996). Our results showing female preference for clustered males over solitary males is consistent with the social mate choice hypothesis. However, this hypothesis cannot explain the relationship between male pairing success and centrality. Moreover, this hypothesis cannot explain the pattern of extrapair paternity being more common in peripheral nests.

Least flycatcher mating behavior and the hidden lek hypothesis

The hidden lek hypothesis has been examined in razorbills (*Alca torda*, Wagner, 1992), purple martins (*Progne subis*, Morton et al., 1990; Wagner et al., 1996), and bearded tits

(*Panurus biarmicus*, Hoi and Hoi-Leitner, 1997), species that breed colonially and not in all-purpose territories. Below we outline one scenario for how the hidden lek might operate in least flycatchers.

Consider the scenario in which female behavior promotes clustering. Most males arrive at the breeding grounds and settle in clusters; some settle solitarily. Males (and possibly territories) vary in quality. Females preferentially visit clustered males to appraise relative male quality, similar to females visiting males at leks. Solitary males are generally avoided and remain unpaired. Female preference for clustered males is the first critical line of evidence required to support the hidden lek hypothesis. Because only one female can pair with a high-quality central male, other females should attempt to pair with males near the central male and seek EPCs from him. Female pursuit of EPCs with central males is analogous to females in classically lekking birds seeking promiscuous matings from central males at leks, and is the second key line of evidence for the hidden lek hypothesis. The third critical piece of evidence necessary to provide the most convincing support for the hidden lek hypothesis is to show that females benefit from EPFs, through genetic benefits for example (for review, see Boag and Ratcliffe, 2000).

We found clear female preferences for males in clusters. Mating behavior data suggested that male and female least flycatchers seek EPCs. Females may be using multiple extrapair mating strategies by soliciting EPCs on territory and/or engaging in extraterritorial forays. One might argue that our results could be explained if males predominantly pursued EPCs. That is, females might prefer clustered males, settle adjacent to central males, and accept EPCs from these males (but resist EPCs from peripheral males). We do not know if female least flycatchers incur costs by resisting EPCs. However, that at least some females can evade males by flying away during copulation attempts or facilitate cloacal contact by remaining in situ and raising their tail during mounting suggests that EPCs are not always accompanied by male aggression and possible risk of injury to females (see also Tarof and Ratcliffe, 2000). The hidden lek hypothesis does not preclude the possibility that males can seek EPCs. However, this male-based scenario is unlikely to maintain cluster stability because sexual selection would favor peripheral males forcing copulations on females. Of the 51 pairs that we observed over 3 years we never witnessed forced copulations by males.

Nonetheless our data are insufficient to conclude that female mating behavior promotes clustering. It is unclear if females in our population solicit EPCs from neighboring males while on territory, or if this behavior typically leads to fertilization. Without data on territory quality, female behavior during forays, and the nesting status of neighboring females, we can only speculate that forays were for EPCs. Extraterritorial forays might instead be related to foraging (see Gray, 1998), conspecific brood parasitism (see Hobson and Sealy, 1990), assessment of neighboring males' quality (see Smiseth and Amundsen, 1995), or a combination thereof (see also Neudorf et al., 1997). In the 4 years of this study we never observed females (or males) feeding on neighboring territories (see also Briskie, 1994), but females were not always in view during forays. Small-scale habitat sampling will be necessary to compare arthropod variation among territories in clusters and to determine if this possible variation is related to mating behavior. Simultaneous radio-tracking of pair members during the fertile and nonfertile periods will be needed to elucidate with greater clarity the frequency and function of forays and the complex nature of least flycatcher mating behavior in clusters. Conspecific brood parasitism is

an unlikely explanation for female forays in our population, based on our genetic data revealing no cases of females laying eggs in the nests of other females. Finally, complete paternity sampling will be necessary to determine potential skews in male genetic mating success and benefits that accrue to females engaging in EPFs.

In conclusion, patterns of male settlement, aggression and song output, and correlations of male arrival, body mass, body condition, and pairing success with centrality support some key predictions of the hidden lek hypothesis. However, one of the most important predictions, that extrapair mating activity and genetic mating success would also relate positively with male position in clusters, was not supported. Current data do not allow us to rule out with confidence alternative hypotheses for clustering or to integrate precisely female behavior with the spatial distribution of males. Centrality in least flycatcher clusters may signal some aspect of male quality to females (Kokko et al., 1999). Other all-purpose territorial birds that have similar resource requirements, such as cerulean warblers (Hamel, 2000) and red-eyed vireos (Cimprich et al., 2000), establish territories that are up to 10 times larger than least flycatcher territories and have unoccupied habitat between neighbors. Least flycatchers seem to have reduced their territory size to an ecological minimum, enabling pairs to cluster in tight social groups that provide improved access to neighbors. It is premature to dismiss the hidden lek hypothesis as an explanation for clustering in least flycatchers. We encourage further tests of the hidden lek hypothesis in this and other territorial birds that cluster, such as the congeneric willow flycatcher (Walkinshaw, 1966), blue-black grassquit (Almeida and Macedo, 2001), or dusky bush-tanager (Bohórquez and Stiles, 2002).

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