ARE NORTHERN SAW-WHET OWLS NOMADIC?

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ABSTRACT.—The first known nesting of a Northern Saw-whet Owl (*Aegolius acadicus*) in the Snake River Birds of Prey National Conservation Area occurred in a nest box in 1986, 4 yr after nest boxes were constructed in the study area. Occupancy of nest boxes by Northern Saw-whet Owls varied substantially over the next 13 yr (0–8 nests per yr). The number of mice counted on nocturnal surveys fluctuated widely during this same period, and the annual number of Northern Saw-whet Owl nests in the boxes was positively correlated with an index of mouse abundance. Only one of the 52 breeding adults that we banded was recaptured in a subsequent year, and none of the 139 nestlings produced in the boxes was reencountered. A male that we banded at a nest in April 1990 was found dead in British Columbia in January 1993, more than 900 km NNW of our study area. Data from the Bird Banding Laboratory were insufficient to evaluate breeding-site fidelity because few researchers have banded adult Northern Saw-whet Owls at nests. Northern Saw-whet Owls seem to exhibit some of the characteristics associated with nomadism in birds (e.g., high fecundity and low survival), but they differ from typical nomadic species because they do not specialize on cyclic prey. We suggest that Northern Saw-whet Owls are nomadic in some parts of their range, settling to breed in areas of high food abundance that they encounter during the nonbreeding season.

KEY WORDS: *Northern Saw-whet Owl; Aegolius acadicus; nomadism; breeding biology; Idaho.*

Es *Aegolius acadicus* una especie nomada?

RESÚMEN.—El primer registro de un *Aegolius acadicus* en anidación en el área de conservacion del Snake River ocurrió en una caja de anidación en 1986, 4 años después que las cajas fueron construidas en el área de estudio. La ocupación de las cajas por los buhos varió substancialmente en los próximos 13 años. (0–8 nidos por año). El número de ratones contabilizados de noche fluctúo ampliamente durante este mismo período y el número anual de nidos de buhos en cajas fue positivamente correlacionado con el índice de abundancia de ratones. Solo uno de los 52 adultos en reproducción anillado, fue recapturado y ninguno de los 139 pichones producidos en las cajas de anidación fue reencontrado. Un macho que fue anillado en el nido en abril de 1990 fue encontrado muerto en Columbia Británica en enero de 1993, a mas de 900 km NNW, del area de estudio. Los datos del laboratorio de anillacion fueron insuficientes para evaluar la fidelidad al territorio de reproducción debido a que pocos investigadores han anillado adultos de *Aegolius acadicus* en los nidos. *Aegolius acadicus* parece mostrar algunas de las características asociadas con el nomadismo en las aves (e.g., alta fecundidad y baja sobrevivencia), pero difieren de las especies nómadas típicas debido a que no se especializan en una presa cíclica. Sugerimos que los buhos son nómadas en parte de su rango, estableciéndose para reproducirse en áreas de alta abundancia de comida que encuentran durante la estación no reproductiva.

[Traducción de César Márquez]

The raptors nesting in the Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho have been under intensive study since the mid-1970s (USDI 1979). Through 1985, six species of owls were known to nest in the area: Barn Owl (*Tyto alba*), Western Screech-Owl (*Otus kennicottii*), Great Horned Owl (*Bubo virginianus*), Burrowing Owl (*Athene cunicularia*), Long-eared Owl (*Asio otus*), and Short-eared Owl (*A. flammeus*). The first three species are permanent residents in the NCA, the Burrowing Owl is a typical migrant, and the two species of *Asio* are year-round residents in some years and migrants in others (J.S. Marks and J.H. Doremus pers. obs.).

The first known nest of a Northern Saw-whet Owl (*Aegolius acadicus*) in the NCA occurred in a nest box in 1986, 4 yr after boxes were constructed in the study area. In marked contrast to the six species of owls that occur regularly in the NCA, the presence of nesting Northern Saw-whet Owls varied substantially over the next 13 yr (0–8 nests per yr). This variation in numbers, combined with a nearly complete lack of recaptures of adults, led us to speculate that Northern Saw-whet Owls are nomadic in the NCA.

Many species of birds exhibit strong breeding-site fidelity, remaining in or returning to the same breeding places year after year (Andersson 1980). Site fidelity may be adaptive because it allows individuals to learn the best places to feed, nest, and avoid predators, which in turn may enhance the ability of territory holders to attract mates (Hinde 1956, Greenwood and Harvey 1976, Greenwood 1980). Nomadism (i.e., lack of breeding-site fidelity) in birds is much less common than site fidelity and tends to be restricted to species that feed on cyclic prey or for which environmental variation (e.g., periodic rains) results in large fluctuations in the availability of suitable breeding habitat (Andersson 1980, 1981).

The classic examples of nomadism in birds come from boreal seedeaters such as finches and crossbills that move large distances in response to changing availability of beechmast and conifer seeds (Newton 1972). In owls, nomadism is best known in vole specialists such as Boreal Owls (*Aegolius funereus*), Long-eared Owls, and Short-eared Owls (Wallin and Andersson 1981, Village 1987, Korpimäki and Norrdahl 1991), although documentation of the same individuals breeding in vastly different locations is rare. Several female Boreal Owls have been captured at nests more than 500 km apart in different years (Wallin and Andersson 1981, Korpimäki et al. 1987), but the extent of nomadism in this species varies widely among populations, and individuals may remain on the same home ranges for two or more years in succession (Korpimäki et al. 1987, Hayward et al. 1993). In short, compared with "classic" nomadism exhibited by boreal seedeaters, the owl species noted above seem to be "periodically" nomadic.

The Northern Saw-whet Owl is common in forested habitats across the northern United States and southern Canada. Despite its abundance, relatively little is known about its breeding biology (Cannings 1993). In this paper, we present data to suggest that Northern Saw-whet Owls are nomadic in southwestern Idaho. If we are correct, then our study birds would constitute the only known example of nomadism in a strigid that does not specialize on cyclic prey.

STUDY AREA AND METHODS

We studied breeding Northern Saw-whet Owls in the NCA in southwestern Idaho from 1986–99. The NCA is a shrubsteppe desert dominated by big sagebrush (*Artemisia tridentata*). Compared with typical breeding habitat for Northern Saw-whet Owls (i.e., coniferous forest), trees are scarce and are confined to riparian areas and human settlements. All of the owls that we studied bred in nest boxes placed in willows (*Salix* spp.), Russian olives (*Elaeagnus angustifolia*), and black locusts (*Robinia pseudoacacia*). We set out boxes in pairs (1–40 m apart) beginning in 1981. Since 1986, when Northern Saw-whet Owls first nested in one of our boxes, two or more boxes have been available at 25–47 sites each year along 95 linear km of the Snake River and its tributaries.

To assess the availability of small mammals, we conducted nocturnal surveys in the NCA each spring from 1984–94 (see Marks et al. 1989). With the aid of a spotlight, observers in a slowly moving vehicle counted all "mice" seen along 547–709 km of secondary roads. Based on these surveys, we calculated an index of mouse numbers by dividing the total number of mice seen by the total length of roads surveyed each year. No surveys were conducted after 1994.

We captured breeding female owls in nest boxes during the brood-rearing period and caught males at night in mist nets set in front of the boxes. We determined the sex of adults by the presence (females) or absence (males) of an incubation patch. Adults were weighed, measured, and banded at first capture, and nestlings were banded about a week before they left the nest.

We used partial correlation analysis to assess the relationship between the mouse index (log transformed) and the number of owl nests in the boxes and to see whether the number of Northern Saw-whet Owl nests was correlated with the number of Western Screech-Owl nests. All tests were one-tailed because we predicted that numbers of nesting owls of both species would be positively correlated with the mouse index. Similarly, we predicted that the number of nesting Northern Saw-whet Owls would be negatively correlated with the number of nesting Western Screech-Owls in the boxes because Western Screech-Owls are permanent residents in the NCA, and their body mass is two to three times that of Northern Saw-whet Owls (J.S. Marks and J.H. Doremus unpubl. data).

RESULTS

The number of Northern Saw-whet Owl nests in our boxes varied considerably among years, ranging from zero to eight ($\bar{x}$ = 2.7 ± 3.09 [±SD]) (Table 1). In contrast, Western Screech-Owls nested in the boxes every year (range 4–13), and the number of nests per year was larger ($\bar{x}$ = 8.8 ±

Table 1. Number of Northern Saw-whet Owl and Western Screech-Owl nests in boxes in the Snake River Birds of Prey National Conservation Area, 1984–99. Pairs of nest boxes were available at 25–47 sites each year. The number of adult Northern Saw-whet Owls captured at nests each year is in parentheses.

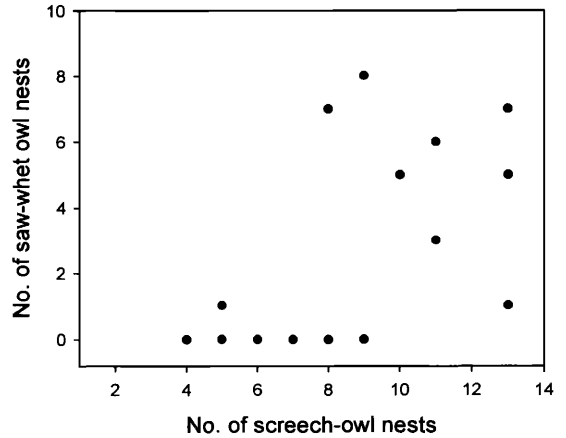| YEAR	NORTHERN SAW-WHET OWL	WESTERN SCREECH-OWL
1984	0	7
1985	0	5
1986	1	5
1987	7 (11)	8
1988	0	4
1989	0	6
1990	8 (11)	9
1991	6 (10)	11
1992	7 (5)	13
1993	1	13
1994	0	8
1995	5 (6)	13
1996	3 (4)	11
1997	0	8
1998	0	9
1999	5 (5)	10

Figure 1. Relationship between the number of Northern Saw-whet Owl nests in boxes and the number of Western Screech-Owl nests in boxes, Snake River Birds of Prey National Conservation Area, 1984–99. Only 15 points are shown because two were identical.

2.93) and less variable than that of Northern Saw-whet Owls (Table 1). Rather than the negative relationship that we expected, the number of Northern Saw-whet Owl nests in the boxes was positively correlated with the number of Western Screech-Owl nests in the boxes each year (partial $r = 0.58$, $N = 16$, $P = 0.038$; Fig. 1). Indeed, in several cases Northern Saw-whet Owls nested in boxes within occupied Western Screech-Owl territories. Thus, the presence of Western Screech-Owls appeared to have no negative effect on yearly fluctuations in the number of Northern Saw-whet Owl nests in the boxes.

The number of mice counted during nocturnal surveys also varied substantially from year to year (Table 2). The years with the highest mouse numbers tended to coincide with the highest numbers of nesting Northern Saw-whet Owls in the boxes (Tables 1, 2), and the number of Northern Saw-whet Owl nests was positively correlated with the mouse index during the years that we had data on small mammals (partial $r = 0.69$, $N = 11$, $P = 0.013$; Fig. 2a). In contrast, no significant correlation existed between the mouse index and the

number of Western Screech-Owl nests in the boxes (partial $r = -0.28$, $N = 11$, $P = 0.21$; Fig. 2b).

We caught 52 adult Northern Saw-whet Owls (29 females, 23 males) at the 43 nests that we monitored (Table 1). Only one returned to breed in a subsequent year, a female that nested in boxes 360 m apart in 1990 and 1991. A male that bred successfully in the study area in 1990 was found freshly

Table 2. Results of nocturnal spotlight surveys for small mammals in the Snake River Birds of Prey National Conservation Area, 1984–94 (no surveys were conducted after 1994).

YEAR	MICE[a]	SURVEY LENGTH (km)	MICE/km
1984	2	547	0.004
1985	30	547	0.055
1986	4	547	0.007
1987	293	612	0.479
1988	20	612	0.033
1989	43	709	0.061
1990	146	700	0.208
1991	24	604	0.040
1992	47	603	0.078
1993	15	660	0.023
1994	21	659	0.032

[a] Total number counted on surveys each year. "Mice" includes *Perognathus parvus, Onychomys leucogaster, Peromyscus maniculatus, Reithrodontomys megalotis,* and *Microtus montanus.*
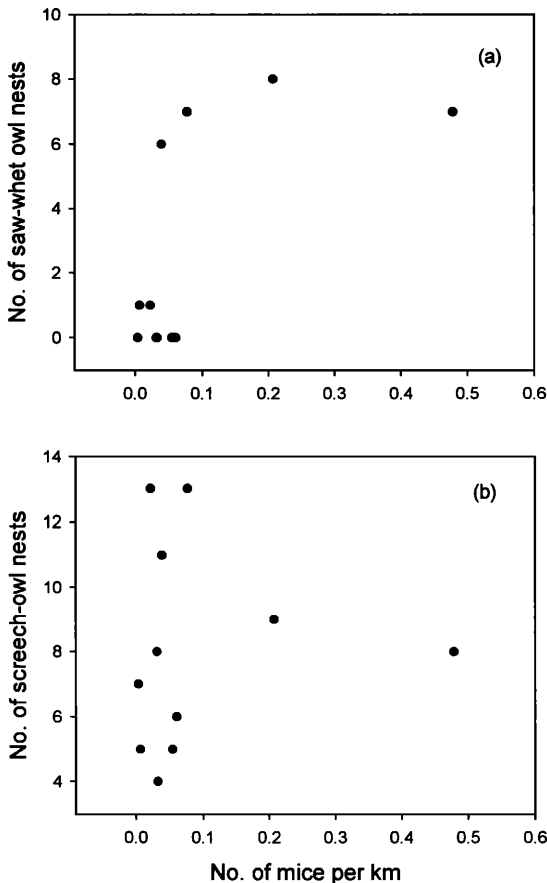
Figure 2. Relationship between the mouse index and the number of Northern Saw-whet Owl nests in boxes (a) and the number of Western Screech-Owl nests in boxes (b), Snake River Birds of Prey National Conservation Area, 1984–94.

dead in British Columbia in January 1993, approximately 920 km NNW of the NCA. No other adults that we banded in the study area have been reencountered, nor have we reencountered any of the 139 nestlings produced in the boxes. Nesting success was rather high, with 29 of 42 nests (69%; one nest was not monitored completely) producing one or more young that survived to leave the nest ($\bar{x}$ = 3.3 young per nesting attempt and 4.8 per successful nest).

In contrast to the situation with Northern Saw-whet Owls, we made hundreds of recaptures of adult Western Screech-Owls, which occupied their breeding territories year-round (indeed, once a Western Screech-Owl settles on a breeding site, it

typically remains there for life). Western Screech-Owl nests were not confined to boxes; some occurred in natural cavities in trees and cliffs, and one pair nested in an old Black-billed Magpie (*Pica hudsonia*) nest (J.S. Marks and J.H. Doremus pers. obs., Marks 1983). We have never found a Northern Saw-whet Owl nest anywhere in the NCA except in a nest box, nor have we heard males singing from tree groves that did not contain a box. Thus, we suspect that few Northern Saw-whet Owls nest in sites other than our boxes.

DISCUSSION

The Northern Saw-whet Owls that we studied appeared to be nomadic. Turnover among breeding adults was high, and no juveniles were known to have returned to the study area to breed. The best evidence for nomadism would be the capture of marked individuals at widely separated breeding sites in different years. Such evidence is absent from banding records, although we note that the banding data are not ideal for assessing breeding-site fidelity.

Our review of the 1276 reencounters (through August 1999) of Northern Saw-whet Owls in the database of the USGS Bird Banding Laboratory showed that less than 3% were of birds banded during the breeding season, and we found no records of birds banded at a nest in one year and recaptured at a distant site in a subsequent breeding season. Indeed, aside from the instance we documented in the NCA, the only known cases of breeding-site fidelity in Northern Saw-whet Owls have come from British Columbia, where 5 of 36 breeding adults (two females, three males) banded over an 8-yr period returned to the same or adjacent territories in subsequent years (Cannings 1993).

Predatory birds that exhibit nomadism typically feed on cyclic prey, and in theory they should produce large clutch sizes, reproduce at one year of age, and have high juvenile survival and low adult survival (Andersson 1980). Northern Saw-whet Owls in the NCA have high fecundity (typical clutches contain 6–7 eggs, which is at the high end of the range of clutch sizes for the continent; Cannings 1993), but they do not specialize on cyclic prey. Rather, their diet consists of a mixture of house mice (*Mus musculus*), harvest mice (*Reithrodontomys megalotis*), montane voles (*Microtus montanus*), and deer mice (*Peromyscus maniculatus*) (Marks and Doremus 1988, Rains 1997). The abun-

dance of these prey species in the NCA varies unpredictably rather than in a cyclic pattern. Elsewhere in the range of Northern Saw-whet Owls, vole populations can be cyclic. However, voles seldom comprise a major portion of the diet during the breeding season (Marks and Doremus 1988, Swengel and Swengel 1992, Cannings 1993). Northern Saw-whet Owls probably reproduce at one year of age, but the age of first breeding is not known for wild birds (Cannings 1993). In addition, little is known about annual survivorship of adults or juveniles, although adult survival appears to be low (ca. 50%; Cannings 1993). Thus, Northern Saw-whet Owls exhibit some of the characteristics of nomadic species, but they differ fundamentally from typical nomads in that they do not specialize on cyclic prey.

Nomadism in owls has been documented most thoroughly in the Boreal Owl (e.g., Wallin and Andersson 1981, Löfgren et al. 1986, Korpimäki et al. 1987). Male Boreal Owls in Fennoscandia tend to remain on their territories year-round, whereas females are more likely to disperse between breeding sites, especially during lows in the vole cycle (Löfgren et al. 1986, Korpimäki et al. 1987). Nomadism and site fidelity have been documented in both sexes of Boreal Owls in Idaho, but the tendency toward nomadism is strongest in females (Hayward et al. 1993:33–35). Thus, unlike the situation in the NCA, where both sexes of Northern Saw-whet Owls almost never display site fidelity, nomadism in Boreal Owls is confined mostly to females and occurs in some years but not others.

Aside from our study population, the only previous hints that Northern Saw-whet Owls are nomadic have come from studies of vocal activity in Colorado (Palmer 1987) and Wisconsin (Swengel and Swengel 1995). In the Colorado study, annual changes in the number of singing birds corresponded with changes in the numbers of voles in the area. In Wisconsin, nightly surveys conducted in late winter and early spring over a 10-yr period revealed a fairly strong 4-yr "cycle" in the amount of singing by adults. Swengel and Swengel (1995) noted that the vole cycle was a possible explanation for the pattern in vocal activity that they observed. Neither study involved finding nests and trapping adults, however, so it is difficult to determine the extent to which changes in vocal activity translate to actual changes in the presence of breeding birds.

Lacking the proof that would be provided if our birds had been captured outside of the NCA in subsequent breeding seasons, two alternative hypotheses could explain the apparent lack of site fidelity that we observed. First, the NCA may be a "sink" in which Northern Saw-whet Owls have low annual survival relative to those nesting elsewhere. We have no way to test this hypothesis, but the presence of one of our males in Canada three years after breeding in the NCA, and the apparently high reproductive success of Northern Saw-whet Owls in our study area (see Cannings 1993), argue against the notion that these birds constitute a sink population. Second, we may have failed to detect adults that returned to breed in the NCA because they used natural cavities. We have not conducted systematic surveys of tree cavities throughout the NCA, but as noted above, we have never heard Northern Saw-whet Owls singing in areas that did not contain nest boxes. We suspect that few owls nest in natural sites relative to the number that use our boxes. Nonetheless, it is possible that we have missed some nests in natural sites and that site tenacity by Northern Saw-whet Owls is more prevalent in the NCA than we believe.

If we are correct in our assertion that Northern Saw-whet Owls are nomadic in southwestern Idaho, then these birds would constitute the first known case of nomadism in a species of owl that does not specialize on cyclic prey. Given the apparent geographic variation in nomadism exhibited by Boreal Owls (Korpimäki et al. 1987), it is likely that the incidence of nomadism in Northern Saw-whet Owls varies geographically. The shrubsteppe desert of southwestern Idaho is not typical breeding habitat for Northern Saw-whet Owls. Indeed, without the presence of nest boxes, we suspect that few Northern Saw-whet Owls would breed in our study area. Northern Saw-whet Owls have probably wintered in the NCA for many years, but the availability of nest boxes has only recently made the area suitable for nesting. We suggest that Northern Saw-whet Owls are nomadic in some parts of their range, settling to breed in the same areas in which they winter or migrate during years when food availability is high. Long-term banding efforts at nests, coupled with monitoring of prey availability, will be necessary to thoroughly address the question of nomadism in Northern Saw-whet Owls.

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