Ann. Zool. Fennici 21: 277–281. 1984

The reproductive constraints on moult in the Ural Owl Strix uralensis

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Pietiäinen, H., Saurola, P. & Kolunen, H. 1984: The reproductive constraints on moult in the Ural Owl Strix uralensis. — Ann. Zool. Fennici 21: 277–281.

The moult was studied retrogressively from breeding individuals in 1979–83. The females did not start moulting their wing feathers until in the late nestling period or early fledgeling period. No males were in active moult during the nestling period. The high number of moulted outer primaries in the first and subsequent moults may be adaptive because of the wear of the sound muffling combs on the leading edges of the outer primaries. There was a decreasing trend in the number of moulted primaries and secondaries in the first six moults.

The number of moulted flight feathers decreased from the birds having failed their breeding attempt to those having 1, 2, 3 or 4–5 young. This was explained by the energetic strain of the presumably long fledgeling period. In addition, the Ural Owls moulted more of their flight feathers in those years when only few females laid eggs compared to those years when almost all females laid.

The results suggest that the reproductive output is a severe constraint on moult in the Ural Owl. On the other hand, the energetic needs of the moult may affect the evolution of the timing of the laying period and the age of first breeding.

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1. Introduction

The temporal overlap of breeding and moulting is to be expected in areas where the amount and availability of food fluctuate seasonally (Payne 1972). These conditions are typically found in the northern coniferous (taiga) zone. In this geographical area the time available for reproduction may become another critical factor, especially for birds with a long period of parental care.

The resident bird species of the taiga must gather considerable fat reserves for the winter. All extra energy expenditures, such as moulting, can jeopardize overwintering, if they occur too late in the season (Sylvén 1982). Thus the timing of moult and its intensity is an important aspect in the evolution of life history patterns in birds.

The Ural Owl *Strix uralensis* is an interesting even if laborious, species for long-term life history studies (e.g. Saurola 1980). As the species nests readily in nest-boxes it is feasible to gather moult records from a ringed population over several years.

In 1979 we incorporated the study of moult into our long-term study on the population biology of the Ural Owl. The main problem of this subproject was whether there were any trade-offs between the production of young and the moult of the parent birds. In this article we report results from our studies in 1979–83 and discuss the observed patterns as a part of an evolved reproductive tactic of the species.

2. Material and methods

Feathers wear and fade with use. This characteristic can be used in distinguishing between feather generations in species, such as larger owls, which moult only a part of their feathers annually (Stresemann & Stresemann 1966). Thus it is possible to study the moult retrogressively, as we have done.

We restricted our observations to the primaries and the ten outermost secondaries (1–10). The feathers were numbered beginning from the carpal joint: the primaries outwards and the secondaries inwards. Both wings were studied and scored, so all figures we present represent the sum of both wings. The feathers were classified into "new" and "old" according to their typical appearance.

In 1979-83 we studied 201 (49 males, 152 females) breeding individuals (344 observations). When analysing the data we did not separate between males and females. In 33 cases we were unable to tell if all or none of the feathers were moulted. The difficulties arose if the birds were studied in too bright a sunlight or too late in the evening. The best results were obtained in cloudy weather. All ambiguous cases were omitted from the analyses. 119 individuals were studied only once in the study period, 44 twice, 18 three times, 17 four times and 3 females in each of the five study years.

We denote the age of the bird as follows: the year of birth = 1st year; second spring and summer = 2nd year etc.

3. Results and discussion

3.1. General

The number of annually moulted feathers ranged from 2 to 40. In both the primaries and the secondaries the range was from 0 to 20. So far we have not been able to confirm the absence of wing feather moult in the Ural Owl. Some feathers are moulted almost every year, some can be in use at least for four years (Fig. 1). This may indicate differences in the importance of different feathers for the flight performance.

The gross pattern of moult in the Ural Owl resembles that of the Tawny Owl (Stresemann & Stresemann 1966, Glutz von Blotzheim & Bauer 1981). Certain feather groups seem to be tied together in their moult. The clearest groups are formed by primaries 1-3 and 4-10 (primaries 9 and 10 form an apparent subgroup). In the secondaries the clearest division lies between the 4th and the 5th feather.

No incubating female was in active moult. Only one female had shed two primaries in the late nestling period in May 1983. No males, caught in the nestling period, were in active moult. In two cases non-breeding birds were observed to have shed feathers in May.

According to Payne (1972) the Snowy Owl *Nyctea scandiaca* and Hawk Owl *Surnia ulula* may start moulting shortly after laying has commenced. Unfortunately Payne did not specify whether the species had moulted wing or body feathers. These species have more northern ranges than the Ural Owl, so the time available for their moulting may be shorter and force them to start the moult earlier during their breeding cycle.

The absence of moult in the Ural Owl during the incubation and nestling periods is in contrast with the moult schedule of two sympatric raptors, the Goshawk *Accipiter gentilis* and Common Buzzard *Buteo buteo.*

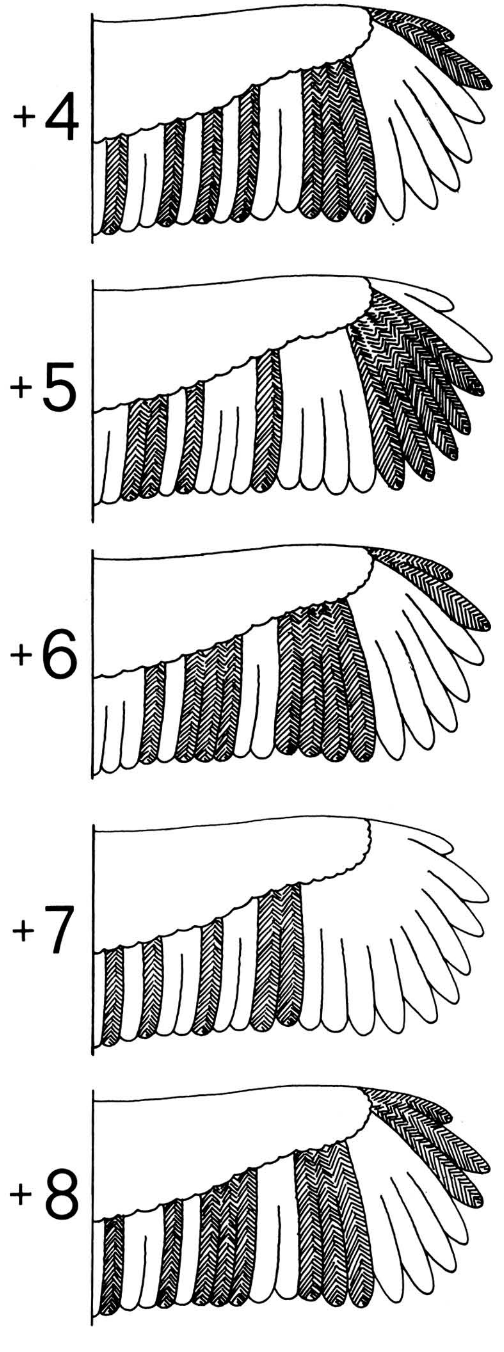

Fig. 1. The moult of the Ural Owl female D-60445 in 1978-82. In 1978 the female was at least 4 calendar years old (+4). The new feathers are shaded.

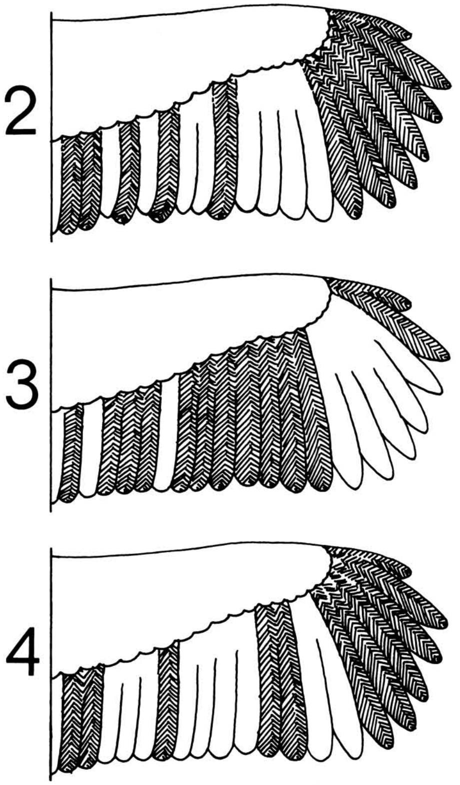

Fig. 2. A generalized presentation of the three first moults of the Ural Owl (age 2, 3 and 4, respectively). The flight feathers are moulted for the first time in the 2nd summer. The new feathers are shaded.

These species start their wing feather moult in the incubation period.

The few museum specimens studied indicate that the moult in the Ural Owl ends in early September.

3.2. The moult in different ages

The first three moults of the Ural Owl are presented schematically in Fig. 2. The high proportion of moulted primaries (always feathers 4–10) in the first wing feather moult (2nd year birds) may have an adaptive function. The owls have comblike projections on the leading edges of the outer primaries, which ensure silent flight (Welty 1964). These combs wear easily because they are not protected by overlaying feathers. The feathers grown in the nestling and fledgeling periods are perhaps of poorer quality than those of the grown-up birds, so the wear may be more pronounced during the first year of life.

In general there are differences in the longevity of different primaries, the outer ones being moulted more often than the inner ones. This is in contrast with the Accipitrids where the moult starts from the first primary and continues outwards. In the North-European eagles the outer primaries are moulted only in the third moult (D. Forsman 1980).

The number of moulted primaries decreases during the first six subsequent moults (Fig. 3). The number of moulted secondaries varies from age to age, but there is a decreasing trend. Between the 8th and the 13th year there seems to be another decreasing "cycle" in the number of yearly moulted primaries or secondaries, but our sample size is too small for definite conclusions to be made; only more data can establish whether the pattern is real.

3.3. Reproduction and moult

In general, reproduction is considered to have an adverse effect on the survival of parents (Williams 1966). The good condition

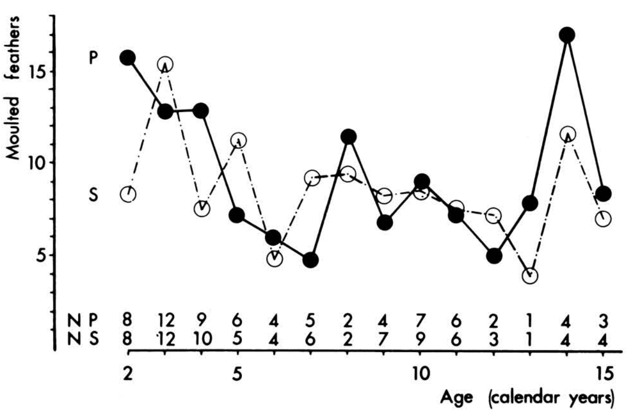

Fig. 3. The number of moulted primaries (P) and secondaries (S) in relation to the age of the bird. N P = number of primary moult observations, N S = number of secondary moult observations.

of the plumage is an important component of the factors promoting survival. The body feathers provide insulation against adverse weather and the condition of the flight feathers affects feeding, especially in raptors preying upon alert prey, such as mammals.

As the Ural Owl is a resident of the cold North it must probably moult all of its body feathers before winter, like the North-American Spotted Owl (*Strix occidentalis*; E.D. Forsman 1981).

There were statistically significant (F = 10.58, P <0.001) differences in the number of moulted flight feathers between birds having failed in their nesting attempt or attending to 1, 2, 3 or 4-5 young (Fig. 4). We did not take into account the birds of unknown age breeding for the first time, or those individuals known to be in their 3rd or 4th year. The non-breeding birds were excluded from the statistical analysis, because the physiological condition of these birds in the beginning of the breeding season may vary more than in the breeding birds. The Ural Owls may skip reproduction because of a poor food situation, being in poor physical condition after a hard winter or, when considering the females, when their mate has died.

The decline in the number of moulted flight feathers with increased reproductive efforts (expressed here by the number of fledgelings) of the parents can be explained by the overlapping fledgeling and moulting periods of the Ural Owl. If we estimate the fledgeling period to be about the same as in the Tawny Owl (about 2.5 months; Southern 1970), the Ural Owl young acquire independence in late August. In the fledgeling period the parent birds must strike a balance between the energy demands of their offspring and their own maintenance (in our study the moult of the flight feathers). Unfortunately we have not yet enough data from large broods in order to analyse the possible survival costs of the diminished number of moulted flight feathers.

The reproductive constraint in the moult may be a factor in the evolution of the age of the first breeding. The Ural Owls may breed successfully in their 2nd year (own observations), but only in the very best food conditions. Generally they start to breed in their 4th or 5th year. We know (Fig. 3) that the proportion of moulted feathers is rather high (60-70%) in the first two moults, when the juvenal feathers are moulted into those of the

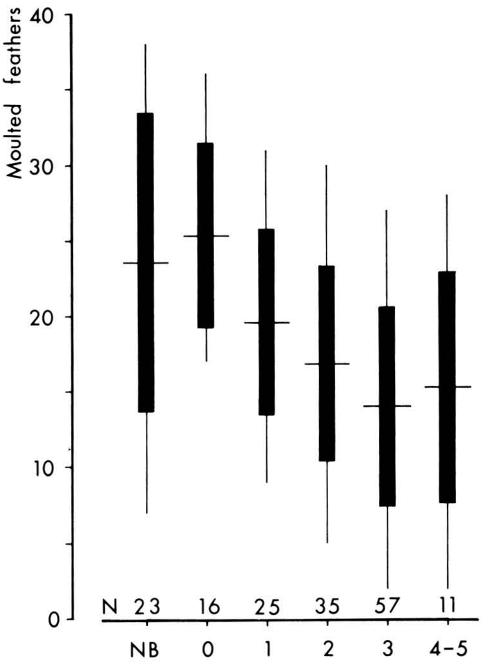

Fig. 4. The number of moulted flight feathers in relation to the breeding status. — NB = no breeding attempt, 0 = failure in breeding, 1 = one young, etc. Horizontal bars indicate mean, narrow vertical bars range and broad vertical bars standard deviation of the sample. N = sample size.

adults. If these moults overlap with breeding, they may cause a decrease in the probability of surviving to the next breeding attempt. Another possibility is that these birds may be in so poor a physical condition the following spring that they cannot start breeding.

As in the Common Buzzard (Sylvén 1982), the Ural Owls must adjust their reproductive efforts and the demands of their own maintenance (moult and autumnal fattening for winter) to the available favourable season. The moult and the autumnal fattening should not co-occur. Thus the schedule of moult can affect the evolution of the timing of the laying period.

Clutches of 3-5 are layed about 10 days earlier than clutches of two, which produce most of the broods containing 1 or 2 fledgelings. However, the former birds, although having more available time, can moult less of their flight feathers than the latter birds starting later and attending to smaller broods.

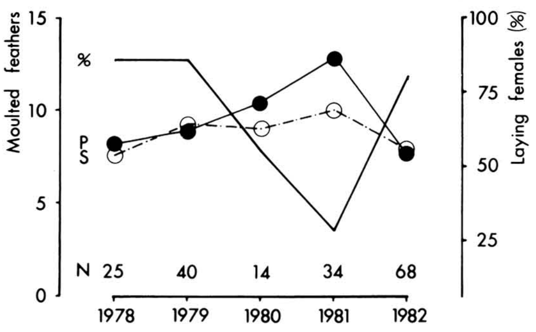

Fig. 5. The number of moulted primaries (P) or secondaries (S) in different years. N = sample size. Percentages indicate the proportion of females laying in each year.

In Fig. 5 we compare the number of moulted primaries or secondaries in different years. The number of Ural Owl pairs in a population attempting to breed follows rather closely the density of small mammal populations (Linkola & Myllymäki 1969). In 1981 when the birds had moulted the highest numbers of primaries and secondaries the proportion of laying females was only 28 %. In general there was an inverse relationship between the proportion of females laying and the total number of moulted flight feathers (r = -0.915, $P < 0.05$). This indicates again that the reproductive efforts diminish the amount of energy allocated to the moult.

Future study years will reveal whether there are any significant survival costs caused by the decreased moult.

Acknowledgements. We thank Juhani Koivu for allowing us to use his unpublished data. Olli Järvinen, Juha Tiainen, Mika Kilpi and Dick Forsman clarified our thinking in many respects.

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Received 23.VIII.1983
Printed 16.XI.1984