Parus montanus, and consequences for reproductive success. Anim. Behav. 48:1143-1154.

- RYTKÖNEN, S., K. KOIVULA, AND M. ORELL. 1990. Temporal increase in nest defence intensity of the Willow Tit (*Parus montanus*): parental investment or methodological artifact? Behav. Ecol. Sociobiol. 27:283-286.
- RYTKÖNEN, S., M. ORELL, AND K. KOIVULA. 1993. Sex-role reversal in Willow Tit nest defence. Behav. Ecol. Sociobiol. 33:275–282.

Rytkönen, S., M. Orell, and K. Koivula. 1995.

Pseudo Concorde fallacy in the Willow Tit? Anim. Behav. 49:1017–1028.

- SOKAL, R., AND ROHLF, F., J. 1981. Biometry. Freeman, San Francisco.
- SONERUD, G. A. 1985. Brood movements in grouse and waders as defence against win-stay search in their predators. OIKOS 44:287-300.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, p. 136–179. *In* B. Campbell [ed.], Sexual selection and the descent of man. Aldine Publishing Company, Chicago.

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RENESTING BY SPOTTED OWLS¹

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Key words: Renesting behavior; Spotted Owl; Strix occidentalis; Great Horned Owl; Bubo virginianus; Barred Owl; Strix varia.

Spotted Owls (*Strix occidentalis*) typically begin courtship in late February or early March and lay eggs in late March or April. Nest success is high in most years (typically 70–90%). Nest failures occur for a variety of reasons, including abandonment or breakage of eggs, predation on eggs or young, collapse of nest structures, and mortality of adults (Forsman et al. 1984; Forsman, unpubl. data). Documented cases of renesting after nest failure are rare. We found only two confirmed cases, one in New Mexico (Kroel and Zwank 1992) and one in Oregon (Lewis and Wales 1993). Here we describe three cases of renesting by Spotted Owls in Washington, and present information on the frequency of renesting by Spotted Owls on four study areas in Oregon and Washington.

The three cases of renesting by wild Spotted Owls included one in 1992 on the east slope of the Cascades Range, and two in 1994 on the Olympic Peninsula. In all three cases, the nesting birds were banded and were being monitored as part of a long-term demographic study. Two of the pairs were comprised of adult birds (3+ years old) and one pair included an adult female and 2-yr-old male.

In all three cases, pairs were initially confirmed as nesting in early April (range = 3-7 April). Nest failure occurred sometime between 3-29 April. In two cases, nest failure was confirmed based on the presence of broken eggshells found in the nest or on the ground under the nest. In the third case, two eggs were seen in the nest, and then disappeared without a trace. Cause of nest failure was undetermined in all three cases.

In all three cases, females moved to a new nest after the first nest failed. Distances between the original nests and new nests were 0.35, 0.40 and 1.0 km. Renesting was initiated between 25 April and 12 May. These dates were based on sightings of females going into new nests or by estimating egg-laying dates based on plumage development of juveniles observed at the new nests (Forsman 1981). Although we were not sure of exact dates when second clutches were initiated, it appeared that the minimum and maximum period between failure and initiation of a new clutch was about 14 and 30 days, respectively. Renesting produced two young at one site (estimated fledging date 15 July) and one young at another site (fledging date 6 July). At the third site, a single fledgling was found dead below the new nest on 13 July.

The three cases of renesting described above were the only instances of renesting observed in 221 cases of apparent nest failure on our study areas in Washington and Oregon between 1985–1994 (Table 1). This suggests that renesting occurred about 1.4% of the time after an initial failure. This estimate of renesting rate should be considered only an approximation, because some cases of apparent nest failure could have been cases where pairs acted like they were nesting but never actually laid eggs. It is also possible that some cases that were labeled as nest failures were actually cases where juveniles fledged, but were killed before being confirmed.

Our observations, and those of Lewis and Wales (1993) and Kroel and Zwank (1992) suggest that re-

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Study area	Years	Failures	Renesting attempts	Renesting frequency (%)
Olympic, Washington	1987–1994	47	2	4.2
Cle Elum, Washington	1989–1994	19	1	5.3
Roseburg, Oregon	1985–1994	126	0	0.0
Siuslaw, Oregon	1990–1994	29	0	0.0
Total		221	3	1.4

TABLE 1. Number of nest failures and renesting attempts of Spotted Owls on four demographic study areas in Washington and Oregon.

nesting by Spotted Owls occurs relatively infrequently. We suspect that renesting is rarely observed for three reasons. One is that juvenile Spotted Owls have a relatively long period of parental care, typically from the time they hatch in late April or May until August or September of their first summer. Late nesting attempts could put juveniles at a disadvantage since they would be relatively inexperienced and underdeveloped when parental care begins to taper off in late summer. The latest date that we have seen juvenile Spotted Owls leaving the nest is 15 July, which would indicate a laying date of approximately 20 May, assuming that owlets spent 35 days in the nest after an incubation period of 30 days (Forsman et al. 1984). The long period of juvenile dependency in Spotted Owls has likely resulted in selection for a pattern of hormone production that allows egg production during a relatively brief period each year (March to mid-May). Thus, for renesting to occur, failure would have to occur relatively early in the nesting season when there is still time for hormone levels to rebound to levels necessary for egg production.

A second factor that probably accounts for the paucity of renesting attempts by Spotted Owls is that females generally lose weight during the incubation period, and unless nest failure occurs early in incubation and in a year of high prey abundance, most females are probably so physiologically stressed that they lack the necessary energy reserves to produce a second clutch. This was suggested by the fact that the three cases of renesting that we observed occurred in years when the majority of pairs were breeding (Forsman, unpubl. data). Southern (1970) noted that renesting in Tawny Owls (*Strix aluco*) occurred only in years when prey levels were high.

The third factor that could account for the small number of reported cases of renesting by Spotted Owls is that renesting can only be confirmed if the identity of the female is known. Thus, renesting is likely to be documented only in demographic studies where females are uniquely marked with color bands and numbered leg bands.

Movement to a new nest tree after a nest failure would be an expected response if failure was caused by predation on eggs or if the initial nest proved unsuitable. For example, one of the nests that failed on the Olympic Peninsula was an exposed platform in which the female and eggs were clearly visible from the ground and from surrounding trees. Such nests are rare on the Olympic Peninsula, where heavy rainstorms are frequent during March and April. After the platform nest failed, the female moved into a cavity nest that offered much greater protection from the elements and from predators.

Although renesting attempts by Spotted Owls appear to be infrequent, it is possible that monitoring programs like ours may underestimate the frequency of renesting. The main source of bias would occur if females renested but did not change nest trees. In these cases it is possible that renesting attempts could not be differentiated from pairs that simply initiated late clutches (Lewis and Wales 1993). We have yet to confirm a case where renesting occurred in the same nest tree as the original attempt.

Renesting appears to be a fairly common response by owls and diurnal raptors to clutch loss during early incubation. Bent (1938), who collected eggs from numerous pairs of Barred Owls (Strix varia), reported that they would sometimes lay a second clutch 3-4 weeks after their initial clutch was removed. In rare cases they produced a third clutch after the second was removed. Although Bent did not specify at what stage in incubation the eggs were removed, we presume they were collected early in incubation. Wolfe (1912) and Sclater (1912) reported renesting by Great Horned Owls (Bubo virginianus) following egg collection, including one female that was reputed to have laid successive clutches of four, three, and two eggs. In the latter case, the female changed nests each time her nest was robbed. Although they presented no details, Fry et al. (1988) reported renesting by Spotted Eagle Owls (Bubo africanus), Long-eared Owls (Asio otus), and African Wood Owls (Strix woodfordii). Bull and Henjum (1990:6) reported renesting by three female Great Gray Owls (Strix *nebulosa*), including two that renested after losing eggs and one that renested after losing nestlings. Renesting occurred 17-20, 28, and 30 days after failure, respectively.

Newton (1979:121) noted that many species of diurnal raptors may renest if their first clutch "... is lost at an early stage. Much depends on latitude, and a given species may lay one or more replacement clutches during the longer season in the south of its range, but not in the north." He also reported that the interval between loss of the first clutch and initiation of a second clutch was typically around two weeks for small and medium-sized raptors, and somewhat longer in large raptors. The interval between loss of the first clutch and initiation of a second was found to be consistently 14 days in the Peregrine Falcon (*Falco peregrinus*) and Gyrfalcon (*Falco rusticolus*) (Cade and Temple 1977), Platt 1977, and averaged 29.4 days for Bald Eagles in Florida (Wood and Collopy 1993). The relatively consistent interval between loss of a first clutch and initiation of a second in raptors is likely controlled by changes in hormone levels (e.g., prolactin) that cause ovulation to cease after incubation begins (Welty 1982). After an initial clutch is lost, it apparently takes a minimum of 1–3 weeks for hormone levels to change enough to stimulate ovulation of a second clutch.

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LITERATURE CITED

- BENT, A. C. 1938. Life histories of North American birds of prey. Part 2. Smithsonian Institution U.S. Natl. Mus. Bull 170.
- BULL, E. L., AND M. G. HENJUM. 1990. Ecology of the Great Gray Owl. USDA For. Serv. Gen. Tech. Rept. PNW-GTR-265.
- CADE, T. J., AND S. A. TEMPLE. 1977. The Cornell University falcon programme, p. 353–369. *In Proc.* International Council For Bird Preservation, World Conf. on Birds of Prey, Vienna.
- FORSMAN, E. D. 1981. Molt of the Spotted Owl. Auk 98:735-742.

The Condor 97:1080-1083 © The Cooper Ornithological Society 1995

- FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87.
- FRY, C. H., S. KEITH, AND E. K. URBAN. 1988. The birds of Africa, Vol. III. Academic Press, London.
- KROEL, K. W., AND P. J. ZWANK. 1992. Renesting of Mexican Spotted Owl in southern New Mexico. J. Raptor Res. 26:267-268.
- LEWIS, J. C., AND B. C. WALES. 1993. Northern Spotted Owl pair successfully renests. J. Field Ornithol. 64:323–325.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.
- PLATT, J. B. 1977. The breeding behavior of wild and captive Gyr Falcons in relation to their environment and human disturbance. Ph.D.diss., Cornell Univ., Ithaca, NY.
- SCLATER, W. L. 1912. A history of the birds of Colorado. Witherby, London.
- SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. London 62:197–285.
- WELTY, J. C. 1982. The life of birds. Saunders College Publishing, New York.
- WOLFE, R. 1912. The Western Horned Owl in western Kansas. Oologist 29:222-224.
- WOOD, P. B., AND M. W. COLLOPY. 1993. Effects of egg removal on Bald Eagle productivity in northern Florida. J. Wildl. Manage. 57:1–9.

REPERTOIRES, TERRITORY SIZE AND MATE ATTRACTION IN WESTERN MEADOWLARKS¹

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Key words: Western Meadowlarks; Sturnella neglecta; *repertoires; signature songs; territories; mating status.*

Male Western Meadowlarks (*Sturnella neglecta*) are conspicuous in their singing activity as they establish and defend their chosen territories (Lanyon 1957). Meadowlark females arrive only after the males have begun this process of defense (Lanyon 1956). The song delivery of a male Western Meadowlark consists of a repertoire of discreet, stereotypical song types, each of which is repeated several times before switching to another (Miller 1952, Falls and Krebs 1975). Each male sings between three and 12 song types, about one third of which are shared by neighboring birds (Horn 1987). The individual song types do not carry different messages (Horn and Falls 1988), nor are they associated with specific behaviors (Horn and Falls 1991). However, the action of switching song types within a repertoire in itself apparently conveys a message that the territory is being actively defended (Falls and d'Agincourt 1982). This is evidenced by the fact that switching is more rapid during boundary defense activity than before or afterward (Horn and Falls 1991).

Several investigators have tested the association between song delivery and territory control in a variety of avian species. Yasukawa (1981) showed that Redwinged Blackbird (*Agelaius phoeniceus*) repertoires conferred an advantage over single song-types in territory defense. Krebs et al. (1978) suggested that in the Great Tit (*Parus major*) large repertoires were more effective than small ones in keeping out intruding males. Correlations between repertoire size and territory size have been found to exist in several species, including the Great Tit (Krebs 1977b), the Northern Mockingbird (*Mimus polyglottos*; Howard 1974), and the Redwinged Blackbird (Yasukawa et al. 1980). Female use of repertoire clues has also been investigated. Catch-

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