



REDUCED PREDATION AT INTERIOR NESTS IN CLUSTERED ALL-PURPOSE TERRITORIES OF LEAST FLYCATCHERS (*EMPIDONAX MINIMUS*)

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ABSTRACT.—Predator deterrence has been widely studied as a potential advantage of colonial breeding. We extend the predator-deterrence hypothesis to the Least Flycatcher (*Empidonax minimus*), a noncolonial species that clusters its all-purpose territories, leaving apparently suitable habitat unoccupied. Under the hypothesis that Least Flycatchers' alarm calls deter some predators from hunting inside their nesting clusters, we predicted that the rate of nest predation would be lower for interior nests than for those on the periphery. In 1995 and 1996 in north-central Minnesota, we monitored 157 Least Flycatcher nests from nine nesting clusters, with locations ranging from directly on the edge to 170 m in from the edge. Using proportional hazards regression, we assessed the effect of distance to cluster edge on nest success. The models best supported by the data all indicated higher success for interior nests, with 34–38% lower predation hazard. This result is the first evidence of reduced predation within nesting clusters of a species that defends all-purpose territories. Combined with earlier results demonstrating a dramatic response by Least Flycatchers to a live predator, our results lend substantial support to the predator-deterrence hypothesis. Received 3 January 2007, accepted 7 December 2007.

Key words: clustered nesting, *Empidonax minimus*, Least Flycatcher, nest predation, predator-deterrence.

Reducción de la Depredación en Nidos de Interior en Agrupaciones de Territorios de Uso General en *Empidonax minimus*

RESUMEN.—La disuasión de los depredadores ha sido ampliamente estudiada como una ventaja potencial de la reproducción colonial. Extendimos esta hipótesis de disuasión de depredadores a *Empidonax minimus*, una especie no colonial que agrupa sus territorios de uso general dejando hábitat aparentemente apropiado desocupado. Bajo la hipótesis de que las llamadas de alarma de *E. minimus* disuaden a algunos depredadores de cazar en las áreas en que se agrupan los nidos, predijimos que las tasas de depredación de nidos serían más bajas para los nidos de interior que para aquellos que se encuentran en la periferia. Entre 1995 y 1996 monitoreamos 157 nidos de *E. minimus* pertenecientes a nueve agrupaciones de nidos en el centro norte de Minnesota. Las posiciones de los nidos variaron entre directamente en el borde hasta el interior a 170 m desde el borde. Utilizando regresiones de riesgo proporcional, determinamos el efecto de la distancia al borde del grupo de nidos sobre el éxito de los nidos. Los modelos mejor apoyados por los datos indicaron un mayor éxito para los nidos de interior, con un 34 a 38% menos riesgo de depredación. Este resultado es la primera evidencia de reducción de la depredación en agrupaciones de nidos, en una especie que defiende territorios de uso general. En combinación con resultados anteriores que demostraron una fuerte respuesta por parte de *E. minimus* ante un depredador vivo, nuestros resultados brindan evidencia substancial para apoyar la hipótesis de disuasión de depredadores.

IN SOME BIRD species that defend all-purpose territories, individuals cluster their territories, leaving apparently suitable habitat unoccupied. Several hypotheses to explain clustered nesting in the forest-nesting Least Flycatcher (*Empidonax minimus*) have been proposed: (1) habitat heterogeneity, (2) food-resources heterogeneity, (3) competitive exclusion, (4) hidden lek, and (5) predator deterrence. The first three have been evaluated at least once without garnering support (Sherry and Holmes 1985,

Canterbury 1993, Perry and Andersen 2003, Tarof and Ratcliffe 2004). The hidden-lek hypothesis, in which females prefer clustered territories for easier access to extrapair mates (Wagner 1998), received mixed support from Tarof et al. (2005). Perry and Andersen (2003) found evidence of predator deterrence in Least Flycatcher clusters, whereas Tarof and Ratcliffe (2004) did not. Here, we further investigate the predator-deterrence hypothesis.

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In Least Flycatchers, collective antipredator behavior takes the form of a chorus of alarm calls in response to predators inside clusters (Perry and Andersen 2003), including corvids and hawks (E. F. Perry pers. obs.). Least Flycatcher clusters produce alarm calls out of proportion to the density of breeding birds (Perry and Andersen 2003). For example, when the density of breeding birds was only 0.87–0.89 birds ha⁻¹ greater inside clusters than outside, the number of alarm calls given in response to experimental presentation of a Broad-winged Hawk (*Buteo platypterus*) was 5.8× greater inside. This difference resulted from the high calling frequency of Least Flycatchers and the relatively infrequent calling by all other bird species (Perry and Andersen 2003). Inside Least Flycatcher nesting clusters, a predator is faced with far more alarm calls than in the surrounding forest, even though the abundance of prey (birds or their nests) is only slightly greater.

A chorus of alarm calls may deter predation and promote clustering by confusing predators (Curio 1978, Ficken 1989), alerting neighbors to a predator's presence (e.g., Hoogland and Sherman 1976), or prompting predators to hunt elsewhere (Curio 1978, Woodland et al. 1980, Hasson 1991, Alvarez 1993, Zuberbühler et al. 1999). Perry and Andersen (2003) observed Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*) less frequently inside clusters than outside, which suggests that some nest predators may be influenced by Least Flycatcher alarm calls. Although predators could potentially use alarm calls as a cue to help find nests, Least Flycatchers avoid their nests while giving alarm calls (E. F. Perry pers. obs.), thereby reducing this risk. Across the Least Flycatcher range, apparent nest success ranges from 38 to 58%, with predation accounting for 66–97% of failures (Briskie 1994, Perry 1998).

The dramatic alarm-call response of Least Flycatchers to a predator and the possible reduction in corvid numbers inside clusters suggest that this territorial species may cluster to reduce nest predation through predator deterrence (Perry and Andersen 2003). Three predictions of this hypothesis are that (1) solitary nests experience a higher predation rate than clustered nests, (2) nests in small clusters experience higher predation than those in larger clusters, and (3) nests on the periphery of clusters experience higher predation than interior nests. We were unable to test the first two predictions because no Least Flycatchers nested solitarily in our study area (Perry 1998) and some clusters were so large that measuring their full size was impractical. We tested the third prediction, for which one previous test produced negative results (Tarof and Ratcliffe 2004). Here, we report the first evidence of higher predation at cluster edges for a species that defends all-purpose territories.

METHODS

Study area.—We conducted our study in 1995 and 1996 on six 25- to 65-ha plots of mature northern hardwoods in north-central Minnesota (described in Perry and Andersen 2003).

Mapping clusters.—We placed orange flagging labeled with grid coordinates at 25-m intervals throughout the study plots to facilitate mapping and navigation. We mapped nesting clusters by recording the approximate point locations of Least Flycatchers detected by sight or sound during 3-min (DellaSala and Rabe 1987), 50-m radius counts at points spaced 100 m apart throughout the

plots. Singing males were often audible >100 m away, but estimating their locations was most accurate within 50 m (they were not marked). Despite their dull coloration, Least Flycatchers are conspicuous, and they call with great frequency (Tarof et al. 2005). Our goal was not to complete a census but to identify which portions of the plots were occupied and which were not. Two clusters extended hundreds of meters beyond the gridlines of the plots, and four others extended shorter distances. We did not survey beyond plot boundaries and concentrated our cluster-mapping and nest-searching within the plots, because delineating the entire clusters would have diverted effort from locating and monitoring nests (and maximizing sample size). Consequently, we were unable to evaluate whether predation rate was related to cluster size.

We conducted all surveys between 0500 and 1200 hours CST in appropriate weather (wind speed estimated at <12 km h⁻¹ and rain not heavy enough to impair our ability to hear calls 50 m away). We sometimes extended surveys later in the day than recommended for point counts because Least Flycatchers continued to call frequently (E. F. Perry pers. obs.) and so that we could survey large clusters in a single morning. In 1995, we surveyed each cluster in late May (during territory establishment) and a second time in early July (peak fledging time). In 1996, we surveyed clusters four times: late May, early June, late June, and early July. In 1995, we counted only male Least Flycatchers heard giving the *chebec* song; in 1996, we counted all individuals, regardless of sex. Although some birds with fledged chicks may have moved off their territory by early July, these males no longer gave the *chebec* song, so we avoided counting them in 1995. In 1996, when we may have counted some birds off their territory in July, we avoided using them to delineate clusters by excluding areas occupied during only one survey (see below).

We plotted the locations of Least Flycatchers recorded during the six surveys on grids representing the six plots, using ARC/INFO, version 3.5 (ESRI 1995), geographic information system (GIS) software. The plots revealed dense clusters of Least Flycatcher observations, clearly distinguishing occupied and unoccupied areas. To delineate clusters, we drew 40-m-radius circles around observations from all six surveys. Forty meters is slightly less than the average diameter of Least Flycatcher territories in similar habitat, assuming circular territories (Martin 1960, Sherry 1979). In 1995, we delineated boundaries of the clusters by combining all 40-m-radius circles from the two surveys. In 1996, we delineated clusters by including all the area inside circles during at least two of the four surveys. We considered occupied areas separated by <80 m (two territory widths) to be disjunct parts of the same cluster.

We found two nests in 1995 and three in 1996 outside delineated clusters, which indicates that the mapping method was not perfect, but these nests were <20 m from delineated cluster edges. Although mapping all individual territories of marked pairs in a cluster would have provided a more precise delineation of cluster boundaries, mapping the large number of territories in our plots (~300) would have precluded finding and monitoring enough nests to adequately address our primary research question. The 3-min point-count surveys enabled us to map each plot in one morning and objectively estimate cluster boundaries. The edges of clusters are often obvious even to casual observers, who can hear songs and calls in one direction but not the other, and our field observations confirmed that mapped edges coincided with cluster boundaries.

Nest predation.—From mid-May to mid-July each year, four or five people searched for nests of all bird species on study plots, both inside and outside Least Flycatcher clusters. We hung a pink flag 5–20 m (horizontal distance) from each nest to aid in relocation and checked all nests every 3–5 days, and every 2–3 days near expected hatch or fledge dates, to assess status. Using mirror poles, we observed the contents of nests ≤ 5 –7 m high. If no clues (e.g., a destroyed nest or visible nestlings) indicated the status of higher nests, observers viewed nests for ≥ 20 min to determine whether nests were being visited by adults or whether nestlings were present. After one to five observations with no activity, depending on visibility, we presumed that nests had fledged or failed. We considered nests that fledged at least one chick to be successful, but we rarely observed fledglings. We estimated each nest's expected fledge date on the basis of estimated dates of initiation (date of first egg laid), start of incubation, and hatch for individual nests and average length of incubation and nestling periods (Ehrlich et al. 1988, Briskie 1994). If parents stopped visiting a nest after incubation had commenced but before chicks could possibly have fledged, we assumed, on the basis of observations of lower nests, that the eggs or chicks had been removed by predators (Perry 1998). When we observed large chicks bulging out of nests within two days of expected fledging and, at a later check, observed no activity, we considered the nest successful. Without direct evidence, such as observing mature chicks, we considered nest fate unknown (Manolis et al. 2000).

In 1995 and 1996, we measured the distance from each Least Flycatcher nest to the closest estimated edge of its nesting cluster (to nearest 1 m) on GIS maps. Along irregular edges, we ignored indentations and protrusions < 40 m wide because these were narrower than average territory size in similar habitat. We did not map cluster edges with 1-m precision, and the measured distance to edge can be no more precise than our mapping. However, we used these distances as measures of relative proximity of nests to the edges of clusters, not as absolute measures of nest location in relation to cluster edges. For some analyses, we categorized nests into 40-m intervals on the basis of average territory

size. When sorting nests into these broad categories, our mapping error should cause relatively few nests to be categorized incorrectly. Distance as a continuous variable was more sensitive to mapping error, which should have reduced our ability to detect a trend in nest success. In our analyses of distance to cluster edge, we treated distance as both categorical and continuous variables, because this approach allowed us to maximize the use of our nest data.

Data analysis.—For nests categorized by year (1995 vs. 1996) and as peripheral or interior (< 40 m from edge vs. > 40 m), we estimated nest success using the Mayfield (1961, 1975) method, which calculates the probability of a nest surviving each day. We estimated these probabilities for the incubation and nestling periods (combined) but not for the egg-laying period. Average period lengths are 13.5 incubation days and 14.5 nestling days (Ehrlich et al. 1988, Briskie 1994) for Least Flycatchers. We present Mayfield rates as the probability of a nest surviving the full length of both periods combined, with standard deviations calculated as described by Hensler and Nichols (1981). We calculated exposure-days for the incubation period by counting the days a nest was under observation between the start of incubation and estimated nest failure or egg hatch. For nests with known fate, nestling exposure-days included the observation days between estimated hatching and the estimated end date, which is half-way between the last observed active date and the first inactive date. For nests with unknown fate, exposure-days ended on the last active date (Manolis et al. 2000).

To examine the effects of predictor variables on nest survival, we used proportional hazards regression, employing the COXPH function in SPLUS, version 7.0 (Insightful Corporation 2005). Among several new approaches for analyzing nest survival (Jehle et al. 2004), proportional hazards regression has two distinct advantages. First, nests with uncertain nest fate can be included in the analysis (Manolis et al. 2000, Nur et al. 2004). Nest fates can be difficult to determine (Weidinger 2007) and, in the present study, we had relatively high numbers of nests with unknown outcome (Table 1). Nest intervals with unknown outcome must be excluded

TABLE 1. Least Flycatcher nests from the interior and periphery (< 40 m from edge) of clusters in 1995 and 1996 combined in north-central Minnesota.

Cluster	Males detected ^a	Hectares ^b	Interior nests			Peripheral nests		
			Successful nests	Failed nests	Unknown fate ^c	Successful nests	Failed nests	Unknown fate ^c
Bro	84 ^d	24	6	9	2	0	3	2
Ced	49	23	13	7	2	0	3	2
Crt-E	42	19	11	3	4	1	3	0
Crt-W	19 ^d	9	10	13	2	1	3	0
Net-N	5	3	1	0	1	2	0	0
Net-S	24 ^d	10	5	3	2	1	0	0
Osp-N	21 ^d	9	3	5	4	0	0	0
Osp-S	23 ^d	10	2	6	1	0	5	1
Por	35 ^d	16	5	5	2	0	0	1
Total			56	51	20	5	17	6

^aHighest count of four counts of singing males inside 1996 clusters.

^bAs mapped in 1996, within plot boundaries.

^cData from nests with unknown fate were included in nest-success estimates and proportional-hazards regression models (Manolis et al. 2000).

^dCluster extended beyond plot boundaries, not surveyed completely.

from analysis in other advanced approaches, such as the nest-survival model in MARK (Dinsmore et al. 2002) or the logistic-exposure method (Shaffer 2004). A second advantage of proportional hazards regression is that it has well-developed theory, practical applications, diagnostics, and graphics, because of its extensive use in medical studies (Nur et al. 2004) over the past 30 years.

We used the “Efron” method of handling ties in failure times and counting-process notation to allow for left truncation of start times for nests that we found after the first day of egg laying. To compare models, we used the information-theoretic approach described by Burnham and Anderson (2002). This approach uses Akaike’s information criterion (AIC; Akaike 1973) to select the model best supported by observed data among a set of carefully chosen *a-priori* models. Our *a-priori* candidate set of models included combinations of the following predictors: distance to nearest cluster edge, cluster, distance*cluster interaction, year, and year*distance interaction. We chose these variables because distance to cluster edge was the main variable of interest, and nest success is known to vary across sites and years (E. F. Perry unpubl. data). We modeled distance*cluster and distance*year interactions because we hypothesized that the magnitude of edge effects could vary among sites or years. We tested for nonproportional hazards using the COX.ZPH function in SPLUS, which employs the approach developed by Grambsch and Therneau (1994). The tests indicated nonproportional hazards among clusters ($P < 0.05$ for cluster; $P > 0.05$ for all other variables), so in subsequent models we adjusted for this nonproportionality via stratification (stratum = cluster in the COXPH statement). An assumption of proportional hazards models is that effects of continuous covariates are linear in the log hazard. We checked this assumption by examining Martingale residuals, as recommended by Klein and Moeschberger (1997). Because the maximum number of parameters considered in our candidate model set was large in relation to sample size, we used a modification of AIC (AIC_c), as recommended by Burnham and Anderson (2002). Again following Burnham and Anderson (2002), we calculated Δ_i (the difference between the lowest AIC_c value and all other AIC_c values for the candidate model set) and w_i (Akaike weights; i.e., approximate probabilities that a given model is the best model in the set of models considered).

We conducted two model comparisons, treating distance to cluster edge as continuous and categorical variables in one comparison and as a categorical variable in the other. When using distance as a continuous variable, we excluded 22 nests ($n = 127$) from analyses because of uncertainty in distance to closest cluster edge (i.e., nests closer to plot edge than cluster edge). Categorical analyses made it possible to increase sample size by classifying these nests into two (<40 m, ≥ 40 m; $n = 149$) or three (<40 m, $40\text{--}80$ m, and >80 m; $n = 140$) distance categories. We excluded eight nests from all models for several reasons: because we were uncertain that predation was the cause of nest failure, because activity at the nest was observed only once (resulting in 0 observation days), or because we were uncertain of the nest age at the beginning and end of observation (a requirement of proportional hazards regression).

Examination of survival plots from the three-category models revealed that survival curves for $40\text{--}80$ and >80 m were very

similar. This suggested a nonlinear distance effect and, potentially, a better fit with a two-category than with a three-category model (i.e., predation hazard decreased up to a certain distance and then leveled off). Examination of Martingale residual plots provided further evidence that a two-category model was more appropriate than a three-category model. In a single assessment, we compared 10 models, including models with distance as a continuous variable and models with distance grouped into two and three categories. To compare this model set using AIC_c , we used the set of nests with known distance to cluster edge ($n = 127$), because a common data set is a requirement of AIC comparisons. For models that included distance to cluster edge as a continuous variable, we estimated distance effects (and 95% confidence intervals [CI]), expressed as the percent change in predation hazard over a 40-m-distance change from cluster edge to interior, to be comparable to categorical analyses. For models that included distance as a categorical variable, we expressed the estimated distance effect as percent change in predation hazard from the edge-most category to farthest interior category. Although the choice of 40-m intervals for categorical analyses was nonarbitrary (based on average Least Flycatcher territory size in other studies), it is possible that other cut points could result in better model fit. Thus, in our final model-refinement stage, we used the log-likelihood approach described by Klein and Moeschberger (1997) to determine the optimal cut point between categories (where log likelihood was maximized).

RESULTS

We mapped nine distinct nesting clusters of Least Flycatchers on the six study plots in 1995 and 1996. Three plots each contained two clusters; the remaining three each had one cluster. All nine clusters were in the same locations both years. Boundaries of some clusters shifted between years, increasing the area of some clusters to a small degree in 1996 (Perry 1998). Disjunct portions of clusters were separated by ≤ 50 m, and the two closest clusters were 130 m apart. Three of the clusters were surveyed completely, and the remaining six extended beyond plot boundaries. The highest count (of four counts) of singing males in 1996 ranged from 5 in the smallest cluster, which was surveyed completely, to 84 in the largest, which was not surveyed completely (Table 1).

We found 157 active nests in the nine clusters, 67 in 1995 and 90 in 1996. With the number of territories involved and the difficulty of finding nests high in the canopy, these nests represent only a portion of all Least Flycatcher nests in the clusters. These open-cup nests were located in vertical crotches at heights ranging from 1.3 m to >20 m (median = 10.0 m). The most interior nest we found was 170 m from the cluster edge. In 1995, apparent nest success was 0.34 ($n = 56$, 11 nest fates unknown). In 1996, apparent nest success was 0.55 ($n = 69$, 21 nest fates unknown). Mayfield rates of nest success were 0.40 ± 0.06 in 1995 ($n = 66$) and 0.67 ± 0.05 in 1996 ($n = 88$). Combining 155 nests from both years, 28 were <40 m from cluster edges and 127 were >40 m from cluster edges (Table 1). Mayfield rates of success were 0.37 ± 0.09 ($n = 27$) for peripheral nests and 0.57 ± 0.05 ($n = 125$) for interior nests.

TABLE 2. Proportional-hazards regression model comparisons for Least Flycatcher predation hazard, including models with a continuous distance variable and models with two (<40, >40 m) and three (<40, 40–80, >80 m) category distance variables ($n = 127$). All models included cluster as a stratifying variable.

Parameters	K^a	AIC_c	Δ_i	w_i	Distance effect ^b	Distance effect 95% CI
Two distance categories and year	3	265.894	0.000	0.506	–34.2	–52 to –9
Continuous distance and year	3	268.895	3.001	0.113	–28	–56 to 4
Three distance categories and year	5	269.188	3.294	0.098	–39	–57 to –13
Distance only, continuous	1	269.615	3.721	0.079	–20	–48 to 0
Year only	1	269.826	3.932	0.071		
Two distance categories	2	270.112	4.218	0.061	–27	–47 to –1.2
Three distance categories	3	271.466	5.572	0.062	–32	–52 to –4
Three distance categories, year, and distance*year	6	272.357	6.463	0.020	–36.9	–62.3 to 5.6
Continuous distance, year, and distance*year ^c	5	272.667	6.773	0.017		
Three distance categories, year, and distance*year	8	275.481	9.587	0.004	–30	–59 to 21.3

^aNumber of estimable parameters in the model.

^bFor models with a continuous distance variable, expressed as the percent change in nest predation hazard over a 40-m distance interval from cluster edge to interior. For models with categorical distance variables, expressed as percent change in predation hazard from the edge-most category (<40 m) to farthest interior category (≥40 m or >80 m).

^cDistance-effect results not reported because the distance coefficient was unreliable, because of missing data in some distance*year and cluster strata combinations.

Best-supported models in two comparisons showed strong evidence of higher predation near the edges of clusters. The first comparison included models with continuous distance and two- and three-category distance variables (Table 2; $n = 127$). The best-supported model included a two-distance category variable and year. The estimated change in predation hazard from the <40-m category to the ≥40-m category was –34% (95% CI: –52 to –9). The second comparison included models with distance only as a two-category variable (Table 3; $n = 149$), and for this set of models we used a refined cut-point between the two categories (45 m), because this was the cut-point that maximized the log likelihood among a set of all possible cut-points (present in the data) between 20 and 100 m (Klein and Moeschberger 1997). The best-supported model included distance and year, and the estimated change in predation hazard from the <45-m category to the ≥45-m category was –38% (95% CI: –53 to –16). In this model, the estimated change in predation hazard when comparing 1996 with 1995 was –41% (95% CI: –55 to –22).

DISCUSSION

Within the nine Least Flycatcher nesting clusters we studied, interior nests exhibited significantly higher nest success than peripheral nests. Because 97% of nest failures in our study area failed as a result of predation (Perry 1998), we conclude that nest predation was lower at interior nests. This result is the first evidence of reduced predation within nesting clusters of a species that defends all-purpose territories. Combined with results of an earlier study (Perry and Andersen 2003) that demonstrated a dramatic response by Least Flycatchers to a live predator, our results lend substantial support to the hypothesis that clustered nesting in Least Flycatchers serves to deter predators.

Predator deterrence is a widely documented factor in the formation of bird colonies, and it can be achieved in a variety of ways, including swamping, selfish-herd effects, and collective antipredator behavior (reviewed by Wittenberger and Hunt 1985). One prediction of the selfish-herd theory is that nests at the edges

TABLE 3. Proportional-hazards regression model comparisons for Least Flycatcher predation hazard, where distance to cluster edge was a categorical variable (<45 m, ≥45 m) ($n = 149$). All models included cluster as a stratifying variable.

Parameters	K^a	AIC_c	Δ_i	w_i	Distance effect ^b	Distance effect 95% CI
Distance and year	4	319.850	0.000	0.823	–38	–53 to –16
Distance, year, and distance*year	6	324.132	4.282	0.10	–40	–66 to 6
Year	2	324.631	4.782	0.075		
Distance only	2	330.236	10.386	0.004	–28	–46 to –5

^aNumber of estimable parameters in the model.

^bExpressed as percent change in predation hazard from the edge-most category (<45 m) to the farthest interior category (≥45 m).

of a colony are at greatest risk of predation. Even though our results are consistent with this prediction, neither the selfish-herd effect nor swamping is likely to be operating in Least Flycatcher nesting clusters. Their nests, though clustered, constitute only a fraction of the nests of all bird species in their forested habitat (Perry and Andersen 2003). The totality of prey is not concentrated, and the theories of swamping and selfish herds explain concentrations of prey.

Collective antipredator behavior, on the other hand, could potentially reduce predation rates in the interior of Least Flycatcher clusters. Although colonial-nesting birds often drive predators out of the nesting area with mobbing behavior (e.g., Elliot 1985, Robinson 1985, Wiklund and Andersson 1994, Picman et al. 2002; reviewed by Wittenberger and Hunt 1985), Least Flycatchers do not mob predators within clusters (Perry and Andersen 2003). They attack predators that approach their own nests (attacks on chipmunk and ground squirrel reported by MacQueen [1950]), but even if they sometimes prevent nest predation, individual nest defense would provide no benefit to clustered nesting. Instead, the collective antipredator behavior of Least Flycatchers is the broadcast of a chorus of incessant alarm calls in response to predators inside clusters (Perry and Andersen 2003).

A chorus of alarm calls may promote clustering and reduce predation at interior nests by confusing predators (Curio 1978, Ficken 1989), alerting neighbors to a predator's presence (e.g., Hoogland and Sherman 1976), or prompting predators to hunt elsewhere because they can no longer surprise their prey (Curio 1978, Woodland et al. 1980, Hasson 1991, Alvarez 1993, Zuberbühler et al. 1999). If alarm calls confuse predators, a stronger chorus in the interior would interfere to a greater extent with a predator's ability to hunt. If alarm calls alert neighbors to a predator's presence, more calling neighbors would better alert individuals to a predator. This mechanism requires that alerted individuals are better able to deter predation, such as by avoiding their nests when a nest predator is present (as observed by E. F. Perry). If alarm calls prompt predators to hunt elsewhere, a stronger chorus would better indicate to a predator that it had lost the element of surprise, prompting it to hunt where prey are not so clearly aware of its presence. This mechanism could reduce nest predation by predators that search for bird nests by watching unaware adults visit their nests or by predators that depredate nests opportunistically.

Regardless of the mechanism of reducing predation, nest predators that generally approach from outside the clusters, rather than residing within them, may find nests near the edges of clusters before the full chorus of alarm calls develops. Predators with home ranges larger than the clusters, such as corvids, hawks, and medium-sized mammals, are most likely to approach from outside clusters, whereas small mammals that depredate nests probably reside within them. We do not know which predators are important to Least Flycatchers on our study plots in northern Minnesota. Alarm calls have been observed in response to corvids and hawks (E. F. Perry pers. obs.) but not in response to Red Squirrels (*Tamiasciurus hudsonicus*) or Eastern Chipmunks (*Tamias striatus*), which were much more common (Perry and Andersen 2003). The only predator observed at a nest was a Blue Jay. Perry and Andersen (2003) detected Blue Jays and American

Crows less frequently inside clusters than outside, but this correlation does not indicate whether Least Flycatchers cluster to avoid corvids or whether corvids avoid their clusters. Other potential predators of arboreal nests include flying squirrels (*Glaucomys* spp.) and American Martens (*Martes americana*). We observed a few Common Garter Snakes (*Thamnophis sirtalis*) on the plots, but never above the ground. The cause of the decrease in nest predation from 1995 to 1996 may have been a population decline in whichever predators were primarily responsible for predation on Least Flycatcher nests.

In a similar study in Ontario, Tarof and Ratcliffe (2004) found no difference in predation rate between interior and peripheral nests or between solitary nests and those in clusters. At least two differences between Tarof and Ratcliffe's (2004) study and ours could account for different results. First, our sample size of nests was considerably larger (149 from 9 clusters vs. 58 from 10 clusters), which resulted in greater statistical power. Second, the Ontario clusters were much smaller, on average, than those in our study, likely because of habitat differences (7 territories per cluster vs. 24 per cluster, where not all clusters were completely surveyed; Perry and Andersen 2003). Perhaps Least Flycatchers cluster all-purpose territories for some reason unrelated to anti-predator behavior, but large clusters have the additional advantage of reducing predation. In addition, the study periods were only two years and three years, respectively, and, by chance, results from either study may not be representative of longer-term patterns in nest success.

Our results indicated reduced predation in the interior of Least Flycatcher nesting clusters, and a previous study (Perry and Andersen 2003) demonstrated greater and faster alarm response to predators within nesting clusters. However, it is not yet evident that alarm calls lead to reduced predation. Whether they do depends on which predators are most responsible for nest depredation (Kruuk 1964, Hoogland and Sherman 1976, Brunton 1997) and whether they are deterred by Least Flycatcher alarm calls. Additional study of predator behavior near clusters is necessary to demonstrate whether predators avoid the interior of clusters and, if they do, what mechanism is involved.

Greater understanding of the social behavior of Least Flycatchers, in addition to their antipredator behavior and the behavior of predators, will also contribute to understanding the phenomenon of clustered nesting. Two studies (Mills et al. 2006, Fletcher 2007) have explored the role of conspecific attraction in the establishment of Least Flycatcher territories. This behavior could be the mechanism that draws Least Flycatchers together and gives them the benefits of clustered nesting, whether those are reduced predation or access to extrapair mates (Tarof et al. 2005). Further research into the hidden-lek hypothesis could reveal that social behavior and predator deterrence act in concert to promote clustered nesting in this species.

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LITERATURE CITED

- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in *Second International Symposium on Information Theory* (B. N. Petrov and F. Csáki, Eds.). Akadémiai Kiadó, Budapest.
- ALVAREZ, F. 1993. Alertness signalling in two rail species. *Animal Behaviour* 46:1229–1231.
- BRISKIE, J. V. 1994. Least Flycatcher (*Empidonax minimus*). In *The Birds of North America*, no. 99 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- BRUNTON, D. H. 1997. Impacts of predators: Center nests are less successful than edge nests in a large nesting colony of Least Terns. *Condor* 99:372–380.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- CANTERBURY, G. 1993. *Modelling habitat use in forest songbirds*. M.Sc. thesis, University of Minnesota, St. Paul.
- CURIO, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie* 48:175–183.
- DELLASALA, D. A., AND D. L. RABE. 1987. Response of Least Flycatchers *Empidonax minimus* to forest disturbances. *Biological Conservation* 41:291–299.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOFF. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- EHRLICH, P. R., D. S. DOBKIN, AND D. WHEYE. 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, New York.
- ELLIOT, R. D. 1985. The exclusion of avian predators from aggregations of nesting Lapwings (*Vanellus vanellus*). *Animal Behaviour* 33:308–314.
- ESRI. 1995. *Understanding GIS: The ARC/INFO Method*. ESRI, Redlands, California.
- FICKEN, M. S. 1989. Are mobbing calls of Steller's Jays a "confusion chorus"? *Journal of Field Ornithology* 60:52–55.
- FLETCHER, R. J., JR. 2007. Species interaction and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76:598–606.
- GRAMBSCH, P. M., AND T. M. THERNEAU. 1994. Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika* 81:515–526.
- HASSON, O. 1991. Pursuit-deterrent signals: Communication between prey and predator. *Trends in Ecology and Evolution* 6:325–329.
- HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. *Wilson Bulletin* 93:42–53.
- HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46:33–58.
- INSIGHTFUL CORPORATION. 2005. *S-Plus 7 for Windows User's Guide*. Insightful, Seattle, Washington.
- JEHLE, G., A. A. YACKEL ADAMS, J. A. SAVIDGE, AND S. K. SKAGEN. 2004. Nest survival estimation: A review of alternatives to the Mayfield estimator. *Condor* 106:472–484.
- KLEIN, J. P., AND M. L. MOESCHBERGER. 1997. *Survival Analysis: Techniques for Censored and Truncated Data*. Springer, New York.
- KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). *Behaviour (Supplement)* 11:1–129.
- MACQUEEN, P. M. 1950. Territory and song in the Least Flycatcher. *Wilson Bulletin* 62:194–205.
- MANOLIS, J. C., D. E. ANDERSEN, AND F. J. CUTHBERT. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117:615–626.
- MARTIN, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. *Ecology* 41:126–140.
- MAYFIELD, H. [F.] 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MAYFIELD, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456–466.
- MILLS, A. M., J. D. RISING, AND D. A. JACKSON. 2006. Conspecific attraction during establishment of Least Flycatcher clusters. *Journal of Field Ornithology* 77:34–38.
- NUR, N., A. L. HOLMES, AND G. R. GEUPEL. 2004. Use of survival time analysis to analyze nesting success in birds: An example using Loggerhead Shrikes. *Condor* 106:457–471.
- PERRY, E. F. 1998. *Clustered nesting of Least Flycatchers (Empidonax minimus) in north-central Minnesota*. M.S. thesis, University of Minnesota, St. Paul.
- PERRY, E. F., AND D. E. ANDERSEN. 2003. Advantages of clustered nesting for Least Flycatchers in north-central Minnesota. *Condor* 105:756–770.
- PICMAN, J., S. PRIBIL, AND A. ISABELLE. 2002. Antipredation value of colonial nesting in Yellow-headed Blackbirds. *Auk* 119:461–472.
- ROBINSON, S. K. 1985. Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *Auk* 102:506–519.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- SHERRY, T. W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwood forest. *Auk* 96:265–283.
- SHERRY, T. W., AND R. T. HOLMES. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests. Pages 283–309 in *Habitat Selection in Birds* (M. L. Cody, Ed.). Academic Press, London.
- TAROF, S. A., AND L. M. RATCLIFFE. 2004. Habitat characteristics and nest predation do not explain clustered breeding in Least Flycatchers (*Empidonax minimus*). *Auk* 121:877–893.

- TAROF, S. A., L. M. RATCLIFFE, M. M. KASUMOVIC, AND P. T. BOAG. 2005. Are Least Flycatcher (*Empidonax minimus*) clusters hidden leks? *Behavioral Ecology* 16:207–217.
- WAGNER, R. H. 1998. Hidden leks: Sexual selection and the clustering of avian territories. Pages 123–145 *in* *Avian Reproductive Tactics: Female and Male Perspectives* (P. G. Parker and N. T. Burley, Eds.). Ornithological Monographs, no. 49.
- WEIDINGER, K. 2007. Handling of uncertain nest fates and variation in nest survival estimates. *Journal of Ornithology* 148:207–213.
- WIKLUND, C. G., AND M. ANDERSSON. 1994. Natural selection of colony size in a passerine bird. *Journal of Animal Ecology* 63:765–774.
- WITTENBERGER, J. F., AND G. L. HUNT, JR. 1985. The adaptive significance of coloniality in birds. Pages 1–78 *in* *Avian Biology*, vol. 8 (D. S. Farner, R. King, and K. C. Parkes, Eds.). Academic Press, London.
- WOODLAND, D. J., Z. JAAFAR, AND M.-L. KNIGHT. 1980. The “pursuit deterrent” function of alarm signals. *American Naturalist* 115:748–753.
- ZUBERBÜHLER, K., D. JENNY, AND R. BSHARY. 1999. The predator deterrence function of primate alarm calls. *Ethology* 105: 477–490.
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