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Source: Ardea, 97(4) : 489-496

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0413

Correlations of Northern Saw-whet Owl *Aegolius acadicus* calling indices from surveys in southern Wisconsin, USA, with owl and small mammal surveys in Manitoba, Canada, 1986–2006

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Duncan J.R., Swengel S.R. & Swengel A.B. 2009. Correlations of Northern Saw-whet Owl *Aegolius acadicus* calling indices from surveys in southern Wisconsin, USA, with owl and small mammal surveys in Manitoba, Canada, 1986–2006. In: Johnson D.H., Van Nieuwenhuyse D. & Duncan J.R. (eds) Proc. Fourth World Owl Conf. Oct–Nov 2007, Groningen, The Netherlands. Ardea 97(4): 489–496.

The Northern Saw-whet Owl *Aegolius acadicus* (NSWO) can be found year-round on its North American breeding range, but considerable numbers migrate south in autumn, with banding data documenting migration movements over 1000 km. Although the timing and routes of migration are better known in eastern North America, there is some evidence of a general movement from Manitoba, Ontario and Minnesota around Lake Superior to Wisconsin, and then south and/or east. We examined NSWO calling indices from annual auditory surveys in Manitoba, Canada (1991–2006) and from another study site over 770 km southeast in Wisconsin, USA (1986–2007) for covariance as evidence of a spring migration in central North America. In Manitoba and Wisconsin, NSWO calling showed a consistent pattern of regular periodicity, with peak calling every 2–7 years (average 3–5). Likewise, NSWO prey (small mammal) abundance in southeastern Manitoba surveys (1986–2006) showed a periodicity of 2–7 years. NSWO calling, both in Manitoba and Wisconsin, covaried significantly with small mammal abundance in southeastern Manitoba. NSWO indices in Manitoba covaried nearly significantly with the same year in Wisconsin, and significantly with the lag year in Wisconsin suggesting a spring migration takes place in central North America that is influenced by prey availability. This study highlights the need for more extensive analyses of long-term data from owl and prey surveys and for spring owl migration banding to better understand NSWO migration in North America.

Key words: Northern Saw-whet Owl, *Aegolius acadicus*, periodicity, spatial synchrony, surveys, migration, *Clethrionomys gapperi, Microtus pennsylvanicus*, Manitoba, Wisconsin

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INTRODUCTION

Nocturnal and cryptic, the Northern Saw-whet Owl (NSWO) *Aegolius acadicus* is a small (18–21.5 cm long) predator of small mammals, especially deer mice *Peromyscus*, voles (*Microtus* rangewide, *Clethrionomys* to the north), and shrews (*Blarina, Sorex*) (Johnsgard 1988, Swengel & Swengel 1992, Cannings 1993). This owl vocalizes primarily during its courtship and early breeding season (late winter to early spring); otherwise it remains nearly mute. Banding studies in eastern North America, especially in fall (reviewed in Swengel & Swengel 1995), indicate that NSWOs regularly migrate and are much more common than sight and sound records indicate (Cannings 1993). Individuals are hard to see during the day in the dense cover of their roosts and relatively few observers frequent this small owl's forest habitats at night during its vocal period.

Since the timing of spring migration and breeding overlap, it is difficult to determine how many vocalizing individuals are wintering, migratory, or resident in an area. The NSWO is present year-round on parts of its breeding range. But substantial numbers, especially hatch-year individuals, migrate each fall, with banding data documenting migration movements over 1000 km (Cannings 1993). Fall migration has been documented from southern Manitoba and western Ontario, Canada around Lake Superior, the westernmost Great Lake between Canada (Manitoba and Ontario) and the USA, to Wisconsin, USA (Evans & Rosenfield 1987, Erdman *et al.* 1997).

We investigated the pattern of NSWO calling on Manitoba and Wisconsin surveys during 1986–2007. We correlated these indices between the two study regions, both within the same year and as a lag (this year's Manitoba index to next year's Wisconsin index). We also correlated the owl indices, by study region, to small mammal abundance indices from southeastern Manitoba and adjacent Minnesota, both within year and as a lag (this year's mammal index to next year's owl index). Because small mammal abundance can be cyclical in boreal habitats (Norberg 1987, Korpimäki 1994), we were particularly interested in any apparent periodicity in the mammal and owl indices. These analyses are useful for understanding the relationship of NSWO calling to prey availability, and provide evidence for a spring NSWO migration between the study regions.

METHODS

The breeding and winter range of the NSWO as mapped in Cannings (1993) is shown in Fig. 1. The southern half of Manitoba coincides with the northern extent of the NSWO's year-round range and Sauk County, southern Wisconsin at the south edge of the year-round range, but the limits of its breeding and winter ranges are not accurately known and likely vary annually.

Manitoba (MB) nocturnal owl survey

Conducted by volunteers in late March or early April. Surveys started 30 min after sunset and finished at least 30 min before sunrise. Owl indices are expressed as individuals/km (Duncan & Duncan 1997, Duncan 2006). The Manitoba owl survey has used two survey protocols as follows.

1991–99. Fixed stations were spaced 0.8 km apart. The survey period was 3 min and 40 s per stop: 1 min listening, 20 s tape playback of a male Boreal Owl *Aegolius funereus*, 1 min listening, 20 s of tape playback of a male Great Gray Owl *Strix nebulosa*, 1 min listening. Volunteers surveyed on average 1202.5 km/year (range 618–1753 km). Because they exhibit strong interspecific responses to broadcasts of other owl calls, many species of owls can be expected to answer broadcasts of just 1–2 species (Swengel & Swengel 1987, 1995, Francis & Bradstreet 1997, Duncan & Duncan 1997, Duncan 2006).

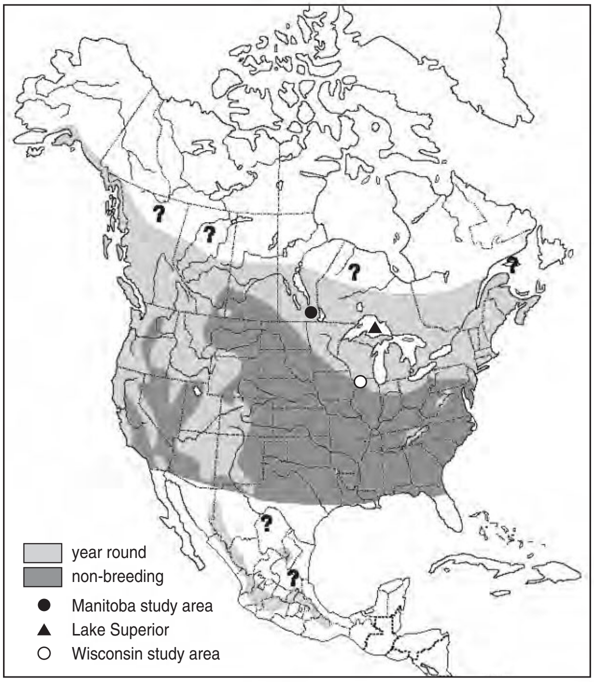

Figure 1. Range of the Northern Saw-whet Owl. The limits of its breeding and non-breeding range are not accurately known and likely vary from year to year. Image and caption modified from Cannings (1993) and used with permission from http://bna.birds.cornell.edu/BNA/ 24 September 2007.

2000–06. Fixed stations were 1.6 km apart and no playback was used. Doubling the interval between stations markedly reduces owl individuals heard at >1 station (Francis & Bradstreet 1997) and lengthens the route covered. Although NSWO calling in Ontario increased slightly after tapes were played, about 60% of total NSWO individuals detected throughout a listening period + broadcast + a second listening period were detected in the single period before a tape was played (Francis & Bradstreet 1997); skipping the tape broadcast and continuing to listen would increase this number. Data presented here reveal that NSWOs per km rates declined <50% after eliminating tape broadcasts in 2000; the decline in NSWOs *per station* was much less than that, because there were fewer stations/km in the later period. The listening period was 2 min per station. Volunteers surveyed on average 1378.7 km/year (range 946–2403 km). Some routes were sampled more than once on different nights, and all survey data were combined here. In both periods, the number of individual owls detected at each station were recorded.

Manitoba small mammal surveys

Small mammals were surveyed annually (1986–2006) at two study areas, one in southeastern Manitoba and one in adjacent Minnesota (hereafter referred to as 'southeastern Manitoba') (Duncan 1987). Trapping occurred in late September to mid-October and prior to snow fall. Trapping effort at each study area totalled 300 stations spaced 10 m apart. One museum special snap-trap, baited with peanut butter, was set at each station and monitored for 3 nights. The stations were checked each morning, trapped mammals removed, and traps reset or re-baited as required. Trap nights averaged 1774.8 per year (range 1582–1814). Mammal indices are expressed as number trapped per number of trap nights per year.

Wisconsin (WI) owl surveys

Each year during 1986-2007, surveys were made in two study areas in Devil's Lake State Park, near Baraboo, Sauk County, southern Wisconsin, USA (43°24' to 43°26'N, 89°42' to 89°46.5'W), c. 770 km southeast of Manitoba. The South Shore Road traverses rugged terrain with deciduous and deciduous-coniferous forests and some open areas. The Steinke Basin contains wet meadow and grassland with scattered pine plantations and oak-pine forest on the perimeter. Surveys occurred at a third site (Baxter's Hollow) near the state park, but only during 1986–97, so this site was included here. Surveys occurred at fixed stations 100 m apart in 1986–87, then 200 m apart in 1988–2007. Study areas and survey methods are described in detail in Swengel & Swengel (1987).

Each station was surveyed up to twice per year, during mid-February to April; averaged 77 stations/year (range 16–146) were surveyed, with 78 (39 done twice) from 10 February to 30 March in 1994–2007. For this analysis, we did not distinguish whether the same or different owl individual(s) were calling in subsequent time slots at the same station. That is, if the same individual Saw-whet Owl called continuously throughout all three time slots at a station, or if a different individual called in each time slot, we totalled three contacts. Thus, the number of contacts per station is an index of the amount of calling heard, not the number of owls responsible for this calling. Indexing auditory results per station rather than using putative number of owls responsible for the calling has been recommended by other owl researchers (Holmberg 1979). The number of contacts (vocalizing individuals) in each time slot (before first playback and during/after each of two playbacks of 20 s of NSWO song) was summed at each station, by owl species.

Statistical analyses

Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado), with statistical significance set at $P < 0.05$. The Manitoba survey data were organized by year (for owls, total owls tallied and km surveyed; for mammals, total individuals trapped and trap nights surveyed). The Wisconsin survey data were organized by listening station. These datasets were too short for time series analysis. Instead, we tested for significant differences in indices among years and noted the apparent peak years. For the Manitoba data, we used the Chi Square Goodness of Fit test. Because Wisconsin data were analyzed at the station level, and hence had a distribution within each year, we used the Mann–Whitney Test to test for significant differences in amount of calling by NSWO between all pairs of consecutive years there. Since the least surveying occurred in 1991 and statistical power for 1991 was likely weak, we also tested 1990 vs. 1992.

In Manitoba, higher NSWO indices occurred in the earlier period (1991–99), when tape playbacks were used, than the later period (2000–06), when no playbacks were used (Fig. 2). This 'trend' is probably the result from a change in methods, rather than a change in owl numbers. Thus, each period was analyzed separately. To use the entire dataset in a single test, the indices were 'detrended' as follows. For each period, a linear regression line was placed through observed value – expected value plots of each year's index. Then the residuals (how far above or below that line) were calculated for each index. Since the residuals are larger in absolute terms for larger indices, the residuals in the two periods were made comparable by converting them into 'residual ratios' (dividing each residual by the mean index for that period). Residuals were also calculated for Wisconsin NSWO indices during 1991–2006, but without ratios inasmuch as the same method was used in the entire period.

We used Spearman rank correlations to examine: (1) Manitoba owl indices to Wisconsin owl indices, and (2) owl indices (in Manitoba or Wisconsin) to Manitoba mammal indices. We did these correlations in two

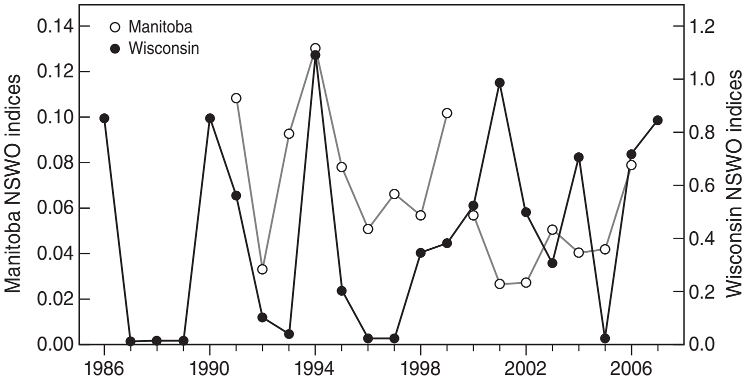

Figure 2. Periodicity of Northern Saw-whet Owl indices.

types of temporal pairings: within year and as a lag (this year's Manitoba owl index to next year's Wisconsin owl index; or this year's Manitoba mammal index to next year's owl index, separately for Manitoba and Wisconsin owl indices).

RESULTS

Periodicity of NSWO indices

In both the Manitoba and Wisconsin surveys, NSWO indices significantly varied among years and peaked about every 3–5 years (Fig. 3). During 1991–99, the Manitoba NSWO indices peaked in 1991, 1994, and 1999; during 2000–06, in 2000, 2003, and 2006. In a Chi-Square Goodness of Fit test for each study period, the number of owls detected each year skewed significantly ($P < 0.0005$) from an expected number proportional to survey effort (km). During 1986–2007, the Wisconsin NSWO indices peaked in 1986, 1990, 1994, 2001, 2004, and 2006–07. The NSWO indices changed significantly ($P < 0.05$) between 9 of the 22 year-pairs tested (Mann–Whitney U test, at scale of individual station, not annual index): 1986–87, 1989–90, 1990–92, 1993–94, 1994–95, 2001–02, 2003–04, 2004–05, 2005–06. All significant tests involved a peak year.

In 1991–99, NSWO indices in Manitoba and Wisconsin (Fig. 2) covaried significantly within the same year but not with the lag year (Table 1). In 2000–06, NSWO indices did not correlate within the same year, but covaried significantly in the lag year. As residual ratios (Manitoba) and residuals (Wisconsin) (Fig. 3), NSWO indices between the two regions covaried near-significantly within year and significantly with the lag year (Table 2).

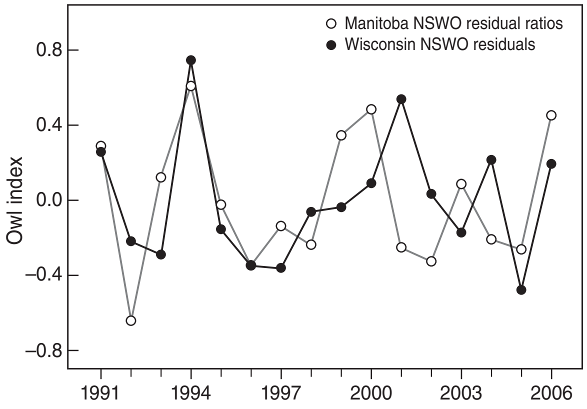

Figure 3. Periodicity of Northern Saw-whet Owl indices as residual ratios (Manitoba) and residuals (Wisconsin).

Periodicity of small mammal indices

For the three small mammal categories sampled in Manitoba (Fig. 4), the top six ranks among years during 1986–2006 occurred with a periodicity of 2–7 years: Red-backed Vole *Clethrionomys gapperi* in 1986, 1990–91, 1993, 1999, and 2006; Meadow Vole *Microtus pennsylvanicus* in 1986, 1991, 1993, 1999, and 2006; Shrews (Soricidae) in 1986, 1993, 1995, 1997, 1999, and 2005.

In a Chi-Square Goodness of Fit test, the number of individuals detected in each of the three small mammal categories each year skewed significantly ($P < 0.0005$) from an expected number proportional to number of trap nights per year. In Spearman rank correlations of annual indices, Red-backed Voles and Meadow Voles significantly covaried ($r = +0.673$, $P < 0.01$), as did Red-backed Voles and shrews ($r = +0.445$, $P < 0.05$).

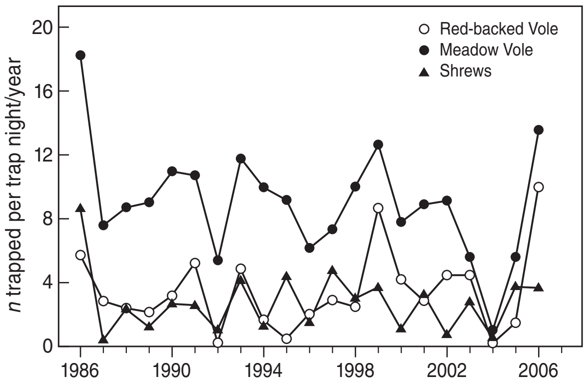

Figure 4. Periodicity of three categories of small mammals trapped in southeastern Manitoba and adjacent Minnesota.

Abundance of meadow voles and shrews did not covary significantly ($r = +0.374$, $P > 0.10$). Red-backed voles were most abundant, followed by meadow voles and shrews. The three categories of small mammals had synchronized peaks in 1986, 1993, and 1999, which were among the top six years for all three categories.

Correlations of NSWO and small mammal indices

NSWO indices in both Manitoba (residual ratios) and Wisconsin significantly covaried with Manitoba small mammal indices in same-year correlations (Table 3). No lag year correlations (this year's mammal index to next year's owl index) were significant, but all were positive.

Table 1. Spearman rank correlations of Manitoba and Wisconsin Northern Saw-whet Owl indices calculated for two study periods (see Methods) and as (A) same year (matching same year in Manitoba and Wisconsin) and (B) lag year (matching this year in Manitoba to the next year in Wisconsin).

(A)	Same year	r_s	P
	1991–99	+0.720	<0.05
	2000–06	–0.143	>0.50
(B)	Lag year	r_s	P
	1991–99	+0.343	>0.25
	2000–06	+0.786	<0.05

Table 2. Spearman rank correlations of Manitoba NSWO residual ratio indices with Wisconsin Northern Saw-whet Owl residual indices using (A) same year (matching same year in Manitoba and in Wisconsin) and (B) lag year (matching this year in Manitoba to the next year in Wisconsin).

(A)	Same year	r_s	P
	1991–2006	+0.471	<0.07
(B)	Lag year	r_s	P
	1991–2006	+0.497	<0.05

Table 3. Spearman rank correlations of Manitoba small mammal indices with owl indices in Manitoba and Wisconsin for (A) same year (matching mammals to same year of owls) and (B) lag year (matching this year for mammals to the next year for owls).

		Manitoba owls[a]		Wisconsin owls[b]	
(A)	Same year	r_s	P	r_s	P
	Red-backed Vole	+0.576	<0.05	+0.430	<0.055
	Meadow Vole	+0.494	<0.055	+0.298	>0.10
	Shrews	+0.174	>0.20	+0.088	>0.50
	Voles (Red-backed & Meadow)	+0.553	<0.05	+0.462	<0.05
	All small mammals	+0.482	<0.07	+0.460	<0.05
(B)	Lag year	r_s	P	r_s	P
	Red-backed Vole	+0.318	>0.10	+0.159	>0.20
	Meadow Vole	+0.182	>0.20	+0.326	>0.10
	Shrews	+0.162	>0.20	+0.178	>0.20
	Voles (Red-backed & Meadow)	+0.294	>0.15	+0.255	>0.10
	All small mammals	+0.215	>0.20	+0.177	>0.20

[a] NSWO residual ratio indices; (A) owls and mammals 1991–2006, (B) mammals 1990–2005 and owls 1991–2006.

[b] NSWO indices, (A) owls and mammals 1986–2006, (B) mammals 1986–2006 and owls 1987–2007.

DISCUSSION

NSWO calling indices showed large fluctuations that peaked about every 3–5 years in both Manitoba and Wisconsin (Figs 2, 3). This was consistent with the results from other auditory surveys for this species (Palmer 1987, Francis & Bradstreet 1997, Swengel & Swengel 1997) and with results from NSWO banding stations (e.g. Weir 1983, Evans & Rosenfield 1987, Duffy & Kerlinger 1992) which found high annual fluctuations in NSWO detection rates that usually peak every 3–5 years.

NSWO calling indices covaried between Manitoba and Wisconsin regions > 770 km apart either within the same year (1991–99, Table 1) or with a lag year (2000–06, Table 1; 1991–2006, Table 2). NSWO peaks in other studies were usually regionally desynchronized (reviewed in Swengel & Swengel 1995), which contrasts with this study during 1991–99. The one-year lag between Manitoba and Wisconsin NSWO peaks for part of the study period suggests that the migration of NSWOs between the two regions is complex and warrants more detailed study (e.g. age-biased migration).

Although simultaneous interspecific owl peaks were not found in our study areas (Duncan 2006), these commonly occur between NSWOs and the congeneric Boreal Owl, with Boreal Owls seeming to peak at 3–4 year intervals (Palmer 1987, Francis & Bradstreet 1997). Owls in northern Europe commonly have simultaneous peaks, such as in Finland where all five species examined had synchronous three-year population cycles (Saurola 1997). Synchronous peaks in small mammal populations in southeastern Manitoba (Fig. 4) were consistent with the well-known population cycles of 3–4 years (range usually 2–5 years) for several small mammals in boreal zones and further north (Krebs *et al.* 1973, Mikkola 1983, Korpimäki 1994). These cycles often exhibit synchrony over large areas within a species, and local synchrony among species (Popp *et al.* 1988, Korpimäki & Krebs 1996, Krebs *et al.* 2002). Northern owl abundance and breeding density appear to be largely driven by cycles in their mammalian prey (Nero 1980, Houston 1987, Norberg 1987, Mikkola 1983, Korpimäki & Krebs 1996).

Besides influencing where owls ‘settle’ (the process of selecting a location for breeding; Korpimäki 1994), variable regional prey availability seems to mediate the degree of migration, winter wandering, and large-scale southerly irruptions in several northern owl species (Mikkola 1983, Cheveau *et al.* 2004). Owls and hawks compete for the same small mammal food base, resulting in complex interactions of predator population sizes (Herrera & Hiraldo 1976, Norberg 1987, Korpimäki & Krebs 1996). As an example, NSWOs had an extremely low calling year in Wisconsin in 2005 (Figs 2, 3); a year when they competed for food with larger northern owls irrupting on a massive scale into the region (Bacon & Paulios 2006). A low calling year may indicate either few individuals present, or instead more individuals present, but many silent and with inadequate resources to breed that year.

Voles and shrews were the main prey trapped in southeastern Manitoba (Fig. 4). Although cyclic microtines made up nearly 30% of the NSWO diet in southern Wisconsin (Swengel & Swengel 1992), these become increasingly important NSWO prey northward (Cannings 1993). *Peromyscus*, which comprised 60% of the NSWO diet in southern Wisconsin, does not exhibit dramatic population fluctuations in southern Wisconsin, but voles are cyclical and shrews (5% of the NSWO diet in Wisconsin) fluctuate strongly (Popp *et al.*1988, Swengel & Swengel 1992).

NSWO indices in both Manitoba and Wisconsin covaried with several mammal population indices from southeastern Manitoba (especially voles) within year, and had positive non-significant correlations with all of the previous year’s mammal indices (Table 3, Fig. 5). These relationships to prey abundance may help explain the same-year synchrony of NSWO indices between the two regions (Tables 1, 2). The lag-year prey–owl correlations also suggest enough of a positive relationship to help explain the one-year lag in NSWO population synchrony between the two regions. But it also seems likely that owl migration between the regions play an important role in the same-year and lag-year synchrony of NSWO indices between the two regions. The lag-year correlation in Manitoba and Wisconsin calling may result from increased NSWO breeding during Manitoba peak years. This might lead to higher numbers of fall migrant first-calendar individuals, which are disproportionately represented in fall migration banding studies (Evans & Rosenfield 1987, Cannings 1993). The following winter and spring, these individuals may contribute to increased calling in Wisconsin. Both same-year and lag-year correlations of Manitoba and Wisconsin NSWO calling may also result from a significant degree of spatial synchrony in small mammal abundance (cf. Cheveau *et al.* 2004). The same-year correlation in owl indices could also relate to initiation of vocalization by migrating NSWOs in Wisconsin prior to their first attempt to settle (possibly further north), or their initial attempt to breed in Wisconsin fails and they try again further north.

Our most surprising finding was evidence for a one-year lag in synchrony between Manitoba and Wisconsin NSWO indices (Tables 1, 2). But there was also a significant (1991–99) to near-significant (1991–2006) same-year synchrony in NSWO indices in the two study regions, suggesting an average lag of perhaps less than one year. In Fennoscandia, wintering and breeding owl and hawk populations strongly covary with the current prey densities (Korpimäki 1985, Korpimäki & Norrdahl 1991), but spring breeding densities of at least three owl species, including Tengmalm's, also covary with the vole index from the previous autumn (Korpimäki 1994) or even nine months before (Hörnfeldt *et al.* 1990). This type of lag may play a role in the NSWO synchrony patterns in this study, but the correlations of NSWO indices were stronger with same-year than with lag-year mammal indices.

We conclude that a return or spring migration from Wisconsin to Manitoba is likely and that there is a predator-prey 'echo' effect or time lag. Like many northern forest owls, the timing and magnitude of this small predator's dispersal behaviour is influenced by the availability of its prey (small mammals) on its breeding range. Comparisons of long-term data from nocturnal owl surveys in more locations across North America will complement information from bird banding stations and help us better understand the timing and scope of dispersal for migratory owl species. Spring NSWO banding efforts are needed to document a regular spring or north migration. The migration of NSWOs between Manitoba and Wisconsin and their relationship to prey density provides a mechanism to explain the synchrony and one-year lag patterns we observed. Local interspecific competition for food must also play a role. The dynamics of multi-species interactions among competing avian predators in the north have been studied (Herrera & Hiraldo 1976, Korpimäki 1994), but much remains to be learned (Korpimäki & Krebs 1996).

ACKNOWLEDGEMENTS

Chelsey Lumb, Dean Berezanski, Robert Nero, Ken De Smet, and David H. Johnson kindly reviewed early drafts of this paper. Dustin Crawford created and printed out a beautiful poster layout for the World Owl Conference. Patsy Duncan co-coordinated the Manitoba owl survey since 1991 and assisted with small mammal surveys since 1986. We thank Ken Lange, Robert Nero, Douglas Trapp, and our sometimes bemused families for encouragement and patient understanding during the course of this study. We also greatly appreciate the many volunteers in Manitoba who conducted surveys, promoted the program, and/or helped in data management. Manitoba's Nocturnal Owl Survey has been supported by the Manitoba Department of Conservation, the James L. Baillie Memorial Fund, Bird Studies Canada, the Saskatchewan Natural History Society Membership Initiatives Fund, the University of Manitoba Alumni Fund, and the Manitoba Conservation Data Centre. Al Vrezec provided a thoughtful and careful review of the final manuscript.

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SAMENVATTING

De Zaaguil *Aegolius acadicus* wordt het gehele jaar door in het Noord-Amerikaanse broedgebied aangetroffen. Er trekken in de herfst echter ook aanzienlijke aantallen naar het zuiden weg. Volgens terugmeldingen van geringde vogels tot 1000 km van de ringplaats. De timing van de trek en de trekwegen in het oosten van Noord-Amerika zijn goed bekend. Er zijn aanwijzingen dat er ook een trekroute loopt van Manitoba, Ontario (Canada) en Minnesota (USA) rond Lake Superior (Bovenmeer) naar Wisconsin en dan verder naar het zuiden en/of het oosten. We onderzochten de roepindex van Zaaguilen tijdens jaarlijkse inventarisaties in Manitoba (1991–2006) en Wisconsin (1986–2007), ruim 770 km verder naar het zuidoosten. Doel van dit onderzoek was na te gaan of er inderdaad voorjaarstrek in het midden van Noord-Amerika plaatsvindt. In Manitoba en Wisconsin werd iedere 2–7 (gemiddeld 3–5) jaar een zelfde roeppiek vastgesteld. Kleine zoogdieren, prooidieren van de Zaaguil, vertoonden in 1986–2006 in het zuidoosten van Manitoba een zelfde periodiciteit van 2 tot 7 jaar. De toppen in de roepindex van de uilen in Manitoba en Wisconsin kwamen beide overeen met pieken van kleine zoogdieren in het zuidoosten van Manitoba. De roepindex in Manitoba vertoonde een verband met de roepindex in het voorjaar erop in Wisconsin. Er was tevens een zwakke aanwijzing dat de roepindices in de twee gebieden binnen een zelfde jaar waren gecorreleerd. Dit suggereert een voorjaarstrek door het midden van Noord-Amerika, die samenhangt met de beschikbaarheid van kleine zoogdieren. Er zijn duidelijk meer uitgebreide analyses van langetermijngegevens van uilen en hun prooien nodig. Het ringen van uilen tijdens de voorjaarstrek kan eveneens een beter inzicht geven van het trekgedrag van de Zaaguil in Noord-Amerika.

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TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

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Research grants – The NOU supports ornithological research and scientific publications through its Huib Kluijver Fund and the 'Stichting Vogeltrekstation'. Applications for grants can be addressed to the NOU Secretary. Donations to either fund are welcomed by the NOU treasurer.

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Editorial address – Jouke Prop, Allersmaweg 56, 9891 TD Ezinge, The Netherlands (ardea.nou@planet.nl)

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World Owl Conference Special

Editors – David H. Johnson, Dries Van Nieuwenhuyse and James R. Duncan, in cooperation with Jouke Prop and Rob G. Bijlsma

Technical editor – Jouke Prop

Dutch summaries – Arie L. Spaans, Dries Van Nieuwenhuyse, Jouke Prop, Rob G. Bijlsma, or authors

Graphs and layout – Dick Visser

Drawings – Jos Zwarts

Cover photos - Serge Sorbi
front – Snowy Owl
back – Snowy Owl, Great Grey Owl and young Tengmalm's Owl

Production – Hein Bloem, Johan de Jong and Arnold van den Burg

Printed by Van Denderen, Groningen, The Netherlands, December 2009