Short communications and comments

Influence of brood size on moult in female Willow Warblers

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Like other tropical passerine migrants adult Willow Warblers *Phylloscopus trochilus* undergo a fast (ca. 40 d) moult of wing and tail feathers after breeding. Moult intensity is sometimes so high that flightlessness occurs (Haukioja 1971). A moulting bird most probably would have a higher energy cost for flight and also reduced manoeuverability. Since reproduction is by far the most important activity, a reasonable assumption would be that the moult is adjusted so as not to coincide with the most intense period of parental care. This has been shown for Sparrowhawks *Accipiter nisus* in Scotland which arrest their moult during the period of peak food demand of the young (Newton and Marquiss 1982).

At higher latitudes the time available for post breeding activities, especially for moult, is shorter than at more southerly latitudes. Since an unsuccessful moult is likely to influence adult survival negatively (Newton 1966), one would expect adults to start moulting as soon as the breeding energy budget allows. This may result in an overlap between breeding and moult. Another adaptation to a short summer would be a faster moulting rate than in southern populations. This has been shown for several passerine species (summarized by Orell and Ojanen 1980).

As part of the LUVRE project (Enemar et al. 1984) we studied Willow Warblers in a subalpine birch forest near Ammarnäs in Swedish Lapland (66.58N, 16.17E) in July and August 1984. The breeding biology of Willow Warblers has been studied there since the early 1970s (Arvidson 1984). R. Nergaard and B. Arvidson gave us information on the breeding status of the ringed females in the study area and data on their broods. During the post-breeding period we caught some of the females in mistnets and their moult status was examined according to Ginn and Melville (1983). An old feather scores zero points, a growing one 1–4, and a full-grown one 5 points. As moult begins with the shedding of the innermost primaries, and we are interested in the onset of moult, we include only the primaries in our calculations. The outermost short primary is not included.

In order to estimate the date for the onset of moult of each female caught in the post-breeding period we calculated the mean moulting rate. To do this we used data from five females recaptured more than five days after their first moult record was taken. The mean rate was 1.23 primary points per day (S.D. 0.17). Moult starts with the simultaneous shedding of 2–4 primaries. Since this gives an immediate increase in the primary score by 2–4 points, we used 3 points as the criterion defining the onset of moult.

During the post-breeding period we caught seven females whose breeding status was known. We calculated the date for the onset of moult for these females assuming a linear rate of moult common to all females. The dates were spread over a period of four weeks. If related to the age of the broods, however (i.e. days after hatching), the spread was reduced to two weeks. This indicates that the timing of the onset of moult depends on the breeding schedule. This has also been shown for e.g., Bullfinch *Pyrrhula pyrrhula* (Newton 1966), White-crowned Sparrow *Zonotrichia leucophrys* (Morton and Welton 1973), Great Tit *Parus major* (Orell and Ojanen 1980), Common Buzzard *Buteo buteo* (Sylvén 1982) and Sparrowhawk (Newton and Marquiss 1982). Tiainen (1981) argues that there is no such connection between female moult and breeding schedule in Willow Warblers.

Male Willow Warblers participate much less than females, if at all, in the raising of the young and start moulting approximately 14 days before the females (whereas they do not moult as fast as the females; Tiainen 1981 and own observations).

If the onset of female moult in relation to hatching date of their brood is analysed as a function of brood

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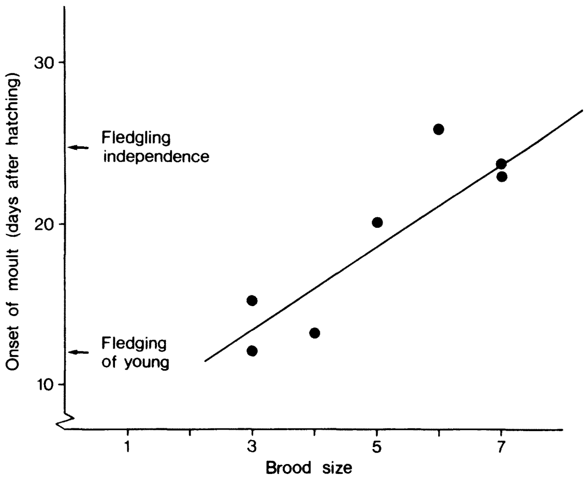

Fig. 1. The relationship between brood size and the onset of moult in female Willow Warblers. Brood size refers to the number of almost fledged young in the nest (8 days old), and the onset of moult is expressed as number of days after the brood hatched. The regression is Y = 2.9X + 4.3.

size, using a linear regression, we obtain a significant postive correlation ($r_s = 0.82$, $p < 0.05$; Fig. 1). This correlation implies that females with smaller broods begin their moult relatively earlier. A brood size dependent regulation of moult has also been shown for the Ural Owl *Strix uralensis* (Pietiäinen et al. 1984). Adults with larger broods replaced fewer flight feathers during the following moult.

Female Willow Warblers with larger broods begin their moult relatively later than females with small broods which gives them a shorter time for moulting. The possible disadvantages of a reduced time for moulting could be either poorer feather quality due to a faster moulting rate or that the bird would have to leave some feathers unmoulted (viz. innermost secondaries). Some late breeding females have shown such a suspended moult (own observations). A further disadvantage is that the energy cost per unit time is higher with a faster moulting rate. These factors could have a negative impact on adult survival.

Sylvén (1982) suggests that the earlier moult of female Common Buzzards, as compared with males, enables a more efficient pre-winter fat accumulation which could be a contributary factor behind the higher survival rate of the females in this species. Newton (1966) found that, in a year when food was unusually sparse in autumn, late-moulting Bullfinches survived less well.

Askenmo (1977) showed a positive correlation between female weight loss during feeding nestlings and brood size in the Pied Flycatcher *Ficedula hypoleuca*. Though this could be an adaptation to reduce flight costs, as suggested by Freed (1981) and Norberg (1981), this observation indicates a possible cost for having large broods. The later start of moult following the raising of a large brood, as shown by our results, adds another cost that might reduce the benefits of a large brood. This cost could be diminished if the females start breeding earlier in the season and/or can obtain more male help in parental care. Could the trade-off between breeding and moult be another factor explaining the decrease in clutch size with laying date, especially the small size of second broods, found in so many bird species?

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