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NATAL DISPERSAL OF EASTERN SCREECH-OWLS[1]

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Abstract. Using radiotelemetry we monitored dispersing juvenile Eastern Screech-Owls (*Otus asio*) in central Kentucky during 1985 and 1986. Juvenile owls (n = 16) from seven families remained on natal territories for an average (±SE) of 55 ± 1.3 days after fledging. The mean dispersal date was 15 July, ranging from 8 to 21 July. The mean number of days between dispersal of the first and last members of a brood was 4.3, ranging from 0 to 9 days. Juveniles (n = 17) dispersed a median distance of 2.3 km from their nest ($\bar{x}$ = 4.4 ± 1.11 km), ranging from 0.4 to 16.9 km, including one juvenile that continued to use portions of its natal home range. Dispersal distance was not significantly correlated with either dispersal date or the number of days that juveniles remained on natal territories. Mean dispersal direction was 210 ± 99.1°, and the distribution of dispersal angles did not differ significantly from random. After departing from natal areas, individuals (n = 7) settled after an average of 5.6 days, ranging from 2 to 11 days. Mortality of juvenile owls was 18.2% during the period prior to dispersal but increased to 67% after dispersal.

Key words: Natal dispersal; Eastern Screech-Owl; Otus asio; *juvenile mortality; central Kentucky.*

INTRODUCTION

Dispersal, the movement from natal to first breeding site (natal dispersal) or between breeding sites (breeding dispersal), has received relatively little attention from field investigators, primarily because of the practical difficulties involved in following individuals as they disperse. Nevertheless, the importance of dispersal to populations has long been recognized. For example, Gadgil (1971, p. 253) stated that, "dispersal is one of the most important and among the least understood factors of population biology," while Horn (1983) noted that dispersal and its patterns affect all aspects of a species' ecology and behavior. Although defined differently by various authors, we defined natal dispersal as the permanent movement of individuals to a new location irrespective of whether or not they reproduced after dispersal (i.e., gross dispersal; Greenwood 1980).

Eastern Screech-Owls (*Otus asio*) are widely distributed and common throughout much of the eastern United States. Most populations appear to be nonmigratory with little movement among adult owls. Previous studies of dispersal by Eastern Screech-Owls have been restricted to the recovery of birds banded as nestlings in populations that use artificial nest boxes (VanCamp and Henny 1975, Gehlbach 1986). Such studies provide information concerning dispersal distances and directions but offer little insight into the behavior of dispersing individuals. Further, information based on band recoveries can be biased (Miller and Meslow 1985).

The objective of our study was to monitor dispersing juvenile Eastern Screech-Owls in central Kentucky. We summarize the timing, duration, rate, distance, and direction of natal dispersal movements, and report the causes, extent, and timing of mortality.

STUDY AREA AND METHODS

We conducted observations between May 1985 and February 1987 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 (see Belthoff [1987] for a description of habitat types and dominant plant species). Areas surrounding the CKWMA were mainly agricultural, with extensively wooded tracts and mountainous terrain located to the east and southeast.

We captured adult Eastern Screech-Owls either

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from 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 removed nestlings from nests and equipped each with a radio transmitter (Wildlife Materials Inc., Carbondale, IL) and a U.S. Fish and Wildlife Service aluminum band several days before fledging. Radio transmitters were attached backpack style (Smith and Gilbert 1981) with woven nylon cord (approximately 0.25 cm in diameter). Complete packages, transmitter plus harness, weighed less than 8 g. Entire broods were fitted with radio transmitters with one exception, the 1986 Trap Range family. Initially, we radio-tagged only two of four young in this family, but one of the radio-tagged young was killed the night it fledged. We captured and radio-tagged an additional 1986 Trap Range juvenile 27 days later by luring it into a mist net during playback of bounce songs on its natal territory. We refer to individual owls by either the last three digits of their U.S. Fish and Wildlife Service bands or by their respective family names.

After young owls fledged, we located the diurnal roost sites of each adult and juvenile an average of four times per week in 1985 and daily in 1986 until dispersal. Thus, we were able to determine the number of days that juveniles remained on natal territories prior to dispersal. We defined the date of dispersal as that date when an owl no longer roosted on its natal territory (juvenile owls actually dispersed the previous night). Because owls were radio-tagged, the date of dispersal was easily detected and was typically unambiguous. However, three young owls departed from natal territories but subsequently returned to roost. We termed such movements "exploratory" movements and, because owls generally remained on natal territories for only a day or so following exploratory movements, we considered dispersal date as the date of initial departure.

After dispersal, we searched for owls in adjacent and surrounding woodlots on foot using a hand-held receiver (Model TR-24, Telonics Inc., Mesa, AZ) and a two-element yagi antenna (Telonics Inc.). If an owl could not be located in this manner, we drove roads surrounding the study area in an automobile with a bumper-mounted omni-directional antenna (Telonics Inc.). If still unable to locate dispersing birds, we used a single engine airplane from which we either held the two-element yagi antenna from an open window or secured it to a wheel support. We traversed areas surrounding the study area at altitudes of approximately 700 m. After determining the general location of dispersing juveniles in this manner, we attempted to locate juvenile owls from the ground. We tried to locate dispersing owls daily but were sometimes unsuccessful. Locations of dispersing juveniles in rugged, inaccessible terrain were determined by the triangulation of at least two compass bearings; owls in more accessible terrain were visually located. We measured dispersal distances and directions from the nest to either the site of first breeding attempt, the center of an animal's activity range during the fall and winter, or to the site of an individual's death using aerial photographs and U.S. Geological Survey topographical maps of the study area. The sex of juvenile owls could not be determined prior to an individual's first breeding attempt, at which time we determined sex by the presence of a brood patch or by behavior.

We used Mann-Whitney U-tests to examine differences in dispersal distances and the timing of dispersal between years and Spearman's rank correlation coefficients to examine the effect of dispersal date on dispersal distance (Zar 1974). Linear means and their standard errors are reported as $\bar{x} \pm$ SE. The degree to which distributions of dispersal distances were skewed (sk) was calculated by subtracting the median from the mean, multiplying the difference by three, and dividing by the standard deviation (Glass and Hopkins 1984, p. 68). Mean dispersal angles ($\bar{a}$) were calculated after Zar (1974). We calculated angular deviation (s), a statistic analogous to standard deviation for linear data, by using the following formula (Zar 1974, p. 316):

$$s = 180/\pi\ [\sqrt{-4.60517 \log r}] \text{ degrees},$$

where r is a measure of concentration that has no units but can vary from 0, when there is so much dispersion that a mean angle cannot be described, to 1.0, when all data are concentrated in the same direction (see Zar 1974, p. 313 for calculation of r). Mean angles and angular deviation are given as $\bar{a} \pm s$. We applied Rayleigh's test (Rayleigh's z) to determine if significant mean directions occurred within the sampled dispersal distributions or whether dispersal directions were distributed randomly (Zar 1974). Finally, we applied the nonparametric Watson's test to deter-

TABLE 1. Timing of juvenile natal dispersal movements in seven families of Eastern Screech-Owls in central Kentucky.

Family	n	Days PF[1] ($\bar{x} \pm$ SE)	Range (days)	Mean date	Range (dates)
Off-property	3	62.7 ± 1.45	60–65	19 July	16–21 July 1985
Muddy Creek	3	57.7 ± 1.20	56–60	10 July	8–12 July 1985
Trap Range '85	3	49.0 ± 2.31	45–53	13 July	9–18 July 1985
Stream	2	55.0 ± 0.00	55	15 July	15 July 1986
Goose Pen	2[2]	53.0 ± 0.00	53	20.5 July	20–21 July 1986
Hilltop	1	58.0 ± 0.00	58	16 July	16 July 1986
Trap Range '86	2	53.5 ± 0.50	53–54	13.5 July	13–14 July 1986
Overall	16	55.4 ± 1.26	45–65	15 July	8–21 July

[1] Number of days postfledging when young owls first left natal territories.
[2] An additional Goose Pen juvenile remained on portions of its natal territory so we could not determine dispersal date for this individual.

mine differences in dispersal directions between years (Zar 1974).

RESULTS

TIMING OF DISPERSAL

We captured and radio-tagged 21 young Eastern Screech-Owls from seven families. The mean fledging date was 21 May ($n = 21$), ranging from 14 to 30 May. Siblings either fledged during the same night or over a 2-night period. Young screech-owls that escaped predation ($n = 16$) remained on natal territories for an average of 55 ± 1.3 days after fledging, ranging from 45 to 65 days (Table 1). The mean number of days that young owls remained on natal territories did not differ between years (Mann-Whitney U-test, $P > 0.05$), averaging 56 ± 2.2 days in 1985 and 54 ± 0.8 days in 1986. The mean dispersal date was 15 July ($n = 16$), ranging from 8 to 21 July.

The date of dispersal varied among siblings. For example, young owls ($n = 3$) in the 1985 Trap Range family dispersed from their natal territory over a 9-day period, while young in the Goose Pen family ($n = 3$) dispersed over a 2-day period (Table 1). Overall, the mean number of days between dispersal of the first and last siblings in a family was 4 ± 1.2 ($n = 6$ families), with no significant difference between years (Mann-Whitney U-test, $P > 0.10$).

We recorded exploratory movements by three young owls. Two owls left natal territories for one day before returning. Although the roost site of one of these owls could not be located the day after dispersal, it was found back in its natal territory the following day. This individual once again left its natal territory that evening and was located at a roost site 0.8 km from its natal territory the following day (owl j; Fig. 1). The second juvenile roosted 0.5 km from its natal territory on the first day after dispersing (owl a; Fig. 1). This individual returned to roost on its natal territory the next day but left again that evening. We failed to locate this owl the next day but found it roosting 1.3 km from its natal territory the following day (day 4 postdispersal; Fig. 1). A third owl (owl g) dispersed on 13 July but was not located until 15 July, when it roosted 1.1 km from its natal territory (day 3; Fig. 1). We located this bird roosting 0.3 km farther from its natal territory 2 days later (day 5; Fig. 1). After roosting in this same general area for several days, we found this owl roosting in its natal territory on 21 July (day 9 postdispersal). After roosting in its natal territory for two additional days, on 24 July this owl returned to the same general area where it had roosted on day 5 postdispersal (owl g; Fig. 1).

One juvenile (Goose Pen 344) continued to roost in its natal territory until 3 October, nearly 11 weeks after its two siblings had dispersed. Although still in an area used by the entire family during the postfledging period, this young owl appeared to be independent of its parents. That is, the adult male was radio-tagged and was never found roosting closer than about 0.4 km away during the period from 19 July (about the time when this owl's two siblings dispersed) through 10 October (when the adult male's transmitter was removed). Although the adult female was not radio-tagged, she was not observed roosting with the juvenile after 28 July. On 3 October we recaptured the juvenile and replaced its transmitter. The following day we were unable to locate a signal from this bird's transmitter. We did, however, observe an owl roosting in a site that had often been used by the juvenile, suggesting failure of the new transmitter rather than movement from the area. Subsequent attempts to capture owls in the area failed and, therefore, we are not certain if this owl made any further movements. Because we are uncertain if or when this individual dispersed, we excluded this owl from analyses of the timing of dispersal and calculated its "dispersal" direction and distance based on the location of its recapture.

RATE AND DURATION OF DISPERSAL

Three young screech-owls were located at roost sites the first day after dispersal from natal territories. These birds traveled 0.5, 1.1, and 3.2 km respectively (owls a, o, and k; Fig. 1). The individual that traveled 0.5 km returned to its natal territory on the following night, and was subsequently located 1.3 km from its nest 3 days after its initial "exploratory" movement (owl a; Fig. 1). Three additional owls located at roost sites 2 days after dispersal were 0.8, 1.5, and 2.4 km from their respective nests (owls b, h, and l; Fig. 1). Other owls were first located 3 to 5 days after leaving natal territories (owls c, d, e, g, and j; Fig. 1). Owls dispersing longer distances had to be located from the air and, therefore, were first located much later (21 to 54 days postdispersal) (owls f, i, p, and n; Fig. 1).

Many young owls settled in areas within a relatively short time after dispersing. The movements of seven owls were well-documented and the mean duration of dispersal for these individuals was 5.6 ± 1.10 days, ranging from 2 to 11 days. One owl was located 2 days after dispersal from its natal territory and was still in the same general area 98 days later when its transmitter failed (owl 1; Fig. 1). Other owls were first located 11, 4, 5, and 6 days after dispersal and remained in the same general areas for 167, 188, 174, and 187 days, respectively, when they were either found dead or their transmitter failed (owls a, e, g, and h; Fig. 1). Another bird (owl i) was known to have moved nearly 3 km some time between days 22 and 46 postdispersal (Fig. 1). After this movement, the owl apparently remained in the same general area until it was found dead nearly 6 months later. Another owl was first located 2.8 km from its nest site 4 days after dispersing from its natal area. This owl was located 16.9 km from its nest site 74 days later (owl c; Fig. 1), but we made no further observations of this bird prior to failure of its transmitter.

Two young owls that had apparently established ranges shortly after dispersal from natal

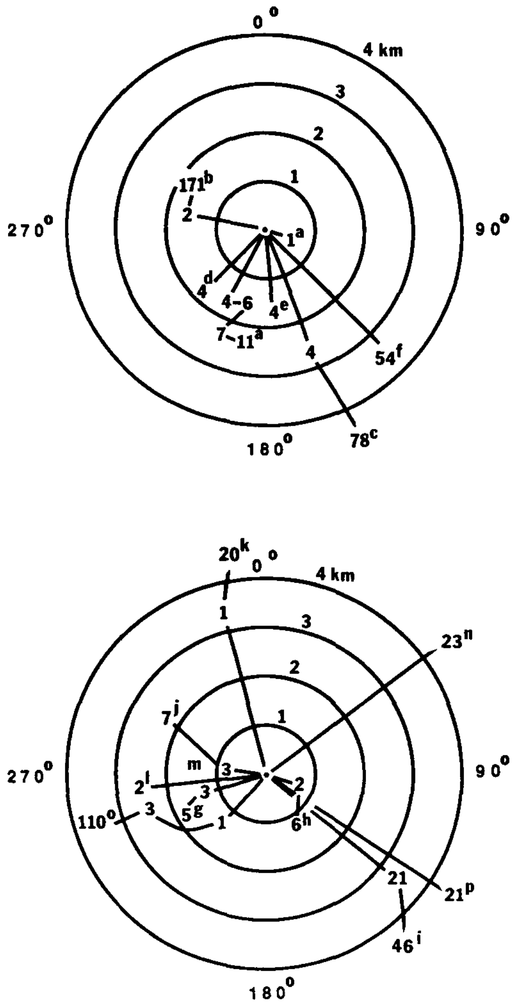

FIGURE 1. Dispersal movements of individual juvenile Eastern Screech-Owls in central Kentucky. Letters refer to individuals identified in Table 2. The central dots represent the respective nest sites of young owls. Numbers indicate the number of days after dispersal that individual owls were first found at that location (Table 2 lists the last date that individuals were known to be at that location). Outside the 4-km circle, refer to Table 2 for actual dispersal distances. Individual m dispersed on 21 July 1986 and was located only once, at the position indicated, on 15 February 1987.

areas exhibited further movements some time later. One young male was first located 2 days after dispersal and remained in the same general area for over 5 months. In mid-February, this young owl (owl b) moved about 0.8 km from this area and paired with a female (Fig. 1). Another young owl (sex unknown) had apparently settled in an area 3 days after its initial dispersal flight.

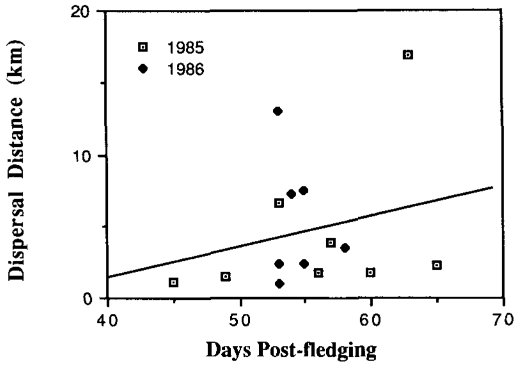

FIGURE 2. Dispersal distances as a function of the number of days that juvenile Eastern Screech-Owls remained on natal territories in central Kentucky during 1985 (n = 9) and 1986 (n = 7). There was no significant correlation between the number of days owls remained on natal territories and dispersal distance (r_s = 0.20, $P > 0.23$). Equation of plotted line is: $y = -7.14 + 0.21x$. Note: n = 2 observations at 60 days postfledging and 1.7 km.

However, this owl moved nearly 1.4 km in early November, after spending over 100 days in the same general area (owl o; Fig. 1). Recapture efforts failed and transmitter failure prevented further observations of this individual.

DISTANCE OF DISPERSAL

Median dispersal distances for 1985 and 1986 were 1.8 km (n = 9) and 3.0 km (n = 8), respectively (Fig. 2). Dispersal distances were slightly skewed (sk = 1.39), resulting in mean dispersal distances that were consistently greater than medians, averaging 4.2 ± 1.60 km and 4.7 ± 1.50 km for 1985 and 1986, respectively (Table 2). Overall, juveniles (n = 17) moved a median distance of 2.3 km ($\bar{x}$ = 4.4 ± 1.11 km). These statistics, however, probably underestimate actual dispersal distances because some birds may not have settled permanently when transmitter failure occurred. Dispersal distances did not differ significantly between years (Mann-Whitney U-test, $P > 0.05$). Because there were no significant differences between years in either number of days on the natal territory or dispersal distance, we pooled data for both years to examine the relationship between the timing of dispersal and dispersal distance. We predicted a priori that early dispersers would settle closer to natal territories than late dispersers (i.e., Murray 1967, Waser 1985) but found no significant correlation between the number of days that individuals remained on natal territories after fledging and the distance of dispersal (r_s = 0.20, P >

TABLE 2. Dispersal distances and fates of 17 juvenile Eastern Screech-Owls in central Kentucky. Individuals with fates listed as unknown were located only by aircraft or made additional movements and radio transmitters could not be replaced prior to their failure. Stable dispersers appeared to be settled prior to transmitter failure (after Gutiérrez et al. 1985).

Family	Owl # and letter[1]	Sex	Dispersal distance (km)	Final sighting	Fate
Off-property	867 a	U	2.25	1-14-86	Dead
	868 b	M	1.68	4-86	Nesting[2]
	869 c	U	16.90	10-4-85	Unknown
Muddy Creek	870 d	U	1.76	10-10-85	Stable
	871 e	U	1.80	1-14-86	Stable
	872 f	U	3.80	9-15-85	Stable
Trap Range (1985)	877 g	U	1.43	1-6-86	Dead[3]
	878 h	U	1.16	1-16-86	Dead[4]
	879 i	U	6.59	3-28-86	Dead[5]
Stream	347 j	U	2.30	10-10-86	Stable
	348 k	U	7.40	8-4-86	Unknown
Goose Pen	343 l	U	2.42	10-26-86	Stable
	344 —	U	0.40	10-3-86	Stable
	345 m	M?	1.05	2-15-87	Possibly paired
Hilltop	342 o	U	3.54	11-3-86	Unknown
Trap Range (1986)	324 p	U	7.16	10-15-86	Stable
	325 n	U	13.00	8-4-86	Unknown

[1] Letters used to identify individuals in Figure 1.
[2] Acquired a mate and nested. Four young hatched but none fledged.
[3] Remains of carcass and radio transmitter found in unidentified underground mammalian burrow.
[4] Scattered feathers and radio transmitter found in open field; suspected Great Horned Owl predation.
[5] Radio transmitter found on ground with no signs of carcass.

0.23, one-tailed test) (Fig. 2). Similarly, there was no significant relationship between dispersal date and distance ($r_s = 0.11$, $P > 0.34$, one-tailed test).

DIRECTION OF DISPERSAL

The mean dispersal direction ($n = 17$) was 211 ± 99.1°. The observed distribution of dispersal directions did not differ significantly from random (Rayleigh's test, $z = 0.86$, $P > 0.05$, $r = 0.22$). There was, however, a significant difference in dispersal direction between years (Watson's test, $U^2 = 0.26$, $P < 0.02$). Mean dispersal direction was approximately 187 ± 55.0° and 332 ± 85.3° for 1985 ($n = 9$) and 1986 ($n = 8$), respectively (Fig. 3). In 1985, dispersal directions differed significantly from random (Rayleigh's test, $z = 3.58$, $P < 0.05$, $r = 0.63$), with most individuals dispersing to the southeast and southwest (Fig. 3). Dispersal directions of the 1986 cohort, however, did not differ significantly from random (Rayleigh's test, $z = 0.87$, $P > 0.05$, $r = 0.33$).

We located several owls more than once prior to their apparent settling. Observation of these individuals suggest that dispersing owls move consistently in the same general direction (Fig. 1). One owl did reverse direction, moving back to an area occupied earlier. This individual was observed 0.8 km from its nest site 3 days postdispersal (Fig. 1j). Four days later this bird moved approximately 1.6 km to another area (see day 7 location; Fig. 1j) where it remained for 5 days before returning to the area where first located 3 days postdispersal. After remaining in this area for 11 days the owl returned to the area first occupied 7 days postdispersal and still occupied that area when its transmitter failed 88 days postdispersal.

MORTALITY—TIMING, CAUSES AND EXTENT

Mortality of juvenile owls after fledging and prior to dispersal from natal territories was 18.2%, with four of 22 young dying. A 1986 Trap Range juvenile was killed by what appeared to be a Great Horned Owl (*Bubo virginianus*) on the night that it fledged, while a Muddy Creek juvenile succumbed to an unidentified mammalian predator 3 days after fledging. The remaining two deaths occurred in the Hilltop family after a Great Horned Owl killed the adult female 3 days before her young fledged, leaving the adult male to care for three young alone. We did not observe a replacement female on the territory or near any of

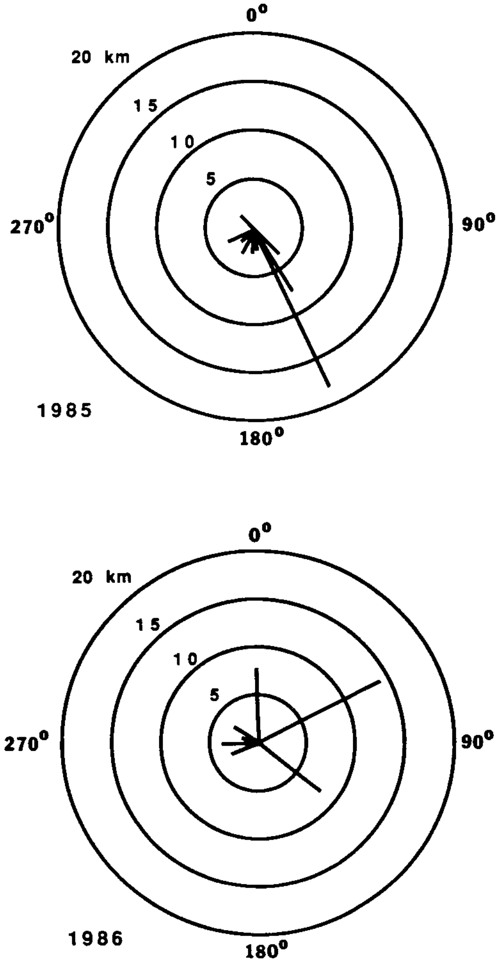

FIGURE 3. Dispersal directions and distances of the 1985 ($n = 9$) and 1986 ($n = 8$) cohorts of Eastern Screech-Owls in central Kentucky.

the young throughout the postfledging period. Five days after fledging, we found the first juvenile's radio transmitter and remains on the ground; the cause of death was unknown. The other owl survived for 41 days, being killed 6 days after injuring its left eye. The remains of this owl were discovered in a tree surrounded by "whitewash," suggesting Great Horned Owl predation.

Only one juvenile from each cohort was known to have survived to the next breeding season. Four of five juveniles known to be alive in December 1985 either starved or were killed by predators prior to the end of March 1986 (Table 2). We were able to recapture and replace the radio transmitter on only one 1986 juvenile but, as noted previously, the transmitter apparently failed. We did, however, locate Goose Pen juvenile 345 roosting in a cavity within the territory of the Muddy Creek family during February 1987, possibly paired with the adult female, which roosted nearby.

DISCUSSION

TIMING OF DISPERSAL

Young Eastern Screech-Owls in the present study remained on natal territories for an average of 55 days after fledging, with owls dispersing from 8 through 21 July. VanCamp and Henny (1975, p. 19) suggested that young screech-owls in northern Ohio "begin dispersing from their natal area in late summer and early fall . . ." Eckert (1974) suggested that young screech-owls disperse by late August. Gehlbach (1986) reported that juvenile screech-owls begin to disperse in late summer in Texas. He further noted that all young screech-owls seem to be dispersing by August or September, as suggested by an increase in the number of descending trills (whinny songs) uttered by resident males. Ritchison et al. (1988) also reported increased use of whinny songs by screech-owls during the period of natal dispersal in central Kentucky. Hough (1960) observed an increase in the use of whinny songs beginning in July in New York, suggesting the initiation of natal dispersal. Thus, it appears that young screech-owls disperse from natal territories in July and August throughout their range.

In the weeks prior to dispersal, juveniles roosted with their parents less often and the distance between the roost sites of young owls and their parents increased (Belthoff 1987). In addition, based on calculations of biweekly home-range overlap between adult owls and their offspring, juvenile owls began to move more widely outside the home ranges of their parents during this same period (Belthoff 1987). Such behavior suggests that there may be little interaction between young owls and their parents immediately prior to dispersal. Similarly, Gehlbach (1986) reported that as the postfledging period continued young screech-owls became increasingly independent but were tolerated within parental territories for most of the summer. In addition, three young owls in the present study returned to roost in parental territories following brief dispersal movements, with one individual roosting within 20 m of its parents for 3 days before finally leaving. Moreover, one young owl in the present study continued to roost in its natal territory for nearly 11 weeks after the dispersal of its two siblings. These observations suggest that young screech-owls are not forced from parental territories due to parental aggression.

Previous investigators have noted an absence of parent-offspring aggression in other species as well. Weise and Meyer (1979) provided evidence that parental aggression was not the driving or initiating force behind dispersal of young Black-capped Chickadees (*Parus atricapillus*), but suggested that interspecific competition could influence the total distances traveled by young chickadees. Similarly, Nilsson and Smith (1985) found no evidence that parental aggression forced young Marsh Tits (*P. palustris*) to initiate dispersal. Furthermore, no evidence of parental aggression has been reported in the Chaffinch (*Fringilla coelebs*, Marler 1956), Great Tit (*P. major*; Royama 1962, Saitou 1979), or Northern Harrier (*Circus cyaneus*, Beske 1982). In contrast, Bunn et al. (1982) suggested that while the oldest Common Barn-Owls (*Tyto alba*) in a brood gradually drift away from natal territories, the youngest owls in a brood are forced away by the growing aggression of the adults. Similarly, in contrast to Weise and Meyer (1979), Holleback (1974) reported that the breakup of Black-capped Chickadee broods may be the result of parental aggression toward the young or of young toward each other. Thus, although parent-offspring aggression may be important in initiating dispersal of the young in some cases, such aggression appears to be of little importance in initiating dispersal in many species. Nilsson and Smith (1985) suggested that parental aggression is not needed to initiate dispersal of young because there may be selective pressure on juveniles to disperse as early as possible. That is, dominant individuals are likely to obtain better quality territories or ranges and early established dispersers may be dominant over later dispersers.

The mean number of days between dispersal of the first and last siblings for six families in the present study was 4.3. Similarly, siblings are reported to initiate dispersal over a period of several days in Eurasian Sparrowhawks (*Accipiter nisus*, Wyllie 1985), 0 to 31 days in Red-tailed Hawks (*Buteo jamaicensis*, Johnson 1973), and up to 15 days in Ferruginous Hawks (*Buteo regalis*, Konrad and Gilmer 1986). Nilsson and Smith (1985) observed similar individual differences in the timing of dispersal among siblings in Marsh Tits and suggested that such variation might be the result of dominance status. These authors found that larger individuals (assumed to be dominants) tended to disperse before smaller individuals (assumed to be subdominants) and suggested that subdominants remained in parental territories longer to increase their self-feeding ability. This increased ability is needed because subdominants may have to move farther before they manage to settle (as a result of losing interactions with more dominant individuals) and they are likely to end up in poorer habitats (Nilsson and Smith 1985). Other factors that could contribute to variation in dispersal date among siblings in screech-owls include age (first young to hatch may be first to disperse), sex (males may disperse prior to females because they must establish territories to gain access to females), and physical condition (individuals must attain the physical condition necessary to disperse).

All but one of the juvenile Eastern Screech-Owls in the present study dispersed from natal territories, and this individual may have dispersed as well. After dispersal of its two siblings in mid-July, this young owl consistently roosted about 0.4 km from the adult male. The roost sites of this young owl after mid-July were in an area that had been used for roosting by the entire family during the postfledging period. However, the family used this area on only five occasions (20 June–24 June). Thus, this apparent nondisperser may simply have "dispersed" to an area on the periphery of its parents' territory. Similar behavior has been reported in other species. Greenwood et al. (1979) observed that nearly 25% of male Great Tits established territories in or adjacent to their natal one. Dunstan (1970) reported a juvenile Great Horned Owl in South Dakota that apparently did not disperse, rather its parents abandoned their territory and moved approximately 1.6 km to another area. Such behavior appears to support Murray's (1967) rule—move to the first uncontested site you find and no farther.

Three young owls in the present study made exploratory movements away from natal territories prior to final dispersal. Similar behavior has been reported in young Great Horned Owls (Dunstan 1970) and Red-tailed Hawks (Johnson 1973). Such behavior has not been observed in Spotted Owls (*Strix occidentalis,* Gutiérrez et al. 1985). Exploratory movements may permit young birds to determine whether surrounding areas are occupied and, if not, whether such areas represent suitable habitat. Or, perhaps individuals exhibiting these movements are unsuccessful at locating suitable cover or adequate prey and return to natal territories where the location of both are more familiar.

RATE AND DURATION OF DISPERSAL

The rate of movement by young Eastern Screech-Owls during dispersal was difficult to determine in the present study because owls could not be located every day. Even owls located relatively close to natal areas may have remained undetected for prolonged time periods because of low sampling effort in areas with rugged topography and limited access, or perhaps such individuals wandered outside the study area and returned later. Nevertheless, our data suggest that actively dispersing screech-owls may travel up to 3.2 km per night, although most appear to travel much shorter distances (0.5–2.4 km per night). Gutiérrez et al. (1985) reported that young Spotted Owls dispersing from natal territories traveled at an average rate of 8 km per day, with a range of 1.6 to 17 km per day. Forsman et al. (1984) reported that a young Spotted Owl left its natal territory and moved 4.4 km within 2 days.

The dispersal movements of seven young owls were well-documented in the present study and these individuals settled in areas an average of 5.6 days after first leaving natal territories. These data, however, must be viewed with caution because they come largely from short-distance dispersers. Screech-owls dispersing longer distances may take longer to reach their final destination. For example, one owl in the present study was known to have traveled nearly 3 km sometime between days 22 and 46 postdispersal. Thus, the earliest that this bird could have settled would have been day 23 postdispersal. Furthermore, all but two owls in the present study either died or were lost due to transmitter failure prior to establishment of breeding territories. It is possible, therefore, that the young owls may have made further movements. In fact, two owls in the present study did make additional movements after spending several months in one area. Nightly home ranges of Eastern Screech-Owls are reportedly largest during winter (Smith and Gilbert 1984, pers. observ.), so it is possible that young owls are forced into making further movements by adjacent adults (or dominant juveniles) that expand their territorial boundaries, possibly in response to decreased prey abundance during this time. Alternatively, young owls may make additional movements during late winter and early spring in search of mates.

Although limited, available data suggest that the dispersal movements of young birds are often of relatively short duration. For example, Weise and Meyer (1979) noted that the dispersal phase for young Black-capped Chickadees persisted for only a few weeks. Matthysen (1987) reported that juvenile European Nuthatches (*Sitta europaea*) may settle and begin territorial defense of areas less than 4 to 6 days after leaving natal territories (or less than 2 weeks after fledging). Band recoveries suggest that young sparrowhawks move chiefly during their first few weeks of independent life, and are relatively sedentary thereafter (Newton and Marquiss 1983). Finally, Bowman and Robel (1977) found that two young Greater Prairie Chickens (*Tympanuchus cupido*) settled only 1 day after leaving their natal areas and two others settled after only 3 days. However, these birds were not monitored throughout the fall and into the next spring, when young prairie chickens may make additional movements (Bowman and Robel 1977).

DISTANCE OF DISPERSAL

Young Eastern Screech-Owls in the present study dispersed a median distance of 2.3 km, ranging from 0.4 to 16.9 km. Similarly, Gehlbach (1986) reported that young Eastern Screech-Owls in Texas dispersed up to 14.5 km from their natal territories, although most dispersed less than 2 km. VanCamp and Henny (1975) reported that Eastern Screech-Owls in the northeastern United States dispersed a mean distance of 32 km, although most moved much shorter distances. Other investigators have reported similar observations of other species, with most individuals dispersing relatively short distances and a few dispersing much greater distances (e.g., Adamcik and Keith 1978, Baker and Mewaldt 1978, Greenwood et al. 1979, Weise and Meyer 1979, Newton and Marquiss 1983). Some investigators have suggested that certain individuals may possess innate tendencies to disperse longer distances (Howard 1960, Lidicker 1962), but such hypotheses have proved difficult to test (Greenwood et al. 1979). Instead, contemporary hypotheses have focused on the possible role of competition and behavioral dominance in determining dispersal distances (Murray 1967, Gauthreaux 1978, Moore and Ali 1984, Liberg and von Schantz 1985, Waser 1985). For example, Waser (1985) suggested that early dispersers may settle closer to their natal territories than later dispersers, filling vacant areas progressively farther from natal territories as the season progresses. In other words, dispersing juveniles are prevented from settling in areas where adults or earlier dispersing juveniles are present. Assuming that early broods disperse before later ones, a correlation would be expected between hatching date and dispersal distance, or between hatching date and the percentage of young from early vs. late broods returning to breed in natal areas. Such a pattern has been observed in Song Sparrows (*Melospiza melodia*, Arcese and Smith 1985), House Wrens (*Troglodytes aedon*, Drilling and Thompson 1988), Marsh Tits (Nilsson and Smith 1985), and Great Tits (Belgian and Dutch populations) (Dhondt and Huble 1968, Dhondt 1971, Dhondt and Olaerts 1981). In contrast, late broods of Eastern Bluebirds (*Sialia sialis*) settle closer to natal areas than early broods (P. A. Gowaty, pers. comm.). Hatching date reportedly has no significant effect on dispersal distance in House Sparrows, *Passer domesticus* (Lowther 1979), Eurasian Sparrowhawks (Newton and Marquiss 1983), Great Tits (Swedish and British populations) (Dhondt 1979, Greenwood et al. 1979), European Nuthatches (Matthysen and Schmidt 1987), and Boreal Owls, *Aegolius funereus* (Korpimaki and Lagerstrom 1988). Similarly, results of the present study (although based on dispersal dates rather than hatching dates) suggest no significant relationship between dispersal date and dispersal distance in young Eastern Screech-Owls.

The optimal strategy for a dispersing juvenile may be to settle in the first unoccupied site encountered in suitable habitat, thereby limiting costs associated with dispersing (Murray 1967). Although it appears that most young owls in the present study could have used such a strategy, the longer-distance dispersers almost certainly passed over unoccupied sites in suitable habitats. Further, at least two young owls dispersed relatively long distances (>2 km) in 1 or 2 days, suggesting that they were not inspecting all available habitat for either suitability or occupancy. Similarly, Weise and Meyer (1979) observed that young Black-capped Chickadees did not simply drift gradually from parental territories to adjacent territories, but exhibited movements of longer distance than would be necessary simply for feeding or escaping the aggressiveness of other birds. It also appears that young House Wrens pass through unoccupied sites before settling (Drilling and Thompson 1988). Such behavior suggests that genetic factors may be influencing dispersal behavior. Newton and Marquiss (1983) speculated that certain aspects of dispersal (distance as well as lack of directional bias and the timing of main movement) may be under some genetic control in sparrowhawks.

DIRECTION OF DISPERSAL

The mean dispersal direction of young Eastern Screech-Owls in the present study did not differ significantly from random. Similarly, VanCamp and Henny (1975) examined dispersal directions of 158 screech-owls banded as nestlings in the northeastern United States and concluded that dispersal direction was random. Our data further suggest that young screech-owls moved consistently in the same general direction during dispersal. Similar behavior has been reported in dispersing Spotted Owls in California (Gutiérrez et al. 1985). Weise and Meyer (1979) noted that a dispersing Black-capped Chickadee also continued moving in the same direction.

MORTALITY OF YOUNG OWLS

Two of six young owls whose fates were known in the present study survived into the next breeding season, a mortality rate of 67%. VanCamp and Henny (1975) estimated that the mortality rate for young screech-owls in the northeastern United States was 69.5%. Three of the young owls in the present study were known to have died in January, while the fourth died in March. We recovered only one of the carcasses. An autopsy revealed an emaciated owl, with no subcutaneous or intra-abdominal fat and an empty proventriculus. Although the small intestine had a moderate infestation of *Coccidia* sp. and nematodes were observed in the ventriculus, the absence of fat suggests that the owl starved to death. During the summer and fall months, Eastern Screech-Owls prey largely on invertebrates (Duley 1979, pers. observ.). As winter progresses the availability of invertebrates declines and screech-owls begin to prey on small mammals and birds (Duley 1979, pers. observ.). Such prey may be more difficult to capture than invertebrate prey, especially for young, inexperienced screech-owls. It is also possible that many young screech-owls are forced into suboptimal habitats (with reduced prey availability) by more dominant adults. Either or both of these factors may increase the susceptibility of young owls to starvation or increased predation by Great Horned Owls and other predators. In any case, our results, although based on a small sample, suggest that the winter months are critical in terms of survival of young screech-owls.

High mortality rates have been reported for first-year individuals in other species of owls. Mortality rates of first-year Tawny Owls (*Strix aluco*) average between 47 and 66% (Southern 1970). Barrowclough and Coats (1985) calculated an expected first-year survivorship for Spotted Owls of 19%. Gutiérrez et al. (1985) radio-tagged and followed seven dispersing Spotted Owls and all of these owls died during dispersal. Miller and Meslow (1985) radio-tagged and followed 18 dispersing Spotted Owls and only three were still alive the following May. Larsen et al. (1987) reported that 78% (seven of nine) of young Eagle Owls (*Bubo bubo*) released in Norway were found dead within 12 weeks. Korpimaki and Lagerstrom (1988) banded 4,311 fledgling Boreal Owls, 53 (1.2%) of which were recovered after surviving at least their first winter. These authors further reported that the proportion of fledglings recovered was significantly larger during the increase phase of vole (*Microtus* and *Clethrionomys* spp.) cycles than during peak, decreasing, and low phases, suggesting that food conditions during the postfledging and independence periods are crucial for the survival of young Boreal Owls.

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