Long-eared Owls, Asio otus: A Review of North American Banding

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In Saskatchewan, at the northern edge of the species' range, the Long-eared Owl (*Asio otus*) is an irruptive species that has appeared in numbers during major vole (*Microtus*) outbreaks in 4 of 44 years. Seven other years have had either no bandings or no sightings over large areas. In a search for possible evidence of food-based nomadism, population trends, length and synchronicity of cycles, and longevity, I reviewed all banding in North America through 1998. Prior to banding office computerization (retroactive to 1955), 803 Long-eared Owls had been banded with 33 band encounters (4.1%). Between 1955 and 1998 there were another 10 250 banded by 426 banders with 86 band encounters (0.8%). Encounter records, especially those involving unexpected directions and distances, tend to support but do not prove food-based nomadism. Peaks of migration movements at different long-term stations occurred in different years. There is soft evidence of both 10- and 3-yr cycles. There is inconclusive evidence for a continuing population decline. The oldest banded bird in North America lived for 11 years, 1 month, but another possibly lived for 15 years, 8 months.

Key Words: Long-eared Owl, Asio otus, nomadism, irruption, Microtus, Short-eared Owl, Asio flammeus, Northern Harrier, Circus cyaneus, Saskatchewan.

In Saskatchewan, the Long-eared Owl, *Asio otus*, shows extreme variations in numbers, common only during obvious but unmeasured increases in vole (*Microtus* sp.) numbers. In other years, none may be seen across substantial areas.

Are Long-eared Owls nomadic in North America as they are in Europe? (Korpimäki and Norrdahl 1991). If so, how far do they travel in search of voles in high vole years? The subsequent year, when voles are low and the owls virtually disappear from favoured Saskatchewan habitat, where have the owls gone?

The first of four long flights by banded owls in unexpected directions in North America was reported in 1939 (Lincoln 1939); do these represent atypical flights, unusual dispersal, or true nomadism? If nomadic, do peaks occur in different years in different regions? Are Long-eared Owl populations cyclic, and if so, are they on a circa 10-yr cycle that roughly parallels Snowshoe Hares (*Lepus americanus*) and Great Horned Owls (*Bubo virginianus*) (Houston 1987) or on a circa 4-yr cycle with small rodents, as occurs in Europe? Because this is a secretive owl, might single individuals or nonbreeding pairs be present but overlooked during low years? Are North American populations of the Longeared Owl steady or declining?

I hoped North American banding data might shed light on some of these questions, as well as on longevity of this species. In particular, would banding records show recoveries in subsequent breeding seasons at a distance from the natal site?

Methods

The Bird Banding Laboratory of the U.S. Geological Survey, which maintains data for the North American Banding Program, provided computerized lists with details of all bandings and all reported band encounters since 1955. Numbers of Long-eared Owls banded each year, 1920-1954, were obtained by perusal of all issues of *Bird Banding Notes* (Fish and Wildlife Service 1922-1965*), yielding 802 Long-eared Owls banded before computerization in 1955. Most early bandings were of nestlings, although a specific code for flightless young, age code "04, local," was not designated by the banding office until the August 1949 issue of *Bird Banding Notes*.

(Three 1930s bandings in Alberta were changed from age code "2" to the later designation of age code "4" in Table 2). Another 10 250 Long-eared Owls were banded by 426 different banders after 1955 (Table 1, Figure 1). Of these, 920 were of unknown age, 3499 were locals, 2075 were immatures, 3293 were adults, 230 were SY (second year), 231 ASY (after second year), one TY (third year) and 1 ATY (after third year). Of the 3499 locals banded, Idaho led with 706, followed by Saskatchewan (699), Alberta (361) and Montana (317).

Because of the intense concentration of Saskatchewan banding in five different years, I paid special attention to the Saskatchewan subset and the relations of their numbers to obvious vole peaks. At large migration stations, banding effort, year to year, of all ages of owls, was more consistent than elsewhere, including 1938 banded in Minnesota (1783 by David Evans at Duluth) and 1261 in Michigan (772 at Whitefish Point under four different permits).

Results

Band encounters: where and how found

Pre-1955 banding resulted in 33 band encounters (4.1%). An Alberta subset of 69 nestlings and seven

TABLE 1. Long-eared Owl banding by state and province

	Recoveries post-1955	Banded Locals	Banded Total	State or Province	Main banders (>80%) of locals
	6	706	976	Idaho	Marks 285; Ulmschneider 227
1	8	698	705	Saskatchewan	Houston 539; Gehlert 76
8	1	361	399	Alberta	Fyfe 160; Gehlert 19
Ü	4	317	864	Montana	D Holt 285
	2	284	296	Oregon	PWRC #124
1	3	217	301	California	Bloom 175
•	2	151	178	Colorado	Ward 85
	1	145	158	Washington	ward ob
3	12	84	734	Wisconsin	
		75	90	British Columbia	
		69	96	Utah	
3	14	53	1261	Michigan	
	9	51	605	New Jersey	
		36	65	Arizona	
	3	30	46	North Dakota	
5	8	29	586	Ontario	
2	O	27	43	Pennsylvania	
-	11	26	1938	Minnesota	
	11	26	27	Nevada	
2	3	21	519	New York	
2	3	11	29	Iowa	
		11	15	Virginia	
2		10	15	Manitoba	
2	1	10	37	Nebraska	
	1	9	16	Kansas	
		8	37	Nova Scotia	
		7	50	Ohio	
		7	21	Quebec	
		6	19	Connecticut	
2	2	4	18	Massachusetts	
2	2	3	9	Maryland	
		3	8	Vermont	
		2	48	Illinois	
		1	6	Indiana	
		1	1	New Brunswick	
		0	1	Atlantic Ocean	
		0	5	Maine Ocean	
		0	8	Missouri	
		0	3	New Mexico	
		0	4	Oklahoma	
		0	1	South Carolina	
		0	8	Texas	
		0	4	Wyoming	
	86	3499	10250	Banded after 1955	
33	00	シサフフ	802	Banded 1920-1954	
33	119		11052		TATES, 8 PROVINCES AND ATLANTIC OCEAN
	117		11032		THE STATE OF THE STATE OF THE STATE OF THE

^{*}Patuxent Wildlife Research Center

Note: 57% of locals banded by 8 of 172 banding permits

None banded in Delaware, District of Columbia, New Hampshire, North Carolina, Rhode Island, Kentucky, South Dakota, or in far south

adult females banded from 1930 to 1937 by W. Ray Salt of Rosebud, Alberta, resulted in a remarkably high six recoveries (7.9%). After 1955, there were only 89 band encounters throughout North America (0.9%).

Of 119 band encounters from the two periods combined, 53 were found dead, 23 shot (12 pre-1955 and 11 post-1955), 8 killed by a car or on a highway, 5 were

injured; 18 other encounters fitted into 11 other coded categories, including 4 re-trapped in the same block of latitude and longitude in a subsequent year, 4 netted or re-trapped in an adjacent block, and 4 re-trapped in a distant ten-minute block of latitude from where banded. Details of the latter four travelers are: a bird of unknown age but probably a nestling, banded on

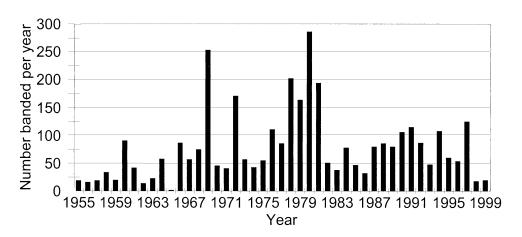


FIGURE 1. Numbers of Long-eared Owls banded each year in North America, 1955-1999.

TABLE 2. Long-eared Owl recoveries banded anywhere in North America.

	Recovery Data							Banding Data								
_	Dista	nce				State/					State/					
Band #	(km)	Mo	Dy	Year	How	Prov.	Lat	Long	Α	S	Prov.	Lat	Long	Mo	Dy	Year
000556933	175	5	42	1932	89*	AB	524	1120	0	5	AB	511	1125	6	25	1931
053526629	225	11	99	1959	0	IL	414	890	0	0	Wl	433	875	10	17	1959
060617751	245	11	30	1969	4	IL	420	895	0	0	Wl	433	874	10	25	1969
057690565	400	1	22	1990	0	NY	410	735	0	0	ON	435	765	9	22	1989
000208816	480	4	19	1933	3	NJ	405	735	0	0	MA	412	707	0	0	1927
055674536	590	1	6	1959	15	MD	390	755	0	0	ON	434	791	11	8	1958
060684563	690	1	2	1967	1	NC	362	794	0	0	ON	423	802	4	20	1965
003661927	730	2	42	1936	89*	VA	373	785	0	0	Ml	424	841	4	27	1932
002573140	870	12	6	1936	1	NE	420	962	0	0	MB	495	970	7	3	1936
068604234	1035	9	10	1980	14	QU	480	665	0	0	ON	435	785	10	8	1978
003661987	3135	10	9	1934	1	ON	465	843	0	0	CA	330	1170	4	22	1934
081606045	3175	3	24	1977	1	PU	184	975	0	0	MN	465	920	9	20	1973
068600215	140	5	25	1976	45	Ml	455	861	1	0	Ml	464	845	4	15	1976
036714113	260	5	8	1940	98	ND	465	1020	1	5	ND	484	1020	5	22	1937
040512026	270	4	5	1944	1	WA	482	1181	1	4	WA	463	1203	6	18	1943
088610415	365	4	1	1998	45	IL	402	885	1	0	Wl	433	874	11	3	1989
220604277	370	9	2	1994	0	ON	485	880	1	0	MN	465	920	10	19	1993
081611315	370	8	5	1978	0	ON	462	800	1	0	Ml	464	845	4	23	1977
081611772	385	12	4	1982	0	Wl	455	894	1	0	Ml	464	845	4	17	1981
220600812	410	9	3	1994	50	ON	453	814	1	0	NY	431	774	4	7	1991
081623324	470	7	30	1981	0	ON	451	791	1	0	Ml	464	845	5	5	1979
056695514	480	6	42	1968	1	QU	484	791	1	0	Ml	464	845	5	20	1966
068600211	480	5	2	1975	57	Wl	453	905	1	0	Ml	464	845	4	22	1975
052624634	500	6	10	1962	0	ON	480	793	1	0	ON	433	792	2	5	1954
056695534	585	1	99	1969	98	Wl	435	911	1	0	Ml	464	845	5	2	1968
081698373	690	11	18	1988	0	MN	462	935	1	0	Ml	464	845	5	1	1988
220615419	825	9	5	1991	0	UT	400	1122	1	0	MT	472	1140	7	17	1990
081625890	1000	4	17	1988	0	QU	465	714	1	0	Ml	464	845	5	10	1985
074546503	1430	1	11	1983	0	MS	341	885	1	0	Ml	464	845	4	28	1981
081693230	3270	5	20	1990	2	GU	200	1004	1	0	MT	472	1140	6	1	1989
038620218	145	11	63	1939	0	IL	420	881	2	0	Wl	430	892	5	15	1939
081620711	145	3	29	1979	0	MN	454	925	2	0	MN	465	920	9	26	1978
081620719	225	10	28	1978	1	Wl	450	905	2	0	MN	465	920	9	27	1978
081641608	240	3	29	1984	45	Wl	450	902	2	0	MN	465	920	10	18	1981
068600523	355	1	24	1972	3	IL	413	881	2	0	Wl	444	875	11	7	1971
220604294	375	3	28	1995	0	MN	444	954	2	0	MN	465	920	10	23	1993

TABLE 2. Long-eared Owl recoveries banded anywhere in North America (continued from previous page)

	Recovery Data									Banding Data							
	Dista	nce				State/					State/						
Band #	(km)	Mo	Dy	Year	How	Prov.	Lat	Long	A	S	Prov.	Lat	Long	Mo	Dy	Year	
081620719	225	10	28	1978	1	Wl	450	905	2	0	MN	465	920	9	27	1978	
081641608	240	3	29	1984	45	Wl	450	902	2	0	MN	465	920	10	18	1981	
068600523	355	1	24	1972	3	IL	413	881	2	0	Wl	444	875	11	7	1971	
220604294	375	3	28	1995	0	MN	444	954	2	0	MN	465	920	10	23	1993	
081604937	440	4	29	1976	89*	Ml	464	845	2	0	Wl	432	875	10	15	1974	
081620400	875	7	12	1978	45	MB	520	1011	2	0	MN	465	920	11	4	1976	
074575003	890	1	41	1992	0	IN	403	863	2	0	ON	482	885	9	29	1991	
081653319	1260	10	28	1992	0	NB	474	650	2	0	NJ	385	745	11	19	1988	
081620108	1305	12	1	1978	0	AR	351	935	2	0	MN	465	920	10	11	1975	
036714117	205	8	21	1937	1	SK	502	1043	3	0	ND	484	1020	6	9	1937	
000226052	290	11	21	1925	1	IN	413	873	3	0	Ml	424	842	5	19	1925	
039669347	330	6	28	1942	0	OH	412	814	3	0	PA	404	775	5	16	1941	
037642104	615	11	28	1938	1	SD	432	995	3	0	ND	484	1020	6	16	1938	
004616735	845	9	4	1933	47	QU	483	770	3	0	Ml	430	843	5	14	1933	
038687566	1400	12	5	1943	0	TX	332	994	3	0	Wl	430	892	5	15	1939	
220616638	255	9	41	1994	0	MT	443	1122	4	0	MT	463	1140	5	7	1991	
057692535	280	10	8	1968	0	NY	424	734	4	0	NJ	402	750	5	25	1968	
057689020	435	6	28	1969	4	MB	505	1005	4	0	SK	520	1065	6	15	1967	
057688448	715	2	10	1967	3	MT	454	1083	4	0	SK	520	1064	6	9	1966	
057692533	995	10	4	1969	1	NB	473	672	4	0	NJ	402	745	5	20	1968	
004629600	1135	2	2	1935	1	UT	410	1115	4	0	AB	511	1125	7	4	1933	
057688480	1415	4	9	1969	0	IA	425	935	4	0	SK	520	1070	6	20	1966	
004629579	1440	3	3	1934	98	NE	425	981	4	0	AB	511	1125	7	4	1933	
050643309	1605	4	1	1961	1	AB	524	1133	4	0	CO	393	1045	6	2	1959	
003664770	1660	10	21	1933	98	MN	442	930	4	0	AB	511	1125	6	25	1933	
057689017	2365	12	99	1972	0	MS	341	903	4	0	SK	520	1064	6	15	1967	
057695906	2385	11	3	1957	1	NL	263	1001	4	0	Ml	433	840	5	17	1957	
056681737	2825	8	64	1972	98	NL	254	1001	4	0	SK	510	1022	6	20	1967	
057612231	3710	1	25	1970	1	DF	191	990	4	0	SK	520	1064	6	13	1969	
052622635	3865	99	99	1960	0	OA	163	964	4	0	SK	510	1020	6	15	1960	
081611823	465	4	41	1997	0	Ml	421	831	5	4	NY	431	774	4	20	1996	
074597414	645	7	5	1999	0	ON	463	842	6	0	NY	431	774	4	5	1989	

In column 6, how found codes are: 0, found dead; 1, shot; 2, injured; 3, starved; 4, caught in trap; 14, struck by vehicle; 15, killed by weather; 45, killed on highway; 47, band removed; 50, skeleton only; 57, entangled in fence; 89, trapped and released in different 10-minute block; 98, band only without information.

In column F. all bird codes indicate death, except for 89*

In columns 7 and 12, standard postal abbreviations for states and provinces are used.

Additional abbreviations for Mexican states in column 7 are:

DF - Federal District; GU - Guanajuoto; NL - Nuevo Leon; OA - Oaxaca; PU - Puebla; QU - Queretaro

17 April 1932 by P. F. English in Michigan, was retrapped during mid-February 1936 in Virginia, 730 km distant; an immature banded in Wisconsin by C. R. Sindelar on 15 October 1974 was re-trapped on 29 April 1976 in Michigan, 440 km distant; an owl of unknown age, banded at Nature Dunes Nature Center, Wisconsin, 9 November 1981, was re-trapped on 30 November 1982, 130 km distant in Wisconsin; a nestling banded at Rosebud, Alberta, by Ray Salt on 25 June 1931, was re-trapped 175 km north and west near Killam, Alberta, in mid-May 1932. All but the Alberta owl were probably in migration when banded.

The map (Figure 2) and Table 2 together depict the movements of 64 owls that traveled more than 100 km.

Fifteen of the 64 were banded as nestlings, and traveled greater distances, an average of 1672 km, than owls banded at other ages. One wandered north 280 km from New Jersey, in the months after it was banded. Another two were shot after "wrong-way-Corrigan" northward movements of 1605 and 995 km, respectively: from near Denver, Colorado, banded by J. A. Neff on 2 June 1959, to Ponoka, Alberta on 1 April 1961, and from near Stockton, New Jersey, banded by O. A. Heck on 20 May 1968, to Saint Quentin, New Brunswick on 4 October 1969. The other 12 nestlings traveled in a southerly direction, 4 reaching Mexico along with 3 of other ages. Once could speculate that the seven recoveries in Mexico might represent "leap-

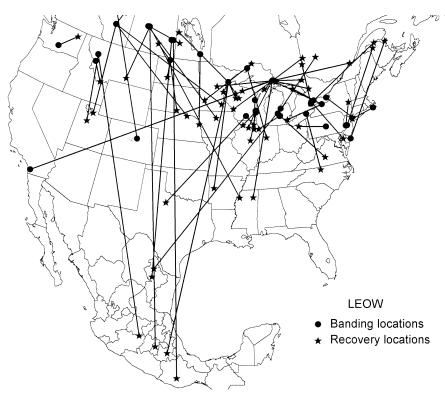


FIGURE 2. Map of Long-eared Owl movements in North America, 1925-1999. Circles represent place of banding. Stars represent place of recovery. Map by K. M. Meeres.

frogging" of northern owls to more southern wintering grounds.

There are four other examples of dispersal in an unusual direction and distance. The first two, presumed to be young in their first year of life, were each recovered in the year of banding. Lincoln (1939: 128) listed a Long-eared Owl of unknown age banded at Escondido, California, 22 April 1934, and shot at Corbeil, Ontario, 9 October 1934, a distance of 3135 km northeast. Considering banding of all species, Lincoln commented "This is one of the most unusual records thus far obtained." Lincoln also listed a juvenile Long-eared Owl that had traveled northeast from St. John, Michigan, to Abitibi, Quebec, between 14 May and 4 September 1933, a distance of 845 km. In each of these instances it is not known whether the northward movement was achieved in the first or second year of life, nor whether either represents migratory movement or dispersal to a very different breeding location.

Four distant recoveries during or immediately after the breeding season might have been construed as evidence in favor of nomadism, had they not been banded during migration.

Two were adults banded as April migrants at Braddock Bay, New York; one flew 465 km to the west to

Michigan in mid-April of the subsequent year and the other was found dead 645 km northwest in Ontario on 5 July, 10 years after it had been netted as an SY bird by subpermittee Frank Nicoletti (see below under Longevity). Two others, banded as late migrants at Whitefish Point, Michigan (on 22 April and 14 May), were recovered two years later; one went northeast 480 km and was shot in mid-June in western Quebec; the other went southeast 470 km and was found dead on 30 July in Ontario.

Longevity

After deleting ten birds inadmissible because they were alive when recaptured (most of them taken in a net at a banding station and released), two bands found on a skeleton, and two reported as "band only," 105 records remained that were acceptable for a life table (Table 2). As with other raptor species, nearly two-thirds of the band encounters, 67 of 105, occurred before the birds were a year old, with 17 in the second year (Table 3).

The Long-eared Owl accepted by the banding office as their oldest to date was banded as a second-year bird at Braddock Bay, New York, by Frank Nicoletti on 5 April 1989, and found dead in Ontario on 5 July 1999, as already mentioned. At least a year old when banded,

assuming hatching near the first of June, it was at least 11 years, 1 month old, recognized as the longevity record for this species (Klimkiewicz 2005*). A potentially older Long-eared Owl is also in the banding records. Number 816-06355, banded as a nestling near Lincoln, Nebraska, on 24 May 1978 by Ross Lock, was reported as killed by a hawk or owl on an unknown date in February 1994, in the same tenminute block of latitude and longitude in which it had been banded. Long-eared Owls regularly winter that far north. The unusual and precise mode of death tends to suggest that the band had not been lying in a desk for months or years before it was reported. Had this owl indeed died in February 1994, it would be the oldest Long-eared Owl in North America, at 15 years, 8 or 9 months. Older birds are expected in future, since in Europe, the longevity record for this species is 27 years, 9 months (Rydzewski, cited in Marks et al. 1994).

Relation to vole numbers in Saskatchewan

In Saskatchewan, between 1969 and 1997, only in three years (1970, 1982, and 1986) were no Longeared Owl nests detected anywhere in extensive travels throughout west-central Saskatchewan (CSH, personal observation). Also in 1982, and in three other years (1976, 1979, and 1981), no birder in the 11 012 km² Saskatoon area reported seeing a single Long-eared Owl at any time (Leighton et al. 2002: 182-183).

The three peak vole years (1960, 1969 and 1997) made a striking contrast. Each occurred in a spring following the rare occurrence of grain crops that were incompletely harvested before snowfall. Some grain crops lay in the swath unharvested all winter, and voles multiplied in the grain beneath the snow. Greatly increased numbers of breeding Long-eared Owls appeared in each of the following springs, together with increased numbers of Short-eared Owls (Asio flammeus) and Northern Harriers (Circus cyaneus). In 1960, there was a striking increase in the numbers of breeding pairs of Long-eared Owls (73 nestlings banded), Short-eared Owls (68 nestlings) and Northern Harriers (25 nestlings). In 1960, productivity of the Great Horned Owl peaked in concert that year with the ten-year peak of the Snowshoe Hare (Houston 1960).

In the spring of 1969, banders capitalized on a recurrence of high vole numbers to band 195 Long-eared Owl nestlings, 104 Short-eared Owl nestlings and 202 Northern Harrier nestlings (Houston 1997). Long-eared Owl sightings by members of the Saskatoon Nature Society also peaked dramatically in 1969, reaching levels four to ten times higher than any year before or since (Figure 1 *in* Houston 1997).

Although not as widely spread as in 1959 and 1968, occasional fields of grain lay unharvested at first snowfall in the fall of 1996. In the subsequent spring, 1997, voles were common, based on direct observation and anecdotal reports. Some days on Highway 6 south of

TABLE 3. Long-eared Owl life table.

Age	Number
+0>1	67
1–2	17
2–3	8
3–4	4
4–5	2
5–6	2
6–7	1
7–8	0
8–9	2
9–10	0
10-11	1
15-16	1
Total	105

119 band encounters 10 inadmissible, because alive when recaptured; 4 excluded, because skeleton (code how found, 50) or 98 (band only), after one year. 105 records available for life table.

Regina, voles crossed the highway in such numbers that vehicles left a patchwork of dead voles on the asphalt surface. The three mouse-eating raptors that year showed only modest increases in banding of nestling Long-eared Owls (18), Short-eared Owls (15), and Northern Harriers (23). Fifteen of these Long-eared Owls were on the Marten J. Stoffel (MJS) dairy farm raptor study area immediately north of Saskatoon, a rectangle 8 km east to west and 13 km north to south. Here MJS had found no nesting Long-eared Owls in 1998, one pair with four young in 1999, and an unprecedented density of 36 pairs of breeding Long-eared Owls, one pair per 2.9 km², in 2000 (Stoffel 2001).

Are irruptions synchronous?

Unlike Great Horned Owls, whose 10-year cycle tends to be roughly synchronous across much of North America (Houston 1987), peak years for Long-eared Owls appeared to vary widely between localities. At Duluth, D. L. Evans banded 172 Long-eareds in 1978 and 163 in 1981, and mist-netted more than 100 during migration in three other years, 1980, 1986 and 1990. At Whitefish Point, Michigan, the overwhelming peak year was 1981. At Cedar Grove, Wisconsin, the peak year was 1982, whereas Erdman's station near Oconto, Wisconsin, had peak numbers in 1977. At Camden, New Jersey, the peak year was 1988, and at Braddock Bay, New York, the peak years were 1993 and 1994.

How pronounced are cycles?

A casual glance at Figure 1 offers only weak support for a ten-year cycle. However, analysis by James R. Duncan (Manitoba Natural Resources, personal communication) showed 14 minor peaks and hence 13 between-peak-periods (BPP). He found four "2-yr BPPs," 5 "3-yr BPPs," and four "4-yr BPPs." Thus, the mean and coincidentally, the mode BPP was 3

years. Further, Evans' Figure 6, in Marks et al. 1994, shows a four-year cycle of incomplete molt.

Numbers banded at migration stations, where annual effort is more consistent than in itinerant travels to locate nests containing young, showed a continuing decline in Long-eared Owls captured. Apart from banding, there is also suggestive evidence for declines in California, Indiana, Maryland, Minnesota, New Jersey, Pennsylvania, and South Dakota, but not for western Montana (Holt 1997). This suggestion of a gradual decline, even better documented for Short-eared Owls from Breeding Bird Survey data, is somewhat at odds with the locally high numbers seen in Saskatchewan in 2000.

Discussion

Long-eared Owl numbers in Saskatchewan fluctuate in relation to vole numbers; during seven years these owls virtually disappeared from major portions of the province. This was not the case in western Montana or southwestern Idaho, where they were found year-round, including winter, every year, especially in sheltered valleys. On Denver Holt's study area north of Missoula, Long-eared Owls were present and banded every year since 1987, although there was some fluctuation in numbers and in 2 of 15 years (1993 and 1995) he banded no nestlings. In southwestern Idaho, Helen Ulmschneider (1993, 1994) and John Doremus banded young in successful nests for 12 consecutive years, 1988 through 1999.

What might explain the differences between Saskatoon, Saskatchewan (52°N), where Long-eared Owls do not winter, and Holt's study area (47°N) in Montana? Because both Saskatchewan and Montana have adequate numbers of corvid nests, nest sites are not a limiting factor. Even in extreme southwestern Saskatchewan where there are sheltered wooded valleys, Long-eared Owls rarely remain through Christmas week. In contrast, large winter roosts are encountered in Idaho and Montana and at least some owls from the winter roosts remain to nest (Ulmschneider 1993. 1994; D. W. Holt, personal communication). Owls occupy pastoral inter-mountain valleys in Montana whereas the Saskatoon area is largely a cultivated, wind-swept plain with pastures for dairy cattle and scattered copses of aspen (Populus sp.).

Because vole cycles are known to be more pronounced in northern Fennoscandia than farther south in Europe (Korpimäki and Norrdahl 1991), and Longeared Owls winter farther north in Finland in years of vole abundance (Korpimäki 1994), it is possible that vole fluctuations are more extreme in southern Saskatchewan than in Montana, although I know of no Saskatchewan mammal trapping data to support such an hypothesis. In Finland, there is no time lag between population fluctuations of vole-eating raptors and their prey (Korpimäki 1994).

When Long-eared Owl numbers peaked at or near the top of the ten-year Snowshoe Hare cycle in 1960 and 1969, Great Horned Owls had ample hares to feed their young. In such years, Great Horned Owls had less need to take voles, and perhaps competed less often with Long-eared Owls for that prey base.

What have I learned from this review? Clearly, Long-eared Owls and Short-eared Owls increase when voles increase, and thus are owl equivalents of the Northern Harrier, which Fran Hamerstrom (1986) termed "the hawk that is ruled by a mouse." Apart from its clear relationship to vole numbers, other answers are as yet incomplete:

- 1. Are Long-eared Owls nomadic? Movements of individual banded Long-eared Owls offer tantalizing clues rather than strong evidence in support of nomadism, at least in the northern portions of the range. Full proof of nomadism requires that marked birds that bred in one area be sighted or captured while breeding in another area at a considerable distance. The Northern Saw-whet Owl, for example, appears to settle to breed in areas of high food abundance that it encounters during the nonbreeding season (Marks and Doremus 2000).
- Are peaks synchronized? No. Numbers of Longeared Owls peak in different years at different migration stations.
- Length of cycle? There is "soft" evidence for both three- and ten-year cycles.
- 4. Is there an overall, continuing population decline? Not proven. Evidence from migration stations, especially at Duluth, 1976-1993 (Evans' figure 5 in Marks et al. 1994), suggests yes; Evans (personal communication) informs me that the average of 90 per year banded at his station, 1974-1993, dropped to 31 for 1991-2003. The evident concentrations that appeared in Saskatchewan in three different years do not exclude a long-term, general downward trend in population.

As Marks et al. said in 1994, similar questions "can be answered only by intensive banding and recapture efforts over many years." Here is an opportunity for all banders to band both nestlings and adults whenever possible. Application of readily visible wing tags or satellite radiotelemetry, should funds and miniaturization permit, might prove invaluable. All of us have a great deal yet to learn about this enigmatic and perplexing species.

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Documents Cited (marked * in text)

- Fish & Wildlife Service. 1922-1965. Bird Banding Notes, volumes 1-5 (mimeographed). Bureau of Biological Survey, Washington, District of Columbia and Fish and Wildlife Service, Patuxent, Maryland.
- Klimkiewicz, M. K. 2002. Longevity records of North American birds. Version 2002.1. Patuxent Wildlife Research Center, Bird Banding Laboratory, Laurel, Maryland. http://www.pwrc.usgs.gov/bbl/homepage/long vrec.htm.

Literature Cited

- Hamerstrom, F. 1986. Harrier: Hawk of the marshes. Smithsonian Press, Washington, District of Columbia.
- Holt, D. W. 1997. The Long-eared Owl (Asio otus) and forest management: a review of the literature. Journal of Raptor Research 31: 167-174.
- **Houston, C. S.** 1960. 1960, the year of the owls. Blue Jay 17: 105-110.
- Houston, C. S. 1987. Nearly synchronous cycles of the Great Horned Owl and Snowshoe Hare in Saskatchewan. *In* Biology and conservation of northern forest owls. *Edited by* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre. General Technical Report RM-142. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

- Houston, C. S. 1997. Banding of Asio owls in south-central Saskatchewan. In Biology and conservation of owls of the northern hemisphere. Edited by J. R. Duncan, D. H. Johnson, and T. H. Nicholls. General Technical Report NC-190, U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, Minnesota.
- Korpimäki, E. 1994. Rapid or delayed tracking of multiannual vole cycles by avian predators? Journal of Animal Ecology 63: 619-628.
- Korpimäki, E., and K. Norrdahl. 1991. Numerical and functional responses of kestrels, short-eared owls, and longeared owls to vole densities. Ecology 72: 814-826.
- Leighton, A. L., J. Hay, C. S. Houston, J. F. Roy, and S. Shadick. 2002. Birds of the Saskatoon Area. Saskatchewan Natural History Society Special Publication 23, Regina, Saskatchewan.
- Lincoln, F. C. 1939. The migration of American birds. Doubleday Doran, New York.
- Marks, J. S., and J. H. Doremus. 2000. Are Northern Sawwhet Owls nomadic? Journal of Raptor Research 34: 299-304
- Marks, J. S., D. L. Evans, and D. W. Holt. 1994. Long-eared Owl (Asio otus). In The birds of North America, 133 (24 pages). Edited by A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, District of Columbia.
- Stoffel, M. J. 2001. Long-eared Owl abundance near Saskatoon in 2000. Blue Jay 59: 129-133.
- Ulmschneider, H. M. 1993, 1994. Wintering and nesting site use by Long-eared Owls in the Snake River Birds of Prey Area. Snake River Birds of Prey Area 1993 Annual Report: 318-323; 1994 Annual Report: 292-295.

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