

- DUNN, E., & I. L. BRISBIN JR. 1980. Age-specific changes in the major body component and caloric values of Herring Gull chicks. *Condor* 82: 398-401.
- FITZPATRICK, L. C., C. G. GUERRA, & R. E. AGUILAR. In press (a). Reproductive energetics in the desert-nesting seagull *Larus modestus*. *Estud. Oceanol.*
- , ———, & T. L. KING. In press (b). Sex determination in Gray Gulls *Larus modestus* using external measurements and discriminant analysis. *Estud. Oceanol.*
- GUERRA, C. G., B. E. AGUILAR, & L. C. FITZPATRICK. 1988. Water vapor conductance in Gray Gull *Larus modestus* eggs: adaptation to desert nesting. *Col. Waterbirds* 11: 107-109.
- , & M. A. CIKUTOVIC. 1983. Un nuevo sitio de nidificación para la garuma *Larus modestus* (Aves, Charadriiformes: Laridae). *Estud. Oceanol.* 3: 13-20.
- , & L. C. FITZPATRICK. 1987. Albinism in the Gray Gull *Larus modestus* in northern Chile. *Le Gerfaut* 77: 275-279.
- , ———, R. E. AGUILAR, & G. S. LUNA. In press (a). Location and characterization of new nesting sites for Gray Gulls *Larus modestus* in the Atacama Desert, northern Chile. *Le Gerfaut*.
- , ———, ———, & B. J. VENABLES. In press (b). Reproductive consequences of El Niño-Southern Oscillation in Gray Gulls *Larus modestus*. *Col. Waterbirds*.
- HARRIS, M. P. 1970. Breeding ecology of the Swallow-tailed Gull, *Creagus furcatus*. *Auk* 99: 236-242.
- HARRISON, P. 1983. Seabirds, an identification guide. Boston, Houghton Mifflin Co.
- HOWELL, T. R., B. ARAYA, & W. R. MILLIE. 1974. Breeding biology of the Gray Gull, *Larus modestus*. Univ. Calif. Berkeley, Pub. Zool. 104.
- LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.
- NICE, M. M. 1962. Development of behavior in precocial birds. New York, Trans. Linn. Soc.
- O'CONNOR, R. 1984. The growth and development of birds. New York, A. Wiley-Interscience Publ.
- RICKLEFS, R. E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48: 879-983.
- . 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 117-201.
- . 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Stud. in Avian Biol.* 8: 84-94.
- . 1984. The optimization of growth rate in altricial birds. *Ecology* 65: 1602-1616.
- , S. C. WHITE, & J. CULLEN. 1980. Energetics of postnatal growth in Leach's Storm-Petrel. *Auk* 97: 566-575.
- SCHREIBER, E. A., & R. W. SCHREIBER. 1980. Breeding biology of Laughing Gulls in Florida. Part II: Nesting parameters. *J. Field Ornithol.* 51: 340-355.
- SCHREIBER, R. W. 1976. Growth and development of nestling Brown Pelicans. *Bird Banding* 47: 19-39.

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Molt of Primaries and Age Determination in Tengmalm's Owl (*Aegolius funereus*)

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In Tengmalm's Owls (*Aegolius funereus*) which are partly nomadic and band recovery rates are low (e.g. Löfgren et al. 1986, Korpimäki et al. 1987), banding is inadequate for age determination. Some European owls (Strigiformes) molt all primaries annually, while Tengmalm's Owls take more than 1 yr to replace primaries of the juvenile plumage (Glutz von Blotzheim and Bauer 1980, Ginn and Melville 1983, Haarhaus 1983). At 1 yr, Tengmalm's Owls in Germany molt an outermost primary group; at 2 yr, a neighboring middle group; at 3 yr, normally the 7-8 outermost primaries for the second time. They commonly do not molt the 2 innermost primaries until 4 or 5 yr (Glutz von Blotzheim and Bauer 1980: 538; referring to B. Kondratzki and R. Altmüller). While there must be

deviations from this pattern from the third year, it should be possible to use the molt pattern to age the owls (Schwerdtfeger 1984).

We investigated the possibility of aging Tengmalm's Owls in northern Sweden from postmolt records. We investigated the pattern of molt in relation to age and sex, and the timing of molt relative to breeding and season. These data are a prerequisite for accurate aging from postmolt records.

We studied birds north of Umeå in northern Sweden (about 64°N, 20°E) in the middle and northern boreal zone (Ahti et al. 1968). The breeding biology of Tengmalm's Owl has been studied here since 1980 (Löfgren et al. 1986, Carlsson et al. 1987). The breeding season is variable and laying dates range from early March until mid-June (Carlsson et al. 1987, Hörnfeldt et al. unpubl.). We followed molt in both captive and wild birds.

We studied 8 captive 1-yr-old owls (collected as nestlings in 1984) and 3 birds when 2 yr old (in 1985-

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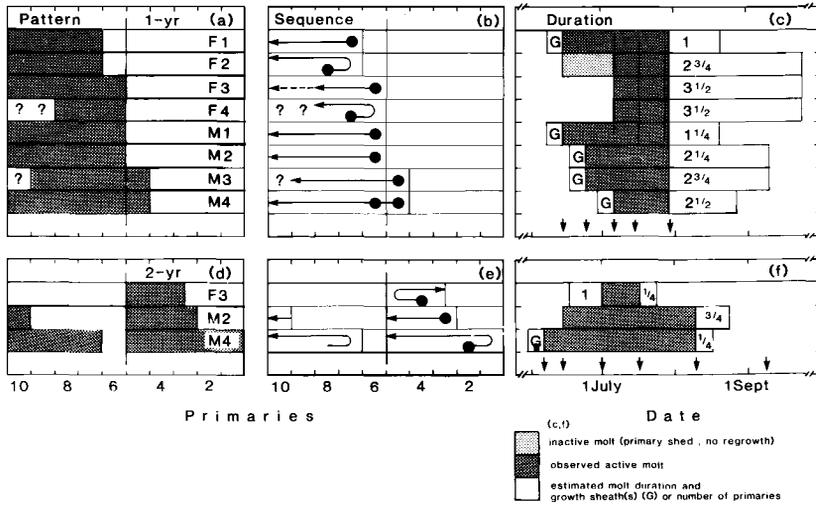


Fig. 1. Pattern, sequence, and duration of primary molt in 1-yr-old (a-c) and 2-yr-old (d-f) captive Tengmalm's Owls (females, F1-4 and males, M1-4). Pattern of molt (a, d) indicated by shaded bars; '?' denotes molt assumed but not observed. Sequence of molted primaries (b, e) illustrated by arrows from first shed primaries (filled circle); broken arrow denotes unknown relative sequence. Duration of molt (c, f) is shown by bars. Vertical arrows (c, f) show inspection dates.

1986). They were held in an outdoor aviary and provided daily with food *ad libitum*. In mid-August 1985, 4 adult owls (F1, F4, M1 and M3; Fig. 1) were killed by a predator. Another female (F2) died in late 1985.

Wild 1-yr-old females were heavier than males during breeding (139-236 g [$n = 107$] vs. 98-128 g [$n = 42$], respectively), and we sexed the aviary birds as 4 females (F1-4; 148-158 g) and 4 males (M1-4; 101-127 g). In 1985 1 female (F4) started laying in late April and reared two owlets. Two other unsuccessful clutches were laid by other females.

Molt was inspected every 1 or 2 weeks from the first half of June until the end of July in 1985 and early September in 1986. Molt stage of primaries in all birds was scored according to a 0-5 scale (0 = old; 1 = shed and missing; 2 = growth sheath, unbroken; 3 = growth sheath with vane $< \frac{1}{2}$; 4 = growth sheath with vane $\frac{1}{2}$ - $\frac{3}{4}$; and 5 = growth sheath with vane $> \frac{3}{4}$ of full length). In addition, the length in mm of growing primaries was estimated. Primaries (P1-10) were numbered from the body (Ginn and Melville 1983). Shed primaries (with primary and bird number) were collected during daily feeding visits in 1985.

We studied wild birds during breeding in 1983-1987 and in autumn 1984-1986. Breeding females were caught in nest boxes; males, when feeding the female or nestlings (Löfgren et al. 1986). In autumn, owls were trapped with mist nets. Birds were sexed only if they had been banded as breeders.

We recorded molt stage as in aviary birds and classed full grown primaries according to their relative age as judged from their darkness (darkest primaries being

last molted) and wear. We defined progressive molt as when at least 2 primaries were missing or growing. A single, asymmetrically missing or growing primary could have been accidentally lost and replaced outside the ordinary molt season (Ginn and Melville 1983).

We used the records from 1983-1986, representing about 400 females and 220 males to time molt. About 25% of the females and 10% of the males were inspected more than once in the same year. We calculated laying date in breeders by backdating (Carlsson et al. 1987). Laying-incubation period of the first egg was taken as 4 weeks and post-hatching period as the next 7 weeks.

We estimated individuals' start of molt in captive owls (first primary shed) and termination (regrowth completed) from the stage when first and last seen in molt (Fig. 1c, 1f). At the onset of molt we added 1 week for unbroken or just broken growth sheaths (vane ≤ 5 mm). This was the condition 4-7 days after the shed primaries were recovered for 2 males in early molt. For later stages of molt, we first calculated the average regrowth time (to nearest number of whole days) per pair of primaries in individual birds. During observed molt, inclusive of period added for sheath stage, regrowth time/primary pair ranged from 16-19 days in females and 9-16 days in males in 1985. In F3, it was 16 and 13; in M2, 16 and 12; and in M4, 9 and 8 days in 1985 and 1986, respectively. Estimates of primary regrowth time were multiplied by the number of early or late regrown primaries in individual birds (assuming that all birds molted the out-

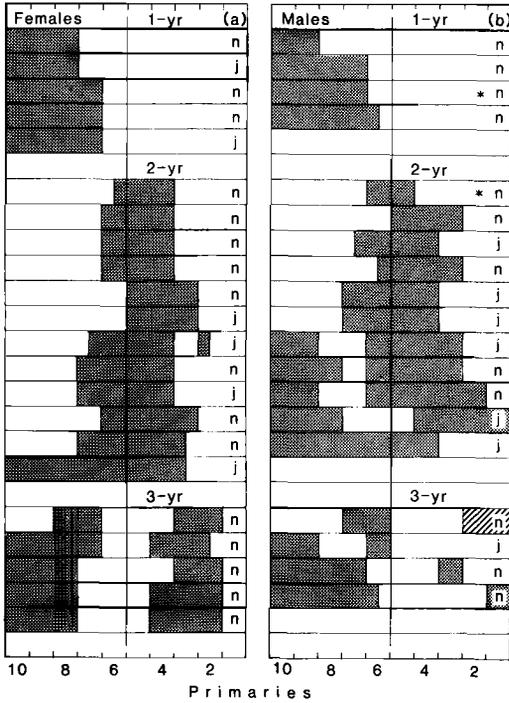


Fig. 3. Primary molt (shaded bars) according to postmolt records (autumn or following spring) in wild known-age Tengmalm's Owls banded as nestlings (n) or juveniles (j). Asterisks refer to the same male. Hatched bar represents primaries that could have been molted at age 3 yr but were regarded as molted at age 2 yr.

if possible. Molt did not overlap laying in females. The later laying dates in 1984 compared to 1985 were associated with later molt in both sexes (Fig. 2). Further, earlier onset of molt in the aviary in 1986 than in 1985 (Fig. 1c, 1f) was associated with absence of laying and older age in 1986. Molt was prevented at least during laying presumably because of energetic constraints.

Our data, as those in Glutz von Blotzheim and Bauer (1980), show that the juvenile primary generation was successively replaced in a variable number of molts (Figs. 1a, 1d; and 3a, 3b). Individuals started to molt primary groups from a variable point, but most of them had a descending (from the body) pattern and only occasionally molted from a point towards the body (ascending) (*sensu* Ginn and Melville 1983; Figs. 1b, 1e; and 4a, 4b). Because the molt season is restricted to summer, nonmolting owls during most of the year can be aged according to postmolt records of molted primaries.

In aviary birds, all old primaries were of the same dark shade at first inspection in 1985. The 1-yr molt had only just begun in 3 of the birds (Fig. 1c). Among

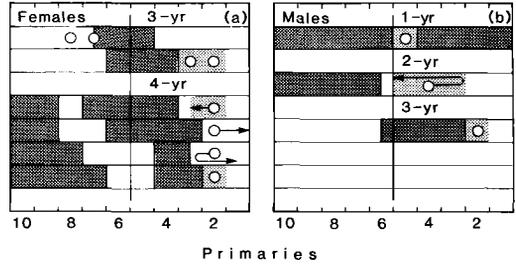


Fig. 4. Molt of wild Tengmalm's Owls. Primaries currently molting are shown by circles or, if sequence was ascertained, circle and arrow from first shed primary. Heavy shade indicates primaries molted in the previous year. Unmolted primaries are unshaded; primaries of unknown status are lightly shaded. Present age was inferred from previous year's pattern as established in known-age birds (see Fig. 3a, 3b).

wild birds banded as nestlings, 7 females and 5 males breeding at age 1 yr and 2 unsexed birds in their first autumn had primaries which were all of the same type. Consequently, owls with all primaries of the same type should be categorized as juveniles. Adults may molt all primaries in the same year. Such occurrences, however, must be very rare and have negligible practical importance. We had no such observations and very few individuals molted 9 primaries in 1 season (e.g. Fig. 5a, 5b).

At age 1 yr, an outermost primary group was molted. It ranged in number from 2-6 (Figs. 1a; 3a, 3b; and 3 unsexed birds in autumn). Glutz von Blotzheim and Bauer (1980) reported 3-6 primaries, $\bar{x} = 4.3$.

Molt was still in progress in all aviary birds on 30 July 1985. By then all except 3 birds (F3, F4, and M3) had shed the outermost primaries. When F3 was checked in 1986, however, she had molted P9-10 at age 1 yr later in 1985. It is reasonable to assume that F4 and M3 also proceeded until P10 was molted. Assuming this, 1-yr-old females molted an average of 4.5 primaries, males averaged 5.5 (Fig. 1a). These values exceed those in wild birds (Fig. 3a, 3b). Wild birds of unknown age which had molted a variable number of the outermost primaries (and showed only 1 other primary age-class) showed bimodal frequency distributions with respect to number of molted primaries (Fig. 5). This suggested that birds of different age were included in our sample. The minima between peaks of the distributions were at 6 primaries in both sexes. The lower frequency distributions corresponded to the range of molt in 1-yr-old birds, and we regarded these birds as 1-yr-olds. These females most commonly molted 4 primaries and males molted 4 or 5. Birds molting more than 6 primaries presumably were older than 1 yr (see below). Although we scored some older birds for the 1-yr pattern (13 out of 55 birds at age 2+ to 6+ yr), 85% (11 out of 13) were identified

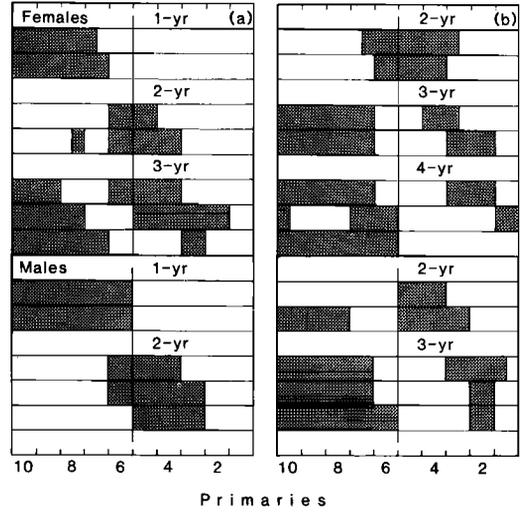
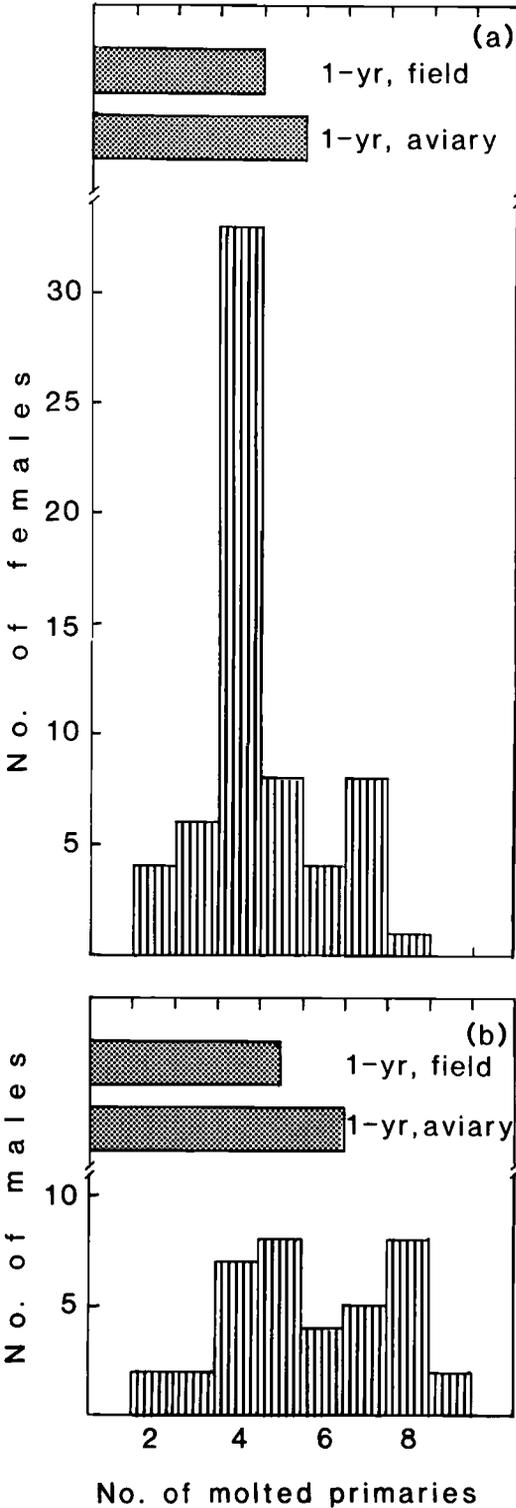


Fig. 6. Successive primary molts (a-b) in wild individuals of Tengmalm's Owls according to postmolt records (shaded bars). Age was inferred from the pattern in (a) of molt in known-age birds (see Fig. 3a, 3b).

from signs of earlier molts. Presumably both females and males that molted an outermost group of up to 6 primaries and exhibited only one other kind of primary should be aged as having passed their 1-yr molt (being 1-2-yr-old).

At age 2 yr, females, and about half the males, typically molted a middle primary group (referred to as the basic 2-yr pattern) (Figs. 1d; and 3a, 3b). This group neighbored the 1-yr group (Fig. 6a, 6b; F3 in Fig. 1a, 1d, and male denoted by asterisk in Fig. 3b). Pooled data for 1984-1985 suggested that 2-yr-old females ($n = 38$) and males ($n = 11$) molted within the range of P3-P8 and P3-P7, respectively. Number of primaries molted ranged from 1.5-4.5 in both sexes.

The basic 2-yr pattern was repeated by some older birds (3 out of 44 birds at age 3+ to 6+ yr), but we recognized 2 of 3 of these birds from signs of earlier molts. We suggest that birds of both sexes could be aged as passed their 2-yr molt (being 2-3 yr old) if

Fig. 5. Frequency of wild Tengmalm's Owls with a variable number of the outermost primaries last molted and with only 1 other primary age class. Eleven females with asymmetric molt were scored for the larger number. Horizontal bars represent the largest extension of molt observed at age 1 yr in owls from the field and aviary, respectively. Data refer to postmolt records as observed in spring (1984-1985). Sample size: 64 females (a), 38 males (b).

TABLE 2. Classification of wild Tengmalm's Owls of unknown age into common molt patterns, corresponding to those observed in known-age birds. Data refer to primaries last molted (if not stated otherwise). Absolute age is inferred for pattern 1-3, and minimum age for pattern 4-7.

| Pattern of molted primaries | Females | | Males | |
|--|----------------------------------|----------|----------------------------------|----------|
| | Inferred age (yr) | <i>n</i> | Inferred age (yr) | <i>n</i> |
| 1. All of same (juvenile) type | 0-1 | 26 | 0-1 | 18 |
| 2. Outermost (1-yr) group, max. 6 primaries (no sign of earlier molt) | 1-2 | 13 | 1-2 | 11 |
| 3. Middle (2-yr) group (only other sign of molt refers to the 1-yr pattern) | 2-3 | 15 | 2-3 | 5 |
| 4. Gap-separated inner and outermost group, ^a ranging 7-9 outermost primaries | 3 ⁺ to 4 ⁺ | 22 | 2 ⁺ to 3 ⁺ | 16 |
| 5. Outermost group, 7-9 primaries | 3 ⁺ to 4 ⁺ | 2 | 2 ⁺ to 3 ⁺ | 11 |
| 6. Gap-separated innermost and outermost group ^a | 3 ⁺ to 4 ⁺ | 3 | 2 ⁺ to 3 ⁺ | 7 |
| 7. Diverse, but P1 (at least 1) molted in last or next last molt | 3 ⁺ to 4 ⁺ | 9 | 2 ⁺ to 3 ⁺ | 16 |
| Uncertain | | 10 | | 16 |

^a One of the groups may be only one primary pair.

they showed the basic 2-yr pattern and in addition exhibited no earlier sign of molt than the 1-yr pattern.

In contrast to Glutz von Blotzheim and Bauer (1980) we found that 2-yr old males showed the basic pattern as often as an extension of this pattern. These extensions represent a continuum from a middle, inner, or innermost group, separated by a gap, and an outermost group to a large outermost group (>6 primaries; Figs. 1d, 3b, and 6b). These patterns resemble those at age 3 yr (Figs. 3b and 6b) and were hard to distinguish objectively. These males, at maximum, should be aged as having molted at age 2⁺ yr and are 2⁺ to 3⁺ yr old. Such birds should include those which last molted a large outermost group (7-9 primaries) or 2 nonneighboring primary groups, and those which have molted P1.

A single female, inferred as 2 yr old, was scored for the outermost 7.5 primaries (Fig. 3a). This deviation was highly unlikely and the record may have been incorrect. If this pattern occurred at the 2-yr molt in females, we would reasonably have observed individuals with a gap. Until there is more evidence, we will not consider this pattern as characteristic for 2-yr molt in females.

According to Glutz von Blotzheim and Bauer (1980), German owls (sex not given) at age 3 yr molted 7-8 of the outermost primaries, sometimes with a gap for P6-P7. We observed the latter in known 3 yr olds (Fig. 3a) and refer to it as the basic female 3-yr pattern. Since we found both types (within the range of the 7-9 outermost primaries) among birds of unknown age, we believe that the "gapless" pattern occurred infrequently (Table 2). Records before and after inferred 3-yr molt imply that the middle primary group which molted at age 2 yr was not usually molted at age 3 yr (Fig. 6a, 6b). If molt is suspended in a late stage and molt sequence is descendant, which seems likely (e.g. male M4 in Fig. 1d and Haarhaus 1983), an outer and not an outermost group of molted primaries may be expected (Fig. 3a). Females at inferred

4-yr molt all showed different patterns with repetition of the 1-yr and of the basic female 3-yr pattern (Fig. 6b). P1 was molted for the first time in some females (Figs. 4a and 6b). Molt of P1 is normal at age 4 or 5 yr (Glutz von Blotzheim and Bauer 1980). The successive molts of a female in captivity, however, suggested molt of P1 at the age of 3 yr (Haarhaus 1983). Females of unknown age, molting innermost and outermost primary groups (Table 2), represent a minor variant of the basic 3-yr pattern (cf. Haarhaus 1983) or alternatively had molted at the age of 4 yr (suggested by molt of P1). Because 3- and 4-yr patterns are difficult to distinguish, our recommendation is to assign females as having molted at the age of 3⁺ yr (being 3⁺ to 4⁺ yr old). These females include those who last molted the 7-9 outermost primaries (inclusive of gap) or an innermost and outermost group and those who have molted P1.

Males in our sample on average molted more primaries and replaced the juvenile plumage faster than females. This difference may be partly explained if males molt at a higher rate than females, as in aviary birds. Both sexes seemed to molt more primaries in the aviary than in the field. This difference may have been related to the continuous and excessive food available.

To estimate the efficiency of classifying and aging from molt records, we sampled 50 females and 50 males from 1984 and 1985, respectively. We grouped the birds, which were of unknown age, into common molt patterns as observed in known-age birds. Most birds matched a known-age pattern (Table 2). Consequently, we found it reasonable to age 90% of females and >80% of males as either juveniles or as having molted at age 1 yr, 2 yr, 2⁺ yr (males) or 3⁺ yr (females). This method obviously has a great potential for aging.

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LITERATURE CITED

- AHTI, T., L. HÄMET-AHTI, & J. JALAS. 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5: 169-211.
- CARLSSON, B.-G., B. HÖRNFELDT, & O. LÖFGREN. 1987. Bigyny in Tengmalm's Owl (*Aegolius funereus* (L.)): effect of mating strategy on breeding success. *Ornis Scandinavica* 18: 237-243.
- DOLNIK, V. R., & V. M. GAVRILOV. 1980. Photoperiodic control of the molt cycle in the Chaffinch (*Fringilla coelebs*). *Auk* 97: 50-62.
- ERKINARO, E. 1975. Zeitpunkt und Dauer der Mauser des Rauhfusskauzes, *Aegolius funereus*, und der Sumpfohreule, *Asio flammeus*. *Beitr. Vogelkd.* 21: 288-290.
- GINN, H. B., & D. S. MELVILLE. 1983. Moults in birds (BTO Guide 19). Tring, Herts., Maund & Irvine Ltd.
- GLUTZ VON BLOTZHEIM, U. N., & K. M. BAUER. 1980. *Handbuch der Vögel Mitteleuropas*, vol. 9. Wiesbaden, Akademische Verlagsgesellschaft.
- HAARHAUS, D. 1983. Die Grossgefiedermauser paläarktischer Eulen in Gefangenschaft. *Beitr. Vogelkd.* 29: 89-102.
- KORPIMÄKI, E., M. LAGERSTRÖM, & P. SAUROLA. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scandinavica* 18: 1-4.
- LÖFGREN, O., B. HÖRNFELDT, & B.-G. CARLSSON. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus* [L.]) in relation to cyclic food production. *Oecologia* (Berlin) 69: 321-326.
- MASMAN, D., S. DAAN, & H. BELDHUIS. 1986. Energy allocation in the seasonal cycle of the Kestrel, *Falco tinnunculus*. Pp. 185-222 in *The annual cycle of the Kestrel Falco tinnunculus: a study in behavioural energetics* (D. Masman). Ph.D. dissertation, University of Groningen.
- PAYNE, R. B. 1972. Mechanisms and control of molt. Pp. 103-155 in *Avian biology*, vol. 2 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- SCHWERDTFEGER, O. 1984. Verhalten und Populationsdynamik des Rauhfusskauzes (*Aegolius funereus*). *Vogelwarte* 32: 183-200.

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Selectivity and Ecological Consequences of Cavity Nesters Using Natural vs. Artificial Nest Sites

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Secondary cavity nesters will use nest boxes in lieu of tree cavities in managed forests (Bellrose et al. 1964, van Balen et al. 1982). Information on use of artificial vs. natural cavities is fragmentary, but preference for boxes is sometimes observed (e.g. Eadie and Gauthier 1985, Korpimäki 1987). This may indicate variation in quality of nest sites regarding expected reproductive success (van Balen 1984; Nilsson 1984a, b). I observed nest-site choice by breeding birds in northern Arizona and offer an alternate hypothesis for nest-site preference.

I examined occupancy of artificial and natural cavities on 3 8.0-ha study plots in ponderosa pine (*Pinus ponderosa*) forests. I observed 5 species: Violet-green Swallow (*Tachycineta thalassina*), Mountain Chickadee (*Parus gambeli*), White-breasted Nuthatch (*Sitta carolinensis*), Pygmy Nuthatch (*Sitta pygmaea*), and Western Bluebird (*Sialia mexicana*). The plots, referred to as "Dense," "Thinned," and "Open," differed in habitat structures. The Dense plot had 637 live trees/ha (583 Ponderosa pine, 54 Gambel's Oak [*Quercus gambelii*]), and 39 dead trees (total); the Thinned plot had 225 live trees/ha (209 pine, 16 oak) and 21 dead trees; and the Open plot had 69 live trees/ha (57 pine, 12 oak) and 7 dead trees. I installed 60 nest boxes on each plot before the 1980 breeding season (see Brawn and Balda 1983). All boxes were identical except for entrance-hole diameter; half the boxes on each plot

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