

HABITAT FRAGMENTATION AND PATERNITY IN LEAST FLYCATCHERS

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ABSTRACT.—We examined the effect of habitat fragmentation, as well as breeding density and synchrony, on realized reproductive success of male Least Flycatchers (*Empidonax minimus*). Both breeding density and synchrony were similar in both continuous (6.75 males/ha, 3.40; respectively) and fragmented (4.04 males/ha, 2.11; respectively) habitats, and no morphological or territorial variables differed between males in either habitat. The number of nests containing extra-pair offspring was lower in fragmented habitat (11%) compared to the continuous habitat (50%). Males in fragmented habitat attracted secondary mates significantly more often than males in continuous habitat (44%, 0%; respectively) resulting in similar estimates of realized reproductive success in either habitat. Although habitat fragmentation does not appear to affect realized reproductive success of male Least Flycatchers, we suggest that males of this species demonstrate a facultative shift in reproductive tactics. Received 21 April 2008. Accepted 17 September 2008.

The complexity of the environment can influence extra-pair paternity (EPP) rates (Westneat and Sherman 1997) as it can alter success of which females foray off territory and the ability of males to successfully guard their mates (Mays and Ritchison 2004). Landscape fragmentation can also alter habitat complexity as it results in loss of original habitat, a decrease in patch size, and increase in distance between patches (Wilcox and Murphy 1985). These factors are thought to negatively influence forest songbird species, and are most often associated with decreases in songbird diversity (Schmiegelow et al. 1997, Drolet et al. 1999, Trzcinski et al. 1999, Hobson and Bayne 2000). Changes in species assemblages can occur quickly (Stratford and Stouffer 1999), and may be due to decreased patch size and an increase in edge habitat (Walters 1998). Greater edge habitat has the potential to increase predation and brood parasitism rates (Hoover et al. 1995, Robinson et al. 1995), and can also result in decreased fitness due to lower pairing (Villard et al. 1993, Van Horn et al. 1995, Roberts and Norment 1999) and fledging success (Roberts and Norment 1999).

Researchers studying fragmentation have not examined its influence on the EPP rate.

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Rates of EPP are altered by other population dynamic factors including breeding synchrony and density (Westneat and Sherman 1997, Yezerinac et al. 1999, Richardson and Burke 2001). Habitat fragmentation could also alter EPP rates as it alters nearest neighbor distances and population density. Fragmentation decreases foray rates as individuals in fragmented habitat are less likely to cross gaps or enter open habitat (Sieving et al. 1996, Desrochers and Hannon 1997, St. Clair et al. 1998), take longer to travel through fragmented habitat (Bélisle et al. 2001), and return if they foray off territory (Norris and Stutchbury 2001). This can lead to fewer opportunities for intraspecific encounters and fewer extra-pair copulations (EPCs). Further decreases in EPP rates can result from situations in which females control EPCs or primarily foray off territory for EPCs (Mays and Ritchison 2004), because females may be less likely to leave fragmented habitats than males (Norris and Stutchbury 2002).

Least Flycatchers (*Empidonax minimus*) settle in clusters which are all-purpose territories with contiguous borders surrounded by unused habitat (Tarof et al. 2005). Previous research in Ontario examining males settling in continuous habitat has shown there is a high rate of EPP in clusters (37% of nestlings are extra-pair) with 62% of broods containing at least one extra-pair offspring (Tarof et al. 2005). Both males and females have been seen to foray off territory, possibly in search of EPCs, although females seem to control

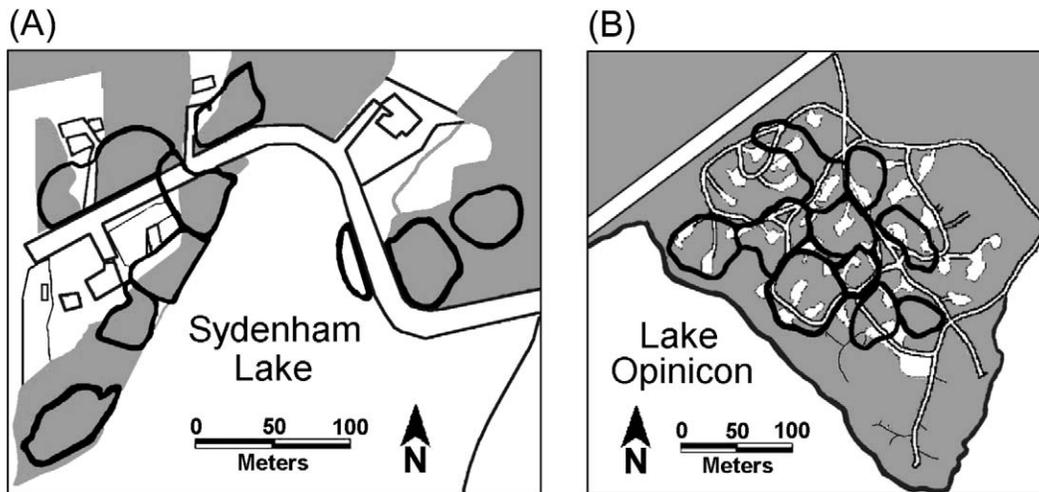


FIG. 1. Fragmented (A) and continuous (B) study sites showing habitat available for settlement (light gray) and location of all territories of Least Flycatchers (outlined in black).

EPCs by either allowing or denying males the opportunity to copulate (Tarof and Ratcliffe 2000). Fragmentation could thus have a large effect on this species since males could no longer form contiguous territories, and foray opportunities for EPCs may decrease.

We examined EPP rates among male Least Flycatchers breeding in continuous versus fragmented habitat to investigate whether variation in male realized reproductive success (RRS, total number of descendant young) is influenced by fragmentation. Our objectives were to compare the EPP rate and male RRS between continuous and fragmented habitats. We also examined whether breeding synchrony and density differed between continuous and fragmented habitat as both of these factors are known to affect EPP rates (e.g., Stutchbury and Morton 1995, Westneat et al. 1990).

METHODS

Study Site.—This study was conducted in 2000 and 2001 near the Queen's University Biology Station (QUBS) south of Chaffey's Lock, Ontario, Canada (44° 34' N, 76° 19' W). The two sites studied were at Sydenham Lake, ~22 km southwest of QUBS and Lake Opinicon, ~3.6 km southwest of QUBS. The proportion of habitat available for settlement was calculated by dividing the area covered by hardwood forests by the area of the polygon that encompassed the entire cluster. Ap-

proximately 71% of the Lake Opinicon site was covered with hardwood forest and suitable for settlement; this site was considered continuous. Only 40% of the Sydenham Lake site supported habitat available for settlement; this site was considered fragmented (Fig. 1). Both study sites were comprised of the same primary tree species, and had similar amounts of canopy cover within forested areas (Kasumovic 2002).

The Lake Opinicon site was studied in 2000 and the Sydenham Lake site in 2001. Only a single site could be studied each year due to the intense mist netting effort required to sample the majority of birds in a cluster. However, we monitored settlement patterns at both sites each year. Clusters of Least Flycatchers also settled in the Lake Opinicon site in 1999 and 2001, and in Sydenham in 1999 and 2000; no individuals settled at the Lake Opinicon site and only three individuals settled at the Sydenham site in 2002 (M. M. Kasumovic, unpubl. data.). Only 4% (4/98) of individuals banded as adults in a previous 4-year study returned to the QUBS area (Tarof 2001), suggesting the return rate is low.

Sampling Methods.—Study sites were surveyed daily, and arrival and pairing dates of all males and females were recorded. Least Flycatchers are an upper canopy species in eastern Ontario (Tarof et al. 2005), and we used mist nets attached to 7-m telescoping

poles (Model 2324, Mr. Longarm, Greenwood, MO, USA) raised into the canopy to capture individuals. Approximately 200 netting hours were spent at each of the two study sites, using a combination of passive netting near nests and a playback lure of conspecific song from a speaker placed below a model of a male Least Flycatcher. Birds were banded with a Canadian Wildlife Service numbered aluminum band and a single plastic colored leg band. All banded individuals were captured within 3 days of arrival and before egg laying. We measured the tarsus length of each individual. Gender of individuals was initially ascertained from tarsus length (Pyle 1997), which was later confirmed by behavior (Tarof and Ratcliffe 2000). We collected 5–30 μL of blood from the brachial vein of adults. Nestlings that survived to day 7 were banded with a single aluminum band and 5–15 μL of blood was collected from the tarsal vein. All blood samples were stored in Queen's Lysis buffer (Seutin et al. 1991).

Nests were located by following females during nest building or by listening to females vocalize from the nest while incubating (Kasumovic et al. 2003b). All female nesting attempts were monitored, and nest building and clutch initiation dates were recorded. Females required a minimum of 4 days to complete nest building and then laid a single egg per day to clutch completion. All accessible nests were monitored each or every other day until clutch completion using an extendable mirror pole. We subtracted the number of eggs from the date found for nests found after clutch initiation to estimate clutch initiation date. We used data on each nesting and re-nesting attempt to calculate an index of breeding synchrony for each female (e.g., Westneat and Gray 1998). We calculated the breeding synchrony index by counting all females that initiated egg laying in the period extending from 2 days prior to clutch initiation by the focal female until she laid her final egg.

First clutches in our study population typically experienced high rates of natural predation (Tarof 2001) and we collected entire first clutches the day after clutch completion (Environment Canada Permit Number CA-0088). We measured success as clutch completion. Typically, females began to re-nest 1–3 days after egg removal, and no subsequent

clutches were collected. Collected eggs were incubated for 7 days in a ©HOVA-BATOR incubator, and frozen until DNA extraction later within the laboratory. We considered a family complete if all young and both social parents were sampled, and partial if all young and only a single social parent were sampled.

Spatial Analyses.—All territories were mapped using Global Positioning System (GPS) following Tarof et al. (2005). Territory boundaries were smoothed using 'heads-up digitizing' in AutoCAD Map 2000 Release 4.0 (Autodesk), and exported into ImageTools Version 3 (UTHSCSA 2002) as a JPEG file, where territory size, perimeter, and centroids could be calculated. Both nearest neighbor and mean neighbor distances were calculated using centroid data for each territory. We used two different methods to calculate settlement density within each cluster. Overall density was calculated by creating a minimum convex polygon around the entire cluster, measuring the area of this polygon, and dividing the number of territories by the area of the cluster. This calculation measured the density of individuals given the habitat constraints. The second calculation of density was similar except that all habitat unsuitable for settlement within the study site (e.g., marshes, fields, lakes etc.) was removed. This measure gave an estimate of the density standardized for available habitat, which could be compared between study sites.

Paternity Assignment.—DNA was extracted within the laboratory and four loci were used to analyze paternity: EMIZ1, EMIZ27, EMIC23, and EMID46 (Tarof et al. 2001). DNA amplification followed Tarof et al. (2005). Paternity was analyzed using programs GERUD1.0 (Jones 2001) and CER-VUS2.0 (Marshall et al. 1998) following Kasumovic et al. (2003a).

Statistical Analyses.—We used JMP 4.02 and SAS Version 8 (SAS Institute Inc. 2000) for all statistical analyses. *t*-tests were used for all pair-wise comparisons involving males and clusters. Paternity (the proportion of young in a nest sired by the male) is not normally distributed but may be binomially distributed. We used separate logistic models (GENMOD in SAS) to analyze whether there was a difference in the EPP rate between habitats and whether the EPP rate was correlated with hab-

itat type, territory size, and tarsus length. These analyses used a logit link and assumed a binomial distribution. We used a General Linear Model (GLM) to analyze whether RRS was correlated with habitat type, territory size, and tarsus length. We used linear regressions to examine if breeding synchrony was associated with other fertility variables. We used a General Linear Mixed Model (GLMM) to examine whether there was any correlation between number of extra-pair young within the nest, and the length of the female's fertile period and breeding synchrony only in the continuous habitat because there was only a single case of EPP in the fragmented habitat. All values are expressed as mean ± SE; test statistics were considered significant at α = 0.05. We provide 95% CI for all non-significant results.

RESULTS

The overall sex ratios were 1:0.9 (male:female) in the continuous cluster and 1:1.2 in the fragmented cluster, not significantly different from 1:1 or from each other (binomial test, all *P* > 0.66). Pairing success in the fragmented cluster (78%, 7/9) was not different (Fisher's exact test, *P* = 0.37) from that in the continuous cluster (90%, 9/10). We calculated the time required for males to pair by subtracting the male's pairing date from his arrival date. Time to pair did not differ between habitats (continuous: 6.9 ± 1.5 days; fragmented: 4.6 ± 1.1 days; 95% CI: 3.4–10.4 days, 1.6–7.6 days, respectively; *t* = 0.84, *df* = 13, *P* = 0.41). Clutch size did not differ between nests in continuous (3.9 ± 0.2; 95% CI: 3.7–4.1) versus fragmented habitat (3.8 ± 0.2; 95% CI: 3.2–4.3) (*t* = 0.60, *df* = 16, *P* = 0.55). Four males in the fragmented cluster attracted a second mate (44%; 4/9), but there were no instances of males attracting second mates in the continuous cluster (0%; 0/10) (Fisher's exact test, *P* < 0.001). Only two of the four males that had a second mate were successful in producing young with both mates.

Mean territory area and perimeter did not differ between the two study sites (both *P* > 0.05, Table 1). Overall density was lower in the fragmented site due to significant increases in nearest neighbor and mean neighbor distances. The mean number of neighbors per

TABLE 1. Territorial features of clusters in continuous (*n* = 10 males) and fragmented (*n* = 9 males) habitats. Corrected density excludes uninhabitable areas such as roads and water. Values are mean ± SE, 95% C.I. in parentheses.

Variables	Continuous		Fragmented		<i>P</i> -value
	Mean ± SE	95% C.I.	Mean ± SE	95% C.I.	
Area, m ²	1361.06 ± 167.95	(981.14–1740.98)	1590.60 ± 266.57	(938.32–2242.88)	0.64
Perimeter, m	168.07 ± 13.02	(137.30–198.83)	171.38 ± 13.72	(137.58–216.65)	0.86
Nearest neighbor distance, m	39.77 ± 3.08	(34.27–45.26)	52.99 ± 3.25	(42.01–65.10)	0.009
Mean neighbor distance, m	80.88 ± 7.44	(66.55–95.20)	130.74 ± 7.84	(103.11–160.37)	0.0002
# of neighbors	3.50 ± 0.36	(2.47–4.53)	1.67 ± 0.38	(1.02–2.41)	0.003
Density, males/ha	6.75		4.04		

territory in the fragmented habitat was also significantly lower due to the decrease in available habitat.

Eleven males were genetically identified in the continuous cluster, although only 10 settled within the cluster. Nine of these males successfully paired, and one male remained unpaired. The last male was not observed within a territory but only identified as a father in one of the nests, and was therefore not used in any further analyses. We sampled 10 nests in the continuous cluster (5 complete and 5 partial families) within the continuous site. Nine males were genetically identified within the cluster in the fragmented site. Seven of these males successfully bred (2 with second mates), one pair abandoned their territory after nest collection, and two males remained unpaired. We collected eight nests (4 complete and 4 partial families) in the fragmented habitat. All nests sampled were first nests. All young were assigned paternity from males within the cluster, except for a single young from the continuous cluster where paternity was assigned to the unknown male that was not sampled. We collected 67 DNA samples from young; 37 from the continuous cluster and 30 from the fragmented cluster. Five of 10 (50%) nests in the continuous cluster and one of eight (11%) in the fragmented cluster contained extra-pair young (EPY). There were two males in the fragmented cluster with two females each and we combined each of their nests to simplify the analysis. There was a significant difference between the number of EPY in the different habitats in our logistic model ($\chi^2 = 10.53$, $df = 14$, $P = 0.0012$). There were multiple extra-pair fathers for some nests in the continuous cluster, but the number of sires did not differ between clusters (mean \pm SE; continuous: 1.7 ± 0.3 , fragmented: 1.1 ± 0.3 ; $t = 1.46$, $df = 16$, $P = 0.16$). All but one of the extra-pair sires in the continuous cluster were immediate neighbors. The only extra-pair sire in the fragmented cluster occurred two territories and 250 m away.

We examined the relationship between the number of extra-pair young and cluster, territory area, and tarsus length using GENMOD in SAS. Males with a larger tarsus sired more extra-pair young ($\chi^2 = 8.00$, $P = 0.005$), and there was a non-significant trend towards a

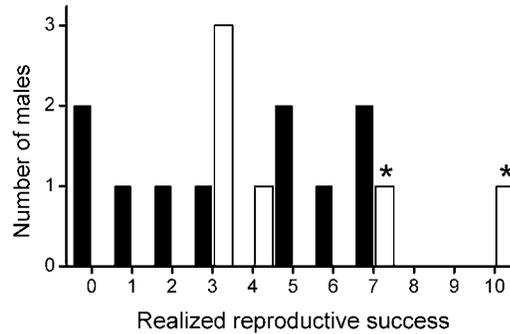


FIG. 2. Distribution of male realized reproductive success in continuous (black) and fragmented (white) clusters. Asterisks represent males that successfully produced offspring with two females.

difference in the number of extra-pair young sired by males between habitats ($\chi^2 = 2.80$, $P = 0.09$). However, there was no effect of territory size on the number of extra-pair young ($\chi^2 = 0.83$, $P = 0.36$). The distribution of RRS for the continuous and the fragmented cluster varied (Fig. 2). We used a GLM to examine whether RRS depended on cluster, territory area, and tarsus length. Males with a larger tarsus had greater RRS ($\chi^2 = 5.47$, $P = 0.019$). There was no effect of territory size ($\chi^2 = 0.80$, $P = 0.37$) or habitat (continuous: 3.6 ± 0.98 , fragmented: 4.0 ± 1.1 ; 95% CI: 1.6–5.6, 1.4–6.9; $\chi^2 = 2.18$, $P = 0.14$) even though differences between habitats were in the same direction.

There was no difference between the number of eggs within the nest and RRS (2.8 ± 0.5 , 3.6 ± 0.9 ; respectively) ($t = 0.79$, $P = 0.44$) for males in the continuous cluster, although there was an increase in variance (0.78 , 1.30 ; respectively). There was no difference in the fragmented habitat between the number of eggs within the nest and RRS, most likely due to the low EPP rate. The variance in RRS (2.45) was higher in the fragmented habitat than the continuous habitat due to males attracting second mates.

Analysis of breeding synchrony was based on 10 females from the continuous cluster and nine females from the fragmented cluster. Breeding synchrony did not differ between the continuous (3.40 ± 0.47 ; 95% CI 2.41–4.39) and fragmented habitat (2.11 ± 0.49 ; 95% CI 1.07–3.15; $t = 1.89$, $df = 17$, $P = 0.075$). We also examined whether the fertile period of

nests that contained extra-pair young overlapped with the fertile period of the female of the extra-pair sire. Four of the six nests that contained extra-pair young did not have overlapping fertile periods. Synchrony in both habitats was significantly negatively correlated with laying date ($r^2 = 0.34$, $F_{1,17} = 8.79$, $P = 0.009$), but not with length of a female's fertile period ($r^2 = 0.056$, $F_{1,17} = 1.01$, $P = 0.33$). The number of EPYs was not correlated with fertility length in our GLMM ($F = 0.85$, $P = 0.47$) or breeding synchrony ($F = 2.08$, $P = 0.20$) in the cluster in continuous habitat.

DISCUSSION

Our results suggest that habitat fragmentation can potentially influence the EPP rate of Least Flycatchers settling in continuous and fragmented habitats. Our EPP results from the cluster in the continuous habitat were similar to EPP rates in four other clusters in 2 previous years (Tarof et al. 2005). This suggests a high EPP rate is common in this species when males settle contiguously in continuous habitat. In contrast, there was only a single instance of EPP in the fragmented habitat along with an increase in the rate at which males attracted second mates. Neither pairing success nor time to pair differed for males in either habitat, suggesting that males did not differ in attracting mates. Males in either habitat did not differ in tarsus length, suggesting the fragmented habitat does not contain lower quality males. Male success at siring extra-pair young in both habitats increased for males with a larger tarsus; males in both habitats performed equally in all aspects of breeding success that we were able to measure. However, due to egg collection, we were not able to identify whether predation rates or fledging success differed between habitats. Thus, our conclusions regarding reproductive success should be regarded with caution. However, these factors suggest fragmentation has few negative effects on mate attraction and clutch size in this species. We suggest that habitat type affected how males maximized RRS. There are potential year effects since clusters were studied in 2 different years, but all the measured variables were similar to previously published values for this species (Tarof 2001). This suggests that a habitat rather than a year effect is more likely for the ex-

planation in differences in EPP and secondary mate attraction rates.

Differences in breeding synchrony and density (Westneat and Sherman 1997) are possible explanations for differences in EPP rates between populations. However, breeding synchrony was similar in both habitats suggesting it is not the main explanation for the decrease in EPP. Four of the six extra-pair sires fertilized females outside of their own female's fertile period, suggesting that Least Flycatcher males attempt extra-pair fertilizations when their female is not laying eggs. High rates of EPP in the continuous cluster may be a by-product of the contiguous borders and proximity of other territories (Westneat and Sherman 1997), as extra-pair young are usually sired by neighboring males (e.g., Yezerinac et al. 1995, Perreault et al. 1997). Male settlement patterns were similar in both clusters with males settling as near as possible to one another given available habitat; the lone exception was a single male in the fragmented cluster. However, density decreased and nearest neighbor distance increased in the fragmented habitat due to gaps of unsuitable habitat between territories. This suggests that even when settling in fragmented habitat there is a strong propensity for Least Flycatchers to settle near one another.

The EPP rate decreased in the fragmented habitat, while the rate at which males attracted a second mate increased. The attraction of a second mate has not been previously documented in other Least Flycatcher clusters studied in continuous habitat in southeastern Ontario (Tarof 2001), and only a single occurrence was documented in over 125 nesting attempts in a population at Delta Marsh, Manitoba, Canada (Briskie and Sealy 1987). Only three instances of males attracting a second mate have been previously observed in our study population; all in the same territory in 3 different years with three different males. These males were solitary (no other Least Flycatcher territories within 500 m), and defended a territory larger than average, which was in continuous habitat (M. M. Kasumovic, unpubl. data). Males with second mates had larger than average territories and were separated by gaps from neighboring males. Therefore, attracting second mates may occur where males can defend sufficient territory to accom-

modate multiple females. Males in both habitats gained similar RRS suggesting fragmentation does not appear to alter mating success in this species, although there are differences in how males maintain their RRS. Whether this is because habitat fragmentation may elicit a facultative change in Least Flycatchers from searching for EPCs in continuous habitat to attracting secondary mates in fragmented habitat, or because male strategies are the same but success rates of attempted EPCs differ in both habitats is unknown.

Most studies have shown that forest songbirds usually avoid fragmented habitat or settle there only after primary continuous habitat is fully occupied (Matthysen and Currie 1996, Huhta et al. 1998). Our study demonstrates that Least Flycatchers settle in fragmented habitat despite the availability of abundant continuous habitat nearby, but that male spacing and settlement patterns may differ due to habitat availability. Our results suggest that further research studying EPP rates and behavior in birds in fragmented habitat may help explain why birds continue to settle in fragmented habitat, and how individuals attempt to maximize fitness when EPCs are more difficult to acquire.

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