

egg laying. Acta XVII Congr. Int. Ornithol. 1129-1135.

SEEL, D. C. 1968. Clutch-size, incubation and hatching success in the House Sparrow and Tree Sparrow *Passer* spp. at Oxford. Ibis 110: 270-282.

WITSCHI, E. 1935. Seasonal sex characters in birds and their hormonal control. Wilson Bull. 47: 177-188.

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Polygyny in the Northern Saw-whet Owl

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Although owls are generally thought to be monogamous (Korpimäki 1988), polygyny has been reported in eight species in Europe (see Watson 1957, Scherzinger 1968, Koenig 1973, Schönfeld and Girbig 1975, Korpimäki 1983, Solheim 1983, Norgall 1985, Lehtoranta 1986, Sonerud et al. 1987). The incidence of polygyny appears rare, however, for all species but the Boreal Owl (*Aegolius funereus*; Carlsson et al. 1987; Korpimäki 1988, 1989).

We report two cases of polygyny for the Northern Saw-whet Owl (*Aegolius acadicus*), including the first apparent case of trigyny known for any owl species. We followed Korpimäki (1988) in inferring polygyny when the same male feeds two or more females (or their young) at different nests at which no other male is detected. We assumed in such cases that the male mated with the females. Given the territorial behavior of cavity-nesting owls (pers. obs.), this assumption is reasonable.

Case 1: Snake River, southwestern Idaho.—The Snake River Birds of Prey Area (BOPA) is a shrubsteppe desert dominated by big sagebrush (*Artemisia tridentata*) and is not typical Northern Saw-whet Owl breeding habitat (Marks and Doremus 1988). Trees are scarce, and most are too small to provide owl nesting cavities.

Beginning in 1982, nest boxes were placed in trees as part of an ongoing study of Western Screech-Owls (*Otus kennicottii*). The first Northern Saw-whet Owl nest known for the BOPA occurred in one of these boxes in 1986. Twenty-six pairs of boxes (paired boxes placed 1-40 m apart) were available in 1987. On 14 March, female Northern Saw-whet Owls were incubating in seven of these boxes. Three nests were very close together: two were in paired boxes 15-m apart and the third was 130 m away. Males were captured at all nesting sites between 22 and 29 March. Four

nests were attended by different males in what appeared to be monogamous relationships. At the three close nests, however, we repeatedly captured and observed the same owl, which we marked in the center of the forehead with a dot of blue paint. This male was captured at both of the paired boxes on 22 March and carried food to all three nests on 12 April. He provisioned young at two of the nests until at least the end of April. No other male was seen or heard near these boxes. We believe this to be a case of trigyny, the first reported for any species of owl.

Nest boxes of the four monogamous pairs ranged from 265 m to >4 km apart. The first eggs hatched on 31 March, 2 April, and 6 April at three monogamous nests, and on 25 March and 9 April at two trigynous nests. A monogamous clutch of seven eggs was vandalized and failed to hatch. The other three monogamous nests produced 2, 4, and 5 fledglings from clutches of 5, 6, and 7 eggs, respectively. The 7-egg clutch from one of the trigynous nests failed to hatch (the eggs were added). The other two nests produced 5 fledglings each from clutches of 5 and 6 eggs. Thus, the trigynous male produced 10 fledglings vs. a mean of 3.7 fledglings for the monogamous males (vandalized nest excluded). The trigynous male weighed 80 g on 22 March, and 76 g on 25 April. Of two monogamous males, one weighed 76 g (24 March) and the other 78 g (29 March); on 25 April, they weighed 73 and 77 g, respectively. These differences in mass loss between trigynous and monogamous males were slight.

Breeding Northern Saw-whet Owls in the BOPA fed almost exclusively on mice (Marks and Doremus 1988). Mice were unusually abundant near owl nests during 1987 (we saw and heard many), and nocturnal spotlight transects conducted each spring from 1984 to 1988 showed that 1987 was a peak year for mice (Table 1).

Case 2: Vaseux Lake, south-central British Columbia.—The Vaseux Lake area, characterized by open ponderosa pine (*Pinus ponderosa*)/Douglas fir (*Pseudotsuga*

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menziesii) forest, is more typical of Northern Saw-whet Owl nesting habitat than is the BOPA. Since 1986, 19 nest boxes have been available to owls.

During 1987, Northern Saw-whet Owls nested in three boxes at Vaseux Lake and in three boxes 30 km to the south. On 27 May, a male was captured and banded while delivering food to four young at a nest box (Nest 1). On 1 June, a second Northern Saw-whet Owl nest (Nest 2), containing three young, was discovered in a box 800 m from Nest 1. The male was captured delivering food to Nest 2 on 20 June, and was the same male that had provisioned young at Nest 1. Based on the probable ages of young when the nests were found, we estimated that hatching dates at nests 1 and 2 were separated by ca. 21 days. The nests of the bigynous male fledged at least 6 young vs. a mean of 3.75 fledglings/male at 4 monogamous nests in 1987. The bigynous male weighed 73.5 g on 27 May and 76 g on 20 June.

Breeding Northern Saw-whet Owls in the Vaseux Lake area fed primarily on deer mice (*Peromyscus maniculatus*; Cannings 1987). Prey remains at the bigynous nests were predominately deer mice (61%), but also included 23% voles (*Microtus* spp.). The monogamous nest at Vaseux Lake also had a relatively high proportion of voles in 1987 (28%). Voles made up only 6% of the prey remains at monogamous nests in similar habitats in 1985 and 1986 (Cannings 1987). The high proportion of voles at the three Vaseux Lake nests implies that voles were abundant.

Oring (1982) identified two preconditions for the evolution of polygamy. First, multiple mates, or the resources necessary to attract them, must be economically defensible. Second, individuals must be able to exploit this potential. Emlen and Oring (1977) coined the term "environmental potential for polygamy" (EPP) to identify the influence of environmental factors on the spatial and temporal distribution of resources critical for obtaining mates. The EPP is highest when limiting resources (e.g. nesting sites and food) are clumped in time and space, and when mates settle asynchronously. The EPP may also increase if the adult sex ratio departs strongly from unity.

We believe that several factors contributed to a high EPP on these study areas. First, the presence of nest boxes created an abundance of high-quality nesting sites. This was especially important in the BOPA, where natural cavities were rare and where nesting sites were clumped because boxes were set out in pairs. Second, small rodents were abundant in the BOPA and appeared to be locally abundant at Vaseux Lake. And third, females mated to the same male settled asynchronously. The egg-laying dates were separated by 15–21 days. Under these conditions, two male owls obtained multiple mates and produced more than twice the mean number of fledglings produced by monogamous males. Males experienced little

TABLE 1. Number of mice counted on nocturnal spotlight transects in the Snake River Birds of Prey Area, mid- to late May 1984–1988.

Year	Mice ^a (n)	Transect 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

^a Includes *Perognathus parvus*, *Onychomys leucogaster*, *Peromyscus maniculatus*, *Reithrodontomys megalotis*, and *Microtus montanus*.

change in body mass (the Vaseux Lake male gained mass), which implies that polygyny is an energetically viable reproductive strategy for Northern Saw-whet Owls, at least during years when food and nesting sites are abundant.

Although we had no data on adult sex ratios, Korpimäki (1989) found high rates of polygyny (11%) in Boreal Owls during years with an excess of males. Thus, a female-biased sex ratio is not requisite for polygyny in *Aegolius* owls.

The Northern Saw-whet Owl is congeneric with the Boreal Owl, the only owl species in which polygyny is common. As seems to be the case with Northern Saw-whet Owls, polygyny in the Boreal Owl occurs only during peak rodent years and in areas where nest sites are increased artificially (Korpimäki 1983, 1989; Solheim 1983; Carlsson et al. 1987). The interval between initiation of primary and secondary nests averages 13–23 days (Solheim 1983, Carlsson et al. 1987, Korpimäki 1989), which agrees closely with the intervals for Northern Saw-whet Owls. Unlike Northern Saw-whet Owls, polygynous male Boreal Owls tend to be polyterritorial, with primary and secondary nests typically separated by 1–3 km (Korpimäki 1983, 1989; Solheim 1983; Carlsson et al. 1987). Indeed, Carlsson et al. (1987) and Korpimäki (1988, 1989) suggest that some male Boreal Owls practice the "deception strategy" (Alatalo et al. 1981), where secondary females are unable to assess correctly the mating status of their mates. We do not know whether the Vaseux Lake male maintained two territories. This clearly was not the case in the BOPA, where one male maintained simultaneous pair bonds with three females that nested within 130 m of each other. The latter case suggests a fundamental difference between Northern Saw-whet Owls and Boreal Owls in the way some males obtain multiple mates.

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LITERATURE CITED

- ALATALO, R. V., A. CARLSON, A. LUNDBERG, & S. ULFSTRAND. 1981. The conflict between male polygyny and female monogamy: the case of the Pied Flycatcher *Ficedula hypoleuca*. *Am. Nat.* 117: 738-753.
- CANNINGS, R. J. 1987. The breeding biology of Northern Saw-whet Owls in southern British Columbia. Pp. 193-198 in *Biology and conservation of northern forest owls: symposium proceedings* (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, Eds.). U.S. For. Serv. Gen. Tech. Rep. RM-142.
- CARLSSON, B.-G., B. HÖRNFELDT, & O. LÖFGREN. 1987. Bigyny in Tengmalm's Owl *Aegolius funereus*: effect of mating strategy on breeding success. *Ornis Scandinavica* 18: 237-243.
- EMLÉN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215-223.
- KOENIG, L. 1973. Das aktionsystem der Zwergohreule. *Z. Tierpsychol. Beih.* 13: 1-124.
- KORPIMÄKI, E. 1983. Polygamy in Tengmalm's Owl *Aegolius funereus*. *Ornis Fennica* 60: 86-87.
- . 1988. Factors promoting polygyny in European birds of prey: a hypothesis. *Oecologia* 77: 278-285.
- . 1989. Mating system and mate choice of Tengmalm's Owls *Aegolius funereus*. *Ibis* 131: 41-50.
- LEHTORANTA, H. 1986. Lapinpöllöjen *Strix nebulosa* lähekkäinen pesintä. *Lintumies* 21: 32.
- MARKS, J. S., & J. H. DOREMUS. 1988. Breeding-season diet of Northern Saw-whet Owls in southwestern Idaho. *Wilson Bull.* 100: 690-694.
- NORGALL, T. 1985. Bigamie bei der Waldohreule (*Asio otus*). *Vogelwelt* 106: 193-194.
- ORING, L. W. 1982. Avian mating systems. Pp. 1-92 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- SCHERZINGER, W. 1968. Bemerkenswerte paarbildung beim Waldkauz (*Strix aluco*). *Egretta* 11: 56.
- SCHÖNFELD, M., & G. GIRBIG. 1975. Beiträge zur Brutbiologie der Schleiereule unter besonderer Berücksichtigung der Abhängigkeit von der Feldmausdichte. *Hercynia* 12: 257-319.
- SOLHEIM, R. 1983. Bigyny and biandry in the Tengmalm's Owl *Aegolius funereus*. *Ornis Scandinavica* 14: 51-57.
- SONERUD, G. A., J. O. NYBO, P. E. FJELD, & C. KNOFF. 1987. A case of bigyny in the Hawk Owl *Surnia ulula*: spacing of nests and allocation of male feeding effort. *Ornis Fennica* 64: 144-148.
- WATSON, A. 1957. The behaviour, breeding and feeding ecology of the Snowy Owl. *Ibis* 99: 419-462.

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Costs to Northern Orioles of Puncture-ejecting Parasitic Cowbird Eggs from their Nests

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The brood parasitic *Molothrus* cowbirds lay eggs with shells that are more than 30% thicker than would be predicted from their volume (Hoy and Ottow 1964, Blankespoor et al. 1982, Spaw and Rohwer 1987). Picman (1989) has shown that two special features—the thick shells and spherical shape—of the eggs of Brown-headed Cowbirds (*Molothrus ater*) contribute about equally in making their eggs about twice as strong as those of other icterids. Three hypotheses—resistance to laying damage (Lack 1968), resistance to accidental damage by the attending host (Blankespoor et al. 1982), and resistance to puncture-ejection (Spaw and Roh-

wer 1987)—have been proposed to explain the unusually strong shells of the eggs of some parasitic cuckoos and of the *Molothrus* cowbirds. Resistance to damage at laying may be important to cuckoos that parasitize hosts with very small nests. In such cases cuckoos sometimes drop their eggs into the hosts' nests from an elevated position. Damage to the hosts' eggs, but not to the strong-shelled cuckoo eggs, has been reported in such layings (e.g. Gaston 1976).

Molothrus cowbirds almost always parasitize hosts whose nests permit the female cowbird to settle fully into them before laying. Neither the accounts of cow-