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NORTHERN SAW-WHET OWL (*AEGOLIUS ACADICUS*) AUTUMN MIGRATION MAGNITUDE AND DEMOGRAPHICS IN SOUTH-CENTRAL INDIANA

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Abstract.—Three banding stations were located in south-central Indiana (2002–07) to study migration patterns of Northern Saw-whet Owls (*Aegolius acadicus*). Saw-whet owl captures ranged from 59 in 2002 (1 station) to 447 in 2007 (3 stations), with 2007 an irruption year in at least one location. The proportion of hatch-year owls was 54.8% on average, but lower in 2004 (30.9%). Hatch-year owls consistently arrived 4–5 d earlier than older saw-whet owls in south-central Indiana. We used morphometric sexing techniques to classify 80% of the saw-whet owls we captured as females, and 7% as males. Encounters of birds banded at other stations indicated that most owls captured in south-central Indiana in fall had migrated around the west side of the Great Lakes. The irruption of 2007 was likely due to a large influx of saw-whet owls moving through the Ohio River Valley from eastern regions. Greatest numbers of saw-whet owl captures were associated with clear nights and relatively calm west-to-northwest winds after the passage of a cold front. For owls captured at our station and another, we calculated the average migration rate of 28.8 ± 15.8 km/d (N = 9).

Key Words: *Northern Saw-whet Owl*; Aegolius acadicus; *autumn*; *banding*; *demographics*; *Indiana*; *migration.*

MAGNITUD Y DEMOGRAFÍA DE LA MIGRACIÓN OTOÑAL DE *AEGOLIUS ACADICUS* EN EL CENTRO-SUR DE INDIANA

Resumen.—Se establecieron tres estaciones de anillamiento en el centro-sur de Indiana (2002–07) para estudiar los patrones migratorios de *Aegolius acadicus*. Las capturas de *A. acadicus* fluctuaron entre 59 en 2002 (una estación) y 447 en 2007 (tres estaciones), con un aumento repentino en 2007 en al menos una localización. La proporción de individuos eclosionados en el año fue en promedio de 54.8%, pero fue menor en el 2004 (30.9%). Los individuos eclosionados en el año llegaron consistentemente 4–5 d antes que los individuos más viejos al centro-sur de Indiana. Usamos técnicas morfométricas para la identificación de los sexos, y clasificamos el 80% de los individuos de *A. acadicus* que capturamos como hembras y el 7% como machos. Las recapturas de individuos anillados en otras estaciones indicaron que la mayoría de las aves capturadas en el centro-sur de Indiana en el otoño habían migrado alrededor del lado oeste de los Grandes Lagos. El aumento repentino en el 2007 se debió probablemente a un gran influjo de individuos moviéndose a través del Valle del Río Ohio desde las regiones del este. Las cantidades más grandes de capturas de *A. acadicus* estuvieron asociadas con noches claras y vientos relativamente calmos del oeste al noroeste, luego del paso de un frente frío. Para los individuos capturados en nuestra estación y en otra estación, calculamos una tasa de migración promedio de 28.8 ± 15.8 km/d (N = 9).

[Traducción del equipo editorial]

The annual fall movements of Northern Saw-whet Owls (*Aegolius acadicus*, hereafter saw-whet owls) are highly variable across regions, age class and sex, as well as magnitude. East of the Mississippi River, the annual fall movement of saw-whet owls southward from their breeding range in the boreal forest suggests partial migration punctuated by a four-year ''irruptive'' cycle when the number of captured saw-whet owls can be 10 times higher than the long-term average (Weir et al. 1980, Swengel and Swengel 1995, Whalen and Watts 2002). However, saw-whet owl migration west of the Mississippi River did not show the four-year irruption cycle in Idaho from 1999 to 2004 (Stock et al. 2006). Fall migra-

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tions east of the Mississippi River generally occur along three corridors: from central Ontario down the Ohio River Valley, from Nova Scotia to North Carolina along the Atlantic coastal lowlands, and around the western side of Lake Superior through Wisconsin and to the southeast (Holroyd and Woods 1975, Rasmussen et al. 2008). Varying numbers of saw-whet owls stopover throughout these migration corridors, some staying the winter at sites along these routes and others continuing as far south as the Gulf of Mexico (Rasmussen et al. 2008). The length of stopover is shorter during large irruptive years, presumably due to density-dependent competition for food (Whalen and Watts 2002). Because >95% of the diet of the saw-whet owl is composed of small mammals, local mammal populations may determine both the number of saw-whet owls migrating south and the duration of their stopovers (Swengel and Swengel 1995, Whalen and Watts 2002).

Saw-whet owls are currently considered uncommon fall migrants and winter residents in Indiana (Brock 2007). Before 2002, documented sightings of this species in the entire state peaked at 29 individuals in the winter of 1987 and averaged 19.4 saw-whet owls per year over the last twenty years (Brock 2007). Many saw-whet owls migrating to Indiana also winter in the state rather than migrating farther south (Brittain 2008). However, in general, very little is known about fall migration for saw-whet owls in this region (Indiana, Illinois, and Kentucky) of the Midwest.

Project Owlnet was established (ca. 1994) to improve the knowledge of saw-whet migrations in North America and has expanded to include over 75 banding stations across the continent. The presence of so many banding stations using similar protocol allows comparisons of the migration patterns in southern Indiana to those in other regions across the continent, particularly the >20 areas with banding stations in the Great Lakes region to the north of our study area. One of the goals of Project Owlnet is to improve knowledge of nocturnal owl migration (Huy 2004), and the purpose of our study was to further this knowledge by characterizing the magnitude and age/sex demographics of migratory saw-whet owls captured in fall in south-central Indiana and to compare them to similar studies in other regions. There are no previously published records of fall migrant saw-whet owl capture data for Indiana, Kentucky, or Illinois; thus our project fills a geographical gap in the database for saw-whet owl movements and seasonal demographics.

METHODS

Owl Captures. As much as possible, the methodology followed the protocol for migratory banding stations recommended by Project Owlnet (Huy 2004). The banding station in Yellowwood State Forest (YSF), Brown County, Indiana (39° 11′ 44″ N, 86° 21′ 51″ W) operated from 2002–07 using five 60-mm mesh mist nets, 2.6 m × 12 m, arrayed with the first three on a line from northwest to southeast, with the fourth net running perpendicular to the northeast from the junction of the first two nets, and the last net running perpendicular to the southwest from the junction of the second and third nets. The station is in the middle of a large parcel (ca. 3300 ha) of forest, dominated by oaks (*Quercus* spp.) and maples (*Acer* spp.) approximately 26 m in height. An audiolure was placed in the middle of the net array and used to broadcast the male solicitation ‘‘toot’’ call of the saw-whet owl at approximately 105 decibels. Mid-October (11–18 October) was chosen as the starting time due to lack of captures from 11–16 October during the first three years of operation. Thereafter the station was in full operation no later than 18 October. Nets were opened within 30 min of dusk each night and the audiolure was started. Mist nets were open for a minimum of 3 hr and remained open until no new saw-whet owls had been captured for more than 1 hr, unless poor weather (precipitation or winds >30 km/hr) forced the cancellation of banding operations due to safety concerns for the owls. Mist-netting continued until migration ended, usually during the first week of December, as evidenced by the lack of new captures for 3 d after the passing of a cold front.

We measured right-wing chord length (nearest mm), tail length (nearest mm), culmen length (nearest 0.1 mm), and mass (nearest 0.1 g) of all captured owls, and attached USGS metal leg bands to those that had not been previously banded. We classified saw-whet owls with no noticeable molt of flight feathers as hatch-year birds and those with a noticeable molt as after-hatch-year (Pyle 1997). Sex-category was assigned, based on morphometrics, using the wing-mass differential function available from Project Owlnet (Brinker 2000). We also recorded date, temperature, humidity, and sky conditions. Meteorological data available online from the National Climate Data Center for the Monroe County, Indiana, Airport (39° 08′ 46″ N, 86° 37′ 00″ W; 22.4 km west of the YSF station) were used to determine the percent of the moon illuminated, barometric pressure, wind speed and wind direction for each night the stations were open and for the time of capture for each owl. A corrected measure of moon illumination was also created by changing the illumination to 0% on cloudy nights.

The second banding station operated at a private residence in rural Newark, Greene County, Indiana, (39° 08′ 02″ N, 86° 48′ 31″ W; 38.9 km west of the YSF station and 16.6 km west of the airport) from 2003–07, using the same protocol as the YSF station. However, the Newark station (NEW) used six 60-mm mesh mist nets measuring 2.6 m × 12 m, and also one 60-mm mesh mistnet measuring 2.6 m × 9 m. Four of the mist nets sloped down the side of a hill and were aligned east to west, with a parallel line of two more nets 7 m to the north. The 9-m mist net connected the two lines of mist nets in an asymmetrical H-shaped configuration. The four nets on the south side of the array were in a brushy field, parallel to a forest edge. All other nets were in a mixed hardwood forest similar to the one in YSF, but only ca. 300 ha in area.

In 2006, a third station was established near YSF using three 60-mm mesh mist nets 2.6 m × 12 m, in a roughly straight line from east to west, approximately 1.6 km south of the YSF station. This substation (SUB) was reconfigured in 2007 with a net array identical to that of YSF, and was run both years using the same protocol as YSF. However, all three stations were open more nights in 2007 than previous years (40 compared to a median of 30), due to an effort by the banders to determine whether the owls were moving during less favorable conditions once it became obvious that 2007 had more migrants.

Data for Previously Banded Owls. Many saw-whet owls were locally recaptured at the same station during the same fall migration season. An index of stopover duration was calculated by taking the difference in number of days between the date of first and last captures of locally recaptured saw-whet owls (Erdman et al. 1997).

Information on owls captured at one of our stations and any other Project Owlnet station during the same fall migration period was exchanged by reporting the capture to Project Owlnet's listserve and the Bird Banding Laboratory. Using the coordinates of the banding stations, we determined average migration rate by calculating the straight-line distance between stations divided by the number of days between captures. The proportion of previously banded owls coming from the northwest versus the northeast between 2007 and the previous five years was compared using Fisher's exact test.

Statistical Analyses. We standardized capture rates to unit of effort on the basis of the number of saw-whet owls captured per 10 m^2 of net per 100 hr of open net time for any given night. Capture rates among years, ages, and sexes were compared using ANOVA and Tukey's multiple comparisons. Capture rates among stations and years were analyzed using MANOVA. Kruskal-Wallis tests were used to test differences in date of capture among years for owls of different ages and sexes, and to test differences in stopover duration index among years. If Kruskal-Wallis tests showed a significant difference, subsequent pairwise Mann-Whitney *U*-tests were run. We used Spearman's rank correlation to test for correlations between capture rates of saw-whet owls and temperature, sky condition, moon illumination, and corrected moon illumination.

Mass, wing chord, tail length, and culmen were compared among stations, years, ages, and sexes using ANOVA and Tukey's multiple comparisons or Student *t*-tests assuming unequal variances where appropriate. Differences in mass and wing chord were not tested between sexes, because those are the criteria we used to sex the owls.

The proportion of sexes and ages in each year were evaluated using χ^2 contingency tables, followed by pairwise χ^2 contingency tables if the log-likelihood showed significant differences. Tests of significant wind vectors among stations, years, ages, and sexes were conducted using Watson-Williams tests in circular statistics as described by Zar (1999).

Where multiple pair-wise tests are presented, 5% experiment-wise error rates were preserved by using sequential Bonferroni methods (Holm 1979). The number of pairwise tests of capture rates per unit effort, mass by year, and wind vector was 15 for YSF and all sites combined and 10 for Newark. The number of pairwise tests of capture rates per unit effort between Newark and YSF, and migration correlations was five.

RESULTS

Owl Captures. The number of saw-whet owls captured across the three stations was highly variable with the most extreme values at NEW which ranged from a low of 21 saw-whet owls in 2006 to 248 in 2007 (Table 1). Overall, the stations were open for 329 station nights and captured at least one saw-whet owl on 57% of those nights. Newark, which

Table 1. Number of nights spent attempting to capture Northern Saw-whet Owls at three south-central Indiana banding stations from 2002–07, and the number of nights with no captures in parentheses. Number of Northern Saw-whet Owls captured and the capture rate per unit effort (owls/10 m^2/100 hr).

	Yellowwood State Forest			Newark			YSF Substation		
	Nights	Owls Caught	Capture Rate	Nights	Owls Caught	Capture Rate	Nights	Owls Caught	Capture Rate
2002	30 (13)	59	2.6	-	-	-	-	-	-
2003	35 (12)	70	3.1	33 (12)	55	2.4	-	-	-
2004	30 (12)	56	2.5	28 (14)	42	1.7	-	-	-
2005	30 (14)	38	1.7	32 (18)	25	0.8	-	-	-
2006	32 (15)	37	1.5	36 (21)	21	0.6	28 (10)	33	1.4
2007	40 (14)	124	3.3	38 (7)	248	7.0	40 (12)	75	2.2
Totals	**197 (80)**	**384**	**3.1**	**167 (72)**	**391**	**2.6**	**68 (22)**	**108**	**2.0**

ranged from a low of at least one owl captured on 18% of nights in 2007 to a high of 58% in 2006, was the most variable site. However, standardized capture rates per unit effort (number of saw-whet owls/10 m^2/100 hr) showed no evidence for differences among the three stations (F = 0.98, df = 2, P = 0.376; Fig. 1). There was no evidence of differences in capture rates per unit effort between the NEW and YSF stations during the five years they were running simultaneously (MANOVA, $F_{1,328} = 0.311$, $P = 0.577$), but the years were different ($F_{4,328} = 12.488$, $P < 0.001$). However, at YSF, capture rates of saw-whet owls did not differ among years (F = 1.44, df = 5, P = 0.213), whereas NEW had higher capture rates in 2007 than in all four previous years (F = 14.92, df = 4, $P < 0.001$). For pooled capture rates of all stations together, 2007 had higher capture rates than 2004, 2005, and 2006 in south-central Indiana (F = 8.31, df = 5, $P < 0.001$).

The earliest capture of a saw-whet was 16 October, which occurred in both 2003 and 2007, and the latest capture occurred on 4 December 2007. The peak of the migration generally occurred between 27 October and 10 November.

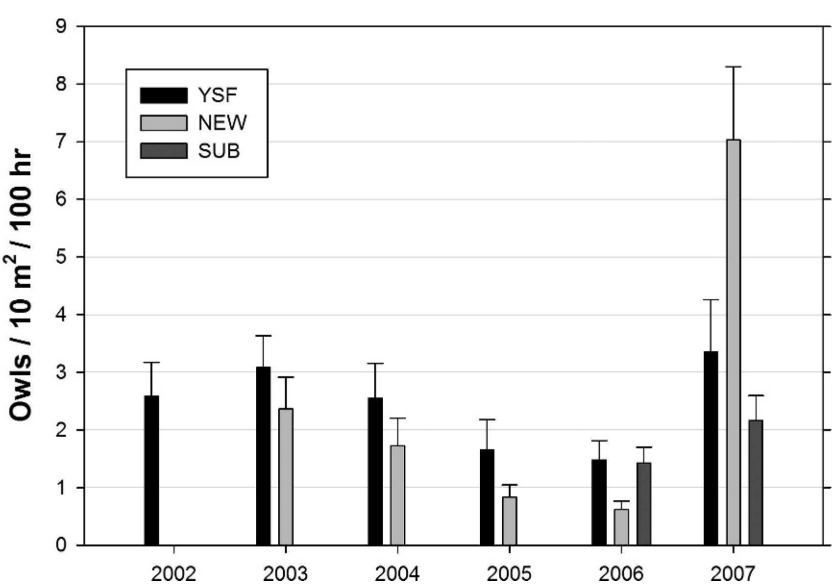

Figure 1. Number (mean ± SE) of Northern Saw-whet Owls captured per unit effort (owls/10 m^2/100 hr) in each of three banding stations in south-central Indiana from 2002–07. YSF = Yellowwood State Forest station in Brown County, Indiana. NEW = Newark station in Greene County, Indiana, and SUB = the substation ca.1.6 km south of YSF.

Table 2. Number of Northern Saw-whet Owls locally recaptured during the same banding season in south-central Indiana from 2002–07, recapture rate (number of local recaptures divided by the total number of owls captured that season), the index of stopover (average number of days between the first and last capture of each owl) and the standard error of the index of stopover.

	NUMBER OF LOCAL RECAPTURES	RECAPTURE RATE (%)	INDEX OF STOPOVER (d)	SE OF INDEX
2002	7	12	9.3	2.0
2003	19	15	11.4	1.6
2004	3	3	3.3	2.3
2005	9	15	13.9	3.2
2006	16	18	9.7	1.2
2007	27	6	6.6	1.0

Age, Sex, and Morphometrics. Of the captured saw-whet owls in south-central Indiana in 2002–07, 60.1% were hatch-year birds and the mean annual proportion over 6 yr was 54.8% (Table 3). The proportion of hatch-year owls differed among years ($\chi^2 = 49.864$, df = 5, $P < 0.001$), with pairwise comparisons showing 2004 (30.9%) was lower than 2002, 2003, 2006, and 2007 ($\chi^2 > 10.333$, df = 1, $P < 0.001$), but not 2005 ($\chi^2 = 2.252$, df = 1, $P = 0.133$).

Based on morphometric sexing (Brinker 2000), the owls we captured included 655 females (78.7%), 73 males (7.1%) and 145 (14.2%) that could not be accurately sexed. There were no significant differences in sex ratios among years ($\chi^2 > 16.457$, df = 10, $P < 0.087$; Table 3).

Hatch-year saw-whet owls had a median arrival date 4 d earlier than after-hatch-year owls ($U = 210508.0$, $N = 875$, $P < 0.001$; Table 4). Wing chords averaged 1.6 mm less in hatch-year owls than after-hatch-year owls ($t = -3.07$, df = 453, $P = 0.002$; Table 4). Similarly, tail length averaged 1.2 mm less in hatch-year owls ($t = -4.88$, df = 711, $P < 0.001$), and mass of hatch-year owls averaged 1.4 g less in hatch-year owls ($t = -2.62$, df = 735, $P = 0.009$). The proportion of female saw-whet owls did not change among the age classes but there was an unexpectedly higher proportion of hatch-year owls among males compared to females ($\chi^2 = 8.909$, df = 1, $P = 0.031$). With data from all sites pooled, we found that saw-whet owls captured in 2007 were lighter than those caught in 2002 and 2004 (ANOVA and Tukey's multiple comparison $F = 5.00$, df = 5, $P < 0.001$).

Recaptured Saw-whet Owls. Of 873 owls caught, 81 were locally recaptured at the same station during the same migration season (9.3%), with a range of only three (3%) in 2004 to 27 (6%) in 2007 (Table 2). The average time between first and last captures in a given season (an index of stopover duration) was 9.3 d over the six-year period (mean range = 3.3 d in 2004 to 13.9 d in 2005), and did not vary by age or sex of the owls. Analysis of local recapture data showed that 7.4% (6 of 81) of the recaptured saw-whet owls were assigned different sex categories, changing from unknown to male or female, or vice versa; however, none of the birds changed from the female category to the male category or vice versa. Three of 54 locally recaptured saw-whet owls that were assigned different sex cate-

Table 3. Annual proportion of Northern Saw-whet Owls by age and sex, and total number of owls captured in south-central Indiana from 2002–07.

	AGE CLASS		SEX CATEGORY		
YEAR	HATCH-YEAR (%)	AFTER-HATCH-YEAR (%)	FEMALES (%)	MALES (%)	TOTAL NUMBER OF OWLS CAPTURED
2002	62.3	37.7	85.2	6.6	59
2003	62.4	37.6	75.2	6.4	125
2004	30.9	69.1	85.1	6.4	94
2005	43.5	56.5	77.4	6.5	62
2006	62.9	37.1	78.7	6.7	89
2007	66.9	33.1	70.5	10.1	444
6-yr mean[a]	54.8	45.2	78.7	7.1	145.5
SD	14.3	14.3	5.7	1.5	148.2
Overall[b]	**60.1**	**39.9**	**75.0**	**8.4**	**873**

[a] Calculated by averaging the percent of owls in each age class and sex category for each year or the total number of owls captured.
[b] Calculated by pooling the data from all six years.

Table 4. Morphometrics (mean ± SE) of captured Northern Saw-whet Owls by age and sex category. The wing chord and mass of the sexes are not reported because sex was assigned on the basis of these variables.

		Age Class		Sex Category		
	N	Hatch-year	After-hatch Year	Females	Males	Unknown
Wing chord (mm)*	872	137.2 ± 0.19*	138.9 ± 0.50*	-	-	-
Mass (g)*	872	90.9 ± 0.33*	92.3 ± 0.41*	-	-	-
Tail (mm)*	860	70.0 ± 0.15*	71.2 ± 0.68*	71.1 ± 0.35	66.5 ± 0.37	69.5 ± 0.57
Culmen (mm)	858	10.5 ± 0.17	10.3 ± 0.10	10.4 ± 0.15	9.7 ± 0.09	10.1 ± 0.09
Date of capture[a]	872	306.0 ± 0.43	311.0 ± 0.51	310.0 ± 0.38	309.0 ± 1.24	309.0 ± 0.79

* Denotes significant differences between age classes.
[a] Julian day.

gories were captured prior to 2007 (5.5%) and three of 27 (11.1%) were captured during the 2007 irruption. A Student *t*-test showed no evidence of differences in the mass of the owls between captures ($t = 1.36$, df $= 86$, $P = 0.177$). Neither did a Kruskal-Wallis test show evidence of a change in the median duration between first and last captures (stopover duration index. $H = 7.24$, df $= 4$, $P = 0.124$).

We encountered 25 saw-whet owls that had been banded at another station (other than our three in south-central Indiana). Five of these were originally banded on the northwest shore of Lake Superior in Lutsen, Minnesota; Tofte, Minnesota; Bigfork, Minnesota; and Sleeping Giant Provincial Park, Ontario, Canada. Another eight were banded in Wisconsin, six at Stevens Point, and two at Two Rivers. Four other saw-whet owls were originally banded in stations at the northern tip of the lower peninsula of Michigan and two were originally banded in Prince Edward County, Ontario. Two more saw-whet owls were originally banded in Timiskaming, Ontario, and one additional saw-whet captured in 2007 was banded at an unknown Ontario location. Two birds were also originally banded in Chilicothe, Ohio. In addition, in 2004, one saw-whet originally banded in Big Oaks National Wildlife Refuge in Ripley County, Indiana, was encountered at NEW five days later, ca. 130 km west northwest of the Big Oaks banding station.

Table 5. Wind vector (direction and speed) analysis for Northern Saw-whet Owl migration in south-central Indiana from 2002–07.

Capture Success, Sex, or Age Category	Sample Size	Wind Direction (°)	Speed (km/hr)
Nights with 1 or fewer saw-whet owls	116	217.1	2.7
Nights with more than 1 saw-whet	89	273.9	0.5
Females	655	280.3	1.1
Males	73	233.0	1.0
Unknown sex	145	219.2	1.0
Hatch-year	525	268.4	1.0
After-hatch-year	352	268.1	1.1
Average of all nights	**207**	**223.8**	**1.6**

Of the saw-whet owls originally banded in south-central Indiana, six were encountered at other stations in subsequent years: two in Whitefish Point, Michigan, two in Timiskaming, Ontario, one in Stevens Point, Wisconsin, and one in Lambs Knoll, Maryland. The longest known distance traveled was 1078 km between Timiskaming, Ontario (47° 49′ 60″ N, 80° 30′ 0″ W) and Newark, Indiana. Of the 434 saw-whet owls banded in Indiana (2002–06) with an opportunity to be recaptured in another year, only four have been recaptured at any Indiana station in subsequent years.

Before the irruptive year of 2007 in Newark, there had been 10 encounters of individuals originally banded on the northwest side of the Great Lakes (Minnesota and Wisconsin) and seven on the northeast side (Michigan, Ohio, and Ontario). However, in 2007 there were three encounters of owls originally banded on the northwest side of the Great Lakes, whereas six were originally banded on the northeast side. The proportion of saw-whet owls from northwestern locations did not differ in 2007, compared to the previous 5 yr ($Z = -1.27$, $P = 0.411$), but the difference is suggestive of a change in direction.

Correlations of Capture Rate with Migration Weather. The number of captures per night was negatively correlated to temperature and cloud cover ($r_S = -0.283$, $N = 706$, $P < 0.001$ and $r_S = -0.301$, $N = 706$, $P < 0.001$, respectively). The number of captures was positively related to barometric pressure and the percent of illuminated moon corrected for cloudy conditions ($r_S = 0.153$, $N = 706$, $P = 0.005$ and $r_S = 0.159$, $N = 706$, $P = 0.001$, respectively).

Wind vectors were also strongly correlated to saw-whet captures as shown by Watson-Williams tests (Table 5). The average wind vector for nights with fewer than two new saw-whet owls captured was more southerly and stronger (217.1° at 2.7 km/hr, $N = 116$) than nights with two or more saw-whet owls captured (273.9° at 0.5 km/hr, $N = 89$, $P < 0.001$). Wind vectors were significantly different among years ($F = 139.657$, $N = 987$, $P < 0.001$). Pairwise comparison showed the wind vector for captured saw-whet owls was more southerly (216.3°) in 2007 compared to 2002 (326.5°), 2004 (272.5°), 2005 (292.7°) and 2006 (274.3°) after correcting with Bonferroni methods ($N > 502$, $P < 0.003$).

The general climate in south-central Indiana was average in 2002, 2003, 2005, and 2006. An outbreak of 17-year periodical cicadas (*Magicicada* ssp.) occurred in 2004, potentially affecting regional productivity of prey species and 2007 was a drought year across much of eastern and southern Indiana.

Migration Rate. Nine saw-whet owls were captured in south-central Indiana after being banded at a different station during the same migration season. The average calculated migration rate for these owls was 28.8 km/night (SD = 15.8).

Discussion

Owl Captures per Unit Effort. During the six-year period of this study, saw-whet owls were consistently captured in south-central Indiana, but with a great degree of variability. Capture rates suggested that 2007 was an irruption year, at least in the vicinity of Newark, Greene County, Indiana, and possibly across south-central Indiana. Data from the Project Owlnet listserve (Huy 2004) also indicated that there was a widespread irruption of saw-whet owls east of the Mississippi River in 2007, particularly in the northeastern U.S. However, captures rates for the YSF station did not indicate a significantly higher rate in 2007, despite the larger number of total captures. The lack of difference in captures per unit effort may have been due to changes in protocol whereby banding was also conducted on less favorable nights than previous years. As a result, 54 more saw-whet owls were captured in YSF in 2007 than in any other year (124 if the substation is included), but net hours were increased by 69.9 over the previous five-year average of 128.2. Alternatively, YSF may not have had the irruption that occurred less than 50 km to the west in Newark, but this was unlikely given the apparent large-scale irruption across eastern North America that year.

Saw-whet owl movements into south-central Indiana did not show the same pattern as in other regions. The lack of an irruption in 2003 did not agree with the four-year periodicity in other regions east of the Mississippi (Swengel and Swengel 1995, Brinker et al. 1997, Whalen and Watts 2002), but was similar to the pattern observed in Idaho (Stock et al. 2006). Saw-whet owl irruptions may not always reach the lower Ohio River Valley, or irruptions along the east coast and Appalachians may be driven by different population factors, such as availability of specific prey. However, the proportion of nights with saw-whet owl captures and captures per unit effort uniformly decreased each year from 2003 to 2006 (Table 1), indicating that 2003 may have simply had an insignificant minor irruption. From 2006 to 2007, the captures of saw-whet owls per unit effort increased more than ten-fold from 0.6 to 7.0 at NEW (Table 1).

Age and Sex Demographics. Researchers at other banding stations on Lake Michigan and Lake Ontario captured similar proportions of hatch-year owls (ca. 60%) as we did at our south-central Indiana stations (Mueller and Berger, 1967, Weir et al. 1980); however, Whalen and Watts (2002) reported a greater proportion (72.5%) of hatch-year owls on the Delmarva Peninsula, and Stock et al. (2006) caught up to 82% hatch-year owls in Idaho. In 2004, the proportion of hatch-year owls caught in south-central Indiana was lower (30.9%), indicating either that saw-whet owls had a poor breeding year in 2004 or that many hatch-year owls died before reaching south-central Indiana that year (Table 3). The proportion of hatch-year owls increased to 43.5% in 2005 and to the more typical proportion (ca. 60%) in 2006 and 2007, indicating annual variability in age demographics of migratory saw-whet owls.

Hatch-year owls consistently arrived 4–5 d earlier than older saw-whet owls in south-central Indiana, whereas age classes differed in timing from year to year in Ontario (Weir et al. 1980) and hatch-year owls only arrived earlier in Idaho during an irruptive year (Stock et al. 2006). In contrast, in New Jersey and Virginia, adult saw-whet owls migrated earlier than did hatch-year birds (Duffy and Kerlinger 1992, Iliff 2000), indicating both spatial and temporal variation in timing of arrival of hatch-year and older birds.

We did not compare sex demographics from this study to that of other studies because the published reports generally did not use the same sexing criteria. The solicitation call of male saw-whet owls may also have biased the sex of captured saw-whet owls, as a study at Cape May, New Jersey, showed that the percent of females captured went from 65% in 9 yr before the use of an audiolure to 80% in 6 yr with the use of an audiolure (Duffy and Matheny 1997). However, females were disproportionately captured at higher rates than males using either technique. Whalen and Watts (1999) similarly found a size bias, with smaller owls being captured farther away from the audiolure. The Whalen and Watts study was conducted before the advent of the current sexing criteria, but suggests a potential reduction in male captures due to audiolure avoidance. Nevertheless, our data may suggest that females were more likely to migrate than males, or that the audiolure increased the difference in capture rates between the sexes.

The sex distribution of saw-whet owls in south-central Indiana was similar to that reported by banding stations to Project Owlnet since the application of Brinker's wing-mass discriminant function sexing criteria (ca. 80% female, 7% male). Even if all of the owls classified as unknown sex were males, the females would still have represented a much greater proportion. The relatively high proportion of hatch-year males compared to after-hatch-year males in our study was similar to the results in Idaho (Stock et al. 2006). The discrepancy among proportions of female and male saw-whet captures, and the high proportion of hatch-year males relative to after-hatch-year males, may be due to higher site fidelity among male saw-whet owls or the bias of capturing using the solicitation call. However, because pre-audiolure captures in Cape May included only had 21% males, the apparent absence of migratory male saw-whet owls may be due to an unwillingness to vacate hard-won nesting territories. Three common hypotheses of differential migration between sexes of the same species are: (1) the larger sex survives better in harsh climates, (2) the dominant sex forces the other sex to migrate farther to avoid competition, and (3) early arrival of one sex to the breeding grounds is favored in intrasexual selection (Arnold 1991). Some combination of these factors may be driving female saw-whet owls to migrate disproportionately. Because it is unlikely that the smaller males force the females into migration to limit competition, it is more plausible that males staying on the breeding territories may receive favorable intrasexual selection. The lack of an increase in male captures during irruptive years in this and other studies suggests that males are not driven south by local prey resources (Brinker et al. 1997, Stock et al. 2006), but that males typically stay further north than females as shown by Brinker and others (1997).

A recent study on the Delmarva Peninsula questioned Brinker's sexing method due to mass variation in the owls (Paxton and Watts 2008). The Delmarva study showed that recaptured males in particular were recategorized as females 14% of the time. The Bird Banding Laboratory currently accepts Brinker's sexing criteria method and the method has been independently verified in another study (Leppert et al. 2006). Our own data showed that 7.4% of the locally recaptured saw-whet owls were recategorized from male or female to unknown or vice versa, but never from male to female or female to male. Of the saw-whet owls we recaptured locally, 5.5% (of 54) were recategorized prior to 2007 and 11.1% (of 27) during the 2007 irruption year, in which the masses of the owls were lower. Although the sample size is limited, the relatively high rate of change in sex recategorization in 2007 may also suggest that when owls may be food-stressed during irruptive years, the sexing criteria do not function as well as predicted and should be applied more cautiously. It is possible that the relationship of wingchord and mass with the sex of saw-whets may have more annual or regional variability than originally thought.

Movement Patterns and Recaptures. It is possible that the saw-whet migration corridor through the Ohio River Valley may be limited to the more extreme eastern side and forested southern third of the state. Because the average wind vector was more southerly for saw-whet captures in 2007 and there was a large number of recaptures of birds banded on the east side of the Great Lakes in 2007, it is likely that the irruption of 2007 in south-central Indiana was due to a larger influx of saw-whet owls moving through the Ohio River Valley from eastern regions and dispersing into the forests of southern Indiana. Typical fall migrations in south-central Indiana appear to include mostly owls migrating through Wisconsin around the west side of the Great Lakes.

Influences of Weather on Migration. Our findings concurred to varying degrees with other studies regarding the magnitude of saw-whet owl migration in response to cloud cover and wind direction (Mueller and Berger 1967, Evans 1980, Weir et al. 1980). South-central Indiana saw-whet owl migration was positively related to the amount of ambient moonlight (corrected for cloud cover), whereas it was negatively related to bright moon phases in other studies (Evans 1980, Stock et al. 2006). This may be due to differences in habitat around the banding stations. The south-central Indiana stations are all located in forested habitats where trees shade the moonlight until leaf-fall sometime in November (well after the peak of migration), whereas the Duluth station (Evans 1980) was located in an open wet meadow and the Idaho station was located in coniferous forest (Stock et al. 2006). The lack of shade in Duluth may have allowed the saw-whet owls to see the nets and avoid capture during a full moon, but this would not explain the differences in moon phase and capture rates between south-central Indiana and Idaho. However, the Idaho and Minnesota studies only looked at moon phase, and our study analyzed the percent of moon illuminated corrected for cloud cover. There was considerable overlap in the percent of moon illumination among the phases, which may have confounded the results and may explain the regional differences.

Index of Stopover Duration. Dozens of saw-whet owls spend the winter in southern Indiana rather than continuing further south (Brittain 2008). However, local recaptures at the stations began to decrease more than a week after the peak of migration, indicating that most of the owls rest in the vicinity of the stations before continuing their migration.

The lighter mass of saw-whet owls in 2007 compared to 2002 and 2004 suggests low prey availability on northern breeding grounds or increased competition for scarce food resources in migration in 2007. Using the time between first and last captures of saw-whet owls as an index of duration of stopover, the shorter indices in 2004 and 2007 also suggest poor food resources for migrating/wintering saw-whet owls in south-central Indiana relative to the number of owls in migration (Table 2), which may have forced the owls to keep moving. In 2004, Yellowwood State Forest had one of the lowest oak masts in 20 yr (J. Allen pers. comm.), possibly due to the effects of the periodical cicada outbreak. Because population sizes of *Peromyscus* spp., the preferred food of saw-whet owls, are known to be positively correlated to oak mast (Krohne et al. 1988, Elias et al. 2004), it is likely that this prey was in short supply, and although the owls may have arrived in south-central Indiana with high body mass, they had to keep moving to find food. The shorter time between captures in 2007 corroborates the results of Whalen and Watts (2002) on the Delmarva Peninsula. They also saw reduced stopover duration indices during irruptive years, presumably due to density-dependent competition. In central Quebec, a positive relationship between saw-whet migration magnitude and small mammal populations suggested that prey availability influences breeding success at the northern extremity of the breeding range (Côté et al. 2007). The relationship among prey populations, saw-whet survivorship, and local recapture rates in the southern regions of the wintering range requires further research.

Migration Rates between Stations in the Same Season. Saw-whet owls are dependent on woodlands throughout their breeding range and dense vegetation in winter (Rasmussen et al. 2008, Brittain 2008). South-central Indiana has few wooded corridors extending from north to south, unlike the Ohio River Valley or Appalachian Mountains, but many small, isolated woodlots that serve as potential stopover locations. The rate of migration of saw-whet owls encountered at one of the three Indiana banding stations after first being banded at a more northern station during the same fall (28.8 km/night) was similar to the migration rates of saw-whet owls captured at Thunder Cape Bird Observatory, Ontario (26.9 km/night, Thunder Cape News 1998). These migration rates were similar to, but slightly higher than the average migration rates in coastal Virginia, which ranged from 14.1 km/night from Cape May, New Jersey to Cape Charles, Virginia, 15.6 km/night from Assateague Island, Maryland to Cape Charles, Virginia, and 23.1 km/night from Cape May, New Jersey, to Assateague Island, Maryland (Brinker et al. 1997).

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LITERATURE CITED

ARNOLD, T.W. 1991. Geographic variation in sex ratios of wintering American Kestrels *Falco sparverius*. *Ornis Scand.* 22:20–26.

BRINKER, D.F., K.E. DUFFY, D.M. WHALEN, B.D. WATTS, AND K.M. DODGE. 1997. Autumn migration of Northern Saw-whet Owls (*Aegolius acadicus*) in the middle Atlantic and northeastern United States: what observations from 1995 suggest. Pages 74–89 *in* J.R. Duncan, D.H. Johnson, and T.H. Nichols [EDS.], Biology and conservation of owls of the northern hemisphere, second international symposium. USDA Forest Service Gen. Techn. Rep. NC-GTR-190, St. Paul, MN U.S.A.

———. 2000. Sex criteria for Northern Saw-whet Owls. Project Owlnet website. http://projectowlnet.org/df.htm (last accessed 30 May 2008).

BRITTAIN, R.B. 2008. Characterizing Northern Saw-whet Owl (*Aegolius acadicus*) winter habitats in south-central Indiana. *Proc. Indiana Acad. Sci.* 117:71–80.

BROCK, K.J. 2007. Brock's birds of Indiana CD. Amos Butler Audubon Society, Indianapolis, IN U.S.A.

CONTRERAS, A. 2000. Changing seasons — fall migration: August–November 1999. *N. Am. Birds* 54:16–17.

CÔTÉ, M., J. IBARZABAL, M.-H. ST-LAURENT, J. FERRON, AND R. GAGNON. 2007. Age-dependent response of migrant and resident *Aegolius* owl species to small rodent population fluctuations in the eastern Canadian boreal forest. *J. Raptor Res.* 41:16–25.

DUFFY, K. AND P. KERLINGER. 1992. Autumn owl migration at Cape May Point, New Jersey. *Wilson Bull.* 104:312–320.

DUFFY, K.E. AND P.E. MATHENY. 1997. Northern Saw-whet Owls (*Aegolius acadicus*) captured at Cape May Point, NJ, 1980–94: comparison of two capture techniques. Pages 131–137 *in* J.R. Duncan, D.H. Johnson, and T.H. Nichols [EDS.], Biology and conservation of owls of the northern hemisphere, second international symposium. USDA Forest Service Gen. Techn. Rep. NC-GTR-190, St. Paul, MN U.S.A.

ELIAS, S.P., J.W. WITHAN, AND M.L. HUNTER, JR. 2004. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. *J. Mammal.* 85:743–747.

ERDMAN, T.C., T.O. MEYER, J.H. SMITH, AND D.M. ERDMAN. 1997. Autumn populations and movements of migrant Northern Saw-whet Owls (*Aegolius acadicus*) at Little Suamico, Wisconsin. Pages 167–172 *in* J.R. Duncan, D.H. Johnson, and T.H. Nichols [EDS.], Biology and conservation of owls of the northern hemisphere, second international symposium. USDA Forest Service Gen. Tech. Rep. NC-GTR-190, St. Paul, MN U.S.A.

EVANS, D.L. 1980. Multivariate analyses of weather and fall migration of saw-whet owls at Duluth, Minnesota. M.S. thesis. North Dakota State University, Fargo, ND U.S.A.

HOLM, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6:65–70.

HOLROYD, G.L. AND J.G. WOODS. 1975. Migration of the saw-whet owl in eastern North America. *Bird-Banding* 46:101–105.

HUY, S. 2004. Project Owlnet. http://www.projectowlnet.org/default.htm. (last accessed 2 December 2006).

ILIFF, M. 2000. Middle Atlantic region. *N. Am. Birds* 54:36–37.

KROHNE, D.T., J.F. MERRITT, S.H. VESSEY, AND J.O. WOLFF. 1988. Comparative demography of forest *Peromyscus*. *Can. J. Zool.* 66:2170–2176.

LEPPERT, L., T.V. ZADOROZHNY, J.R. BELTHOFF, A.M. DUFTY, JR., S.L. STOCK, G. KALTENECKER, AND J.F. SMITH. 2006. DNA sexing of owls: a comparison of three methods. *J. Raptor Res.* 40:291–294.

MUELLER, H.C. AND D.D. BERGER. 1967. Observations on migrating saw-whet owls. *Bird-Banding* 38:120–125.

PAXTON, B.J. AND B.D. WATTS. 2008. Mass variation in Northern Saw-whet Owls: implications for current sexing criteria. *J. Field Ornithol.* 79:53–57.

PYLE, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA U.S.A.

RASMUSSEN, J.L., S.G. SEALY, AND R.J. CANNINGS. 2008. Northern Saw-whet Owl (*Aegolius acadicus*). *In* A. Poole [ED.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY U.S.A. http://bna.birds.cornell.edu/bna/species/042doi:10.2173/bna.42

STOCK, S.L., P.J. HEGLUND, G.S. KALTENECKER, J.D. CARLISLE, AND L. LEPPERT. 2006. Comparative ecology of the Flammulated Owl and Northern Saw-whet Owl during fall migration. *J. Raptor Res.* 40:120–129.

SWENGEL, A.B. AND S.R. SWENGEL. 1995. Possible four-year cycle in amount of calling by Northern Saw-whet Owls. *Passeng. Pigeon* 57:149–155.

THUNDER CAPE NEWS. 1998. Saw-whet owl migration monitoring at Thunder Cape Bird Observatory. Thunder Cape Bird Observatory, Thunder Bay, Ontario, Canada. http://www.tbfn.net/owl.htm (last accessed 10 May 2008).

WEIR, R.D., F. COOKE, M.H. EDWARDS, AND R.B. STEWART. 1980. Fall migration of saw-whet owls at Prince Edward Point, Ontario. *Wilson Bull.* 92:475–488.

WHALEN, D.M. AND B.D. WATTS. 1999. The influence of audio-lures on capture patterns of migrant Northern Saw-whet Owls. *J. Field Ornithol.* 70:163–168.

——— AND ———. 2002. Annual migration density and stopover patterns of Northern Saw-whet Owls (*Aegolius acadicus*). *Auk* 119:1154–1161.

ZAR, J.H. 1999. Biostatistical analysis, Fourth Ed. Prentice Hall, Upper Saddle River, NJ U.S.A.

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