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Annual Migration Density and Stopover Patterns of Northern Saw-whet Owls (*Aegolius acadicus*)

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ABSTRACT.—Northern Saw-whet Owls (*Aegolius acadicus*) exhibit large fluctuations in annual number of individuals migrating in eastern United States. Underlying large differences in the magnitude of the migration may be important density-dependent effects on body condition and stopover patterns. We investigated such effects using data from saw-whet owls that were trapped and banded during autumn migration at the southern tip of the Delmarva Peninsula (near Cape Charles, Virginia) from 1994 to 2000. Irruptive migration events occurred in 1995 and 1999 when 1,002 and 700 owls were captured, respectively. Capture totals ranged from 22 to 105 owls during five nonirruptive years. Irruptive migration years were dominated by immature owls (82% of captures) and were characterized by low recapture rates (13%) and shorter minimum stopover lengths (median = 5 nights) for all owls. Body masses and body-condition index scores were significantly lower for both immature and adult age classes during years when owl density was very high. During such years, a smaller percentage of owls elected to stopover and, among those that did, individuals in good condition departed sooner than individuals

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in poor condition. Conversely, during nonirruptive years, adults constituted 67% of captures, recapture rates were nearly 3× higher (35%), and stopover lengths were twice as long (median = 10 nights). Recapture rates were significantly higher for adults (43%) than for immature owls (23%) and initial body condition of adults was positively correlated with their length of stopover. During light migration years, conditions may be conducive for extended residency, particularly for adult owls in good condition. Our results suggest that density-dependence is an important mechanism driving migration and stopover patterns of saw-whet owls.

RESUMEN.—*Aegolius acadicus* presenta grandes fluctuaciones en el número anual de individuos que migran en el este de Estados Unidos. Subyacentes a las grandes diferencias en la magnitud de la migración pueden estar los importantes efectos de la denso-dependencia sobre la condición corporal y los patrones de paradas durante la migración. Investigamos estos efectos usando datos de captura y marcaje de *Aegolius acadicus* durante la migración de otoño desde 1994 al 2000, en la punta sur de la Península de Delmarva (cerca de Cape Charles, Virginia). Los eventos de migración masiva ocurrieron en 1995 y 1999 cuando se capturaron 1,002 y 700 búhos, respectivamente. Los totales de captura variaron entre 22 a 105 búhos durante los cinco años no masivos. Los años de migración masiva fueron dominados por búhos inmaduros (82% de las capturas) y se caracterizaron por bajas tasas de recaptura (13%) y por tiempos mínimos de parada más cortos (mediana = 5 noches) para todos los búhos. El peso corporal y el índice de condición corporal para las clases de edad inmadura y adulta fueron significativamente más bajos durante los años en que la densidad de búhos fue muy alta. Durante aquellos años, un menor porcentaje de búhos hizo escalas durante la migración, y entre aquéllos que pararon, los individuos en mejor condición partieron antes que los individuos en condición más pobre. Por el contrario, durante los años no masivos, los adultos constituyeron un 67% de las capturas, las tasas de recaptura fueron casi 3 veces superiores (35%), y el tiempo de la parada fue dos veces más largo (mediana = 10 noches). Las tasas de recaptura fueron significativamente más altas para los adultos (43%) que para los búhos inmaduros (23%) y la condición corporal inicial de los adultos se correlacionó positivamente con el tiempo de parada. Durante los años de migración menos masiva, las condiciones locales pueden favorecer la extensión de la residencia, particularmente para los búhos adultos en buena condición. Nuestros resultados sugieren que la denso-dependencia es un mecanismo importante que influencia los patrones de migración y paradas de los búhos.

Seasonal availability of resources has long been considered the primary cause of bird migration (Lack 1954, 1968; Gauthreaux 1982). Each year, billions of birds withdraw from high latitudes to avoid severe food shortages and maximize their probability of survival during the nonbreeding season. However, migratory movements are very energetically demanding (Blem 1980). As a result, most migrating birds stop periodically to replenish energy reserves and therefore resource availability continues to play an important role during migration (Hutto 1985, Martin and Karr 1986).

In addition to seasonal declines in absolute levels of food resources, resource availability may be affected by consumer density through competition. Indeed, leading models of bird migration have incorporated population density and competition as important factors that drive migratory movements (Cohen 1967, Fretwell 1972). Empirical evidence also suggests that competition plays an important role during migration (Rappole and Warner 1976, Moore and Yong 1991). Although numerous studies have shown that energetic condition (i.e. fat stores or size-adjusted body mass) is an important factor influencing stopover decisions (e.g. Moore and Kerlinger 1987, Dunn et al. 1988, Morris et al. 1996), the influence of migrant density on body condition and stopover patterns has been scarcely studied.

One of the most common nonpasserine bird species banded during autumn migration in the eastern United States is the Northern Saw-whet Owl (*Aegolius acadicus*; Brinker et al. 1997). Recent banding studies, employing electronic audiolures that broadcast a continuous saw-whet owl call to attract migrating owls, have demonstrated that the species is an irruptive migrant in the region (Brinker et al. 1997, Whalen et al. 1997). Despite fairly consistent trapping efforts, there has been huge variation in the annual number of owls captured on the Atlantic coast during recent years. Irruptive migration events occurred in 1995 and 1999 as capture rates were several times higher than in any other year. Relatively high passive (without the use of an audiolure) capture rates of owls at Cape May, New Jersey, during 1980 and 1981 (Duffy and Kerlinger 1992) and at songbird banding stations in the eastern United States during 1965 (Davis 1966) suggest that those years also constituted major migration events.

Compared to most raptorial birds, saw-whet owls are a very small-bodied species (60–120 g) with high mass-specific metabolic costs (Nagy 1987). In addition, as a nocturnal species, saw-whet owls fly using powered flapping flight (Cannings 1993), an energetically expensive mode of locomotion (Hedenstrom 1993). Presumably to fuel such high rates of energy expenditure, owls continue to forage during migration (Russell et al. 1991, Whalen et al. 2000).

The aim of this study was to investigate body condition and stopover patterns of migrating saw-whet owls in relation to the irruptive nature of their migration. We examined effects of annual owl density
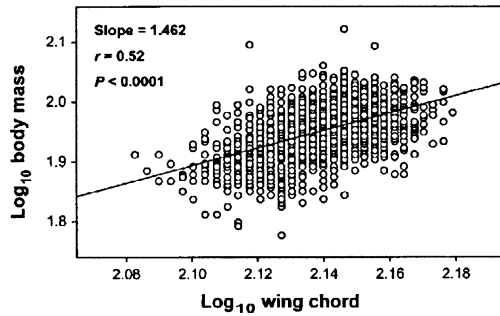
FIG. 1. Log–log plot of body mass versus wing chord for all saw-whet owls captured ($n = 2,048$). The slope of this relationship was used as the scaling exponent in the body-condition index mass/wing chord[1.462]. This technique eliminates residual correlation between body condition scores and wing chord.

on body condition, probability of extended stopover, and length of stopover. By controlling for annual owl density, we also addressed more direct relationships between body condition and stopover patterns. Finally, because experience is likely to influence competitive abilities and stopover decisions of migrating birds (Woodrey 2000), we studied age-specific effects.

Methods.—Migrating saw-whet owls were trapped and banded on the Eastern Shore of Virginia each autumn from late October to mid-December, 1994–2000. To enhance both capture and recapture rates, owls were trapped at three separate wooded sites located within a 10 km² area at the southern tip of the Delmarva Peninsula. The three sites were located on the Eastern Shore of Virginia National Wildlife Refuge, Gatr Tract Wildlife Management Area, and Kiptopeke State Park. Birds arriving in that area during autumn migration are faced with a barrier of ~30 km of open water in the form of the Chesapeake Bay.

Most individuals trapped on the Delmarva Peninsula are believed to come from breeding populations in Canada and the northeastern United States (Brinker et al. 1997).

Each of the three trapping sites in our study consisted of a continuous line of mist-nets 72 m long and 2 m tall. An electronic audiolure, consisting of a cassette tape player, amplifier, loudspeaker, and 12 volt marine battery, was situated at the center of each net lane to attract migrating owls. A continuous-loop broadcast of a saw-whet owl ''advertising call'' (Cannings 1993) was played at an estimated sound output of 100 db at 2 m.

Mist-netting was initiated at dusk and continued until dawn each night. Owls were not trapped on nights with significant precipitation or strong winds. Captured owls were banded with federal aluminum leg bands. Wings were inspected for evidence of molt to determine age (Evans and Rosenfield 1987). Because immature (hatching-year, hereafter HY) saw-whet owls retain all juvenal flight feathers during their first year (Cannings 1993), birds were classified as immature if all primary and secondary remiges and coverts appeared uniform in color. Because adult (after-hatching-year, hereafter AHY) saw-whet owls undergo a definitive prebasic molt in which the remigial molt is incomplete in summer (Cannings 1993), owls were classified as adults if primary and secondary remiges were not uniform in color, indicating the presence of more than one generation of feathers. Unflattened wing-chord measurements were recorded to the nearest millimeter and body mass was recorded to the nearest gram using a Pesola spring scale or a digital scale.

A conventional body condition index of mass/wing chord was not used because mass and wing chord do not scale linearly. As a result, body condition scores based on such an index would be correlated with wing chord ($r = 0.18$, $t = 8.05$, $P < 0.0001$, $n = 2,048$). Hence, size biases could confound

TABLE 1. Annual number of saw-whet owl captures, distribution by age class, and number of recaptures on the Lower Delmarva Peninsula near Cape Charles, Virginia. HY (hatching-year) indicates immature owls. AHY (after-hatching-year) indicates adult owls.

Year	Owl captures	HY captures[a]	AHY captures[a]	Owl recaptures[b]	HY recaptures[b]	AHY recaptures[b]
1994	52	21	31	21 (40.4)	4 (19.0)	17 (54.8)
1995[c]	1,002	825	162	130 (12.9)	109 (13.2)	19 (11.7)
1996	105	15	90	33 (31.4)	1 (6.7)	32 (35.6)
1997	99	59	39	35 (35.4)	19 (32.2)	16 (41.0)
1998	22	11	11	8 (36.4)	1 (9.1)	7 (63.6)
1999[c]	700	562	137	89 (12.7)	63 (11.2)	26 (19.0)
2000	100	17	83	36 (36.0)	3 (17.6)	33 (39.8)
Total	2,080	1,510	533	352 (16.9)	200 (13.2)	150 (27.1)

[a] Row totals for age classes may not sum to owl captures because age was undetermined for a small number of owls (<1%).

[b] Recapture frequencies with percentage of owl captures that were recaptured that year in parentheses.

[c] Irruptive migration years.

interpretation of body condition. Instead, body condition scores were calculated for individual owls using the index mass/wing chord[1.462]. The scaling exponent for this index was determined as the slope of the log–log plot of mass versus wing chord for all owls captured in this study (Fig. 1). That technique successfully eliminated any significant correlation between body-condition scores and wing chord ($r = -0.008$, $t = -0.35$, $P = 0.72$, $n = 2,048$). Therefore, the resulting body-condition index is robust against structural size differences between groups of owls. Body-condition scores were standardized to units of standard deviations based on the mean body condition of all owls captured during nonirruptive years.

During two of the seven years of this study, capture rates were an order of magnitude higher than during the other five years (Table 1). To analyze annual patterns relative to the magnitude of the migration, the two large migration years were classified as irruptive years and the other five years were classified as nonirruptive years.

Numerous owls were recaptured during the same year. The proportion of owls recaptured was assumed to reflect probability of extended stopover by migrating owls. In addition, the duration of time between initial date of capture and date of final recapture was used as an estimate of minimum length of stopover for recaptured owls. That technique is conventionally used in banding studies of migratory stopover (e.g. Rappole and Warner 1976, Moore and Kerlinger 1987). Recapture events occurring on the same night as the initial capture for a given owl were excluded from all analyses.

Morphometric patterns were compared between irruptive and nonirruptive migration years using Student's t-tests. Chi-square tests were employed to compare age ratios among years and to compare recapture rates between age groups and years. Because length of stopover was not normally distributed, nonparametric Mann-Whitney U-tests were used to compare length of stopover between age groups and years, and Spearman rank order correlations were used to analyze relationships between age-specific stopover lengths and body condition scores. Incidence of recapture was recorded as a dichotomous dependent variable for each owl (1 = recaptured, 0 = never recaptured) and logistic regression was used to estimate the probability of recapture as a function of body condition for specific age groups and migration years.

Results.—From 1994 to 2000, a total of 2,080 individual saw-whet owls were banded on the Eastern Shore of Virginia. Considerable variation occurred in number of owls captured each year (Table 1). Age ratio of saw-whet owls differed markedly depending on the magnitude of the migration ($\chi^2 = 387.0$, df = 1, $P < 0.0001$; Table 1). Immature owls were in the minority during nonirruptive years, constituting
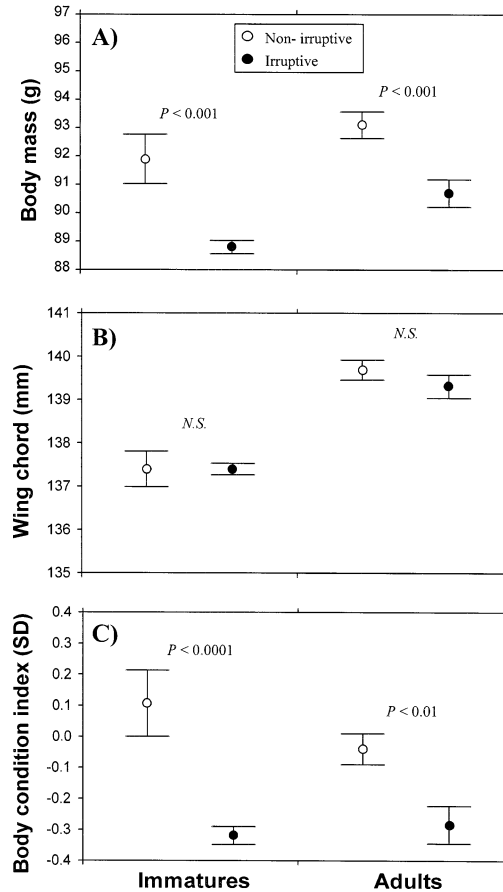

FIG. 2.   (A) Body mass, (B) wing chord, and (C) body condition of immature and adult saw-whet owls captured during nonirruptive and irruptive migration years. Body condition (mass/wing chord[1.462]) was standardized to units of standard deviations based on the mean body condition of all owls captured during nonirruptive years. Points indicate means and whiskers show ±1 SE. P-values from pairwise t-tests are shown. *NS* indicates nonsignificant ($P > 0.10$).

only 33% of captures. Conversely, immature owls dominated irruptive migration events by constituting 82% of individual captures. During the two irruptive years combined, a total of 1,387 immature owls were captured compared to 299 adults. However, both age groups exhibited irruptive patterns of migration. Although capture rates of immature owls were more than 28× higher during irruptive years, capture rates of adults also increased three fold during irruptive years.

Morphometric patterns suggest that large migration events negatively affected body condition. Body masses of both immature and adult owls were sig-
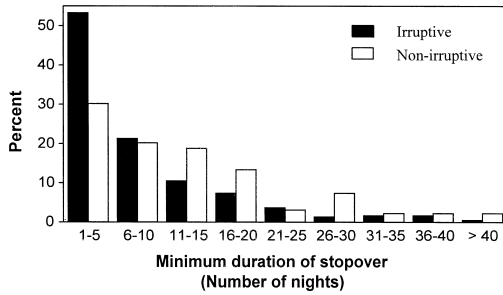
FIG. 3. Percentage distribution of minimum stopover lengths for all saw-whet owls recaptured during irruptive ($n = 219$) and non-irruptive ($n = 97$) migration years. Stopover lengths were aggregated into five night intervals.

nificantly lower during large migration years (immatures, $t = -3.73$, df $= 1,498$, $P < 0.001$; adults, $t = -3.43$, df $= 544$, $P < 0.001$; Fig. 2A). Mean body mass of immature owls was $88.8 \pm$ SE of 0.23 g ($n = 1,378$) during irruptive years versus 91.9 ± 0.87 g ($n = 122$) during nonirruptive years, whereas mean body mass of adults was 90.8 ± 0.48 g ($n = 295$) during irruptive years versus 93.1 ± 0.47 g ($n = 251$) during non-irruptive years. However, age-specific wing chords were not significantly different between irruptive and nonirruptive migration years (immatures, $t = -0.04$, df $= 1,506$, $P = 0.96$; adults, $t = -1.62$, df $= 549$, $P = 0.11$; Fig. 2B). Body condition scores were lower for both immature and adult owls during irruptive years (immatures, $t = 4.14$, df $= 1,497$, $P < 0.0001$; adults, $t = 2.72$, df $= 542$, $P < 0.01$; Fig. 2C). Thus body mass differences apparently reflect poorer body condition during large migration events rather than structural body-size differences.

In addition to adverse effects on body condition, high owl densities may have affected stopover behavior of migrating owls. The proportion of owls recaptured during a given year was inversely related to the magnitude of the migration (Table 1). During each of the nonirruptive migration years, 31–40% of individual owls banded were subsequently recaptured during the same year. During the two irruptive migration years, however, <13% of owls banded were recaptured. Thus, on an annual basis, there appeared to be an inverse density-dependent probability of recapture of migrating saw-whet owls.

Minimum length of stopover for recaptured owls was also inversely related to the magnitude of the migration. Length of stopover was significantly shorter during the two irruptive years than during the nonirruptive years (Mann-Whitney $U = 10,176.5$, $z = -4.74$, $P < 0.0001$, $n_1 = 219$, $n_2 = 133$; Fig. 3). Median duration of stopover was only 5 nights ($\bar{x} = 7.7 \pm 0.5$ nights) during irruptive years compared to 10 nights ($\bar{x} = 12.7 \pm 0.9$ nights) during nonirruptive years. During irruptive years, 53% ($n = 117$) of stop-

A) Immature owls (irruptive years only).
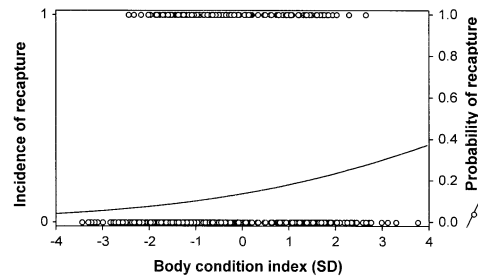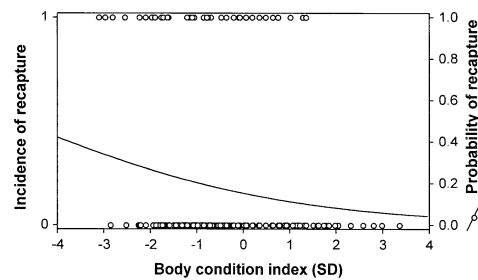

B) Adult owls (irruptive years only).

FIG. 4. Incidence of recapture and body condition of (A) immature and (B) adult saw-whet owls captured during irruptive migration years. ''1'' indicates an owl was recaptured, ''0'' indicates it was never recaptured. Body condition (mass/wing chord[1.462]) was standardized to units of standard deviations based on the mean body condition of all owls captured during nonirruptive years. Curves estimate probability of recapture as a function of body condition based on logistic regression. Both regressions are statistically significant (immatures: $P < 0.001$, adults: $P < 0.01$).

overs lasted for five nights or less. During nonirruptive years, 70% ($n = 93$) of stopovers lasted for more than 5 nights and 50% ($n = 66$) lasted for more than 10 nights.

Adult owls were more likely to be recaptured than immature owls during nonirruptive years but not during irruptive years. In the nonirruptive years, 42% ($n = 105$) of adults were recaptured versus only 23% ($n = 28$) of immature birds ($\chi^2 = 12.52$, df $= 1$, $P < 0.001$). In the irruptive years, however, there was no significant difference in recapture probabilities between age groups ($\chi^2 = 1.93$, df $= 1$, $P = 0.17$) and only 15% ($n = 45$) and 12% ($n = 172$) of adult and immature owls were recaptured, respectively. Apparently when number of migrating owls was low, adults were more likely to stopover than immature owls. In large migration years, however, migrating owls saturated local habitats. High owl densities

may have prevented a large percentage of owls from stopping over, regardless of their age class.

Although minimum stopover lengths were greater for adults than for immature owls ($U = 12,549$, $z = -2.62$, $P < 0.01$), that difference resulted from a large proportion of immature owls being captured during irruptive years when stopover lengths were markedly shorter. Stopover lengths did not vary between age groups within nonirruptive years ($U = 1,376.5$, $z = 0.52$, $P = 0.61$) nor within irruptive years ($U = 4242.5$, $z = -0.74$, $P = 0.46$). The median duration of stopover was 10 nights for each age group during nonirruptive years and only 5 nights for each age group during irruptive years.

Logistic regression was used to test the relationship between probability of recapture and body condition for each age group during irruptive and nonirruptive years. Our results indicate that the probability of recapture declined with body condition for adults during irruptive years ($\chi^2 = 8.99$, df $= 1$, $P < 0.01$; Fig. 4). Conversely, probability of recapture increased with body condition for immature owls during the same years ($\chi^2 = 7.50$, df $= 1$, $P < 0.01$; Fig. 4). Finally, body condition and probability of recapture were unrelated for both age classes during nonirruptive years (immatures, $\chi^2 = 0.13$, df $= 1$, $P = 0.72$; adults, $\chi^2 = 0.45$, df $= 1$, $P = 0.50$).

Minimum length of stopover for recaptured owls was related to initial body condition. During irruptive years, stopover lengths were negatively correlated with body condition of immature owls (Spearman $R = -0.22$, $t = -2.91$, $P < 0.01$, $n = 172$). For adult owls, the relationship was marginally nonsignificant; however, the sample size of recaptured adults was fairly small and the trend was consistent with immature owls ($R = -0.29$, $t = -1.96$, $P = 0.06$, $n = 43$). During large migration years, individuals in good condition departed sooner than individuals in poor condition. During nonirruptive migration years, on the other hand, stopover lengths of adult owls were positively correlated with body condition ($R = 0.30$, $t = 3.18$, $P < 0.01$, $n = 105$). This relationship was nonsignificant for immature owls ($R = -0.17$, $t = -0.88$, $P = 0.39$, $n = 28$).

Discussion.—Intensive efforts to trap saw-whet owls with audiolures in recent years have demonstrated that the species is an irruptive migrant in the eastern United States. Previous researchers have suggested that annual variation in the number of saw-whet owls migrating is a function of the number of immature birds involved, and therefore depends on variation in breeding success (Weir et al. 1980). Although age ratios were heavily skewed toward immature birds during irruptive years, adults also migrated in irruptive fashion. Therefore, breeding success alone cannot explain the irruptive pattern of migration. The underlying cause of irruptive migration events by saw-whet owls remains to be determined. However, we suggest that density-dependent processes play an important role in causing owls to move.

Our data show that energetic condition was related to annual magnitude of the migration. During irruptive years, body masses and body-condition index scores were significantly lower for all owls, but particularly so for immature owls. Based on age-specific wing chord data, there was no evidence of any major differences in sex ratio or general structural body size among years. Instead, we suggest that increased competition for limited resources along the migration route had negative effects on body condition. Relationships between owl density, resource availability, and food-intake rates have not been directly tested for migratory owls. However, Moore and Yong (1991) demonstrated that migratory passerines depress resource abundance during stopover and that rates of energetic intake are negatively correlated with migrant density. Their results suggest that food-based competition among high concentrations of migrants negatively affects energetic condition. Likewise, reduced body condition of saw-whet owls may also result from density-dependent effects of competition during large migration events.

In addition to energetic condition, stopover patterns also depended on magnitude of the migration. During irruptive migration years, recapture rates were several times lower and, among owls that were recaptured, stopover lengths were about half as long. Access to food, habitat, or high-quality perch sites may be greatly reduced when number of migrating owls is very high. As a result, individuals may be more likely to forego stopover and continue migrating or to make shorter stays. Studies have demonstrated that migrant passerines do seem to track measures of habitat quality (Hutto 1985, Martin and Karr 1986). If local resource availability is low, migrating birds are more likely to move on in search of better stopover sites (Lindstrom and Alerstam 1986). We suggest that during irruptive migration years, high owl densities translate to low prey or habitat availability per owl, thus forcing owls to resume migrating sooner. Conversely, during nonirruptive years, recapture rates were very high and long stopover times were more common, suggesting that local habitats were more suitable for extended stopover when the number of migrants was low. Experienced adults in particular may be more likely to reside in a local area until migration becomes absolutely necessary.

Much of the literature on stopover ecology has dealt with the relationship between energetic condition and stopover patterns. Studies of passerines and shorebirds have demonstrated that birds in poor energetic condition (i.e. low body mass or fat content) usually tend to have higher probabilities of recapture (Morris et al. 1996), longer stopover times (Dunn et al. 1988), or both (Moore and Kerlinger 1987). Birds with depleted fuel reserves must stop

longer to replenish energy supplies before continuing to migrate. However, in a study of migrating Bald Eagles (*Haliaeetus leucocephalus*), Restani (2000) found no relationship between body condition and stopover patterns. He proposed a hypothesis that only small-bodied species and birds that migrate by powered flight are likely to show stopover patterns that are sensitive to body condition. Indeed, the relationship between body condition and stopover in saw-whet owls, which are relatively small-bodied and use powered flapping flight, was consistent with results from studies of passerines and shorebirds, but only during irruptive migration years. During such years, we found negative correlations between body condition and stopover length of all owls and between condition and probability of recapture of adults. Owls may be minimizing length of stopover to the extent that energetic condition allows. Individuals that maintain good body condition tend to make very brief stopovers and adults in good condition may forego stopover altogether. Birds in poor condition, on the other hand, may have to stay longer, perhaps in an attempt to replenish energy supplies before continuing to migrate.

During nonirruptive years, however, only adult owls showed any significant relationship between body condition and stopover patterns. A positive relationship was found between body condition of adults and length of stopover. Individuals arriving on the Lower Delmarva Peninsula may be evaluating local areas for the potential of extended stopover. During light migration years, not only do a high percentage of adults elect to stopover, but among those that do, individuals in good condition make longer stopovers. Perhaps adults in good condition are better able to establish extended residency than owls in poor condition and immature owls.

Various factors are likely to contribute to migration patterns of saw-whet owls. Proximate cues such as weather and topographic features are likely to influence migration routes and timing (Weir et al. 1980). The role of those factors in irruptive migration and stopover patterns needs further study. However, among irruptive migrants in general, the ultimate factor believed to contribute to the magnitude of migration is temporal variation in consumer to resource ratios (Lack 1954, Newton 1972, Gauthreaux 1982). High consumer densities can exacerbate seasonal food shortages and force birds to migrate. Although data on prey availability along the migration route are not available, we suggest that resource availability per migrating owl is limited during years when the volume of migrants is very large. As a result, the energetic condition of owls is depressed and local habitats are much less suitable for long-term stopover. During such years, stopover patterns of saw-whet owls are consistent with conventional time-minimization strategies seen in many other species of migratory birds. Conversely, during years when migrant density is low, local conditions may be more conducive for extended stay, and therefore migration proceeds more casually.

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