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AUTUMN MIGRATION ECOLOGY OF THE NORTHERN SAW-WHET OWL (*AEGOLIUS ACADICUS*) IN NORTHERN MONTANA

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ABSTRACT.—Characterizing the migration strategies of Northern Saw-whet Owls (*Aegolius acadicus*) has proved difficult due to variation in movement patterns within and among regions. Such variation underscores the need for information from sites throughout the species' range. To elucidate regional patterns in Northern Saw-whet Owl migration ecology, I studied migration in northern Montana from 2001–06, banding a total of 668 owls between 30 August and 31 October. Capture rates varied greatly among years, as did age ratios. Capture rates peaked between mid-September and early October. Weather variables did not have detectable effects on migration magnitude, but capture rates decreased approximately 2% for every 10% increase in moon illumination. Two owls originally banded in Alberta were captured at my banding site during this study. Additionally, two owls banded during this study were encountered elsewhere: one found dead in southern Montana and the other recaptured in Massachusetts, approximately 3322 km east of my study site. Results were consistent with the hypothesis that high rates of breeding dispersal and density-dependent migratory responses yield annual, latitudinal migrations that vary in magnitude and have a nomadic component.

KEY WORDS: *Northern Saw-whet Owl*; Aegolius acadicus; *migration*; *Montana*; *stopover.*

ECOLOGÍA DE MIGRACIÓN OTOÑAL DE *AEGOLIUS ACADICUS* EN EL NORTE DE MONTANA

RESUMEN.—Se ha demostrado que la caracterización de las estrategias migratorias de *Aegolius acadicus* resulta difícil debido a la variación en los patrones de movimiento dentro y entre regiones. Esta variación subraya la necesidad de información de distintos sitios a través del área de distribución de la especie. Para elucidar los patrones regionales de la ecología de migración de *A. acadicus*, estudié la migración en el norte de Montana del 2001 al 2006, anillando un total de 668 lechuzas entre el 30 de agosto y el 31 de octubre. Las tasas de captura variaron ampliamente entre años, como también la relación de edad. Las tasas de captura llegaron a su nivel más alto entre mediados de septiembre y comienzos de octubre. Las variables meteorológicas no tuvieron efectos detectables en la magnitud de la migración, pero la tasa de captura disminuyó aproximadamente un 2% por cada 10% de incremento en la iluminación lunar. Durante este estudio, dos lechuzas anilladas originalmente en Alberta fueron capturadas en mi sitio de anillado. Adicionalmente, dos lechuzas anilladas durante este estudio fueron encontradas en otros sitios: una encontrada muerta en el sur de Montana y otra recapturada en Massachusetts, aproximadamente 3322 km al este de mi sitio de estudio. Los resultados fueron consistentes con la hipótesis de que altas tasas de dispersión reproductiva y respuestas migratorias dependientes de la densidad producen migraciones anuales y latitudinales que varían en magnitud y que tienen un componente nómade.

[Traducción del equipo editorial]

Marks and Doremus (2000) hypothesized that Northern Saw-whet Owls (*Aegolius acadicus*; hereafter ''NSWO'') are nomadic in at least some portions of their range, and recent research has provided additional support for their hypothesis (Bowman et al. 2010). However, although NSWO appear to respond to temporal fluctuations in prey abundance with a nomadic breeding strategy (i.e., high rates of breeding dispersal; Andersson 1980, Greenwood 1980), annual migrations occur with fairly predictable seasonal timing (e.g., Weir et al. 1980, Duffy and Kerlinger 1992, Whalen et al. 1997). This is inconsistent with true nomadism: ''unpredictable, unseasonal and irregular movements across landscapes and regions'' (Dean 2004). Despite this seeming inconsistency, Newton (2008) notes that in many bird species ''nomadic movements are superimposed on regular north-south migrations.'' Available information on breeding and migration patterns suggests that this form of facultative migration may be an accurate

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general description of the migration strategy employed by NSWO across much of the species' range.

Specific avian migration strategies, however, exhibit a high degree of evolutionary plasticity (Berthold 1999), and it is unlikely that the variable movement and breeding patterns observed in NSWO can be uniformly categorized. The breeding range of NSWO comprises a broad range of ecological systems, with a corresponding diversity of selective pressures. Identifying specific migration strategies underlying the heterogeneous movements exhibited by individuals will require regional information from across the species' range. Relatively few studies of NSWO migration have been conducted in western North America, but recent investigations have described aspects of migration in the Pacific Northwest (Frye and Gerhardt 2003, Nightingale 2009), the Rocky Mountain region (Stock et al. 2006), and western Canada east of the Rocky Mountains (Priestly and Priestly 2005, Priestly et al. 2010). To elucidate regional patterns in migration magnitude, timing, and movements, I studied autumn migration of NSWO on the Rocky Mountain Front in northern Montana. Here I describe migration patterns observed from 2001–06 and movements of NSWO banded or recaptured at the study site.

METHODS

Study Site. The study site was located on the Rocky Mountain Front, approximately 39 km west of Choteau, Montana, U.S.A. (47°52′N, 112°41′W). Vegetation at the site was a mosaic of Douglas-fir (*Pseudotsuga menziesii*)-lodgepole pine (*Pinus contorta*) forest, small grass- and forb-dominated meadows, and small patches of limber pine (*Pinus flexilis*). The banding station was situated atop a ridge at the eastern base of Wind Mountain, between the North and South forks of the Teton River. The ridge has a latitudinal orientation with prominent longitudinal ridges leading toward it from the north. Elevation at the site is approximately 1750 m with steep slopes on both the north and south faces of the ridge. Heading easterly from the site, the ridge tapers gradually into the Great Plains, approximately 7 km distant.

Owl Capture. I followed standard capture and marking procedures for migrant NSWO. A contiguous array of five to seven mist nets (38 mm and 60 mm) was erected adjacent to patches of net-height vegetation on the edge of a 2-ha meadow (seven and five nets were used on 77% and 23% of nights, respectively). Mist nets were located within 40 m of an audiolure (Erdman and Brinker 1997) broadcasting the male NSWO primary call (Cannings 1993). Owls were captured after sunset and before sunrise. Mist nets were checked approximately every hour and captured owls were transported to a banding station approximately 250 m distant. Each owl was marked with a U.S. Geological Survey numeric aluminum leg band. Unflattened wing chord, mass, maximum tail length, culmen length, estimates of fat reserves, and molt and plumage details were recorded. Each owl was assigned an age on the basis of remigial molt criteria outlined by Pyle (1997). Owls were placed in one of six age categories: hatch year (HY), second year (SY), third year (TY), after-hatch-year (AHY), after-second-year (ASY), or unknown (U). The U age class was the result of failing to record molt data prior to release. I did not classify NSWO by sex due to the uncertain reliability of current morphology-based sexing techniques (Paxton and Watts 2008).

I recorded weather conditions (wind speed, wind direction, temperature, cloud cover, precipitation) before each net check. When sustained wind speed exceeded 25 km/hr or there was steady precipitation, capture efforts were suspended. Nightly moon illumination proportions were obtained from U.S. Naval Observatory data (U.S. Navy 2011) for midnight, Mountain Standard Time.

Prolonged periods of high wind are typical of autumn weather on the Rocky Mountain Front, and temperatures may fluctuate dramatically. During this study nightly temperatures ranged from −30°C to 18°C. Snow was encountered as early as August, but did not remain on the ground throughout the season. Start and end dates were weather-dependent, but in all years (2001–06) capture efforts began after 30 August and ended before 31 October.

Analyses. Capture rates corrected for number of mist nets and effort are presented as number of owls captured/net-hr. For analyses, however, capture rates were standardized as number of owls captured/hr. This rate facilitates more direct interpretation and did not alter the outcome of analyses due to the low variation in number of mist nets used.

I used descriptive statistics to compare annual capture rates and annual age ratios (HY/AHY) among the six years in which sampling occurred. Multiple linear regression (MLR) was used to model the influence of moon phase, temperature, wind speed, and cloud cover on capture rates. Capture rate was log-transformed to acquire homogeneity

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Table 1. Capture rates of Northern Saw-whet Owls during autumn migration in northern Montana, 2001–06.

YEAR	NO. OWLS	% HY OWLS	OWLS/HR	OWLS/NET-HR
2001	54	72	0.99	0.14
2002	139	84	0.75	0.11
2003	101	92	1.22	0.20
2004	26	81	0.69	0.10
2005	145	63	0.87	0.13
2006	203	77	1.58	0.23
All years	668	77	1.02	0.15

of residual variance. Year and proximity to median capture date (number of days) were included as independent covariates in these models to control for seasonal and annual fluctuations in migration magnitude. Linear regression assumptions were validated prior to drawing inference from MLR models. For the purpose of analyses, I grouped NSWO into either the HY or AHY category (i.e., immature or adult). Owls placed in the U age class ($n = 3$) were not included in age-based analyses. Age ratio (AHY/HY) partitioned by six-day period was used to graphically assess differential migration timing by age. Six-day periods were used because they partitioned the season into equally sized temporal categories. I used SAS version 9.0 (SAS Institute 2002) for statistical analyses.

RESULTS

Annual Captures. Capture rates varied substantially among years (Table 1). The highest annual capture rate (2006) was 2.3 times greater than the lowest annual capture rate (2004). When annual capture rates were partitioned by age group, HY capture rates peaked in 2003 and 2006 (Fig. 1). The mean HY capture rate for 2003 and 2006 ($\bar{x} = 1.16$, SD = 0.06, $n = 2$) was 1.9 times larger than that of other years ($\bar{x} = 0.62$, SD = 0.07, $n = 4$). The coefficients of variation for these mean values were small (5% and 11%, respectively), indicating a consistent pattern for the years sampled. Combined annual capture rates also peaked in 2003 and 2006, but, because AHY capture rates did not fluctuate with the same pattern, the difference between those years and all other years was less pronounced than that for HY captures alone.

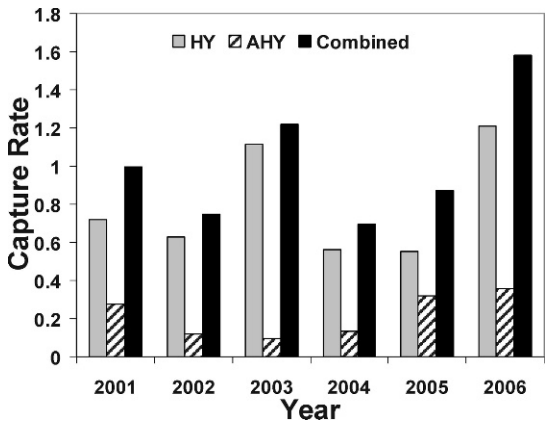


Figure 1. Annual capture rates (owls/hr) partitioned by age for Northern Saw-whet Owls captured during fall migration in northern Montana from 2001–06.

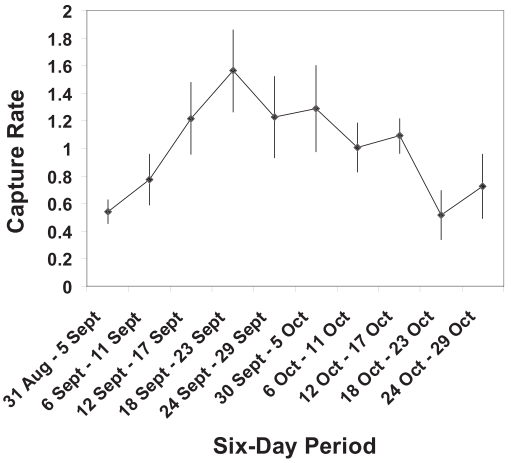


Figure 2. Capture rates of fall migrant Northern Saw-whet Owls (owls/hr ±SE) by six-day period from 2001–06 in northern Montana.

Age ratios of captured NSWO changed dramatically among years. The largest HY/AHY ratio observed (11.5/1.0 in 2003) was 5.8 times greater than the smallest ratio observed (1.7/1.0 in 2005).

Seasonal Captures. NSWO were captured throughout the sampling period each year, including the earliest and latest sampling dates. Capture rates peaked between mid-September and early October (Fig. 2). An increase in the AHY/HY capture ratio (Fig. 3) indicated a later migration peak for AHY owls than HY owls.

MLR models did not indicate effects of weather variables on capture rate. However, a model containing only moon phase and the annual and seasonal covariates ($r^2 = 0.37$, $F_{7,80} = 6.75$, $P < 0.001$) indicated a decrease of approximately 2% in capture rate for every 10% increase in moon illumination ($\beta = -0.20$

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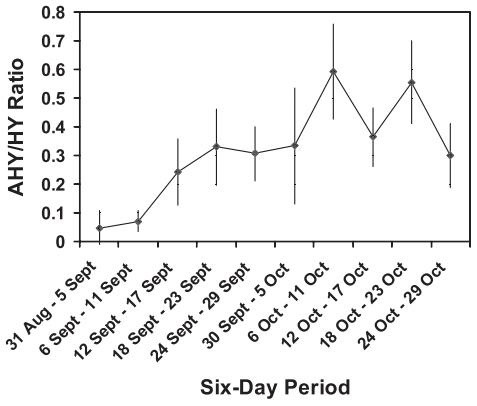


Figure 3. Age ratios of migrant Northern Saw-whet Owls (AHY/HY ±SE) by six-day period from 2001–06 in northern Montana.

± 0.08 SE, $P = 0.02$), given a constant year and proximity to median capture date.

Band Encounters. I captured two NSWO that had been banded at other sites. One was banded in central Alberta, Canada (55°24′N, 114°48′W), as a HY on 18 September 2005 and recaptured at my site on 11 October 2005 (Fig. 4C). The other was banded in southern Alberta (50°45′N, 114°26′W) as a HY on 4 October 2004 and recaptured on 21 October 2005 (Fig. 4A). The former was the only owl in this study to be banded and encountered in the same year (excluding domestic recaptures). The elapsed time between banding and recapture was 23 d. The direct distance between these points of approximately 855 km necessitated a minimum average travel speed of 37 km/d.

Additionally, two NSWO banded at the study site were subsequently encountered at other locations. One was banded as a HY on 27 September 2003 and found dead on a road in southern Montana (45°30′N, 111°50′W) on 16 September 2004 (Fig. 4B). The

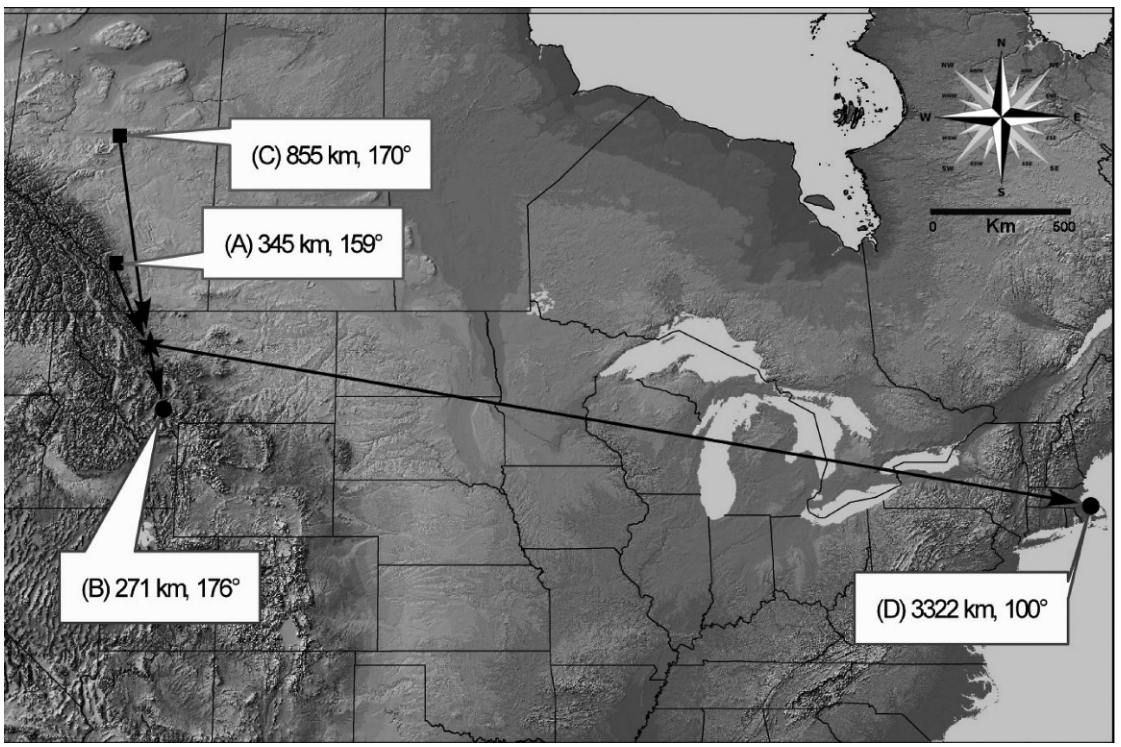


Figure 4. Banding and encounter locations of Northern Saw-whet Owls captured in northern Montana. Star represents the study site in Montana; squares are the origins of recaptures originally banded elsewhere; circles are encounter locations for owls banded at the study site; and arrows indicate straight-line distance and bearing from banding site to subsequent encounter location. Arrows do not indicate actual movement trajectories.

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second was banded as an AHY on 27 September 2003 and recaptured in eastern Massachusetts (42°5′N, 70°42′W) on 4 November 2005 (Fig. 4D).

DISCUSSION

Annual Captures. The observed variation in annual capture rates was driven primarily by HY captures (Fig. 1). Weir et al. (1980) observed that annual variation in NSWO migration magnitude depended primarily on the number of HY NSWO migrating, and postulated that migration magnitude is a function of annual reproductive success. However, Whalen and Watts (2002) argued that reproductive success alone could not explain fluctuations in NSWO migration magnitude. Rather, they hypothesized that density-dependent processes drive fluctuations, and that reproductive success is only one of several factors that may stimulate density-dependent NSWO movements. For example, high reproductive success, increases in abundance of interspecific competitors, and decreases in prey abundance can decrease relative resource availability, yielding a migratory response. Density-dependent migration has been postulated for many other facultative migrants as well (e.g., Lack 1954, Newton 1975, Berthold 2001).

Seasonal Captures. Peak migration timing at my study site was similar to that noted in other published studies in western North America. Priestly and Priestly (2005) reported that NSWO migration peaked in the first week of October at Beaverhill Lake, Alberta. Peak migrations in southwestern Idaho occurred between 27 September and 11 October (Hamilton 2002). In north-central Oregon, migration appeared to peak during October (Frye and Gerhardt 2003). Nightingale (2009) reported peak migration in the first week of October on Vancouver Island, British Columbia. In eastern North America, reported capture rates peaked between mid-October and mid-November (Mueller and Berger 1967, Weir et al. 1980, Duffy and Kerlinger 1992, Whalen et al. 1997, Jobes 2002, Brittain et al. 2009).

Previous researchers have reported differential migration timing with respect to age, consistent with that observed in my study. To my knowledge, all published results of NSWO migration timing by age have found either migration of immatures peaking slightly earlier than that of adults (Duffy and Kerlinger 1992, Iliff 2000, Frye and Gerhardt 2003, Brittain et al. 2009) or a lack of consistent age difference (Weir et al. 1980, Whalen et al. 1997, Jobes 2002, Stock et al. 2006).

Several authors have reported higher NSWO capture rates associated with new moon phases (Catling 1971, Evans 1980, Jobes 2002, Stock et al. 2006). Regression parameters from this study suggest a capture rate decrease of approximately 2% for a moon illumination increase of 10%, assuming a constant year and number of days from median capture date. Thus, given a constant year and time of season, the model estimates that a full moon would cause a 20% (95% CI: 5–34%) decrease in capture rate over a new moon. It is unclear whether migration magnitude decreases along with capture rates on brightly lit nights. Mist nets are more visible in moonlight, which may simply help the owls avoid the nets. Brittain et al. (2009) observed a slight positive correlation between owl captures and ambient moonlight. At their Indiana banding stations, deciduous trees shaded the nets on moonlit nights, suggesting that this difference in results was influenced by differences in vegetative structure. Vegetation adjacent to mist nets was not substantially taller than net height at my study site. Nets were thus fully illuminated when the moon was bright. A synthesis of these results suggests that moonlight affects NSWO capture, but not the magnitude of migration.

Band Encounters. Topography can have a profound influence on avian migration routes (Newton 2008), and is thought to influence NSWO migration patterns (Weir et al. 1980). The Rocky Mountain Front is a region of extreme topographic variation, where steep montane ridges forming the eastern flank of the Rocky Mountains emerge from the relatively gentle topography of the Great Plains. Three of the four individual NSWO movement trajectories documented in this study roughly parallel the eastern flank of this geological formation southward (Fig. 4A, B, C). This small sample of band encounters suggests that the Rocky Mountain Front may form a corridor along which NSWO regularly move. Only one of these owls, however, was banded and recaptured in the same year (Fig. 4C). At least one year elapsed between banding and encounter of the others. Thus, it is unknown what trajectories their actual movements followed in the intervening time. Priestly et al. (2010) reported an additional NSWO movement that appeared to follow the eastern flank of the Rocky Mountains just north of my study site. The NSWO movement illustrated in Figure 4 (D) suggests that dramatic shifts in migration route can occur between years. This owl was captured on the Rocky Mountain Front during the 2003 migration,

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whereas it was captured on the Atlantic coast during the 2005 migration. To my knowledge this is the longest documented movement for the species, and the first in which a NSWO moved between western and far-eastern North America.

Long-distance band encounters with significant longitudinal components (such as that shown in Figure 4 (D) occur with sufficient regularity to indicate some directional complexity in NSWO migration patterns. For example, Priestly et al. (2010) reported a relatively large proportion of longitudinal movements for NSWO encountered in Alberta and Saskatchewan. Farther east, Brinker et al. (1997) reported that a small number of owls banded in the western Great Lakes region had been recaptured during migration in the mid-Atlantic states, both within ($n = 2$) and among (n not specified) seasons. Such movements suggest that a large-scale model of NSWO migration based solely on latitudinal migration is insufficient for understanding the migration ecology of this species. Observed breeding patterns, highly variable migration magnitudes, and longitudinal movements suggest that NSWO may generally be described as a species that exhibits nomadic movements that are integrated into annual, latitudinal migrations.

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