Auditory Surveys for Northern Saw-whet Owls (*Aegolius acadicus*) in Southern Wisconsin 1986-1996

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Abstract.—During auditory surveys with tape playback between 13 February and 27 April during 1986-1996, our detection of calling by Northern Saw-whet Owls (*Aegolius acadicus*) varied dramatically and regularly in an apparent 4-year cycle: 1986, 1990, and 1994 were significantly high calling years; 1987-1989, 1992-1993, and 1995-1996 were significantly low; and 1991 was intermediate. Calling was also significantly affected positively by increasing time since sunset and negatively by date. Results from daytime searches during 1986-1990 for saw-whet owl individuals, roosts, and pellets did not show annual fluctuation. Three other owl species were also heard during these auditory surveys. Calling by Eastern Screech-owls (*Otus asio*) was not significantly affected by any variable tested. Calling by Great Horned Owls (*Bubo virginianus*) was signicantly affected by annual cycle and year, each with opposite effects than for the saw-whet owl. Calling by Barred Owls (*Strix varia*) showed no year or cycle patterns, but was negatively affected by date and wind, positively affected by increasing cloud cover, and positively correlated with saw-whet owl calling.

Auditory surveys by imitating owl calls or by tape playback have often been used to survey nocturnal owls. Many factors must be considered in designing and interpreting such surveys, including daily and seasonal variability in the species' tendency to vocalize, type of vocalization to use as the stimulus, technical aspects of broadcasting, and harmful effects of broadcasts on the survey species' behavior. Well known problems of such auditory surveying concern both responses to broadcasts and the converse, accommodation (reduced responsiveness) with increasing exposure to the stimulus call, so that moderation in frequency and intensity of broadcasts is advised. To account for individuals known to be present through other means but undetected by auditory surveys, correction factors have been calculated so that local population size can be determined (Fuller and Mosher 1981, Johnson *et al*. 1981).

Auditory surveys of nocturnal owls produce valuable distributional and abundance data, but an understanding of the species' vocal behavior is necessary for proper interpretation. Here we report on inter-year variability in amount of calling by Northern Saw-whet Owls (*Aegolius acadicus*), as well as other factors affecting their vocal responsiveness. We also report statistical analyses of calling by other owl species heard during these auditory surveys.

METHODS

Each year during 1986-1996, we conducted auditory surveys for saw-whet owls in the Baraboo Hills, Sauk County, southwestern Wisconsin, USA (43°23' to 43°34'N, 89°41' to 89°49'W). The westernmost site was Baxter's Hollow, a stream gorge with mixed deciduous-coniferous forest. At the nearest point 5.3 km to the east, the second site was the south shore of Devil's Lake State Park, which has rugged terrain with deciduous and deciduous-coniferous forests plus some open areas. At the nearest point 1.6 km to the north, the third site was Steinke Basin in Devil's Lake State Park, containing wet meadow and grassland with scattered pine plantations and oak-pine forest on the perimeter. These study areas were described in more detail in Swengel and

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Swengel (1987, 1992b). Cannings (1993) mapped these areas within but at the southern edge of the saw-whet owl's year-round range, but noted the limits of its breeding and wintering ranges are not accurately known and likely vary annually.

Listening stations (stops) held constant in location among years were spaced 100 m apart along four set walking routes totaling 9 km in 1986, then 12-14 km in 1987-1996. Two routes totaling 7.2 km at Devil's Lake State Park south shore are mapped in Swengel and Swengel (1987). At each station in 1986, then at alternate stations starting part way through the 1987 survey season, we played 20 seconds of taped Northern Saw-whet Owl song (the series of single, short, high-pitched notes repeated at consistent intervals) obtained from "Voices of New World Nightbirds" (ARA Records, Inc.) with a cassette recorder, paused 1 minute to listen, played another 20 seconds of song, and paused again 1 minute to listen. All surveys were conducted by the two of us together and occurred on evenings after sunset with wind <16 km/hr and little or no precipitation. Surveys occurred on at least three evenings each year, with the temperature in the first survey period varying from -11 to 15.5°C (mean 0.15°) and in the second from -15 to 24°C (mean 0.9°).

Each station was surveyed once or twice per year at least 2 weeks apart. During the entire study, the first survey period occurred between 13 February and 29 March and the second between 2 March and 27 April (table 1). Within each year, the two survey periods did not overlap, except in 1986 by 1 day. Surveys occurred a bit earlier over the years to avoid the earlier change to daylight savings time, which would force surveys to be inconveniently later relative to our daytime schedules, set according to clock rather than sun time. The years varied in how soon and how much of the routes could be surveyed in each period because of weather, time, and health constraints. However many stations we sampled in a year, all were in the same general area and habitat. In 1991, very little surveying was done; the surveying that was done occurred only in prime saw-whet owl habitat immediately along the south shore of Devil's Lake. In all other years, surveys occurred in all sections of the three study sites; saw-whet owls were heard in all these subareas during this study. Ten stations were surveyed every year of the study in the first survey period, including in 1991. Analysis restricted to results from these 10 stations provides a common baseline for evaluating of timing and location possible in this study.

Table 1.—*Span of dates for the first and second survey periods in southern Wisconsin 1986-1996.*

Year	First period	Second period
1986	9.III[1] - 29.III	28.III - 27.IV
1987	5.III - 20.III	27.III - 4.IV
1988	2.III - 16.III	30.III - 11.IV
1989	7.III - 21.III	2.IV - 12.IV
1990	28.II - 21.III	23.III - 3.IV
1991	23.II - 25.II	5.IV
1992	13.II - 16.II	27.III - 4.IV
1993	14.II - 3.III	5.III - 26.III
1994	11.III - 16.III	25.III - 30.III
1995	16.II - 27.II	2.III - 18.III
1996	15.II - 25.II	9.III - 14.III

[1] II = February, III = March, IV = April.

At each station for each owl species heard, we recorded the type and direction of each call made by each contact (vocalizing individual) in three time periods: before first tape playback and during/after each of the two tape playbacks. We listened a few seconds prior to the first tape playback upon our arrival at the station to determine whether an owl was calling prior to turning on the tape recorder. The number of contacts in each time period was then summed for each species at each station. For this analysis, we did not distinguish whether the same or different owl individual(s) were calling in subsequent time periods per station. For example, if the same saw-whet owl individual called continuously throughout all three time periods at a station, or if a different individual called in each time period, we totaled three contacts. Thus, the number of contacts per station is an index for the amount of calling, not the number of owls calling. Indexing auditory results per station rather than the number of owls responsible for the calling has been suggested by other owl researchers (Holmberg 1979).

These calling indices (number of contacts) at each station on each survey date were natural log-transformed to allow parametric tests for statistical significance ($P < 0.05$) with ABstat 7.20 (1994 Anderson-Bell, Parker, Colorado). Significant results associated with independent variables are described here as "effects" in the sense of statistical correlations, not as causal relationships proven by experiment. Analysis of variance (ANOVA) analyzed differences in number of contacts among years with Duncan's post-hoc test. Stepwise multiple linear regression was set to indicate P values up to 0.1, and included these independent variables:

1. *annual variables*: year and cycle model (explained below);
2. *survey* (whether first or second);
3. *date* (Julian date);
4. *circadian cycle* (time since sunset);
5. *weather variables*: percent cloud cover, temperature, wind;
6. *moon* (phase in days);
7. *contact indices for other owl species*: Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Eastern Screech-owl (*Otus asio*), Northern Saw-whet Owl, excluding whichever species is the dependent variable.

Since regression is a type of correlation, the year variable would detect a progressive trend in amount of calling (i.e., a general increase or decrease over the years) but probably not other annual effects (such as an increase or decrease in the middle years of the study). To allow the regression to test for cyclic tendencies, we created two cycle models. The first regression used cycle model 1, which assumed 1 year of high calling followed by 3 low years. The second regression used model 2, which assumed 1 high year, 1 intermediate, then 2 low. Both models were suggested by the survey data during 1986-1991, when it first became apparent that the annual variation in saw-whet owl contacts might be cyclic.

Prior to the statistical testing for this paper, it appeared to us that model 1 fit 1986-1990 better, model 2 1990-1996; hence the testing of two cycle models. These models were intended to test how appropriate it is to group the years of saw-whet owl contacts into classes by amount, with either two classes (high, low) or three classes (high, intermediate, low). As a further test of how much of the variation in those annual indices could be attributed to a cycle model, we conducted a linear regression of the 11 annual means of contacts per station in both survey periods (one mean per year), including only one independent variable, the cycle model.

RESULTS

A total of 329 contacts (as defined in Methods) with Northern Saw-whet Owls occurred at 172 (18 percent) of 979 stations (counting all surveys at all stations) during 1986-1996. A minimum of two different individuals (as determined by spatial separation or overlap of calls, such as applied to spot mapping in Swengel and Swengel 1987) were detected each year except in 1988 and 1996, when only one individual was heard at one station. At 147 (15 percent) stations during 1986-1996, one or more other owl species were heard: Great Horned Owl at 36 (4 percent), Barred Owl at 90 (9 percent), Eastern Screech-owl at 30 (3 percent). We occasionally found Long-eared Owls (*Asio otus*) during diurnal searches for owl pellets and roosts, but never heard them during auditory surveys. It is beyond the scope of this paper to analyze the numbers and locations of each owl species detected in these surveys.

Northern Saw-whet Owl

The mean saw-whet owl calling index (contacts) per listening station exhibited significant, regular inter-year variation as much as 80-fold (table 2) (Swengel and Swengel 1995). The ANOVA of indices during both survey periods indicated that the means in 1986, 1990, and 1994 were similar and significantly high, 1987-1989 and 1992-1993 and 1995-1996 were similar and significantly low, and 1991 was intermediate (table 2). ANOVAs restricted to indices from the first or second survey periods produced similar patterns, as did the ANOVA further restricted to the *same* ten stations surveyed each year in the first survey (table 2).

In regression, slightly more of the variation in saw-whet owl calling was described by the first regression and by cycle model 1, with 1 high, then 3 low calling years (table 3). In the second regression, year also had a positive effect; i.e., the years of low calling in the 1990s weren't as low as in the 1980s. Next most significant in each regression was a positive effect of increasing time since sunset. In the first regression only, calling also significantly decreased with increasing date.

Table 2.—*Mean ± SD of total Northern Saw-whet Owl* (Aegolius acadicus) *contacts per station (N) each year in both survey periods, the first survey period, the second survey period, and the same ten stations in the first survey period in southern Wisconsin 1986-1996. Within survey sample, means with no similar letters after them are significantly different (ANOVA with Duncan's post-hoc test, P < 0.05). N is the total number of listening stations surveyed within that period; for both periods, it is the sum of stations surveyed in the first and second periods. For each ANOVA, respectively, F values were 32.13, 16.98, 20.14, 10.32; df were 10 and 968 (residual), 10 and 558, 9 and 399, 10 and 99; and P values were 0.0000 for all.*

Year	Both periods					First period					Second period					Same stations			
	N	*mean*	±	*SD*		*N*	*mean*	±	*SD*		*N*	*mean*	±	*SD*		*mean*	±	*SD*	
1986	106	0.84	±	1.2	A	82	0.82	±	1.2	B	24	0.92	±	1.1	A	1.5	±	1.4	A
1987	175	0.011	±	0.11	C	106	0.012	±	0.14	D	69	0			B	0			B
1988	63	0.016	±	0.13	C	48	0.021	±	0.14	D	15	0			B	0			B
1989	74	0.027	±	0.16	C	43	0.047	±	0.21	D	31	0			B	0.10	±	0.32	B
1990	113	0.90	±	1.4	A	56	0.89	±	1.7	B	57	0.91	±	1.0	A	0.40	±	0.70	B
1991	16	0.56	±	1.2	B	15	0.60	±	1.2	BC	1	0			-	0.30	±	0.67	B
1992	59	0.085	±	0.28	C	24	0.17	±	0.38	D	35	0.029	±	0.17	B	0.20	±	0.42	B
1993	86	0.058	±	0.28	C	48	0.10	±	0.37	D	38	0			B	0			B
1994	91	0.96	±	1.2	A	49	1.2	±	1.3	A	42	0.67	±	1.0	A	2.2	±	1.3	A
1995	98	0.21	±	0.52	C	49	0.24	±	0.52	CD	49	0.18	±	0.53	B	0.20	±	0.63	B
1996	98	0.020	±	0.20	C	49	0.041	±	0.29	D	49	0			B	0			B

Only in the first regression did survey period have a positive effect, apparently indicating that more calling occurred on a particular date if in the second survey rather than the first. This was not immediately apparent in the field (table 2). In all low and intermediate years (1987-1989, 1991-1993, 1995-1996), we heard relatively more owl calls in the first survey than the second, but relatively few owl calls were heard in those years overall. By contrast, we heard relatively more owl calls in the second survey in 2 (1986, 1990) of the 3 high years. Since those high years represent most of the owl contacts in our sample, they affect the statistics more. The 3 high years are comparable in timing, since the first survey occurred within the same rather narrow span of dates, as did the beginning of the second survey (table 1). No weather variables had significant effects.

Table 3.—*Regression statistics and results for the first and second regressions of total Northern Saw-whet Owl* (Aegolius acadicus) *contacts per station in southern Wisconsin 1986-1996. Significant (P < 0.05) results are boldfaced.*

	First			Second		
Statistics	*N*	*r*	*P*	*N*	*r*	*P*
	922	0.5197	**0.0000**	922	0.4687	**0.0000**
Variables	*Step*	*r*	*P*	*Step*	*r*	*P*
Year				2	+0.1243	**0.0000**
Cycle (1)	1	+0.5210	**0.0000**			
Cycle (2)				1	+0.4508	**0.0000**
Survey	4	+0.0950	**0.0196**			
Date	3	-0.1677	**0.0000**			
Time since sunset	2	+0.1239	**0.0000**	3	+0.0961	**0.0013**
Barred Owl	5	+0.0538	0.0582	4	+0.0506	0.0843

The preceding analyses of saw-whet owl calling were all on the basis of contacts at each listening station during each survey. In univariate regressions of the 11 annual indices of saw-whet owl contacts (i.e., the mean contacts per year, as presented in table 2), either cycle model accounted for 80-83 percent of the annual variation, but cycle model 2 (1 high, 1 intermediate, 2 low years of calling) accounted for slightly more (table 4).

Table 4.—*Regression results for Northern Saw-whet Owl* (Aegolius acadicus) *annual vocal index (N = 11) in southern Wisconsin 1986-1996. Significant (P < 0.05) results are boldfaced.*

	r	P
Cycle model 1	+0.8936	**0.0002**
Cycle model 2	+0.9116	**0.0000**

Table 5.—*Mean ± SD of total contacts per station (N) each year in both survey periods for Great Horned (*Bubo virginianus*), Eastern Screech-(*Otus asio*), and Barred Owls (*Strix varia*) in southern Wisconsin 1986-1996. Within species, means with no similar letters after them are significantly different (ANOVA with Duncan's post-hoc test, P < 0.05). For each ANOVA, respectively, F values were 2.32, 3.40, 4.83; df were 10 and 968 (residual) for all; and P values were 0.0106, 0.0002, 0.0000.*

Year	N	Great Horned Owl				Eastern Screech Owl				Barred Owl			
		mean	±	*SD*		*mean*	±	*SD*		*mean*	±	*SD*	
1986	106	0.019	±	0.19	B	0.028	±	0.64	B	0.032	±	0.66	AB
1987	175	0.12	±	0.53	A	0.0057	±	0.076	B	0.11	±	0.51	C
1988	63	0.19	±	0.56	A	0.17	±	0.52	A	0.016	±	0.13	C
1989	74	0.081	±	0.36	AB	0.014	±	0.12	B	0.14	±	0.56	BC
1990	113	0.080	±	0.43	AB	0.0088	±	0.094	B	0.062	±	0.31	C
1991	16	0			B	0.063	±	0.25	B	0.13	±	0.34	ABC
1992	59	0.017	±	0.13	AB	0			B	0.34	±	0.82	AB
1993	86	0.093	±	0.48	B	0.035	±	0.18	B	0.047	±	0.26	C
1994	91	0			B	0.055	±	0.27	B	0.19	±	0.55	ABC
1995	98	0.020	±	0.14	B	0.020	±	0.14	B	0.33	±	0.81	A
1996	98	0.020	±	0.14	B	0.092	±	0.38	AB	0.041	±	0.32	C

Other Owl Species

In ANOVA, the three other owl species heard on auditory surveys exhibited no clear patterns of cyclicity (table 5), and Eastern Screech-owl contacts showed no significant effects in regression (multiple r = 0.0588, N = 922, P = 0.0746). But although no strong annual variation in Great Horned Owl calling was apparent in the field, this species had only two significant effects in regression, cycle and year (table 6). Both of these variables had opposite effects than for saw-whet owl, and cycle model 2 fit better than cycle 1. There was a rather strong pattern of higher Great Horned Owl calling in years with less saw-whet owl calling, and the drop in Great Horned Owl calling in more recent years is also apparent (table 6). But our sample of Great Horned Owl calling was too small to test for the two species directly influencing each other's calling. Thus, it is unclear whether and how the annual patterns of Great Horned Owl and saw-whet owl calling might relate to each other, if at all.

Table 6.—*Regression statistics and results of total Great Horned Owl (*Bubo virginianus*) contacts per station in southern Wisconsin. Significant (P < 0.05) results are boldfaced.*

	First			Second		
Statistics	*N*	*r*	*P*	*N*	*r*	*P*
	922	0.1114	**0.0032**	922	0.1146	**0.0023**
Variables	*Step*	*r*	*P*	*Step*	*r*	*P*
Year	1	-0.0919	**0.0053**	1	-0.1016	**0.0025**
Cycle (1)	2	-0.0716	**0.0299**			
Cycle (2)				2	-0.0778	**0.0203**

In regression, Barred Owl contacts had no year or cycle effects, but showed negative date and wind effects, plus positive effects from cloud cover as well as from saw-whet owl contacts (table 7). To elucidate this last significant correlation further, we compared a graph of the mean annual calling indices of Barred Owls (provided in table 5) to those of saw-whet owls (provided in table 2). Years of higher Barred Owl calling appeared to cluster somewhat around years of higher saw-whet owl calling,

Table 7.—*Regression results for total Barred Owl (*Strix varia*) contacts per station; first and second regressions were identical in southern Wisconsin. Significant (P < 0.05) results are boldfaced.*

Regression Statistics	*N*	*r*	*P*
	922	0.1780	**0.0000**
Variables	*Step*	*r*	*P*
Cloud Cover	1	+0.1058	**0.0018**
Northern Saw-whet Owl	2	+0.0868	**0.0077**
Wind	3	-0.0875	**0.0082**
Date	4	-0.0705	**0.0393**

even though Barred Owl contacts did not show significant annual effects (table 7), but saw-whet owls did (table 3). Similarly, a scatterplot of Barred Owl calls by saw-whet owl calls at each listening station in each survey was mildly consistent with this pattern (i.e., the least-squares regression line was weakly positive in slope), indicating a weak positive correlation between Barred Owl and saw-whet owl calling by listening station within a survey. It was not within the scope of this study to test whether a similar habitat preference between these two species might contribute to this correlation.

We could examine further the possibility that Barred Owl calling might affect saw-whet owl calling, or vice versa. The mean amount of saw-whet owl calling at a station heard after the second tape was slightly higher (mean 0.23 saw-whet owl contacts) following previous Barred Owl calling at the same station compared to no Barred Owl calling earlier at the same station (mean 0.17 saw-whet owl contacts). But this minor difference was not significant in a Mann-Whitney U test (P = 0.2096). Likewise, the mean amount of Barred Owl calling after the second tape was higher (mean 0.19 Barred Owl contacts) after previous saw-whet owl calling at the same station compared to no saw-whet owl calling previously at the station (mean 0.089 Barred Owl contacts), but was not significant in a Mann-Whitney U test (P = 0.1856).

DISCUSSION

Of the owl species analyzed, contacts by Northern Saw-whet Owls produced the most significant effects in regression. The saw-whet owl was the target of the surveys and it was heard more frequently than the other species.

Weather conditions were relatively unimportant in explaining variation in owl contacts (we surveyed in conditions with wind at 16 km/h and little or no precipitation)—only Barred Owl calling had significant weather effects (table 7). Smith and McKay (1984) likewise found weather factors relatively unimportant in explaining variation in Christmas Bird Counts of Great Horned, Barred, and Eastern Screech-owls, although increasing temperature did covary somewhat. Smith *et al*. (1987) found little effect of weather conditions on results of auditory surveys for Eastern Screech-owls, although extreme temperatures and wind decreased response frequency. Holmberg (1979) reported little effect of weather on calling by Tengmalm's Owl (*Aegolius funereus funereus*) within minimal prescriptions for weather conditions during surveys that were roughly comparable to ours, and Palmer (1987) found no significant effects of cloud cover, temperature, and wind on vocalization by Boreal Owls (*A. f. richardsoni*) and saw-whet owls. Lunar phase also had no significant or near-significant effects for any species, similar to Palmer's (1987) finding of an apparently slight but non-significant tendency of greater calling by *Aegolius* during the full moon.

Significant effects were primarily ones of timing: daily (time since sunset), seasonal (both date and survey period), and annual (year, cycle model). The positive effect of time since sunset for the saw-whet owl contrasts with Palmer's (1987) report of no detectable change in vocal intensity for *Aegolius* from sunset until after midnight. The only interspecific relationships occurred between Barred and saw-whet owls.

Northern Saw-whet Owl

Much more so than any other owl species heard on the surveys, the saw-whet owl exhibited pronounced and regular variation in vocal response among years. The first cycle model (1 high year, 3 low) appeared to describe this pattern better in the regression based on contacts per station (table 3), but the second cycle model (1 high year, 1 intermediate, 2 low) was slightly more significant in the regression based on mean annual vocal indices (table 4). The exact pattern of this inter-year variation remains unclear. Palmer (1987) also reported a strong variation in the number of saw-whet owls detected on auditory surveys over 5 years, in a pattern consistent with ours but desynchronized by year: 3 low years (1981-1983), 1 high year (1984), 1 low year (1985).

In one regression, number of saw-whet owl contacts positively covaried quite strongly with year, as a second step following cycle model (table 3). An improvement in our ability to hear faint calls and identify unusual vocalizations might explain this positive year effect, at least in part. But we have no evidence that we failed to recognize certain calls during the early years of the study that we succeeded in identifying in later years; in our field notes, we described all sounds heard on the surveys that were plausibly made by an owl, even if we could not identify it. Furthermore, most contacts with saw-whet owls included the song (like our stimulus tape), which we recognized from the beginning of the study. Even if our ability to recognize saw-whet owl vocalizations did improve markedly during the study, this could not fully explain the annual variability, since the positive year effect is secondary to the significant cycle effect.

It is beyond the scope of this paper to analyze saw-whet owl contacts by habitat type, which is certainly important in explaining their distribution (Swengel and Swengel 1987). However, in all years except 1991 (when we did little surveying), all areas of all study sites were surveyed at least once. Although the exact timing and location could certainly influence the number of saw-whet owl contacts, the annual variation in saw-whet owl contacts was so dramatic it cannot be fully accounted for by subtle variation in timing and location of surveys among years.

Annual indices for saw-whet owl abundance in most migrational banding studies also show annual variability with regional desynchrony and apparent periods of 3-5 years in most cases (reviewed in Swengel and Swengel 1995). This annual variability was so pronounced that it could not be fully explained as simply variation in observer effort and weather conditions among years. But these results, as well as our study, were too short in timespan to prove true cyclicity of saw-whet owl indices.

Hatch-year individuals represent a bigger proportion of migrant saw-whet owls captured in fall than would be expected in the population as a whole (reviewed by Johnsgard 1988). Thus, juveniles may tend to migrate more or be more prone to capture during the banding time period than adults. But numbers of juveniles and adults both vary markedly among years in these studies (Duffy and Kerlinger 1992, Evans and Rosenfield 1987, Weir 1983). The juvenile cohort therefore greatly contributes to annual variation in migrant saw-whet owl indices, perhaps a reflection at least in part of differential breeding success as well as the behavioral factors relating to capturability and migration mentioned above. But the juvenile cohort does not account fully for this inter-year variability in saw-whet owl numbers in banding studies.
Cyclicity in prey availability appears to drive the regular irruptive behavior of Boreal Owls, including the closely related Tengmalm's Owl (reviewed by Norberg 1987). Since the study region lies near the border between the saw-whet owl's year-round and wintering ranges and this border likely shifts around among years (Cannings 1993), perhaps because of prey conditions as well as weather or demographic factors, variation in size and movements of migrational cohorts could certainly influence annual variation in numbers of saw-whet owls present in our study region during the auditory survey season.

While our nocturnal auditory surveys resulted in great inter-year variation in number of contacts with saw-whet owls, our diurnal searches during 1986-1990 did not. These searches yielded 1,148 saw-whet owl pellets, 623 saw-whet owl roosts, and 17 roosting saw-whet owl individuals in these study areas (Swengel and Swengel 1992a,b). Those daytime observations occurring during the auditory survey season did not indicate any strong patterns of annual variation in owl abundance. These diurnal results can only be used as crude measures of saw-whet owl abundance. However, they did prove presence of saw-whet owl individuals in the study sites during the auditory survey season. In years of high calling (1986, 1990), our diurnal searches were much less efficient and precise at detecting saw-whet owl individuals than calling surveys. This is consistent with the recent discovery of breeding by Boreal Owls well south of previously known range by use of auditory surveys (review in Palmer 1987; Stahlecker and Duncan 1996). However, in the years of low calling (1987-1989), our diurnal seaches detected many more saw-whet owl individuals than the nocturnal auditory surveys. Overall, the variation in number of saw-whet owl individuals present during the survey season was clearly lower than the variation in the amount of saw-whet owl calling.

Our observed variation in vocal response appears to be a function not just of the number of owls present, but also of their behavioral inclination to vocalize. A possible explanation for this is based on the assumption that response to tape playback is an aggressive (or territorial) response. In such a scenario, variation in responsiveness corresponds to variation in levels of defense, which in turn might relate to variation in amount and intensity of breeding effort. Breeding by high-latitude owl species has been documented to vary dramatically as a consequence of prey availability, with both breeding attempts and success declining in years of low prey availability (reviewed by Norberg 1987 and Johnsgard 1988). Holmberg (1979) reported that Tengmalm's Owls vocalized earlier and more often in years of higher prey availability. Palmer (1987) reported that the peak calling year (1984) of both Boreal and saw-whet owls correlated with high prey availability of *Clethrionomys* and *Microtus* but not *Peromyscus*. Hayward *et al*. (1987b) reported that Boreal Owl calling rates vary widely among years, with almost no calling by males in poor prey years. Swengel and Swengel (1995) reviewed the possibility that cyclicity in abundance of saw-whet owl prey might occur nearer to our study region than in their boreal populations, well known to be cyclical.

Conversely, high prey availability might also affect vocal response, assuming it is a sign of territorial defense. In a shorebird, higher prey density within a winter feeding territory led to increased intrusion from conspecifics, so that feeding territory size indirectly declined with increasing prey density because of increased costs in territorial defense (Myers *et al*. 1979). Hayward *et al*. (1987a) reported that home range size of Boreal Owls increased with decreasing prey availability, but found no evidence that the owls defended foraging territories.

We cannot determine how much of our observed annual vocal variation results from differences in the number of individuals present and from differences in calling behavior, but this distinction is of interest in interpreting auditory surveys. Although we cannot demonstrate why saw-whet owl (and Great Horned Owl) calling might vary annually, we hope others will come forward with observations to clarify this phenomenon. In the meantime, caution is indicated in interpreting auditory surveys, because their results reflect not only distribution but also calling behavior. We concur with Palmer (1987) that because the owl populations themselves appear relatively more stable than their calling behavior, auditory surveys should be conducted for at least several consecutive years (preferably a minimum of 4) to assess owl occurrence in an area, to avoid all study years being low calling years.

Other Owl Species

It is not only unclear why the Great Horned Owl showed significant effects of both year and cycle (table 6), but also why this might significantly fit a cycle assuming a 4-year period. In Canadian research, Houston (1987) and Houston and Francis (1995) reported pronounced 10-year cyclicity in Great Horned Owl breeding attempts, breeding success, and juvenile dispersal, coinciding with cyclic variation in prey abundance of snowshoe hares (*Lepus americanus*). It is possible that the correlational year effect relates to this 10-year period, since our study has lasted 11 field seasons.

The mechanism underlying the significant covariance of Barred Owl contacts with saw-whet owl contacts (table 7), and vice versa near-significantly (table 3), is also unclear. Habitat sympatry may largely explain this effect. The saw-whet owl has appeared strongly associated with forest canopy, our subsequent years of field data being consistent with the habitat analysis in Swengel and Swengel (1987). While we have not analyzed Barred Owl contacts by habitat structure, they also appear forest-associated, more so than Eastern Screech-owl contacts previously analyzed (Swengel and Swengel 1987). These preferences regarding habitat structure are consistent with the literature (reviewed in Johnsgard 1988).

It remains possible that a behavioral component contributes to this effect. While the effect was far from significant, the tendency was slight for more calling by one species to follow calling by the other. At the least, this demonstrates that in our surveys, calling by one species did not suppress the calling of another, also found by McGarigal and Fraser (1985). At most, it suggests the possibility that one species' calling stimulates the other's, more so the calling of the saw-whet owl (the smaller species) inciting the Barred Owl. Much more sampling is required to analyze this conclusively. At present, our analysis on this point is statistically weak, since the vast majority of surveys at the listening stations had no contact with the one species before the second playback (no contacts with saw-whet owls at 864 stations; no contacts with Barred Owls at 937). For whatever reason, with multiple linear regression, this interspecific pattern became significant, although the causality of this correlation remains unclear.

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LITERATURE CITED

Cannings, R.J. 1993. Northern Saw-whet Owl (*Aegolius acadicus*). In: Poole, A; Gill, F., eds. The birds of North America, no. 42. Philadelphia, PA: The Academy of Natural Sciences; and Washington, DC: American Ornithologists' Union.

Duffy, K.; Kerlinger, P. 1992. Autumn owl migration at Cape May Point, New Jersey. Wilson Bulletin. 104: 312-320.

Evans, D.L.; Rosenfield, R.N. 1987. Remigial molt in fall migrant Long-eared and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 209-214.

Fuller, M.R.; Mosher, J.A. 1981. Methods of detecting and counting raptors: a review. Studies in Avian Biology. 6: 235-246.

Hayward, G.D.; Hayward, P.H.; Garton, E.O. 1987a. Movements and home range use by Boreal Owls in central Idaho. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station:175-184.

Hayward, G.D.; Hayward, P.H.; Garton, E.O.; Escano, R. 1987b. Revised breeding distribution of the Boreal Owl in the northern Rocky Mountains. Condor. 89: 431-432.

Holmberg, T. 1979. Punkttaxering av pärluggla *Aegolius funereus* – en metödstudie. Vår Fågelvärld. 38: 237- 244.

Houston, C.S. 1987. Nearly synchronous cycles of the Great Horned Owl and snowshoe hare in Saskatchewan. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 56-58.

Houston, C.S.; Francis, C.M. 1995. Survival of Great Horned Owls in relation to the snowshoe hare cycle. Auk. 112: 44-59.

Johnsgard, P.A. 1988. North American Owls: biology and natural history. Washington, DC: Smithsonian Institution Press. 295 p.

Johnson, R.R.; Brown, B.T.; Haight, L.T.; Simpson, J.M. 1981. Playback recordings as a special avian censusing technique. Studies in Avian Biology. 6: 68-75.

McGarigal, K.; Fraser, J.D.1985. Barred Owl responses to recorded vocalizations. Condor. 87: 552-553.

Myers, J.P.; Connors, P.G.; Pitelka, F.A. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. Auk. 96: 551-561.

Norberg, R.Å. 1987. Evolution, structure, and ecology of northern forest owls (keynote address). In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 9-43.

Palmer, D.A. 1987. Annual, seasonal, and nightly variation in calling activity of Boreal and Northern Saw-whet Owls. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 162-168.

Smith, D.G.; Devine, A.; Walsh, D. 1987. Censusing screech owls in southern Connecticut. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 255-267.

Smith, D.G.; McKay, B. 1984. The effects of weather and effort on Christmas Bird Counts of owls in Connecticut. American Birds. 38: 383-387.

Stahlecker, D.W.; Duncan, R.B. 1996. The Boreal Owl at the southern terminus of the Rocky Mountains: undocumented longtime resident or recent arrival? Condor. 98: 153-161.

Swengel, S.R.; Swengel, A.B. 1987. Study of a Northern Saw-whet Owl population in Sauk County, Wisconsin. In: Nero, R.W.; Clark, R.J.; Knapton, R.J.; Hamre, R.H., eds. Biology and conservation of northern forest owls: symposium proceedings; 1987 February 3-7; Winnipeg, MB. Gen. Tech. Rep. RM-142. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 199-203.

Swengel, S.R.; Swengel, A.B. 1992a. Diet of Northern Saw-whet Owls in southern Wisconsin. Condor. 94: 707-711.

Swengel, S.R.; Swengel, A.B. 1992b. Roosts of Northern Saw-whet Owls in southern Wisconsin. Condor. 94: 699-706.

Swengel, A.B.; Swengel, S.R. 1995. Possible four-year cycle in amount of calling by Northern Saw-whet Owls. Passenger Pigeon. 57: 149-155.

Weir, R. 1983. Northern Saw-whet Owl studies. Ontario Bird Banding. 16(3): 8-9.