

Irruptive fall migrations are linked to elevated breeding abundance but are not associated with body condition or stopover duration in Northern Saw-whet Owls

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ABSTRACT

Bird species that undertake irruptive migrations are good candidates for assessing density-dependent effects on stopover ecology because the number of birds using stopover sites varies considerably from year to year. Using morphometric data from a 9-year banding program and radiotelemetry ($n = 25$ females), we found that increases in the annual density of Northern Saw-whet Owls (NSWO; *Aegolius acadicus*) encountered at a fall stopover site in Nova Scotia, Canada, were not linked to female body condition or minimum stopover duration. Rather, most NSWO spent no more than 1 or 2 full days at the stopover site following radio-tagging and during their return visits to the site. Body condition indices were highest for NSWO captured near the end of the migration monitoring season, possibly reflecting birds that had recently established wintering ranges and were elevating energy stores. We used breeding abundance indices derived from Birds Canada's Atlantic Nocturnal Owl Survey to help test the hypothesis that irruptive fall migrations in NSWO were driven by elevated breeding productivity and dispersal of immature birds (breeding success hypothesis). Indeed, irruptive fall migrations were characterized by elevated densities of immatures, but not adults, and mean breeding abundance indices for the Maritime provinces during years with irruptive migrations were higher than those for non-irruptive years. We hypothesize that prey abundance during years with irruptive migrations was sufficient to enable high breeding densities and minimize effects of elevated fall densities of NSWO on rates of mass gain and stopover duration.

Keywords: *Aegolius acadicus*, body condition, breeding abundance, capture date, density-dependent effects, irruptive migration, Northern Saw-whet Owl, stopover duration

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LAY SUMMARY

- Elevated migrant densities can affect a bird's rate of mass gain, and individuals in poor condition may need to extend duration of their stopovers to acquire energy to resume migration.
- Using a banding dataset and radiotelemetry, we assessed whether densities of Northern Saw-whet Owls (*Aegolius acadicus*; NSWO) encountered at a fall stopover site in Nova Scotia, Canada, were associated with owl body condition and stopover duration.
- Annual densities of NSWO detected at the stopover site varied across the 9-year study period; however, female body condition and stopover duration were not linked to owl densities.
- Irruptive migrations consisted of elevated densities of immature, but not adult, NSWO, and mean breeding abundance indices for years with irruptive migrations were higher than those for non-irruptive years, consistent with the hypothesis that irruptive movements can be driven by high breeding productivity in this species.
- We hypothesize that prey availability during years with irruptive fall migrations was sufficient to enable elevated breeding abundance of NSWO and reduce effects of increased fall densities on rates of mass gain and stopover duration.

Les migrations automnales irruptives sont liées à une abondance élevée de reproducteurs mais ne sont pas associées à la condition physique ni à la durée de la halte migratoire chez *Aegolius acadicus*

RÉSUMÉ

Les espèces d'oiseaux qui entreprennent des migrations irruptives sont de bons candidats pour évaluer les effets dépendant de la densité sur l'écologie de la halte migratoire car le nombre d'oiseaux utilisant les sites de halte migratoire varie considérablement d'une année à l'autre. En utilisant les données morphométriques provenant d'un programme de baguage s'étendant sur 9 ans et la radiotélémétrie ($n = 25$ femelles), nous avons trouvé que les hausses de densité annuelle d'*Aegolius acadicus* (NSWO) rencontrées sur un site de halte migratoire automnale en Nouvelle-Écosse, au Canada, n'étaient pas liées à la condition physique des femelles ni à une durée minimale de halte migratoire. Au contraire, la plupart des NSWO n'ont pas passé plus d'un ou deux jours complets au site de halte migratoire après avoir été munis d'un émetteur et lors de leurs visites de retour sur le site. Les indices de condition physique étaient plus élevés pour les NSWO capturés vers la fin de la saison de suivi de la migration, lesquels pourraient être des oiseaux ayant récemment établi leur aire d'hivernage et qui étaient en train d'accumuler des réserves d'énergie. Nous avons utilisé des indices de l'abondance de reproducteurs dérivés de l'Inventaire des Strigidés Nocturnes de l'Atlantique d'Oiseaux Canada pour vérifier l'hypothèse que les migrations automnales irruptives chez NSWO étaient motivées par une productivité reproductive élevée et la dispersion d'oiseaux immatures (hypothèse du succès de la reproduction). En effet, les migrations automnales irruptives étaient caractérisées par des densités élevées d'immatures, mais pas d'adultes, et les valeurs moyennes des indices de l'abondance de reproducteurs pour les provinces maritimes pendant les années de migrations irruptives étaient plus élevées que celles des années sans irruption. Nous émettons l'hypothèse que l'abondance des proies durant les années avec des migrations irruptives était suffisante pour permettre des densités de reproduction élevées et limiter les effets des densités automnales élevées de NSWO sur les taux d'accroissement de la masse et la durée de la halte migratoire.

Mots-clés: *Aegolius acadicus*, condition physique, abondance de reproducteurs, date de capture, effets dépendant de la densité, migration irruptive, durée de la halte migratoire

INTRODUCTION

Avian migration is energetically demanding (Wikelski *et al.* 2003), so many birds stop regularly to rest and feed before resuming their journeys (Alerstam 1990, Schmaljohann and Eikenaar 2017). Among stopovers' most important roles are to allow birds to replenish energy stores used to support migratory flight (Jenni and Jenni-Eiermann 1998, Mehlman *et al.* 2005) and to recover from physiological impacts of migration (Skríp *et al.* 2015, Schmaljohann *et al.* 2022). Stopovers also reduce the overall energetic costs of migration. For example, selection can favor stopovers when environmental conditions elevate costs of flight, such as when facing strong headwinds (Loonstra *et al.* 2019) or heavy rain and fog (Erni *et al.* 2002, Panuccio *et al.* 2019).

Stopover decisions are shaped by various factors encountered at stopover sites, though an individual's energy reserve level is among the most important cues used in deciding whether to remain at a stopover site or to resume migration (Biebach 1985, Eikenaar and Schläfke 2013). The duration of time spent at a stopover site is a function of an energy store threshold, above which it is optimal for birds to leave and below which it is better to stay and acquire energy to reach the next destination (Klinner *et al.* 2020). Indeed, birds with low energy reserves often remain at stopover sites longer and exhibit less migratory restlessness than individuals in good condition (Dunn *et al.* 1988, Fusani *et al.* 2009, Seewagen and Guglielmo 2010). Migrants may also be forced to extend their stopover during adverse weather (Shamoun-Baranes *et al.* 2017), or alternatively, a quick departure could reflect predation pressure (Lank *et al.* 2003), seasonal time constraints on completing migration (Alerstam and Lindström 1990), short-distance movements within a stopover landscape (Taylor *et al.* 2011), or food availability (Ferretti *et al.* 2019). Moreover, elevated migrant densities at stopover sites can intensify food-based competition (Moore and Yong 1991), which in turn reduces rates of refueling and mass gain (Kelly *et al.* 2002) and can affect timing of departure (Ellengren 1991).

Species that undertake irruptive migrations are suitable candidates for assessing associations between migrant densities and (1) body condition and (2) stopover duration because the number of individuals using stopover sites can vary considerably from year to year (Gauthreaux 1982). Irruptive fall migrations occur among boreal granivorous passerines (Koenig and Knops 2001) and for some owl species that prey on small mammals, and in both these groups of birds, irruptive movements are influenced by changes in food abundance on breeding grounds (Newton 2006). For example, food shortages can underlie irruptive migrations by forcing adult and immature birds to disperse from breeding sites in search of prey (food scarcity hypothesis; Koenig and Knops 2001). Alternatively, irruptive fall migrations may be driven by elevated breeding productivity due to abundant prey followed by dispersal of large numbers of immature birds (breeding success hypothesis; Robillard *et al.* 2016).

The Northern Saw-whet Owl (NSWO; *Aegolius acadicus*) is an ~100-g nocturnal raptor that preys on small mammals, notably voles (*Microtus* spp.) and mice (*Peromyscus* spp.), that can fluctuate in abundance from year to year (Swengel and Swengel 1992, Bowman *et al.* 2010). Most NSWO breed in boreal and northern hardwood forests of Canada and northern and western United States (Rasmussen *et al.* 2020), and many individuals migrate south during fall though some are found on breeding grounds throughout the year (Confer *et al.* 2014). Banding data have revealed that NSWO undertake irruptive fall migrations generally with a periodicity of at least once every 4 years (Beckett and Proudfoot 2011, De Ruyck *et al.* 2012, Brittain and Jones 2014). The underlying causes of irruptive movements in this species are poorly understood, though some researchers have posited that they can be driven by elevated breeding productivity and dispersal of immatures (breeding success hypothesis; Weir *et al.* 1980, Côté *et al.* 2007).

We tested whether patterns of fall migration in NSWO were consistent with predictions of the breeding success hypothesis and if fall densities of NSWO were linked to body

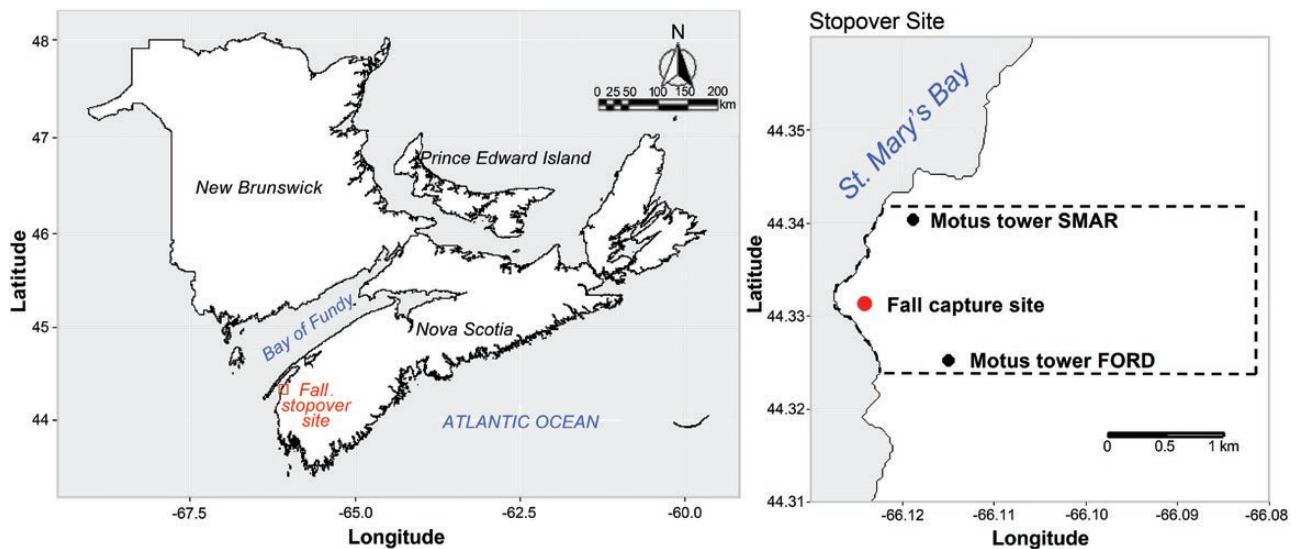


FIGURE 1. (Left) Location of fall stopover site on the campus of Université Sainte-Anne, Church Point, Nova Scotia, Canada. (Right) Position of 2 Motus telemetry stations (SMAR and FORD towers) relative to Northern Saw-whet Owl capture site on the campus of Université Sainte-Anne. Dashed black line represents the approximate outline of the stopover site (i.e., stands of mixed forest) monitored by the 2 telemetry stations.

condition and stopover duration. Banding and radiotelemetry data were obtained at a fall stopover site in southwest Nova Scotia, Canada, a region in which the species is found throughout the year (Rasmussen *et al.* 2020). The study had 3 objectives. First, we tested whether irruptive fall migrations of immatures occurred during years with elevated breeding abundance of NSWO in the 3 Maritime provinces of Canada (Nova Scotia, New Brunswick, and Prince Edward Island; i.e., a test of the breeding success hypothesis; Figure 1). Second, we assessed the relationship between body condition and NSWO densities at the fall stopover site. Finally, we examined if stopover duration was related to body condition or fall owl densities by following radio-tagged NSWO during an irruptive year and a non-irruptive year. If greater migrant densities at stopover sites elevate prey-based competition and decrease rates of mass gain (Moore and Yong 1991, Whalen and Watts 2002), we predicted that (1) body condition would decline with greater owl densities, (2) stopover duration would generally decline with greater owl densities because birds in good condition would quickly move in search of more favorable foraging conditions, and (3) stopover duration would be longest for individuals with low body condition indices.

METHODS

Study Site

NSWO were captured during fall migration on the Church Point campus of Université Sainte-Anne, Nova Scotia (44.332°N, 66.120°W; Figure 1). The campus is on the shore of St. Mary's Bay, a sub-basin of the Bay of Fundy and arm of the Gulf of Maine, and the site includes a ~30-ha mixed forest of red maple (*Acer rubrum*), birch (*Betula* spp.), tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), spruce (*Picea* spp.), and American mountain ash (*Sorbus americana*). Immediately to the east of the campus is an ~25-ha tract of mixed forest with a similar tree species composition as that on the campus of Université Sainte-Anne. We

defined the limits of the NSWO stopover site as the forest on campus and that on the adjacent lands (Figure 1). Saltmarsh, rocky coastline, and fields surrounding the stopover site were generally unsuitable habitats for NSWO (Rasmussen *et al.* 2020).

Data Collection

Captures at the fall stopover site

NSWO were captured at the stopover site each year from 2012 to 2020 with capture procedures following those outlined by Project OwlNet, a program that facilitates standardization of NSWO migration monitoring (Huy 2010). NSWO were captured using four 12-m long mist nets (60-mm mesh size; Avinet, Inc., Dryden, NY, USA) positioned linearly within a forest stand consisting mostly of tamarack and spruce. A 100-dB audiolume (FoxPro Inc., Lewiston, PA, USA) was placed near the center of the net line and broadcasted continuously NSWO male advertising calls (Erdman and Brinker 1997). Male advertising calls result in female-biased captures (Neri *et al.* 2018); and indeed, only 9 of the 225 (4%) NSWO captured during our study were confirmed as male. Nonetheless, the strong bias in female captures may also reflect adult males remaining on their breeding territories throughout the year, a strategy documented in closely related Boreal (Tengmalm's) Owls (*Aegolius funereus*; Korpimäki 1986). Capture efforts began immediately following evening twilight, continued for 3 hr, and occurred over a similar date range each year except for 2017 when logistical constraints resulted in capture attempts restricted to one night only (Table 1). Timing of captures likely spanned most of NSWO migration activity at the stopover site because capture rates were lowest during the earliest (late September to early October) and latest capture efforts (mid-November).

We weighed NSWO with a Pesola scale (± 1 g), measured wing length (± 1 mm), and banded them with a standard USGS metal band on the right leg. A bird's sex was determined using a discriminant function relying on a combin-

Table 1. Summary statistics for Northern Saw-whet Owl captures at a fall stopover site in Church Point, Nova Scotia, Canada, 2012–2020.

Year	Number of owls captured	Number of immatures captured	Number of adults captured	Ratio of immatures to adults	Capture rate immatures ^a	Capture rate adults ^a	Date range of capture attempts
2012	25	17	8	2.1	0.49	0.19	October 5–November 17
2013	19	9	10	0.9	0.12	0.13	September 28–November 16
2014	31	23	8	2.9	0.29	0.10	September 27–November 4
2015	29	6	23	0.3	0.04	0.13	October 4–November 19
2016	31	28	3	9.3	0.26	0.03	October 4–November 20
2017	9	4	5	0.8	– ^b	– ^b	October 28
2018	27	22	5	4.4	0.44	0.10	October 6–November 18
2019	10	5	5	1.0	0.09	0.09	October 16–November 17
2020	44	42	2	21.0	0.58	0.03	October 12–November 22
Overall	225	156	69	2.3	0.29	0.10	September 27–November 22

^aNumber of NSWOW captured per net-hour.^bNot computed because captures were attempted during one evening only.

ation of body mass and wing length (Brinker *et al.* 1997). NSWOW whose body mass and wing length did not lead to a likely determination of sex using the discriminant function were recorded as unknown. Assignment of age was based on remigial molt characteristics (Pyle 1997). NSWOW were classified as immature if they were in their first year of life, and as adults for all subsequent years. Six of the 225 (2.7%) NSWOW captured during the study were recaptured within the same season; and for each of these individuals, we used body mass data from the first capture for body condition analyses. For each year, we calculated (1) the ratio of immature to adult NSWOW captured and (2) capture rate, expressed as the number of NSWOW captured per net hour, as an index of owl density (Frye 2012). Annual capture rate was estimated using data collected on nights with wind speed below 25 km hr⁻¹ because NSWOW were rarely captured during gustier winds, and from the first night to the last night in which ≥ 1 NSWOW was captured.

Fall irruptive migrations in NSWOW are typically characterized as seasons with relatively high capture rates (Whalen and Watts 2002, Stock *et al.* 2006) and captures dominated by immature birds (Côté *et al.* 2007, Beckett and Proudfoot 2011, Confer *et al.* 2014). In our study, migration seasons in which captures were dominated by immatures (i.e., ratio of immature to adult > 2) were also those with the highest capture rates (Figure 2).

Breeding abundance index

The breeding origin of NSWOW captured at the stopover site was unknown, but some birds likely originated from breeding sites in the Maritime provinces, because NSWOW move south along the Atlantic coast during fall (Holroyd and Woods 1975, Confer *et al.* 2014). Annual breeding abundance

indices of NSWOW were derived for the Maritime provinces from data collected by Birds Canada's Atlantic Nocturnal Owl Survey (NOS). Data were not available for Cape Breton Island, Nova Scotia. Ethier *et al.* (2022) provide full details regarding collection of NOS data. Briefly, volunteer citizen scientists trained in owl vocalization identification conducted annual roadside owl surveys between April 01 and May 15 consisting of 10 stops spaced 1.6–2 km apart. At each stop, participants conducted a 2-min point count (i.e., silent listening period), and then played a standardized set of Boreal Owl and Barred Owl (*Strix varia*) calls over a speaker to elicit responses from target species that included NSWOW (Takats *et al.* 2001). The full listening period at each stop was ~9 min for Nova Scotia and ~13 min for New Brunswick and Prince Edward Island. Surveyors conducted their first stop 30 min after sunset and finished their last stop ~180 min later. For each stop, the number of NSWOW detected was recorded and information on local environmental conditions was noted to facilitate standardization of detection probability (Nichols *et al.* 2009). All data were entered into a customized online data entry system available on NatureCounts (www.naturecounts.ca), a service provided by Birds Canada. Surveys were conducted during each year of our study, except in 2020 when COVID-19 public health guidelines prevented most volunteers from conducting their surveys.

Stopover duration

We used radiotelemetry to determine the minimum number of days that NSWOW remained at the fall stopover site during a non-irruptive year (2015) and an irruptive year (2016; Figure 2). We equipped 21 and 18 female NSWOW with a NTQB-4-2 radio transmitter (Lotek Wireless Inc., Newmarket, ON, Canada) in 2015 and 2016, respectively.

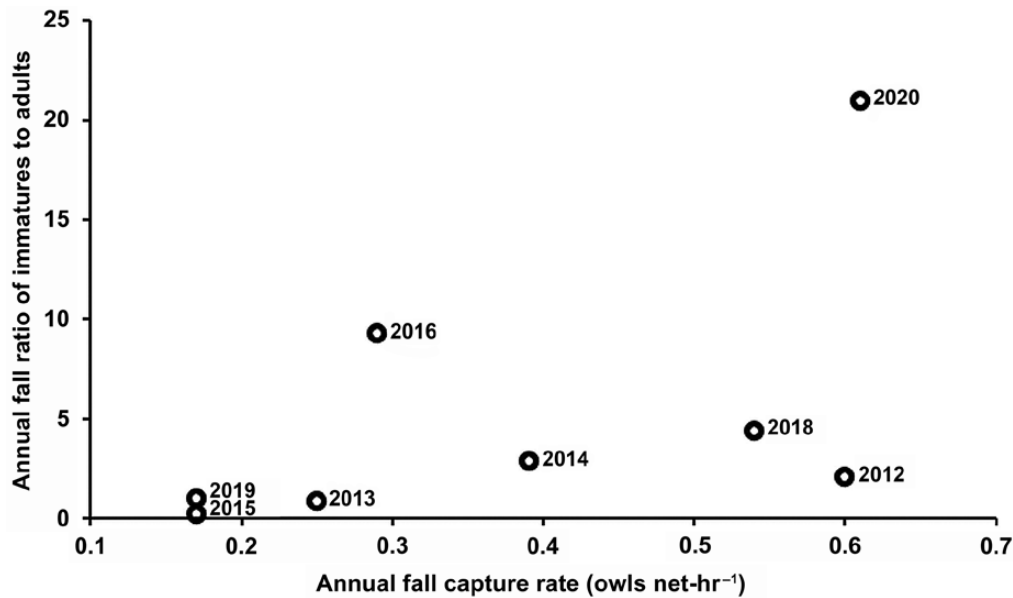


FIGURE 2. Relationship between annual ratio of immatures to adults and annual capture rate for Northern Saw-whet Owls at a fall stopover site in Church Point, Nova Scotia, Canada, 2012–2020.

Tagging dates were distributed throughout the migration monitoring period (October 15 to November 10, 2015; October 4 to November 17, 2016). Transmitters were attached to NSWOW using a leg harness (Rappole and Tipton 1991, Streby et al. 2015), and each tag weighed 1.6 g (1%–2% of NSWOW body weight) and had an antenna length of 20 cm. Transmitters deployed in 2015 emitted a signal every 15 s for up to 306 days and those used in 2016 emitted a signal every 6 s for up to 183 days. Aging, sexing, and transmitter attachment required ~15 min for each NSWOW. Birds were released at the banding station located 300 m from the capture site.

Radio-tagged NSWOW were followed with the Motus Wildlife Tracking System (Taylor et al. 2017). Prior to fall migration in 2015, we established 2 telemetry receiving stations with Yagi-antenna systems within 1 km of the stopover site (i.e., FORD to the southeast and SMAR to the northeast; Figure 1). Receiving stations recorded tag number, date, time, and antenna ID for each tag detection. Tag detections from antennas pointed at the stopover site were used to determine NSWOW stopover duration. The FORD receiving station had one antenna directed toward the forest on the campus of Université Sainte-Anne and a second toward the adjacent forest, and SMAR had one antenna directed toward the forest at Université Sainte-Anne. Tags detected by these antennas were likely at the stopover site because St. Mary's Bay is immediately west of the campus (Figure 1). On several days following radio-tagging NSWOW, we hiked through the stopover site with a hand-held receiving system to visually locate tagged owls and identify dropped tags. From these efforts, we confirmed that one tag dropped from a NSWOW in 2015 and one tag deployed in 2016 either dropped from an owl or we failed to see the tagged owl. Manual tracking efforts resulted in the discovery of 7 roosting perches at the stopover site, and prey identified from 38 pellets collected under these perches consisted primarily of eastern meadow voles (*Microtus pennsylvanicus*) and mice (*Peromyscus* spp.; E. Knighton personal communication).

Data Analysis

For all analyses, we used data from immature and adult females only because the number of confirmed males was small ($n = 9$). A body condition index (BCI) value for each female NSWOW was derived using mass/wing length^{0.5021}; the equation's exponent was obtained from the slope of the logarithm of body mass as a function of the logarithm of wing length for female NSWOW (Whalen and Watts 2002). The BCI is robust against differences in structural size among owls because it eliminates correlations between BCI and wing length (Pearson correlation; $r = 0.003$, $t = 0.04$, $df = 166$, $P = 0.96$), resulting in a quantitative proxy of energetic condition.

Linear models and model selection were used to identify factors predicting BCI of NSWOW. Linearity of data, homogeneity of variance, and normality of residuals were confirmed by inspecting residual plots. Four radio-tagged birds that spent portions of the winter at the stopover site (up until February or March) were not included in analyses. One NSWOW was captured in 2 yr, and we treated both years as independent capture events. For linear models, BCI was a continuous response variable, and age (immature or adult), annual capture rate, and capture date were explanatory variables.

We generated a candidate set of 32 linear models consisting of all combinations of single and additive explanatory variables (including a global model), an intercept-only (null) model, and interaction effects between age and (1) capture rate, (2) capture date (Grueber et al. 2011). Akaike's information criterion for small sample size (AIC_c) was used to assess the relative strength of each model (Akaike 1973, Burnham and Anderson 2002). We considered the best-approximating models as those with $\Delta AIC_c < 2$, where ΔAIC_c is equal to the difference of values in AIC_c between the model in question and the best-approximating model (Burnham and Anderson 2002). For each model, its weight (w_i) was computed because models with larger weights better approximate the data. We inferred that an explanatory variable had strong predictive power when the unconditional 95% confidence interval (CI)

of the parameter's model-averaged slope did not include zero (Arnold 2010).

The basic statistical unit of the NOS breeding abundance index was the sum of NSWO counted by citizen scientists on their spring survey route within a given year, collected over the entire listening period. The model describes the sum of counts $\lambda_{i,k,t}$ for grid cells i encompassing unique combinations of observer-routes k during a year t , where routes were assigned to cells on a regular 50-km² grid (Ethier *et al.* 2022). Our analysis encompassed 105 grid cells containing 183 NOS routes within Nova Scotia (51 routes), New Brunswick (108 routes), and Prince Edward Island (24 routes; Supplementary Figure S1). Counts were modeled from a negative binomial distribution, where the expected counts per grid cell $\mu_{i,t}$ were assumed to be a function of spatially structured grid cell and year effects, plus unstructured variation among observer-routes and cell years. The linear predictor took the form:

$$\log(\mu_{i,t}) = \alpha_i + \tau_i T_{i,k,t} + \kappa_k + \epsilon_{i,t}$$

i = grid cell number

k = combinations of observer routes

t = year

T = transformed year value

α = random intercept

μ = expected count

Parameters included a cell-specific random intercept α_i with an intrinsic conditional autoregressive (CAR) structure (Besag *et al.* 1991), which allows for information on relative abundance to be shared among neighboring cells. Year T was transformed so the maximum year was 0, and each preceding year was a negative integer. This scaling means that the $\exp(\alpha_i)$ could be interpreted as the cell-specific expected count during the final year of the time series. Annual indices of breeding abundance of NSWO for the Maritime provinces were calculated as the exponential mean count from the posterior distribution of the model. Models were fit using a Bayesian framework with Integrated Nested Laplace Approximation using the R-Integrated Nested Laplace Approximation package (Rue *et al.* 2009). See Ethier *et al.* (2022) for more details on model parameterization.

We followed Crewe *et al.* (2020) for treatment of tag detection data. The number of consecutive days starting from the date that an NSWO was tagged to the last day on which it was detected at the stopover site was designated as the minimum apparent stopover duration (Taylor *et al.* 2011); "minimum" because some birds may have used the stopover site prior to their capture and it is possible that some tags failed, or that individuals shed their tags. A stopover duration of 1 day was assigned to NSWO that departed the stopover site during the night of tagging, and an additional stopover day was assigned to each subsequent 24-hr period that birds were detected at the stopover site. Manual radio-tracking of NSWO at the stopover site revealed that it was possible for owls to be at the stopover site without being detected by the telemetry stations. NSWO often perched within 2–3 m of the ground in dense forest cover, which could have affected tag detection probabilities by the telemetry stations (Tremblay *et al.* 2017). However, we presumed that owls not detected at the stopover site for > 24 hr had departed because NSWO are active at night as they move between roosts and hunting habitat (Forbes and Warner 1974).

Eleven of 21 female NSWO tagged in 2015 and 14 of the 18 females tagged in 2016 were used for stopover duration

analyses. Of these 25 owls, 16 were immature and 9 were adult. The 4 radio-tagged NSWO that wintered at the stopover site were not included in analyses of stopover duration. The other 10 radio-tagged NSWO either lost their transmitter within 24 hr of tagging or were never detected by the telemetry stations.

We used linear models to assess whether minimum stopover duration varied according to BCI or between the non-irruptive (2015) and irruptive (2016) years. Stopover duration (in days; log-transformed) was a continuous response variable, and BCI, year, capture date, and age (immature or adult) were explanatory variables. We generated a set of 16 candidate models consisting of all combinations of single and additive explanatory variables and an intercept-only model. AIC_c was used for selection of the best-approximating models and effect sizes for explanatory variables were determined using model averaging as described above. Statistical analyses were performed with R 4.0.2 (R Core Team 2020). Descriptive statistics reported are mean $\pm$ SE.

RESULTS

Patterns of Fall Migration

Of the 225 NSWO captured at the fall stopover site, 180 (80%) were female (119 immature, 61 adult), 9 (4%) were male (8 immature, 1 adult), and 36 (16%; 29 immature, 7 adult) could not be sexed based on the discriminant function. Median capture date was October 19 and capture rates generally peaked during mid-to-late October and declined through November.

Fall migration seasons that were characterized by a combination of captures dominated by immatures (ratio of immature to adult > 2) and highest capture rates occurred in 2012, 2014, 2016, 2018, and 2020, whereas immatures never outnumbered adults during the other years (Figure 2). Thus, irruptive movements were observed every other year, though their magnitude varied considerably throughout the study period. For example, ratios of immature to adult NSWO were particularly high in 2016 (9:1) and 2020 (21:1; Table 1). Annual capture rate for all NSWO was strongly correlated with annual capture rate of immature owls (Pearson correlation; $r = 0.96$, $t = 9.2$, $df = 6$, $P < 0.001$) but not with capture rate of adults (Pearson correlation; $r = 0.03$, $t = 0.1$, $df = 6$, $P = 0.95$). The elevated densities of NSWO encountered each two years therefore reflected densities of immatures.

BCI increased with later capture dates (Figure 3), whereas owl age and annual capture rate did not predict BCI. Capture date was included in each of the 3 best-approximating models (Table 2), and it was the only explanatory variable for which the unconditional estimate of the 95% CI of the model-averaged slope did not include zero ($\beta = 0.015$; 95% CI: 0.010–0.020). A model describing interaction effects between capture date and age on BCI had little support.

Link Between Breeding Abundance and Irruptive Fall Migrations

Years with the highest capture rates at the fall stopover site were typically those with the highest NSWO breeding abundance indices for the Maritime provinces (Figure 4), although the relationship between the two variables was not significant ($F = 3.3$, $df = 1$ and 5 , $P = 0.13$). Mean breeding abundance indices for years with irruptive fall migrations (1.05 ± 0.06 ;

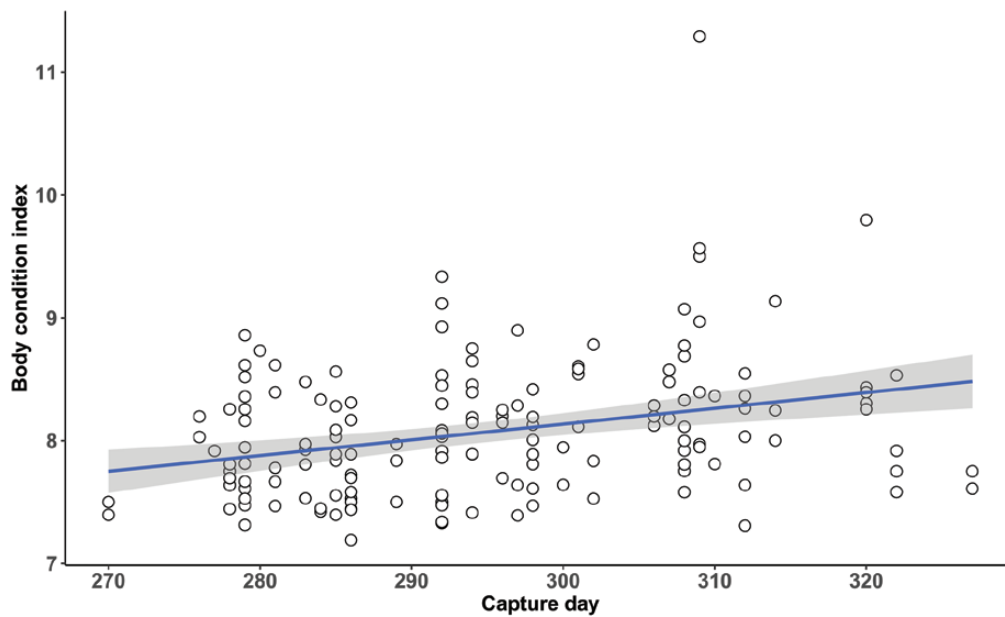


FIGURE 3. Relationship between body condition index and capture day (e.g., 270 = 27 September; 320 = November 16) for 164 female Northern Saw-whet Owls at a fall stopover site in Church Point, Nova Scotia, Canada, during 2012–2020. Shown is a linear regression slope bounded in gray shading by 95% confidence interval estimates.

TABLE 2. The 5 best-fitting models predicting variability in body condition index (BCI) for 164 female Northern Saw-whet Owls captured at a fall stopover site in Church Point, Nova Scotia, Canada, 2012–2020. Each model is shown with corresponding number of parameters (k), deviance, difference in AIC_c value from the best-approximating model (ΔAIC_c), and relative ΔAIC_c weights (w_i). Age was a categorical variable with two levels (immature and adult). Interaction effects are represented by an asterisk. All models include an intercept term,

Model	k	Deviance	ΔAIC_c^a	w_i
Capture date	3	256.984	0.000	0.367
Capture date + Capture rate	4	256.144	1.262	0.195
Capture date + Age	4	256.313	1.430	0.180
Capture date + Age + Capture rate	5	255.864	3.110	0.078
Capture date + Age*Capture rate	6	253.980	3.381	0.068

^aThe lowest AIC_c value was 263.134.

$n = 4$ years) were greater than those for years with non-irruptive migrations (0.90 ± 0.05 ; $n = 3$ years).

Stopover Duration and Movements

Minimum stopover duration averaged 2.7 ± 0.8 days and ranged from 1 to 19 days. All but 3 of the 25 tagged NSWOW spent 1–3 days at the site after capture (Figure 5). The fact that so few NSWOW were recaptured during the same season (6 of the 225 [2.7%] of birds; see Methods) supports the premise that stopover duration for many NSWOW was short. Year and age were not included in the 3 models that best-approximated variability in stopover duration (Table 3). Average stopover duration in 2016 (2.9 ± 1.3 days; $n = 14$) was similar to that in 2015 (2.4 ± 0.6 days; $n = 11$), despite a capture rate in 2016 being nearly twice that for 2015. Stopover duration averaged 2.8 ± 0.8 days for 9 adults and 2.6 ± 1.1 days for 16 immatures. BCI and capture date were each included in one of the best-approximating models; however, their effect sizes did

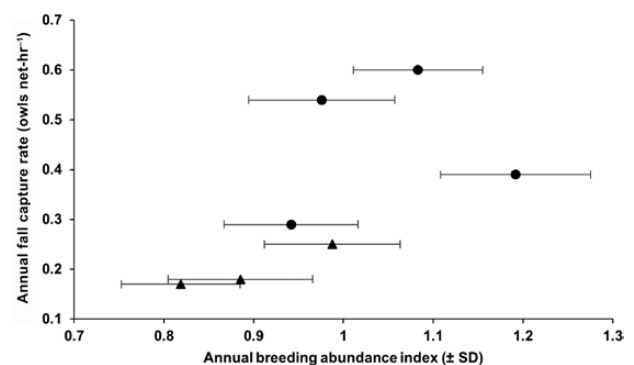


FIGURE 4. Relationship between annual fall capture rate for Northern Saw-whet Owls (NSWO) at the stopover site in Church Point, Nova Scotia, Canada, and annual NSWOW breeding abundance index for the Maritime provinces. Triangles represent years with non-irruptive fall migrations and circles represent years with irruptive fall migrations (see Results for how irruptive and non-irruptive migrations were defined).

not deviate from zero (BCI: $\beta = 0.10$; 95% CI: $-0.21, 0.40$; capture date: $\beta = 0.005$; 95% CI: $-0.010, 0.010$).

Tag detection data revealed that 3 NSWOW made return visits to the stopover site within 4 days of their departure following radio-tagging, and these return stopovers were either 1 or 2 days in duration. Two of these birds were detected by a Motus telemetry station located 60 km from the stopover site (Cape Forchu, Nova Scotia) prior to their return to the stopover site. Three other NSWOW were briefly detected by the telemetry stations directed toward the stopover site (<10-min detection interval) within 8 days of their departure following radio-tagging.

Two other NSWOW were detected by Motus telemetry stations outside of Nova Scotia within several days of radio-tagging. One owl was an immature that was last detected using the stopover site on October 27, 2015 and subsequently detected by telemetry stations on Grand Manan Island archi-

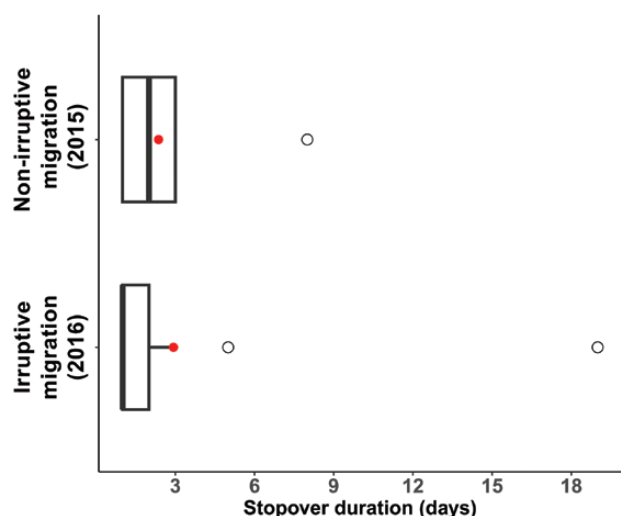


FIGURE 5. Boxplots showing statistics for minimum stopover duration of 25 radio-tagged Northern Saw-whet Owls at a fall stopover site in Church Point, Nova Scotia, Canada, during a non-irruptive migration (2015; $n = 11$ females) and an irruptive migration (2016; $n = 14$ females). The dark vertical line represents the median, and the vertical line(s) adjacent to the median represent(s) quartiles. The horizontal line (whisker) extends to the largest value no more than 1.5 times the interquartile range, with data beyond whiskers shown as outlying points (open circles). The solid circle shows the mean.

pelago, New Brunswick, on November 03, 2015 (60 km straight-line distance from the stopover site) and in northern Massachusetts on November 16, 2015. The second owl was an adult last detected at the stopover site on October 31, 2015 and then detected in southeastern Maine on November 03, 2015 (130 km straight-line distance from the stopover site). It is conceivable that both NSWOW flew over the Gulf of Maine to reach destinations in New Brunswick and Maine.

DISCUSSION

Nearly half a century ago, Weir et al. (1980) suggested that irruptive fall migrations in NSWOW could be driven by elevated breeding productivity (breeding success hypothesis). Several banding studies have provided some support for the breeding success hypothesis in this species by demonstrating that irruptive fall migrations consist primarily of elevated densities of immature birds (Brinker et al. 1997, Côté et al. 2007, Frye 2012, Confer et al. 2014). Similarly, the trend in fall densities of NSWOW observed in southwest Nova Scotia consisted of years with elevated densities of immature females, but not adult females, and years in which immatures never outnumbered adults. Some NSWOW originating from breeding sites in the Maritime provinces move southward along the coast during fall (Holroyd and Woods 1975), so fall densities of immatures in southwest Nova Scotia are expected to be linked to breeding productivity. Indeed, mean breeding abundance indices for the Maritime provinces during years with irruptive fall migrations were greater than those for non-irruptive years. In contrast, we would have expected fall irruptive migrations to include elevated densities of adult NSWOW if food scarcity was a primary cause of irruptive movements, because diminished prey forces adults to leave breeding sites in search of food (Koenig and Knops

TABLE 3. The six best-fitting models predicting minimum fall stopover duration for 25 female Northern Saw-whet Owls during 2015 ($n = 11$) and 2016 ($n = 14$) at a stopover site in Church Point, Nova Scotia, Canada. Each model is shown with corresponding number of parameters (k), deviance, difference in AIC_c value from the best-approximating model (ΔAIC_c), and relative ΔAIC_c weights (w_i). Year was a categorical variable with 2 levels (irruptive and non-irruptive migration), and age was a categorical variable with 2 levels (immature and adult). All models include an intercept term,

Model	k	Deviance	ΔAIC_c^a	w_i
Body condition index	3	12.577	0.000	0.240
Intercept only	2	15.474	0.300	0.206
Capture date	3	14.119	1.541	0.111
Age	3	14.910	2.332	0.075
Body condition index + Capture date	4	12.465	2.745	0.061
Body condition index + Year	4	12.515	2.795	0.059

^aThe lowest AIC_c value was 19.720.

2001). Our observations are therefore most consistent with the breeding success hypothesis, and not food scarcity, as an explanation for patterns of irruptive fall migrations in NSWOW. Nonetheless, these observations should not be generalized beyond females because male NSWOW were not included in analyses.

Similar to NSWOW observed in our study, fall migration patterns in the Snowy Owl (*Bubo scandiacus*) can follow predictions of the breeding success hypothesis (Robillard et al. 2016, Curk et al. 2018, Santonja et al. 2019), whereas irruptive movements in some other rodent-specialist owls, notably Boreal Owls and Great Gray Owls (*Strix nebulosa*), and in some finches (e.g., White-winged Crossbills [*Loxia leucoptera*]) correspond to crashes in food abundance on breeding grounds (Sonerud et al. 1988, Koenig and Knops 2001, Graves et al. 2012). Irruptive migrations may therefore be multi-causal even within species that specialize in similar types of food (Robillard et al. 2016). Moreover, breeding densities and food abundance may interact in shaping fall migration patterns. For example, fall irruptive migrations of NSWOW observed at some stopover sites consist of elevated densities of adult and immature birds (Whalen and Watts 2002, Stock et al. 2006, Brittain and Jones 2014), which could reflect high breeding productivity followed by a decline in prey abundance that causes adults and immatures to search for improved foraging conditions. Similarly, winter irruptions in some boreal granivorous passerines can occur when large seed crops resulting in high breeding productivity are followed by a poor seed crop that forces birds to move in search of food (Koenig and Knops 2001). Underlying mechanisms of fall irruptive migrations may therefore not only vary among species but also among populations, though food availability on breeding grounds is likely an important driver of irruptive movements (Newton 2006).

Fluctuations in breeding densities for irruptive species can reflect adults tracking prey and settling to breed where food is abundant (Newton 2006). Numerical responses to prey abundance during breeding have been demonstrated in NSWOW (Bowman et al. 2010) and other owls specializing in rodents that vary in abundance from year to year, including Snowy Owls (Therrien et al. 2014), Boreal Owls (Korpimäki and Norrdahl 1989), Long-eared Owls (*Asio otus*), and

Short-eared Owls (*A. flammeus*; Korpimäki and Norrdahl 1991). Bowman *et al.* (2010) showed that the abundance of breeding NSWOW in central Ontario, Canada, was correlated with the abundance of red-backed voles (*Myodes gapperi*), an important prey species for NSWOW. Similarly, the highest densities of breeding NSWOW in Idaho, USA, occurred during years with elevated prey abundance, and Marks and Doremus (2000) found that almost all breeding owls did not return to nest at their study site in subsequent years. Low breeding-site fidelity is expected for irruptive species (Andersson 1980) because individuals may need to disperse hundreds of kilometers between consecutive breeding sites to find abundant prey and avoid breeding failure (Newton 2006). Fluctuations in annual breeding densities of NSWOW in the Maritime provinces may have reflected years of immigration of breeding birds that alternated with years in which many birds reproduced elsewhere. Prey availability also affects clutch size and survival of newly hatched owls (Cheveau *et al.* 2004, Confer *et al.* 2014). We hypothesize that movements leading to elevated concentrations of breeding NSWOW in the Maritime provinces played a role in producing localized abundances of immature owls during fall in southwest Nova Scotia.

Most radio-tagged NSWOW spent no more than a couple of days during visits to the stopover site. Some owls may have used the site for roosting only, such as those departing within a few hours after radio-tagging, whereas individuals remaining for longer periods of time likely roosted and foraged at the site because NSWOW may hunt each night (Forbes and Warner 1974). Stopover departure probabilities are expected to increase when conditions favor short-distance movements with minimal risk of starvation (DeSimone *et al.* 2022). Bennetts and Kitchens (2000) found that the greatest movement probabilities of Snail Kites (*Rostrhamus sociabilis*) corresponded to periods of abundant prey across the landscape, and they suggested that these movements allowed individuals to gain knowledge about prey distribution. Our telemetry data revealed that NSWOW undertook flights from the fall stopover site that may not have resulted in continuation of fall migration, such as return trips between the stopover site and other areas in southwest Nova Scotia. Similarly, NSWOW tracked during fall at Long Point, Ontario, Canada, made short flights (mean = 7 km) among sites on the peninsula before leaving the area (Taylor *et al.* 2011). Short-distance flights among sites within a broad “stopover landscape” may help NSWOW gain knowledge about the distribution of foraging and roosting sites and allow them to relocate to favorable habitats.

Migration theory predicts that irruptive migrants in poor conditions should extend the duration of their stopovers to obtain the energy needed to reach the next destination (Dunn *et al.* 1988). Indeed, Whalen and Watts (2002) found that stopover duration in NSWOW during irruptive fall migrations in the southeastern United States decreased for birds with greater BCI. We found that stopover duration in NSWOW was not associated with BCI and that owls with the lowest BCI were often among the quickest to depart the stopover site. These observations indicate that newly arrived NSWOW may have had the energy stores required to depart when they chose to do so, and that the stopover site was unlikely to be a major refueling destination for this species.

Compared to long-distance migrants, birds undertaking short- to medium-distance migrations can face weak time constraints for completing their fall migration (Alerstam

1990) and thus may evolve strategies that minimize energy expenditure during migration (Packmor *et al.* 2020, de Zwaan *et al.* 2022). Female NSWOW are generally considered short- to medium-distance migrants (i.e., movements restricted to within North America; Rasmussen *et al.* 2020) and the rate of their fall migration is slow for a raptor, in part because they may migrate no more than 20–30 km night⁻¹ (Brinker *et al.* 1997, Beckett and Proudfoot 2011) and can spend several days within stopover landscapes. NSWOW may alternate between periods of migratory flight and foraging during the same evening (Brittain and Jones 2014). Capture rates for NSWOW can be particularly high during nights with light tailwinds (Rasmussen *et al.* 2020), suggesting that stopover departure probabilities are tightly linked to conditions favoring reduction of energy expenditure during migration. NSWOW may not be under strong time constraints to complete their fall migration, and a relatively casual-paced migration should help facilitate maintenance of good body condition, including for owls at the earliest stages of their migratory journeys (e.g., stopover sites in the Maritime provinces and other northern areas). Still, NSWOW use an energy-demanding method of flight (wing flapping; Hedenstrom 1993), so birds making large-scale movements, such as those over the Gulf of Maine, may need to extend the duration of their stopover to increase energy stores.

Compared to late in the season, BCI was generally lower for NSWOW captured during October, a period that coincided with the highest seasonal capture rates at the stopover site. Indeed, peak migration activity for NSWOW in eastern Canada occurs in October and declines throughout November (Beckett and Proudfoot 2011). By mid-November, some NSWOW in Nova Scotia may have established their wintering ranges and begun increasing energy stores. Similarly, Snowy Owls may increase fat stores upon reaching their wintering grounds in late fall (Chang and Wiebe 2016, Curk *et al.* 2018). For raptors such as Snowy Owls and NSWOW that hunt small mammals in fluctuating temperatures and snow depths, elevating energy stores at the conclusion of fall migration would help prepare them against variable environmental conditions.

The often unpredictable nature of irruptive migrations makes them challenging to study, yet their consideration is necessary to comprehend the role of density-dependent processes on avian stopover ecology. Data from a banding program and radiotelemetry showed that increases in NSWOW density at a fall stopover site were not linked to owl body condition or stopover duration. We hypothesize that prey availability during years with irruptive migrations was sufficient to enable elevated breeding productivity in the Maritime provinces and subsequently reduce effects of increased fall owl densities on rates of mass gain and stopover duration. Telemetry data showed that the stopover site was likely part of a broad landscape in which NSWOW undertook “within-stopover” relocations during the fall migration period. More research is required to identify the underlying motivation of these movements. Nonetheless, our study further highlights the need for researchers to consider movements at the level of the stopover landscape (Taylor *et al.* 2011, Wright *et al.* 2018) when quantifying avian stopover behavior.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethical statement

All procedures involving animals were in accordance with (1) the Canadian Council on Animal Care (CCAC) guidelines and (2) the ethical standards of the Université Sainte-Anne Animal Care Committee (protocol #09-15).

Conflict of interest statement

The authors have no conflict of interest.

Author contributions

S.R.C. and P.D.T. conceived the study design. S.R.C., A.D., M.M., C.R., T.M.B., and R.F.L. assisted with data collection. S.R.C., A.D., T.M.B., E.J.K., and D.E. analyzed data. S.R.C., A.D., T.M.B., D.S., R.F.L., D.E., A.L.K., and P.D.T. wrote or substantially edited the paper. S.R.C., D.S., and P.D.T. supervised student research. S.R.C. and P.D.T. contributed materials and resources.

Data availability

Analyses reported in this article can be reproduced using the data provided by Craik *et al.* (2023).

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