

HOME RANGES OF ADULT AND JUVENILE EASTERN SCREECH-OWLS: SIZE, SEASONAL VARIATION AND EXTENT OF OVERLAP

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ABSTRACT.—We monitored the home ranges of radio-tagged adult ($N = 10$) and juvenile ($N = 7$) Eastern Screech-Owls (*Otus asio*) and examined spatial relationships between paired males and females, adults and their young, and neighboring conspecifics. Adult owls occupied home ranges that averaged slightly under 50 ha in size. We detected no significant differences in home range size of adult males and females during either the breeding season or non-breeding season. The ranges of paired screech-owls overlapped less during the non-breeding season, perhaps reducing competition between members of the pair. While still occupying parental territories, juvenile owls had significantly larger home ranges during the second half of the nine-week pre-dispersal period, and juveniles wandered outside the ranges of their parents more often during this time. Home ranges of juveniles were generally larger following dispersal from parental territories. We found more overlap in ranges between neighboring individuals than reported for many species of owls. Shared areas were usually used more by one owl, with only occasional excursions by the other owl. Such behavior is consistent with the notion that Eastern Screech-Owls defend exclusive areas or territories throughout the year. Finally, adult screech-owls and their young remained in close proximity during most of the post-fledging period, suggesting that Eastern Screech-Owls do not divide their broods between parents.

Extensión del territorio del Tecolote Nororiental (*Otus asio*) adulto y joven: tamaño, variación estacional y extensión del solapo entre territorios

EXTRACTO.—Hemos controlado las extensiones del territorio habitado por búhos *Otus asio* adultos ($N = 10$) y jóvenes ($N = 7$), los que para este efecto estuvieron radioequipados; y hemos examinado la relación de espacios habitados por parejas de ellos con los de sus crías, y con los de otros de su especie de zonas vecinas. Los búhos adultos ocuparon territorios que promediaron ligeramente en menos de 50 ha de extensión. No hemos detectado significativas diferencias entre la extensión del territorio habitado por búhos adultos machos y la del territorio de las hembras, durante tanto el período reproductor como en el no reproductor. Durante la estación no reproductora hubo un menor solapo entre los territorios habitados por cada miembro de las parejas de estos búhos, tal vez así reduciendo la competencia entre ellos.

Durante la segunda mitad de las nueve semanas en que las crías aún no dejaban permanentemente el territorio paterno, ellas ocuparon territorios significativamente más extensos; en este período los jóvenes volaban más a menudo fuera del territorio de sus padres. Las extensiones habitadas por ellos generalmente se expandieron más después que dejaron permanentemente ese territorio.

Hemos encontrado más solapos, de los que se ha referido para muchas especies de búhos, entre los territorios de individuos vecinos. Áreas cohabitadas por dos individuos generalmente fueron usadas mayormente por uno de ellos, con sólo ocasionales excursiones hacia ese territorio hechas por el otro. Tal conducta es consistente con la idea que sostiene que el búho *O. asio* defiende áreas o territorios exclusivos durante el año. Finalmente, las parejas de búhos y sus crías permanecieron en territorios cercanos durante la mayoría del período que siguió al de haber dejado el nido; lo que sugiere que en estos *O. asio*, el número de las crías no se divide entre los progenitores.

[Traducción de Eudoxio Paredes-Ruiz]

Radiotelemetry studies have provided information on the movements, ranging behavior, and spatial relationships among many wide-ranging species of raptors. However, these studies reveal much varia-

tion among and within species in the size of ranges and their overlap with conspecifics, and factors contributing to this variation are not completely understood (e.g., Dunstan 1970, Nicholls and Warner 1972, Elody and Sloan 1985, Ganey and Balda 1989, Finck 1990). Existing evidence suggests that specific habitat requirements, population density, season of

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the year, whether or not parents divide their broods, and various other factors could influence home range characteristics in birds (e.g., Southern 1970, Krebs 1971, Knapton and Krebs 1974, McLaughlin and Montgomerie 1985).

Eastern Screech-Owls (*Otus asio*) are relatively small, nocturnal predators that inhabit forested areas throughout much of eastern North America. Individuals generally do not migrate, and they apparently occupy the same areas throughout the year (VanCamp and Henny 1975). Limited information is available concerning the ranging behavior of and spatial relationships among Eastern Screech-Owls. Thus, the objectives of our study were to 1) determine the home range sizes of adult and juvenile Eastern Screech-Owls, 2) determine if owls vary the size of their home ranges during the year, 3) determine the extent to which ranges overlap, and 4) examine spatial relationships among adult screech-owls and their young during the post-fledging period.

METHODS

We radiotracked 17 Eastern Screech-Owls between 30 May 1985 and 5 July 1986 in and near the 680-ha Central Kentucky Wildlife Management Area (CKWMA), located 17 km southeast of Richmond, Madison County, Kentucky. The management area consisted of small deciduous woodlots and thickets interspersed with cultivated fields and old fields (Belthoff 1987, Sparks 1990). Areas surrounding the CKWMA were mainly agricultural, but extensively wooded tracts occurred in nearby Jackson County.

We captured adult Eastern Screech-Owls either at artificial nest boxes and natural tree cavities or by luring them into mist nets by broadcasting bounce songs (Ritchison et al. 1988). Nests were located by following radio-tagged adults and by examining suitable tree cavities. We captured nestlings at nests several days prior to fledging. Adults and nestlings were equipped with radiotransmitters (Wildlife Materials, Inc., Carbondale, IL) and banded with U.S. Fish and Wildlife Service aluminum bands. Transmitters (4–5 g) were attached backpack-style with woven nylon cord (Smith and Gilbert 1981), and the transmitter plus harness generally weighed less than 6 g.

We determined the locations of owls by triangulating with receivers (TRX-24, Wildlife Materials, Inc. or TR-2, Telonics Inc., Mesa, AZ) and handheld two-element yagi antennas. Two recorders at separate stations and in radio contact with one another took simultaneous readings. Tracking periods usually began at or shortly after sunset and ranged from 2–4 hr in duration. We conducted all tracking between 1800–0400 H. Average locational error in all habitat types and at different times during the study averaged ± 1 degree (Sparks 1990). We calculated home range areas with the TELEM program (Koeln 1980) using the minimum convex polygon method. In doing so,

the outermost 5% of locations (i.e., those farthest from the mean center of activity) were deleted to avoid overestimating home range sizes (Burt 1943). We typically located individual owls at 20–30-min intervals during tracking periods. Because a 20-min interval was presumably sufficient for owls to cover their entire home ranges, we considered successive locations biologically independent (Lair 1987).

We determined home range sizes of adult Eastern Screech-Owls for two distinct biological time periods: breeding (1 March to 31 July) and non-breeding (1 August to 28 February). Home range sizes of juveniles were also determined for two biological periods: pre-dispersal (defined here as the period beginning the day young owls left nest cavities and ending the day young permanently left the parental home range) and post-dispersal. Juvenile screech-owls in central Kentucky typically leave the nest cavity during the third week in May, and they disperse from natal home ranges (i.e., those ranges used prior to dispersal from parental home ranges) in mid-July (see Belthoff and Ritchison 1989, 1990a). The post-dispersal period began the day after a juvenile dispersed from its parental home range and continued until the juvenile died or its radiotransmitter could no longer be located.

To examine spatial relationships among adult screech-owls and their young, we radiotagged all individuals in two families (both adults and three juveniles in each family). We determined the locations of each family member in a sequential fashion. For each sequence, the location of each family member was plotted on a map according to Universal Transverse Mercator (UTM) coordinates. We then calculated distances between adult males and females and each of their young.

Using a compensating polar planimeter, we measured areas within the home range that an individual owl shared with conspecifics. We also determined the number of locations of each owl in both overlapping and non-overlapping areas. We performed Chi-square tests to examine the frequency of use of shared versus non-shared areas (as determined by number of locations). The expected numbers of locations in shared and unshared areas were determined by multiplying the total number of locations in an individual's range by the proportion of that range that was shared and unshared, respectively. We used analysis of variance (ANOVA) to perform multiple comparisons among means and, if significant effects were detected, performed post-hoc tests using the Student-Newman-Keuls procedure (SNK). We used Mann-Whitney *U*-tests and Wilcoxon signed-ranks tests when comparing only two means. We calculated Spearman rank correlation coefficients to examine the relationship between number of locations and home range size. All statistical tests were two-tailed, and we set rejection levels at $\alpha = 0.05$. Means and standard errors are reported as $\bar{x} \pm SE$.

We obtained 3453 locations of radio-tagged Eastern Screech-Owls ($N = 10$ adults and 7 juveniles) during 340 hr of tracking over 88 nights. Most locations ($N = 2237$) were during the breeding/pre-dispersal period ($N = 10$ adults and 6 juveniles), with fewer locations ($N = 1216$) obtained during the non-breeding/post-dispersal period ($N = 6$ adults and 4 juveniles). We radiotracked both members of three pairs during both the breeding and non-

Table 1. Home range size and extent of overlap with mate during the breeding period, non-breeding period, and overall period for mated pairs in five families of Eastern Screech-Owls (N = number of telemetry locations).

FAMILY	SEX	TIME PERIOD								
		BREEDING			NON-BREEDING			OVERALL (ANNUAL)		
		SIZE (ha)	N	% OVERLAP ^a	SIZE (ha)	N	% OVERLAP ^a	SIZE (ha)	N	% OVERLAP ^a
1	M	60.6	184	84.8	25.8	70	45.6	68.4	254	75.2
	F	59.7	153	86.0	33.0	61	35.5	59.7	214	86.0
2	M	34.8	208	34.1	30.2	143	59.2	46.6	351	66.1
	F	11.9	186	100.0	44.1	261	40.6	48.4	447	69.7
3	M	29.3	44	46.1	35.6	79	41.8	38.6	123	49.8
	F	16.9	79	92.9	14.6	45	88.0	20.9	124	92.0
4 ^b	M	36.7	208	81.8	33.3	82	—	57.0	290	—
	F	35.4	210	84.9	—	—	—	—	—	—
5 ^c	M	15.9	57	32.4	—	—	—	—	—	—
	F	8.0	54	64.8	—	—	—	—	—	—

^a Percentage of home range encompassed by mate's home range.

^b Adult female killed several nights after young fledged.

^c Tracked only during the breeding season.

breeding periods, while both members of two additional pairs were tracked only during the breeding period. Three juveniles were tracked during both the pre- and post-dispersal periods, and we tracked three additional juveniles only during the pre-dispersal period. We tracked one juvenile during the post-dispersal period only.

Initially, we detected a significant relationship (Spearman rank correlation, $r_s = 0.47$, $P < 0.024$) between the number of locations and home range size. However, this relationship was no longer significant ($r_s = 0.41$, $P = 0.058$) when we had at least 120 locations for a given owl. Therefore, we only report home range sizes for which we obtained at least 120 locations per owl (note: percent overlap was calculated no matter how many locations we obtained). For this reason, sample sizes reported within the results section may vary from the overall number of owls radiotracked.

RESULTS

Home Range Sizes. Overall, adult Eastern Screech-Owls ($N = 6$) occupied home ranges that averaged 48.5 ± 5.9 ha in size (Table 1). We noted no significant difference (Mann-Whitney U -test, $U = 11.0$, $P = 0.859$) between mean overall home range size of males (52.6 ± 6.5 ha, $N = 4$) and females (43.0 ± 11.5 ha, $N = 2$). During the breeding season, adult Eastern Screech-Owls ($N = 6$) occupied home ranges that averaged 39.9 ± 7.5 ha in size. There was no significant difference (Mann-Whitney U -test, $U = 12.0$, $P = 0.663$) in mean home range size between males (44.1 ± 8.3 , $N = 3$) and females (35.7 ± 13.8 , $N = 3$) during the breeding period. During the non-breeding period, the two

adult screech-owls for which we obtained >120 locations used home ranges that averaged 37.7 ± 6.9 ha in size (Table 1).

During the pre-dispersal period, juvenile Eastern Screech-Owls ($N = 6$) occupied home ranges that averaged 34.0 ± 6.3 ha in size (range 12.3–53.3 ha). Juvenile owls expanded their ranges as the post-fledging period progressed, such that they occupied significantly smaller home ranges (Wilcoxon signed-ranks test, $z = 2.201$, $P = 0.028$) during the first half of the pre-dispersal period (13.5 ± 2.0 ha) than during the second half (29.6 ± 4.9 ha). The home ranges of two juveniles during the post-dispersal period were 88.9 ha and 154.8 ha in size.

Home Range Overlap. The overall home ranges of three adult males overlapped the ranges of their mates by an average of 63.7 ± 7.4 percent, while the overall ranges of adult females ($N = 3$) overlapped those of their mates by an average of 82.6 ± 6.7 percent (Table 1). During the breeding season, adult males ($N = 5$) overlapped the ranges of their mates by an average of 55.8 ± 11.5 percent, and adult females ($N = 5$) overlapped the ranges of their mates by an average of 85.7 ± 5.9 percent. One female used a home range entirely within the boundaries of her mate's range. During the non-breeding period, adult males ($N = 3$) overlapped the ranges of their mates by an average of 48.8 ± 5.3 percent, and adult females ($N = 3$) overlapped the ranges of their mates by an average of 54.7 ± 16.7 percent.

We tracked no owls with adjacent ranges during the breeding season, but we did monitor two pairs with adjacent ranges during the non-breeding period. Neighboring males overlapped ranges by 40 and 56 percent, while neighboring females overlapped ranges by 26 and 51 percent. Among the neighboring males, one individual used the shared area significantly more than expected ($\chi^2 = 12.62$, $P < 0.001$). One neighboring male and female did not overlap their ranges, while another neighboring male and female overlapped by 62 and 57 percent, respectively.

Within two families, juvenile owls ($N = 3$ per family) overlapped the ranges of adults (male and female combined) by an average of 80 percent and 54 percent, respectively. Home ranges of juvenile owls overlapped those of adult males by an average of 78 and 61 percent ($N = 2$ families), and those of adult females by 82 and 47 percent. Adult males ($N = 2$) overlapped the ranges of juveniles ($N = 3$ per family) by an average of 60 and 34 percent, while the ranges of adult females ($N = 2$) overlapped ranges of these same juveniles by an average of 63 and 78 percent.

Prior to dispersal from parental ranges, siblings ($N = 3$ per family) in two families overlapped ranges by an average of 71.5 ± 5.8 percent and 65.0 ± 8.9 percent. Following dispersal, two juvenile screech-owls overlapped non-breeding ranges with three unrelated adult males by an average of 17.8 ± 4.2 percent. These same males overlapped the ranges of the two juveniles by an average of 65.7 ± 13.6 percent. The post-dispersal ranges of these two juveniles overlapped ranges with unrelated adult females ($N = 2$) by an average of 30.3 ± 12.4 percent, while the ranges of these females overlapped the juveniles' ranges by an average of 66.1 ± 26.0 percent. The post-dispersal home ranges of two juveniles also overlapped (by 28.8 and 50.1 percent, respectively), and both juveniles used the shared area equally.

Distances Between Adults and Juveniles. We monitored distances between adult males and females and their young in two families. We radio-tracked individuals in Family 1 on 14 nights during the period between 30 May (12 d post-fledging) and 17 July (60 d post-fledging). Juveniles in this family initiated dispersal 60, 63, and 65 d after fledging. We tracked individuals in Family 2 on 11 nights during the period from 6 June (23 d post-fledging) through 11 July (58 d post-fledging), and juveniles

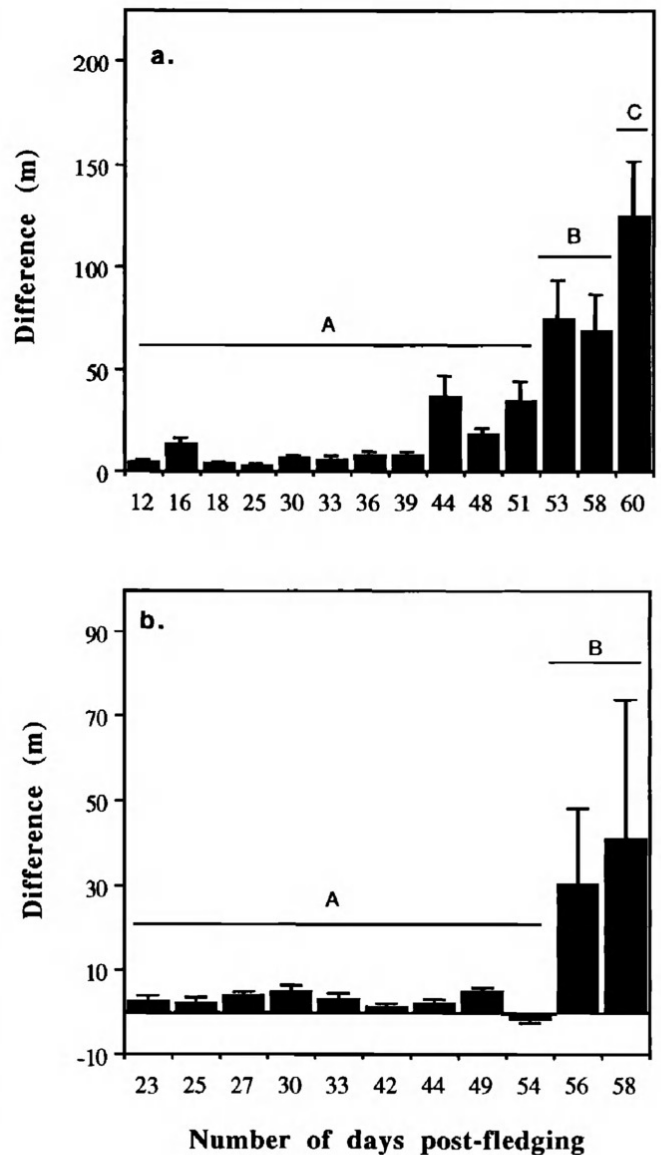


Figure 1. Nightly mean distance ($\pm$ SE) that the adult male Eastern Screech-Owl was farther from juveniles than was the adult female in Family 1 (a) and Family 2 (b). Means with the same letter are not significantly different from each other.

in this family initiated dispersal 56, 57, and 60 d after fledging.

Overall, juveniles ($N = 3$) in Family 1 were significantly closer (Wilcoxon signed-ranks test, $z = 5.597$, $P < 0.0001$) to the adult female ($\bar{x} = 45.0 \pm 4.6$ m, $N = 232$ locations) than to the adult male ($\bar{x} = 75.6 \pm 6.2$ m, $N = 278$ locations). No differences were found among siblings in their respective mean distances from either the adult female ($F = 0.52$, $df = 2, 229$, $P = 0.597$) or the adult male ($F = 1.04$, $df = 2, 275$, $P = 0.355$).

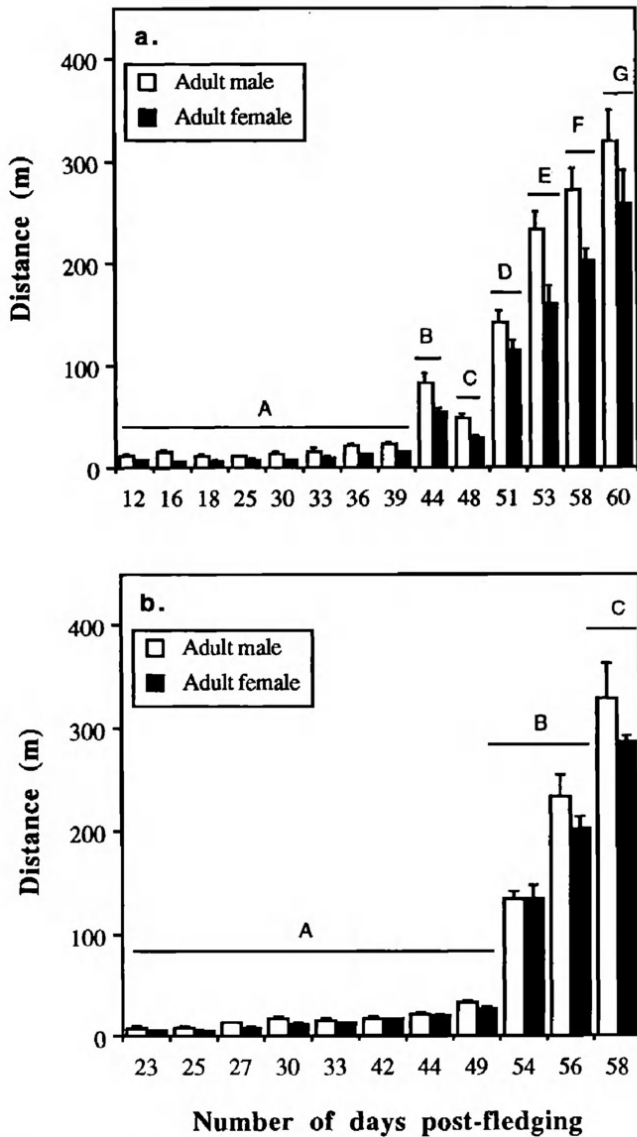


Figure 2. Nightly mean distance ($\pm$ SE) between juvenile and adult Eastern Screech-Owls during the pre-dispersal period in Family 1 (a) and Family 2 (b). Means with the same letter are not significantly different from each other.

Examination of the differences in distance between juveniles and the adult male and female among nights revealed significant variation ($F = 15.33$, $df = 13$, 218 , $P < 0.0001$), with juveniles significantly closer to the adult female during the last three tracking sessions (days 53, 58, and 60 post-fledging; SNK, $P < 0.05$; Fig. 1a). The mean distance between juveniles and the adult female ($F = 106.3$, $df = 13$, 218 , $P < 0.0001$) and male ($F = 106.4$, $df = 13$, 264 , $P < 0.0001$) varied significantly among nights, with distances significantly greater from both the

female and the male beginning on day 44 post-fledging (SNK, $P < 0.05$; Fig. 2a).

Overall, juvenile owls in Family 2 ($N = 3$) were also located significantly closer (Wilcoxon signed-ranks test, $z = 2.720$, $P = 0.006$) to the adult female ($\bar{x} = 31.8 \pm 3.5$ m, $N = 240$ locations) than to the adult male ($\bar{x} = 35.9 \pm 3.8$ m, $N = 240$ locations). Siblings in Family 2 differed significantly in their respective mean distances from both the adult female ($F = 3.69$, $df = 2$, 237 , $P = 0.0263$) and the adult male ($F = 4.52$, $df = 2$, 237 , $P = 0.012$). Further analysis revealed that one juvenile (the same one in both cases) was located significantly farther (SNK, $P < 0.05$) than its siblings from both the adult male and adult female.

Examination of the difference in distances between juveniles and the adult male and female among nights revealed significant variation ($F = 3.48$, $df = 10$, 227 , $P = 0.0003$), with juveniles significantly closer to the adult female during the last two tracking sessions (days 56 and 58 post-fledging; SNK, $P < 0.05$; Fig. 1b). The mean distance between juveniles and the adult female ($F = 228.2$, $df = 10$, 227 , $P < 0.0001$) and adult male ($F = 300.4$, $df = 10$, 227 , $P < 0.0001$) varied significantly among nights, with distances significantly greater from both the female and the male beginning on day 54 post-fledging (SNK, $P < 0.05$; Fig. 2b).

DISCUSSION

Eastern Screech-Owls occupy ranges that vary in size, with published estimates ranging from as small as 4 ha in Texas (Gehlbach 1986) to nearly 400 ha in Virginia (Hegdal and Colvin 1988). The home range sizes of individual Eastern Screech-Owls in our study were typically smaller than reported in previous studies using radiotelemetry. For example, Smith and Gilbert (1984) reported home range sizes of 130 ha for a female Eastern Screech-Owl tracked from January through June and 95 ha for a male tracked from May through June. Hegdal and Colvin (1988) reported a mean home range size of 134 ± 86.3 (SD) ha (range 54–388 ha) for 19 Eastern Screech-Owls. Although his methods were not reported, Gehlbach (1986) suggested that Eastern Screech-Owls in Texas occupied ranges that were smaller than observed in our study, averaging about 30 ha in rural areas and 4–6 ha in suburban areas.

Eastern Screech-Owls apparently prefer areas with varied habitats and abundant edge, i.e., ecotonal areas (Smith and Gilbert 1984). Woods, orchards, and

field-pasture are used more frequently than urban areas (Lynch and Smith 1984, Smith and Gilbert 1984) and cropland (Hegdal and Colvin 1988). Thus, one factor contributing to larger screech-owl home ranges in Connecticut and Virginia may have been the presence of large areas of poor quality habitats. While 39.3% of the Connecticut study area consisted of lawns (Smith and Gilbert 1984) and 23.2% of the Virginia study area was cropland (Hegdal and Colvin 1988), our study area in Kentucky contained no lawn habitat, and no screech-owl home range contained more than 4.5% cropland (Sparks 1990).

High population densities are another potential factor limiting the size of home ranges in owls. Male Flammulated Owls (*Otus flammeolus*) may expand their ranges when adjacent territories are vacant (Reynolds and Linkhart 1987). Similarly, Clark (1975) suggested that surrounding territories might serve to compress territories of Short-eared Owls (*Asio flammeus*). The density of screech-owls on our study area was relatively high (Belthoff and Ritchison 1990b), and this could have contributed to smaller home ranges. In fact, following the disappearance of one territorial male, one neighboring male in our study area expanded its range into the vacated area (unpubl. data).

The availability of prey is another factor that potentially influences home range size in owls, and negative correlations between prey availability and home range size have been either observed or suggested for many species (e.g., Clark 1975, Petersen 1979, Elody and Sloan 1985, Palmer 1986, Ganey and Balda 1989). If availability or relative abundance of prey decreases, as might be the case during the non-breeding period when screech-owls rely more on small mammals and less on invertebrates (Ritchison and Cavanagh 1992), owls may respond by increasing the size of their range (cf. Myers et al. 1979). However, the ranges of adult screech-owls in the present study did not increase in size during the non-breeding period. Therefore, it is possible that prey availability did not decrease during winter on our study area, or that owls compensated in some other manner; e.g., they reduced areas of overlap with mates (see below).

We noted no differences in either overall or seasonal range sizes between adult male and female Eastern Screech-Owls. Fuller (1979) reported that both a male Barred Owl (*Strix varia*) and a male Great Horned Owl (*Bubo virginianus*) had much larger ranges than their respective mates during the

incubation/early brooding period (see also Petersen 1979). During incubation, female Eastern Screech-Owls spend most of their time in the nest cavity and are fed by their mates (Gehlbach 1986). We obtained few locations during the incubation period (typically from mid-March to mid-April in central Kentucky), but detailed observations during this time period (approximately 30 d; Gehlbach 1986, pers. observ.) would probably reveal that the relatively sedentary females have smaller ranges than actively hunting males.

Juvenile screech-owls occupied significantly larger home ranges during the latter half of the pre-dispersal period. Increases in the size of home ranges may be the result of both increased mobility on the part of juveniles and their decreased dependence on the adults (Southern et al. 1954, Fuller 1979). Our results and those of Belthoff and Ritchison (1990c) suggest that juvenile Eastern Screech-Owls become independent of adults around six or seven weeks after leaving the nest (i.e., well into the second half of the eight- or nine-week period between fledging and the initiation of dispersal). Young screech-owls also exhibit increased locomotor activity in the weeks just prior to initiating dispersal (Ritchison et al. 1992), which may have contributed to the larger ranges observed during the second half of the pre-dispersal period.

The ranges of paired screech-owls overlapped more extensively during the breeding season (see also Craig et al. 1988, Ganey and Balda 1989). At least two factors may have contributed to this increased overlap: 1) males and females spent more time together during the period just prior to nesting (perhaps to facilitate courtship and copulation or because of mate guarding by males) and 2) both males and females focused their activities around the nest site during the nesting period. Reduced overlap during the non-breeding period may reduce competition during a period of decreased prey availability.

In contrast to other owl species (e.g., Clark 1975, Nicholls and Fuller 1987, Reynolds and Linkhart 1987, Bull et al. 1988, but see Hayward et al. 1987), neighboring Eastern Screech-Owls overlapped ranges during the non-breeding season (see also Gilbert 1981). Gehlbach (1986:58) suggested that Eastern Screech-Owl ranges in suburban areas overlapped and, further, that "males defend only the cavities and areas in the immediate vicinity." Areas of overlap in the present study were typically used more than expected by only one individual. This suggests

that only occasional excursions were made into the shared area by the other individual (i.e., the neighbor). Raptors may reduce competition by using shared areas at different times with priority of access determined by dominance status (Fuller 1979). If boundaries of total ranges are not regularly patrolled, excursions by neighbors into ranges of dominant conspecifics could occur.

Our data concerning spatial relationships among adult screech-owls and their offspring are useful in assessing the likelihood of brood division. In many species with biparental care, parents apparently divide their brood after young leave the nest (McLaughlin and Montgomerie 1985). Soon after fledging, for example, young Flammulated Owls divide into subgroups, each of which is tended by a different parent (Linkhart and Reynolds 1987). Flammulated Owl subgroups disperse from the nest in different directions and apparently do not come into contact during the remainder of the fledgling dependency period (Linkhart and Reynolds 1987). In contrast, our results corroborate those of Belthoff and Ritchison (1990c) and suggest that adult Eastern Screech-Owls do not divide their broods. Brood division may provide several benefits, including minimizing losses to predators, increased foraging efficiency, and helping young learn to forage (McLaughlin and Montgomerie 1985). However, there may also be advantages in not dividing broods. Young may benefit from remaining together if they learn foraging skills from each other (e.g., Edwards 1989a, 1989b). In addition, young in a subgroup being cared for by only one parent may not survive if that parent is killed. On the other hand, a brood that remains together will still be cared for by the surviving adult (and young are perhaps more likely to survive) following the death of one of the parents. Zaias and Breitwisch (1989) noted that researchers should be cautious of accepting brood division as the general rule because convincing demonstration of brood division requires detailed observations. Clearly, additional studies of fledgling care in birds are needed.

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