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COMPARATIVE ECOLOGY OF THE FLAMMULATED OWL AND NORTHERN SAW-WHET OWL DURING FALL MIGRATION

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ABSTRACT.—We compared the migration ecology of two owl species that exhibit different migration strategies: the Flammulated Owl (*Otus flammeolus*) and the Northern Saw-whet Owl (*Aegolius acadicus*). During fall 1999–2004, we captured 117 Flammulated Owls and 1433 Northern Saw-whet Owls in the southern Boise Mountains of southwestern Idaho. These owl species exhibited contrasting seasonal timing and body condition. Flammulated Owl captures peaked in mid-September and Northern Saw-whet Owl captures peaked in early to mid-October. Flammulated Owls displayed greater body condition than Northern Saw-whet Owls and increasing condition scores during the season, whereas Northern Saw-whet Owls had no apparent seasonal condition patterns. Based on seasonal timing of captures, both species showed unimodal movement patterns characteristic of fall migrants. However, in 1999 both species' capture rates were at least double those in other years of this study. Flammulated Owls' earlier arrival and departure, coupled with superior body condition, were consistent among years and typical of a long-distance migration strategy. In contrast, the Northern Saw-whet Owls' later arrival, more lengthy passage, and variable body condition were more characteristic of a short-distance migrant strategy. Furthermore, Northern Saw-whet Owls' body condition was significantly lower during the irruptive year than during nonirruptive years, supporting the notion that population density affects their migratory condition.

KEY WORDS: *Aegolius acadicus*; *Flammulated Owl*; *Idaho*; *migration*; *Northern Saw-whet Owl*; *Otus flammeolus*; *body condition*.

ECOLOGIA COMPARATIVA DE *OTUS FLAMMEOLUS* Y *AEGOLIUS ACADICUS* DURANTE LA MIGRACION OTOÑAL

RESUMEN.—Comparamos la ecología migratoria de dos especies de búhos (*Otus flammeolus* y *Aegolius acadicus*) que presentan diferentes estrategias de migración. Capturamos 117 individuos de *O. flammeolus* y 1433 de *A. acadicus* en el sur de las montañas Boise, suroeste de Idaho, durante las temporadas de otoño de 1999 a 2004. Estas especies de búhos presentaron diferente estacionalidad y condición corporal. Las capturas de *O. flammeolus* alcanzaron su máximo al principio y a la mitad de octubre. Los individuos de *O. flammeolus* tuvieron una mejor condición corporal que los de *A. acadicus* y su condición incrementó a través de la temporada, mientras que *A. acadicus* no presentó un patrón temporal definido en su condición. Con

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base en la estacionalidad de las capturas, ambas especies mostraron patrones unimodales de movimiento, los cuales son característicos de aves migratorias otoñales. Sin embargo, en 1999 las tasas de captura de ambas especies fueron al menos dos veces mayores que las tasas observadas durante los años subsecuentes de este estudio. La llegada y partida temprana de *O. flammeolus*, asociada con una mejor condición corporal, se mantuvo entre años, siendo éste un patrón típico de una estrategia de migración de larga distancia. En cambio, la llegada tardía, la estadía más larga y la condición corporal variable de *A. acadicus* fueron más características de una estrategia de migración de corta distancia. Además, la condición corporal de *A. acadicus* fue significativamente menor durante los años de incursiones migratorias invernales que durante los años sin incursiones migratorias, lo que apoya la noción de que la densidad poblacional afecta la condición migratoria.

[Traducción del equipo editorial]

The Flammulated Owl (*Otus flammeolus*) and Northern Saw-whet Owl (*Aegolius acadicus*) are two species of small forest owls whose migratory strategies are presumed to differ, yet their migratory habits are largely unknown. Flammulated Owls are considered long-distance migrants (Balda et al. 1975, McCallum 1994), whereas Northern Saw-whet Owls are considered short-distance migrants (Duffy and Kerlinger 1992, Cannings 1993, Brinker et al. 1997) or nomadic wanderers in some geographic locations (Marks and Doremus 2000).

The breeding range of Flammulated Owls extends from southernmost British Columbia (Godfrey 1966) south to Central Mexico (Sutton and Burleigh 1940) and from the Pacific Coast Mountains (except Oregon and Washington; Winter 1974) east to the Rocky Mountains (Linkhart et al. 1998). The diet of Flammulated Owls consists almost entirely of insects, primarily owl moths (Noctuidae), beetles (Coleoptera), crickets and grasshoppers (Orthoptera; Ross 1969, Balda et al. 1975), and occasionally small vertebrates (Cannings 1994, Linkhart and Reynolds 1994, Oleyar et al. 2003). This diet probably forces them south of locations where low fall/winter temperatures drastically reduce insect abundance (McCallum 1994). Flammulated Owls are thought to engage in long-distance migrations, wintering from central Mexico south to the highlands of Guatemala and El Salvador (Phillips et al. 1964). Migration timing and environmental cues used by Flammulated Owls, such as wind, temperature, and moon phase, are mostly unknown (McCallum 1994). Body condition and age and sex ratios during migration have not been documented (McCallum 1994).

The Northern Saw-whet Owls' breeding range spans forested regions from the Pacific Coast to the eastern seaboard and from tree line in Canada and Alaska south to the Mexican highlands (Cannings 1993). Individuals generally winter within the breeding range of the species, yet data collected

from eastern North America document dispersal to new locations, mostly by hatching-year (HY) birds (Mueller and Berger 1967, Weir et al. 1980, Duffy and Kerlinger 1992). Marks and Doremus (2000) suggested that Northern Saw-whet Owls are nomadic in parts of their range, moving to areas of high food availability to breed. Wintering Northern Saw-whet Owls have been observed southeast along the Atlantic Coast to Florida and south to the Gulf Coast (U.S.); some birds in the western mountains and Appalachians have been detected in lowland areas (Cannings 1993). These owls are carnivorous (Swengel and Swengel 1992) and occasionally demonstrate mass movements following the breeding season, presumably during times when small mammal populations are low (Whalen and Watts 2002). Results from past banding efforts in eastern and central North America indicated that autumn movements of the Northern Saw-whet Owl are "irruptive, sporadic, and unpredictable" (Brinker et al. 1997). Banding sites in the East reported that fall movements occurred from September through November (Duffy and Kerlinger 1992, Brinker et al. 1997). Body condition was described by Whalen and Watts (2002) who used a body condition index to determine the effect of saw-whet owl density on fall migration and stop-over patterns.

Migrating birds enhance their body condition during migration to provide them with energy necessary to fly long distances (King 1970). Fats are the major fuel source for migrating birds, and the amount of fat present is an indication of energetic condition (Walsberg 1990). Short- and long-distance migrants fatten to differing degrees according to their energetic requirements. Short-distance migrants refuel regularly and store small to medium fat reserves of 13% to 25% of their body mass (Berthold 1975). Migrants that engage in longer-distance flights, such as Blackpoll Warblers (*Dendroica striata*), are capable of almost doubling their mass (Nisbet et al. 1963).

We investigated the migration ecology of Flammulated and Northern Saw-whet Owls by describing and comparing annual and seasonal timing, body condition, and molt. First, we examined whether captures were related to time of season and moon phases. We then compared the timing of migration using seasonal and annual capture rates, and by comparing age and sex ratios. Finally, we compared body condition between the two species over the course of the season and among years.

METHODS

Study Area. We conducted this study 12 km east of Boise in the Boise Foothills in Ada County, Idaho (43°37'N, 116°03'W) from fall 1999–2004. Our banding stations were on Lucky Peak (1845 m elevation) which lies at the southern end of the Boise Mountains on the northern edge of the Snake River Plain. The topography and habitat diversity along the Boise Foothills concentrate southbound migrants, including raptors and passerines (e.g., Carlisle et al. 2004), and Lucky Peak is one of the most prominent high-elevation wooded habitats encountered before the Snake River Plain. The site is bound by two major habitat zones. The north and east slopes are dominated by Douglas-fir (*Pseudotsuga menziesii*) forest with mountain ninebark (*Physocarpus monogynus*) understory. The south and west slopes are characterized by high desert shrub-steppe vegetation, primarily big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus nauseosus*), and mountain deciduous shrubland, primarily bitter cherry (*Prunus emarginata*) and chokecherry (*P. virginiana*).

Net Operation. From 1999–2004, we captured owls in the conifer forest at two locations approximately 350 m apart, using five to seven nets per station, from approximately 25 August through 27 October. We used an audiolure protocol modified from Erdman and Brinker (1997) and broadcasted Flammulated Owl territorial hoots (Peterson's Western Birds series) and Northern Saw-whet Owl male solicitation calls (Brinker et al. 1997). To maximize captures of Flammulated Owls, we alternated a tape of Flammulated Owl vocalizations with a tape of both Flammulated and Northern Saw-whet Owl vocalizations at each of the two stations from the last week of August through 8 October. After 8 October, we broadcast only vocalizations of Northern Saw-whet Owls at both stations. Nets were checked every 75 min. For each individual, we recorded species, date, age, sex, wing length, mass, and body molt. We also recorded time of net opening and closing, net area (m²), and moon phase. We recorded recaptured birds (excluding same-night recaptures), but did not include them in analyses.

Age and Sex Determination. We were unable to determine ages of most Flammulated Owls and were limited to aging only after-hatching-year (AHY) individuals engaged in flight feather molt (Pyle 1997). We determined ages of Northern Saw-whet Owls by examining molt patterns and plumage characteristics according to Pyle (1997).

Because Flammulated Owls are the least sexually dimorphic North American owl (Earhart and Johnson

1970), we used DNA from blood samples to determine sex. We determined sex by targeting the chromodomain-helicase-DNA (CHD) genes on the W and Z chromosomes and by restriction fragment length polymorphism, shown to be reliable in Northern Spotted Owls (*Strix occidentalis caurina*) (Fleming et al. 1996) and most avian species (Griffiths et al. 1998, Lessells and Mateman 1998, Norris-Caneda and Elliott 1998). We extracted the DNA from the red blood cells and used polymerase chain reaction according to Griffiths et al. (1998) to amplify the homologous parts of the CHD-W and CHD-Z genes using primers P2 and P8. Polymerase chain reaction incorporated noncoding introns in both CHD-W and CHD-Z that differed in length between the two genes. Gel electrophoresis revealed one band for males and two bands for females.

Because the Northern Saw-whet Owl exhibits slight sexual dimorphism, we determined sex using a discriminant analysis function based on wing chord and mass that used a within-covariance matrix (Brinker et al. 1997, Brinker 2000). We examined the validity of this tool by comparing the results with DNA-based sex identification. When we compared results from the DNA-based sex determination of Northern Saw-whet Owls to the results from the discriminant analysis function (Brinker 2000), we found that the function assigned the identical sex to 239 out of 249 owls, a 96% accuracy rate. We then used the function to assign sex to 694 additional Northern Saw-whet Owls.

Body Condition. To calculate the body condition index, we used mass/wing chord raised to the 0.683 and 1.693 power for Flammulated and Northern Saw-whet Owls, respectively. We derived these exponents by determining the slope of the log-log plot mass versus wing chord for all individuals of each species (Whalen and Watts 2002). The resulting index eliminated any significant correlations between body condition scores and wing chord (Flammulated Owl [FLOW]: $r = 0.01$, $t = 0.05$, $N = 115$, $P = 0.96$; Northern Saw-whet Owl [NSWO]: $r = 0.01$, $t = -0.26$, $N = 1430$, $P = 0.80$), thus providing a measure of an individual's fat content without biases incurred from potential structural size differences. For each species we standardized body condition scores to units of standard deviations based on the mean body condition of all individuals captured during nonirruptive years (Whalen and Watts 2002). We reported results from the body condition index exclusively and have eliminated numerical fat and muscle scores (Hamilton 2002) because the body condition index resulted in a more quantitative and robust measure of the species' energetic condition.

Statistical Analyses. During 1 yr of the study (1999), captures were several times greater than the subsequent 5 yr (Table 1). To examine trends relative to the extent of migration and to avoid disproportionate among-year sampling, we categorized the large migration year as the irruptive year and the others as nonirruptive years (Whalen and Watts 2002). Capture rates of owls were based on number of owls captured/10 m² net/100 hr. We used independent two-tailed t -tests (Ott 1993) to investigate differences in body condition scores between irruptive and nonirruptive years and to compare capture rates between new and full moon phases. We also used independent two-tailed t -tests to determine if sex or age

Table 1. Flammulated and Northern Saw-whet Owl individuals and capture rates (no. owls/10 m² net/100 hr) among years.

YEAR	FLAMMULATED OWL		NORTHERN SAW-WHET OWL		COMBINED	
	N	CAPTURE RATE	N	CAPTURE RATE	N	CAPTURE RATE
1999 ^a	49	0.14	847	2.42	896	2.56
2000	7	0.02	137	0.43	144	0.45
2001	17	0.07	159	0.63	176	0.70
2002	12	0.04	67	0.21	79	0.25
2003	17	0.05	163	0.51	180	0.57
2004	15	0.07	60	0.28	75	0.35

^a Irruptive migration year.

were related to differences in capture rates corresponding to irruptive versus nonirruptive years, Julian date, body condition scores, and body molt. We used one-way analysis of variance (Ott 1993) to test if body condition scores varied by year. We examined data for departures from normality by plotting probability plots of the residuals; the data did not depart from normality. All tests used $P \leq 0.05$ for statistical significance. We report values as means \pm SE.

RESULTS

Annual Variation in Capture Rates. The number of Flammulated and Northern Saw-whet Owl captures varied dramatically among years (Table 1), yet timing of peak captures was similar in each year. Most Flammulated Owls were captured between 1 and 25 September and most Northern Saw-whet Owls were captured between 26 September and 26 October (Fig. 1). Flammulated Owl peak captures (median capture date) ranged from 5 September in 2003 to 21 September in 2004; the mean peak capture date for all 6 yr combined was 15 September. Northern Saw-whet Owl peak captures ranged from 6 October in 1999, 2003, and 2004 to 13 October in 2001; the mean peak capture date for all 6 yr combined was 8 October.

Moon phases were related to capture rates. The greatest number of captures occurred during a new moon compared with a full moon for all 6 yr combined ($t_{27} = 2.5$, $P = 0.02$).

Capture Rates by Age and Sex. Northern Saw-whet Owl age ratios varied among years, but HY birds were consistently more numerous than adults. The numbers of HY and AHY birds captured were most similar during the irruptive year when captures consisted of 56% HY birds. During the following 5 nonirruptive yr, HY birds comprised 63%, 72%, 82%, 82%, and 65%, respectively, of captures. The AHY females were most numerous during the irru-

ptive year, whereas HY females were most numerous during nonirruptive years; AHY males were rare in all years. During the irruptive year, there was a significant relation between age and Julian date, with HYs preceding AHYs ($t_{840} = 6.1$, $P < 0.001$). In contrast, timing between ages did not differ during nonirruptive years ($t_{582} = 0.3$, $P = 0.73$).

Of the 43 Flammulated Owls assigned sex using DNA analysis, 44% ($N = 19$) were male and 56% ($N = 24$) were female. Of the 976 Northern Saw-whet Owls assigned sex using DNA analysis ($N = 273$) and the discriminant analysis function ($N = 703$), 23% were male and 77% were female; 32% ($N = 457$) of total individuals could not be sexed using the function. For Flammulated Owls, males and females did not differ in migration timing over the course of the season ($t_{42} = 0.2$, $P = 0.81$). For Northern Saw-whet Owls during the irruptive year, males preceded females by 4 d ($t_{579} = -3.8$, $P < 0.001$). During nonirruptive years, there was no significant difference between the timing of sexes ($t_{393} = -1.9$, $P = 0.06$). For AHY birds in all years, there was no significant difference in timing between sexes ($t_{383} = -1.2$, $P = 0.22$).

Age and sex composition of migrating Northern Saw-whet Owls varied relative to the magnitude of migration. During the irruptive year, AHY females (41% of captures) were more numerous than HY females (36%), followed by HY males (17%) and AHY males (6%). During nonirruptive years, HY females (52% of captures) were more numerous than AHY females (25%), followed by HY males (19%) and AHY males (4%).

Body Condition. Flammulated Owl body condition scores did not differ between irruptive and nonirruptive years (Table 2). However, Northern Saw-whet Owl condition scores were significantly higher in nonirruptive years (Table 2). For all years

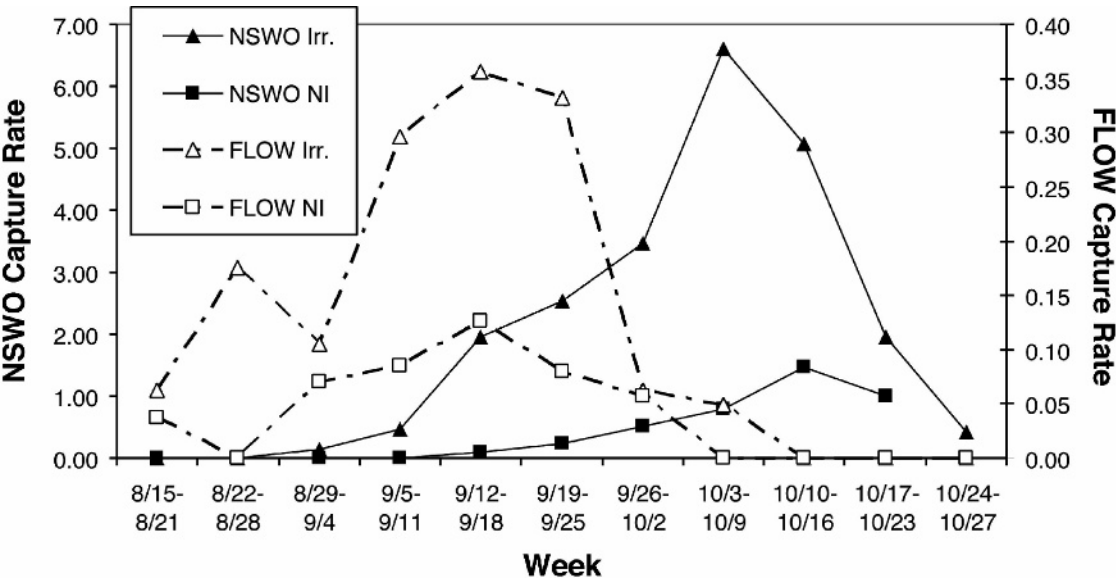


Figure 1. Comparison of Flammulated (FLOW) and Northern Saw-whet Owl (NSWO) weekly capture rates (no. owls/ 10 m² net/100 hr) during fall migration in southwestern Idaho during an irruptive yr (Irr) in 1999 and nonirruptive yr (NI) from 2000 to 2004.

combined, Flammulated Owl body condition scores increased significantly over the course of the season ($r^2 = 0.21$, $N = 115$, $P < 0.001$). In contrast, Northern Saw-whet Owls exhibited variable body condition in irruptive and nonirruptive years ($r^2 = 0.11$, $N = 846$, $P = 0.001$; $r^2 = 0.02$, $N = 585$, $P < 0.001$, respectively).

Hatching-year Northern Saw-whet Owls had significantly lower body condition scores compared with AHYs in both irruptive and nonirruptive years ($t_{839} = 2.4$, $P = 0.02$; $t_{581} = 2.1$, $P = 0.04$, respectively). All ages had lower body condition scores

during the irruptive year compared to nonirruptive years (Table 2).

For Flammulated Owls body condition scores did not differ between males and females (irruptive: $t_{34} = 0.9$, $P = 0.35$; nonirruptive: $t_{15} = 0.2$, $P = 0.83$). In contrast, Northern Saw-whet Owl females had higher body condition scores than males in both irruptive and nonirruptive years ($t_{579} = -15.6$, $P < 0.001$; $t_{393} = -13.3$, $P < 0.001$, respectively). Male body condition scores did not differ among years, whereas female scores were lower during the irruptive year compared to nonirruptive years (Table 2).

Table 2. Body condition scores (mean \pm SE) for Flammulated (FLOW) and Northern Saw-whet Owls (NSWO) compared between irruptive (1999) and nonirruptive years (2000–04) using *t*-tests.

	IRRUPITIVE	NONIRRUPITIVE	IRR. ^a N	NI ^a N	<i>t</i>	df	<i>P</i>
FLOW	0.21 \pm 0.11	0.00 \pm 0.12	47	68	-1.21	113	0.230
NSWO	-0.16 \pm 0.03	-0.00 \pm 0.04	845	585	3.01	1428	0.003*
NSWO HY ^b	-0.23 \pm 0.05	-0.05 \pm 0.05	469	427	2.79	894	0.005*
NSWO AHY ^b	-0.07 \pm 0.05	0.14 \pm 0.08	372	156	2.17	526	0.031*
FLOW Male	0.93 \pm 0.19	0.80 \pm 0.21	18	13	-0.45	29	0.653
FLOW Female	0.66 \pm 0.22	0.67 \pm 0.85	18	4	0.03	20	0.978
NSWO Male	-0.90 \pm 0.06	-0.83 \pm 0.08	137	84	0.69	219	0.491
NSWO Female	0.35 \pm 0.04	0.55 \pm 0.05	444	311	3.15	753	0.002*

^a Irr indicates irruptive year; NI indicates nonirruptive years.
^b HY indicates hatching-year owls; AHY indicates after-hatching-year owls.
* Indicates statistical significance.

Molt. In 1999 four Flammulated Owls (caught between 10 and 16 September) were symmetrically molting their flight feathers, indicative of AHY birds. Of the 51 owls caught in 1999, eight (16%) were molting greater and/or primary coverts. In contrast, Northern Saw-whet Owls were not regularly engaged in flight feather molt. Regardless of the magnitude of migration, Flammulated and Northern Saw-whet Owls showed a negative linear relation between body molt and Julian date (irruptive and nonirruptive combined: $r^2 = 0.57$, $N = 117$, $P < 0.001$; $r^2 = 0.25$, $N = 1432$, $P < 0.001$, respectively). During the irruptive year, Flammulated Owls had significantly more body molt than during non-irruptive years ($t_{106} = -3.5$, $P = 0.001$), whereas Northern Saw-whet Owls had significantly less body molt ($t_{1430} = 4.5$, $P < 0.001$).

For both species in all years, males had significantly more body molt compared with females (FLOW: $t_{53} = -2.1$, $P = 0.04$; NSWO: $t_{974} = 5.5$, $P < 0.001$). Northern Saw-whet Owl adult males also molted later in the season than adult females (slope of Julian date versus molt plot: males = -3.4 , females = -4.3). During the irruptive year, female and AHY Northern Saw-whet Owls had less body molt than males and HYs, respectively ($t_{753} = 4.7$, $P < 0.001$; $t_{839} = -9.2$, $P < 0.001$, respectively). Northern Saw-whet Owl molt did not differ between ages during nonirruptive years.

DISCUSSION

Assuming capture patterns reflect movement patterns, Flammulated and Northern Saw-whet Owls shared similar broad migration trends typical of fall migrants. However, they exhibited contrasting timing and body condition which probably reflect the long-distance migration strategy of the Flammulated Owl and the short-distance migration strategy of the Northern Saw-whet Owl.

Seasonal Movement Patterns. For Flammulated Owls, timing of migration remained fairly consistent among years, with the bulk of the captures occurring between 1 and 25 September. The timing of Northern Saw-whet Owl captures also was fairly consistent among years, but the capture period lasted roughly twice as long (September and October), compared with that of the Flammulated Owl. By October, temperatures regularly fell below freezing, which may have reduced the number of insect prey available. Consequently, Flammulated Owls probably benefited by moving through Idaho before the onset of these lower

temperatures. In contrast, Northern Saw-whet Owls could continue to hunt successfully for small mammals throughout October, in occasionally freezing temperatures.

Higher capture rates were associated with the new moon, corresponding to other studies on Northern Saw-whet Owl migration (Catling 1971, Evans 1980). We do not know if the full moon depressed owl movements (e.g., because of increased visibility to predators or some other reason) or if the light of the moon illuminated the nets, making them more visible to the owls.

Molt and Body Condition. Both Flammulated and Northern Saw-whet Owls were actively engaged in molting their body feathers. Body molt significantly decreased over the course of the season for both species, indicating the near completion of their preformative molt. For Northern Saw-whet Owls, body condition scores were lower and the extent of body molt was less during the irruptive year than during the nonirruptive years. However, molt and body condition did not appear to be related. For example, males were in heavier molt, yet had lower body condition scores than females, regardless of the magnitude of migration.

Age- and Sex-related Differences in Timing of Migration. Hatching-year and male Northern Saw-whet Owls preceded AHY and female birds during the irruptive year exclusively. Perhaps the later migration of AHYs and females during the irruptive year may partly explain their lesser molt, since body molt decreased with Julian date. Duffy and Kerlinger (1992) indicated that HY birds moved slightly ahead of AHY birds from 1980–88 at Cape May, New Jersey U.S.A., but body condition and molt were not reported. At Prince Edward Point, Ontario, Canada, Weir et al. (1980) observed that females tended to migrate earlier in the season than males, but stated that the cause of differential sex migration was unknown. There were no timing differences between adult males and females in our study. Compared to adult females, adult males were scarce, suggesting males may not migrate as far or as often as females. Brinker et al. (1997) reported fewer captures of males than of females in southern latitudes among mid-Atlantic states. However, comparisons of timing and abundance of female and male Northern Saw-whet Owls based on our study are somewhat suspect because we used male solicitation and territorial calls for attracting owls, potentially biasing toward female captures.

Because age determination for Flammulated Owls was limited to eight molting adults, the small sample size of known-aged birds precluded any analyses of age-related migration timing. Future Flammulated Owl migration studies may contribute to the understanding of age-related migration timing and body condition by implementing the aging technique described by DeLong (2004), who identified HY owls by the presence of juvenile contour feathers prior to the completion of preformative molt.

Flammulated Owl males and females did not display different timing of migration, nor different body condition. In contrast, during the irruptive year Northern Saw-whet Owl males preceded females, and in all years males exhibited lower body condition scores and later molt than females. These data suggest that movement patterns of males and females do not differ for Flammulated Owls, but probably differ for Northern Saw-whet Owls in southwestern Idaho.

Annual Movement Patterns. Flammulated Owls eat primarily insects and are long-distance migrants; thus we expected them to show regular annual movements. Although arrival and departure dates were consistent, abundance unexpectedly varied greatly among years (Fig. 1). Nocturnal insects may undergo population fluctuations from year to year that could potentially affect productivity and juvenile survivorship of Flammulated Owls. However, body condition scores were similarly high among years, suggesting birds had ample food and were engaged in long-distance nocturnal flights. Variation in annual abundance of Flammulated Owls at our study site was probably a result of factors other than fluctuating prey populations, such as wildfires throughout much of the northern Rockies in fall 1999, weather, and/or differing migration routes.

Northern Saw-whet Owls eat primarily small mammals and do not typically engage in long-distance flights, yet they showed a unimodal capture pattern by Julian date (Fig. 1). This unimodal pattern (1999–2004) and comparable number of captures in 5 of the 6 yr (2000–04) support the hypothesis that the populations of Northern Saw-whet Owls we captured in our study area were fall migrants. However, a five-fold increase in captures in 1999 indicated that the Northern Saw-whet Owl is also capable of irruptive movements in the western United States, comparable to fluctuations reported from the eastern United States where banding studies have demonstrated that the Northern Saw-whet Owl is an irruptive species (Brinker et al. 1997,

Whalen and Watts 2002). Irruptive migration is the phenomenon of unusually high densities of birds migrating outside their normal range. The underlying cause of irruptive migration events by Northern Saw-whet Owls is probably variation in the ratio of individual owls to prey population (Whalen and Watts 2002). Because southern limits of the Northern Saw-whet Owls' winter range experience greater annual variation in the magnitude of migration than more northern portions, the spatial component of irruptive migration constrains our ability to generalize movement patterns for the population at large, including age and sex classes, beyond our banding location in southwestern Idaho.

Adult Northern Saw-whet Owls comprised a greater proportion of the captures during the irruptive year (44%) compared with the following 5 non-irruptive yr (mean = 27%). In contrast, Whalen and Watts (2002) reported age ratios skewed toward HY birds during irruptive years, with capture rates exceeding nonirruptive years by a magnitude of 28. Their reported capture rates of adults also increased in an irruptive fashion with capture rates exceeding those in nonirruptive years by a magnitude of 3 (Whalen and Watts 2002). The increase in number of migrating adults reported in both studies discounts the suggestion by Weir et al. (1980) that breeding success alone predicts irruptive years. For instance, food reserves were probably scarce during the irruptive year, causing a greater proportion of adults to increase their movements (resulting in higher capture rates) in search of prey, compared with subsequent years when consumer competition was reduced. Data on annual fluctuations of small mammal prey along migration routes are needed to understand underlying causes of density-dependent effects on capture patterns.

Given that population dynamics of nocturnal insects and small mammals differ, yet Flammulated Owls and Northern Saw-whet Owls displayed similar migration patterns across all years and peak migration numbers in 1999, different factors probably influenced the increase in the respective species' capture rates during the irruptive year. The concept of irruptive migration does not apply to neotropical migrants such as the Flammulated Owl; thus, Flammulated Owl migration patterns were not dictated by variation in the ratio of consumers to available resources. In 1999 environmental factors (e.g., forest fires or weather) probably influenced capture rates of Flammulated

Table 3. Summary of migration characteristics for Flammulated and Northern Saw-whet Owls during fall migration in southwestern Idaho (1999–2004).

	FLAMMULATED OWL	NORTHERN SAW-WHET OWL
Capture rates	Lower	Higher
Variation in capture rates among years	Large	Large
Variation in seasonal timing among years	Little	Little
Duration of fall passage	Shorter	Longer
Most frequently captured sex	No difference	Females
Difference in timing between sexes	No	Yes (irruptive year only)
Variation in body condition among years	Small	Large
Seasonal increase in body condition	Yes	No
Sex class and body condition	Not related	Related
Flight feather molt in adults	Some	None
Seasonal body molt	Negative trend	Negative trend
Most body molt	Irruptive year	Nonirruptive years
Sex class and molt	Related	Related

Owls, whereas a drop in small mammal populations probably drove the irruption of Northern Saw-whet Owls into southwestern Idaho.

Conclusions. Past studies have suggested that the Flammulated Owl is a biannual long-distance migrant, largely based on their insectivorous diet that compels them to move south during the fall and north in spring in response to seasonal changes in insect abundance. Also, past studies have reported that the Northern Saw-whet Owls' migratory movements are unpredictable and perhaps nomadic. In this study, some migration characteristics were similar between species (e.g., annual variation in capture rates and seasonal timing), whereas other characteristics contrasted significantly (e.g., duration of fall passage and body condition; Table 3). Compared with Northern Saw-whet Owls, Flammulated Owls arrived and departed earlier in the fall and exhibited enhanced body condition that was virtually immune to seasonal fluctuations in capture rates and presumed magnitude of migration. In contrast, Northern Saw-whet Owls arrived later and passed through the study area over a longer period of time. Their body condition was highly variable, exhibiting a wide range of body condition scores that differed between the irruptive and nonirruptive years. In spite of their lengthy passage through the study area and variability in energetic condition, Northern Saw-whet Owl captures increased, peaked, and subsequently declined over the course of the season. We consider this regular capture pattern, consistent for all years (1999–2004), indicative of a short-distance migrant. However, the variable body condition of Northern

Saw-whet Owls in all years suggests that many individuals may be offsetting the costs of short-distance migration with resources obtained *en route* to their wintering grounds, as also suggested for Nearctic-Neotropic migrants in Benson and Winker (2005). The influx of Northern Saw-whet Owls that occurred in 1999 demonstrates the capacity for irruptive behavior in certain years. Our findings on the migration timing and body condition of these two owl species further support the idea that the Flammulated Owl is a long-distance migrant and that the Northern Saw-whet Owl is a short-distance migrant capable of irruptive behavior, at least in this region.

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