Ibis (2002), **144** (on-line), E11–E18

Moult strategies in the Common Whitethroat *Sylvia c. communis* in northern Nigeria

JONAS WALDENSTRÖM[1,2]* & ULF OTTOSSON[2]
[1]*Evolutionary Biology Centre, Department of Animal Ecology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden*
[2]*Ottenby Bird Observatory, Pl 1500, SE-380 65 Degerhamn, Sweden, Corresponding address: Ottenby Bird Observatory, Pl 1500, SE-38065 Degerhamn, Sweden*

Moult strategies in the Common Whitethroat *Sylvia c. communis* trapped in northern Nigeria in April 1999 are analysed. Differences in the extent of moult between age and sex classes are presented. The secondary moult of adult birds is considered to belong to a new pre-breeding moult or an arrested moult, beginning at the normal starting positions on the wing, and not as a continuation of a suspended post-breeding moult. Eccentric moult of primaries was found in nearly 19% of the yearling birds, a pattern that is unusual for Western Palearctic passerines. Some individuals showed resemblance to the split moult pattern described for the Barred Warbler *S. nisoria*.

Most adult European warblers, *Sylviidae*, fall into two categories with regard to remex moult (Kjellén 1994). They either commence the complete moult of flight feathers directly after breeding, while still on their breeding grounds (post-breeding moult), or they delay the moult until the winter quarters following autumn migration (pre-breeding moult). Additional categories are: the split moult (Hasselquist *et al.* 1988, Lindström *et al.* 1993), in which the moult cycle is divided between winter and summer, and the biannual complete moult, found in the Willow Warbler *Phylloscopus trochilus* (Underhill *et al.* 1992). The time available for moult on the breeding grounds differs between species due to latitude and diet. About half of the long distance, insectivorous migrants breeding in northern Europe delay the complete moult to the winter quarters (Kjellén 1994), and half moult in the breeding areas. Phylogenetic analysis of the evolution of moult strategies (Svensson & Hedenström 1999) has suggested that the complete post-breeding moult is ancestral, and that the pre-breeding moult has arisen as taxa increased their migratory distance and colonized northern breeding areas. Also worth noting is the fact that many long-distance migrants are territorial in their winter quarters, e.g. Marsh Warblers *A. palustris* (Kelsey 1989), Great Reed Warbler *Acrocephalus arundinaceus* (Hedenström *et al.* 1993) and Greenish Warbler *Phylloscopus trochiloides* (Price 1981). Performing the autumn migration without a preceding moult of flight feathers may in this case be an adaptation to arrive early at the wintering grounds, increasing the chance of finding a good territory.

*Corresponding author.
Email: jonas.waldenstrom@zoockoi.lu.se

Some plasticity occurs in the extent of moult within populations and age classes of a species. This plasticity is observed as interruption of primary and secondary moult. Harper (1984) differentiated between two different types of moult interruptions: suspended moult, where the moult is resumed at the point of interruption, and arrested moult, where the subsequent moult starts at the normal site of initiation. Interruption in moult occurs among (1) late breeders that do not have time to finish the post-breeding moult before autumn migration, but instead suspend and resume moult after migration (Cramp 1992, Svensson 1992, Hall & Fransson 2001); (2) birds that suspend pre-breeding moult while migrating between two different wintering areas, e.g. eastern races of Common Whitethroats *Sylvia communis icterops* and *S. c. volgensis* in Kenya (Pearson & Backhurst 1976); (3) birds that suffer seasonal adverse conditions during the pre-breeding moult, as seen in Sedge Warblers *A. schoenobaenus* in Nigeria (Aidley & Wilkinson 1987) and Ghana (Bensch *et al.* 1990) during the peak of the dry season in West Africa; (4) some opportunistic breeders in their annual complete moult, e.g. cuckoos of the genus *Clamator* and some species of weavers (Payne 1969).

The Common Whitethroat exhibits an unusually wide array of different moult strategies, both within and between populations (Pimm 1973, Mead & Watmough 1976, Pearson & Backhurst 1976, Swann & Baillie 1979, Karlsson *et al.* 1985, Aidley & Wilkinson 1987, Bensch *et al.* 1990, Cramp 1992, Jenni & Winkler 1994). Common Whitethroats of the nominate race are long-distance migrants breeding in the west, north and central parts of continental Europe and in the British Isles (Cramp 1992), and wintering in bush savannah of the Sahel zone in West Africa at approximately 12–18°N (Moreau 1972, Cramp 1992). The present paper describes the moult strategies in migrating Common Whitethroats of the nominate race trapped in northern Nigeria, and links variation in moult among different age classes and sexes to ecological and phylogenetic aspects of feather renewal.

MATERIALS AND METHODS

Study area

The field study was carried out in north-east Nigeria at two localities close to the former Lake Chad Research Station of the Nigerian Federal Fisheries Service (13°33′N, 13°23′E) outside the town of Malamfatori. The area is within the Sahel zone, a belt with dry savannah just south of the Sahara, which during the last 20 years has been subject to desertification because of decreased rainfall, increased land use and overgrazing by cattle to meet the demands of the growing population (Jones *et al.* 1996). The study area is mainly a stopover site for migratory birds, either before or after crossing the desert, but some Common Whitethroats are likely to winter there (Fry *et al.* 1970). The study areas were of a seminatural habitat and the vegetation was dominated by dense stands of the saltbush *Salvadora persica*, growing up to 3 m in height. Also present were a few scattered *Acacia tortilis* and *A. senegal* and some *Mimosa* sp. trees. The weather during the study period (April 1999) was hot and very dry, midday temperatures ranging between 39 and 46 °C.

Mistnets were set in cleared patches in the vegetation and operated daily from *c.* 05:30 to 09:00 h, from 2 to 24 April 1999. No more than 12 nets, 9 or 12 m long, were used at any locality. Birds were ringed with aluminium rings, wing-lengths were measured to the nearest mm (maximum chord, Svensson 1992), weights were taken to the nearest 0.1 g and visible fat load measured on a nine-point scale by examining the subcutaneous fat in the tracheal pit and on the abdomen (Kaiser 1993).

Ageing, sexing and recording moult

Birds were aged according to characters presented in Svensson (1992), Jenni and Winkler (1994) and Karlsson *et al.* (1985), as either adult or 2Y (second calendar year). Sex was determined in the field following characters presented in Svensson (1992) and Cramp (1992).

Numbering of primaries and secondaries follows Svensson (1992) where each feather tract is numbered ascendently from the outermost to the innermost feather. Tertials are numbered descendently, the smallest innermost having number T1. Moult of primaries, secondaries and tertials was recorded according to Ginn and Melville (1983): an old feather was scored 0; a new full-grown feather was scored 5; growing feathers were scored on a scale from 1 to 4. The minute outermost primary (P1) was not scored in this study. Moult was recorded on the left wing.

The moult status was assessed on the basis of differences in wear between feathers of different ages, meaning that the bird does not need to be in active moult for the examination of moult patterns. In the Common Whitethroat, assigning feathers to different feather generations can be difficult because of differential wear between individuals and feather tracts (Karlsson *et al.* 1985, Svensson 1992). In this study, feathers that were fresh and glossy, contrasting with dull and worn old feathers, were considered to have been moulted during the bird's stay in the wintering quarters. We avoided distinguishing between moult in early and late winter, except when growing feathers were found.

Genetic sexing

Blood samples, of approximately 20 µl, were taken from a vein in the right wing of the birds, and were stored in 500 µl of 99.5% EtOH. Storage temperatures in the field were ambient, but later the samples were kept at 8 °C.

DNA was extracted by standard molecular methods involving digestion by proteinase K and subsequent extraction with phenol and chloroform. The extracted DNA was resolved in ddH_2O and the final concentration measured with a photospectrometer.

The chromosomal sex of individuals was determined following Fridolfsson and Ellegren (1999), where a pair of sex-linked genes with a difference in intron length (CHD1W and CHD1Z) are detected with the *2550F* and *2718R* primers. DNA was amplified using the PCR technique and the PCR products were separated in agarose gels and later visualized by ethidium bromide staining and UV-light. For full details of the protocol used see Waldenström and Ottosson (2000).

RESULTS

Age differences in moult

In total 653 Common Whitethroats were ringed and 196 moult cards were recorded. Blood samples were taken from 96 individuals where moult was recorded and these samples were later used for the genetic analysis. Of the birds whose moult was recorded, only five were found in active moult; all others had old or fully grown renewed feathers. The extent of moult among different age classes at given positions in the tertials, secondaries and primaries can be seen in Fig. 1. In total, 45 adult and 151 2Y birds were scored for each feather tract.

Adult birds

Nearly all birds examined (93%) had renewed all three tertials during the pre-breeding moult. Only two birds had old tertials: both had moulted T1-T2, and left T3 unmoulted.

Moult of one or more secondaries in winter had occurred in 20% of all adult birds studied. Most frequently the innermost (S6; four birds), or the two innermost (S6-5; three birds) secondaries were moulted. One individual had renewed the four inner (S6-3) and left the two outer unmoulted. Finally, one individual had moulted all six (S6-1) secondaries. The mean number of moulted secondaries was 0.4 in all studied birds, and 2.2 among birds that had renewed at least one secondary (n = 9). No pre-breeding moult of primaries was observed in the recorded birds.

2Y birds

A complete moult of all three tertials was recorded in 96% of the 2Y birds. One bird showed no moult at all, with very worn tertials, which presumably were juvenile. Another five birds had not completed their tertial moult: three birds had moulted T2-T3, one bird T1-T2, and one bird only T3. One bird caught on 7 April was still in active moult, with T3 in stage 4.

Moult of secondaries had occurred in 86% of all examined yearling birds, and the mean number of moulted secondaries was 1.5. Among birds that had renewed at least one secondary, the mean number of moulted secondaries was 1.8 (n = 130). Most frequently, the innermost (S6; 76 birds), or the two innermost (S6-5; 32 birds) secondaries had been renewed. Other less common patterns were also observed; the three inner (S6-4; six birds); the four inner (S6-3: seven birds); the five inner (S6-2; one

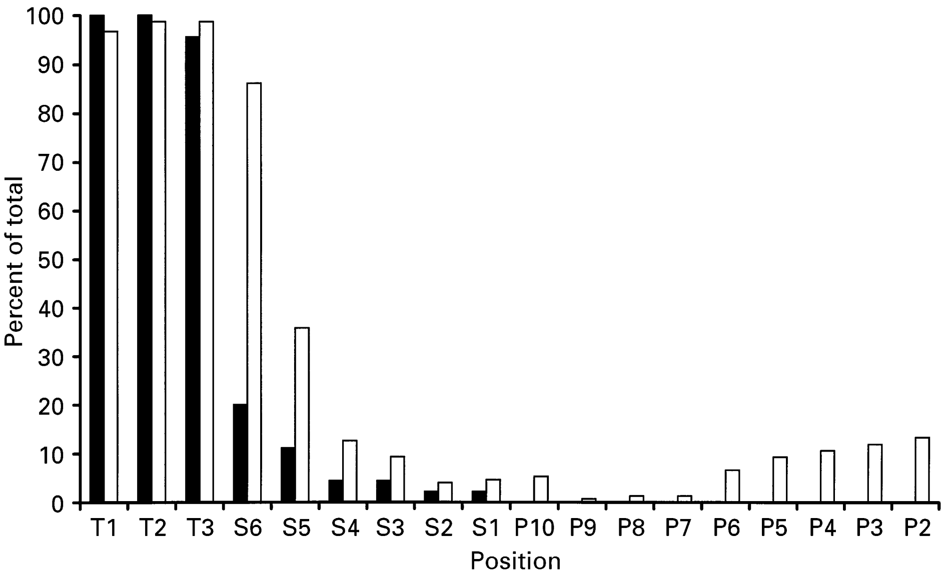

Figure 1. Extent of moult at given positions in adult (solid bars) and 2Y (unfilled bars) Common Whitethroats *S. c. communis* ringed in NE Nigeria 1999.

bird); or all six secondaries (S6-1; four birds) had been moulted. Four birds showed more irregular patterns; three of them having one to three central (S4-2 or S2) unmoulted juvenile feathers, surrounded by feathers moulted in the pre-breeding moult (S6-5 and S1 or S6-3 and S1). One bird had moulted S6-5 and S3, leaving juvenile S4 and S2-1. Four birds caught on the 2, 3 (two birds) and 14 April were in active moult, with S6 growing in stages 3 or 4.

Moult of primaries occurred in 19% of the 2Y birds. The mean number of moulted primaries was 0.6 in all birds, and 4.8 among the birds that had renewed at least one primary (n = 29). Six different patterns of moult were detected; 10 birds had moulted the 2-7 outermost large primaries (P8-2, 6-2, 5-2, 4-2, 3-2) in an eccentric sequence, not starting the moult at P10 (the normal starting position for primary moult, Svensson 1992); eight birds had moulted a single primary at an eccentric position (P7, 6, 5 or 2); two birds moulted two or three central primaries in an eccentric sequence (P6-3, 5-4); seven birds had started moult sequences both at the normal position P10 and at an eccentric position (P10 + 6-2, 5-2, 4-2, 3-2 or 5); one bird had moulted only P10; one bird had started two different eccentric sequences (P8 + 6-2).

Correlates of moult

None of the variables was normally distributed (Shapiro–Wilk, $W \le 0.941$, $P \le 0.01$), so non-parametric tests were used throughout.

Moult scores in the primaries, the secondaries, the tertials and the combined scores of these tracts were correlated with the morphological variables, e.g. the weight, the wing-length and the fat score for 2Y birds (n = 145). A significant relationship was found between weight and moult score in secondaries ($r_s = 0.17$, $P < 0.05$), all other correlations were non-significant ($r_s \le 0.15$, n.s.). Correlations between variables when genetically sexed 2Y males and females were treated together (n = 65) were non-significant ($r_s \le 0.15$, n.s.), as were correlations between variables within genetically determined females ($n = 30$, $r_s \le 0.24$, n.s.) and males ($n = 35$, $r_s \le 0.29$, n.s.).

Observed moult in winter – suspended or arrested moult?

We compared the observed pattern of pre-breeding secondary moult in adult birds in this study with the expected moult pattern using post-breeding moult data from Swann and Baillie (1979). We assumed that the birds recorded with interrupted secondary moult during autumn migration in Crete (Swann & Baillie 1979) only renewed those feathers in winter that were not moulted in the post-breeding moult prior to migration. This gives an opportunity to compare the observed pattern of winter moult, with the pattern expected if the secondary renewal during the winter is simply a continuation of the suspended post-breeding moult. If the data deviate from the expectations, an arrested moult sequence is more likely than a suspended. Feathers were tested feather-by-feather and significant differences found in positions S1 ($\chi^2_1 = 4.51$, $P < 0.05$), S2 ($\chi^2_1 = 19.50$, $P < 0.001$), S3 ($\chi^2_1 = 33.95$, $P < 0.001$), S4 ($\chi^2_1 = 44{,}17$, $P < 0.001$), S5 ($\chi^2_1 = 9.10$, $P < 0.001$), but not in position S6 ($\chi^2_1 = 0.42$, n.s.).

Sex differences in moult

No significant differences were found between the sexes in tertial moult score, secondary moult score or primary moult score (Kruskal–Wallis, n.s.) in 2Y birds of known sex (males = 35, females = 30).

DISCUSSION

Moult strategies and the timing of moult

Adults

Adult birds quite frequently renewed secondaries in the winter quarters, with the number of moulted feathers varying from none to all. No obvious difference in coloration was found between moulted tertials and moulted secondaries. All renewed feathers were fresh and rather glossy, implying that these feathers had been moulted during late winter. During the period when the tertials are missing or growing, there is a higher degree of exposure of the inner, and in particular, the innermost secondary (S6). This accords with the anatomy of the folded wing, where the tertials cover and protect the secondaries and primaries. A renewal of the inner secondaries, after tertial moult, could thus be seen as a renewal of the most worn feathers in that tract.

The general view (Cramp 1992, Jenni & Winkler 1994) is that flight feather moult in the Afrotropics during October–November is best considered as a continuation of the suspended post-breeding moult, and that feathers renewed in this moult mainly replace previously unmoulted secondaries. Our data do not support this view but suggest that the winter moult of secondaries among adult Common Whitethroats represent either a new pre-breeding moult sequence, including renewal of feathers that were also replaced in the post-breeding moult, or represent an arrested moult sequence (Harper 1984). Both of these strategies start at the normal starting positions and not in the eccentric positions that would be expected in a suspended moult. This conclusion can be drawn from the pattern in which secondaries are normally moulted, namely from two loci; S1 inwards and S6 outwards (Swann & Baillie 1979, Cramp 1992). Old feathers, which had not been renewed during the post-breeding moult, would thus be more likely to be found in position S2-5. No bird was found to have renewed only its middle secondaries, but all of the moulting individuals had renewed either S6, S6 plus adjacent feathers or all secondaries (S6-S1). The positions of renewed secondaries differed significantly from the pattern expected from a suspended post-breeding moult (data from Swann & Baillie 1979).

Fully grown, recently renewed, secondaries have been reported in Common Whitethroats examined in northern Ghana (Bensch *et al.* 1990) in November and December, and active secondary moult in all months from September to April in northern Nigeria (Aidley & Wilkinson 1987). However, no separation between adult and 2Y birds was made in these studies, making differences between suspended post-breeding and pre-breeding moult of adults indistinguishable from extensive pre-breeding moult of 2Y birds. Of interest here is the fact that Karlsson *et al.* (1985) reported that one individual at Falsterbo, southern Sweden, had not replaced some of its middle secondaries either in the post-breeding moult or in the pre-breeding moult.

One adult bird renewed all secondaries in a pattern resembling the split moult strategy originally found in the Barred Warbler *Sylvia nisoria* (Hasselquist *et al.* 1988). This is a special type of suspended moult where adult birds replace most of their secondaries and all tertials in their winter quarters in Africa, and all their primaries, frequently one or a few of the outer secondaries, and all tertials on the breeding grounds in Europe (Lindström *et al.* 1993). However, we do not know if the individual in our study failed to renew most secondaries on the breeding grounds, or renewed these feathers in both the post-breeding and pre-breeding moults. The split moult pattern was also implied in eastern individuals of the Orphean Warbler *S. hortensis* (Nikolaus & Pearson 1991), and in two studies of the nominate race of the Common Whitethroat in Sweden (Karlsson *et al.* 1985) and northern Ghana (Bensch *et al.* 1990).

No pre-breeding moult of primaries was recorded among adults in this study, although other studies of European Common Whitethroats have found a small percentage of individuals performing what was considered to be completion of a suspended post-breeding moult: on winter quarters in Ghana one individual was in active moult on 11 November (Bensch *et al.* 1990), and during spring migration in Italy 3% had moulted some outer primaries (Jenni & Winkler 1994). A complete pre-breeding moult of primaries was reported in two adult birds caught on spring migration from Sweden (Karlsson *et al.* 1985), a pattern normally found only in the eastern subspecies of Common Whitethroats (Svensson 1992).

2Y birds

Nearly all 2Y birds (96%) moulted all their tertials, and one individual was still in active moult on 7 April, indicating that tertials were renewed in a pre-breeding moult after autumn migration. It should be noted, however, that a few (less than 10%) juvenile birds renew some or all tertials during a post-juvenile moult preceding autumn migration (Jenni & Winkler 1994). In this study all moulted tertials were fresh and prominently edged with rufous. A tertial retained from the post-juvenile moult would be rather worn and bleached from the migration and wintering periods, but still not be as worn as juvenile feathers (Karlsson *et al.* 1985); however, such differences can be hard to detect reliably.

Variation in the pre-breeding moult of secondaries was high among 2Y birds and the number of moulted feathers varied between none and all. The moult of secondaries was considered as belonging to the pre-breeding moult, probably occurring in late winter, since all moulted feathers were fresh and rather glossy, contrasting with the much more worn and bleached juvenile ones. Further support for this conclusion can be drawn from the four birds found to be in active moult of S6. The post-juvenile moult rarely includes secondaries (Cramp 1992), and when it does most frequently only S6 is renewed.

Post-juvenile moult of primaries in juveniles on autumn migration has not been recorded in any study of the nominate race of the Common Whitethroat (Karlsson *et al.* 1985, Cramp 1992, Svensson 1992, Jenni & Winkler 1994). However, pre-breeding moult of primaries was frequent and extensive in our study. The normal pattern of primary renewal in passerines is descendent, starting with P10 (Ginn & Melville

Table 1. Comparison between three moult studies of Common Whitethroats in spring; Sweden[1] (Karlsson *et al.* 1985); Italy[2] (Jenni & Winkler 1994); Nigeria[3] (this study). Per cent of birds with juvenile greater coverts, per cent of adult birds with moult limit within greater coverts, per cent of birds that have moulted all, 1–2 or no tertials, per cent of birds that have moulted all, part or no secondaries, mean number of moulted secondaries among birds that renewed at least one secondary.

	Sweden		Italy		Nigeria	
	2Y	Adult	2Y	Adult	2Y	Adult
Greater coverts						
Juvenile GC left	33		16		17	
Moult limit in GC		16		56		60
Tertials						
All	50	50	91	59	96	96
1–2	30	30	9	26	3	4
None	20	20	0	15	1	0
Secondaries						
All			2	–	3	2
Part			55	–	83	18
None			43	–	14	80
Mean no. of moulted SS			2.0	4.3	1.8	2.2

[1]2Y n = 69, adult n = 44; [2]2Y/adult n = 85–200 depending on feather tract studied; [3]2Y n = 151, adult n = 45.

1983, Svensson 1992). In this study primary moult started at two loci, either at P10 or at an eccentric position. Renewal of outer primaries also occurs in the seasonally divided wing-moult pattern found in the Barred Warbler (Lindström *et al.* 1993). In this pattern first winter birds renew on average 2.0 of the outermost primaries, some secondaries and all tertials. Pre-breeding moult of primaries has been noted in Italy (Jenni & Winkler 1994) where 24% of 2Y birds on spring migration had renewed feathers, mostly in an eccentric fashion, and in Sweden (Karlsson *et al.* 1985) where two individuals had renewed P10 or P8-10. A previous study from Nigeria (Aidley & Wilkinson 1987) found only one individual, of 152 birds studied in September–April, that showed evidence of primary moult. However, this individual was not aged, so it may have been an adult with suspended post-breeding moult.

Ecological aspects of moult

Renewal of flight feathers is an energy- and protein-demanding process (Murphy & King 1992). Variation in the extent of moult clearly implies that there seems to be a cost associated with the primary and secondary moult. For instance, yearling birds faced with the possibility of renewing just a few primaries, seem to have moulted the longest, and thus most 'expensive', feathers. Renewal of the outer primaries has been argued to improve the aerodynamic performance of flying birds (Lindström *et al.* 1993), as new feathers are not worn and abraded. This pattern is also well known in first-year waders from the Northern Hemisphere wintering in the tropics (Prater *et al.* 1977). Long-distance migrants have, in general, longer primaries giving a larger wing area with more pointed wing formula than short-distance migrants (Marchetti *et al.* 1995).

Only a few studies have been published that deal with moult patterns in Common Whitethroats observed in winter or spring (Karlsson *et al.* 1985, Aidley & Wilkinson 1987, Bensch *et al.* 1990, Jenni & Winkler 1994). The results differ between studies (Table 1). Birds may have belonged to different populations, each population migrating via a very narrow and defined geographical route. Strongest correspondence is found between birds from this study and an Italian one (Jenni & Winkler 1994), but unfortunately the number of trapped birds is not clearly stated for each feather tract in that study, precluding statistical comparisons. Nevertheless, to date, seven ringing recoveries of Common Whitethroats ringed in Malamfatori have been reported during subsequent migrations (Elgood *et al.* 1994, this study), three from Libya (two in autumn), two from Egypt (one in autumn), one from Tunisia and one from Poland. These recoveries also indicate an eastern or central passage over the Mediterranean Sea.

The post-breeding moult of flight feathers has been identified as the ancestral moult pattern of adult birds in Western Palearctic warblers, and the pre-breeding moult more recently evolved as taxa increased their breeding ranges northwards, increasing their migratory distance (Svensson & Hedenström 1999). Adult Common Whitethroats of the nominate race exhibit a range of moult patterns including complete post-breeding moult (Cramp 1992, Svensson 1992), complete pre-breeding moult (Karlsson *et al*. 1985), split moult (Karlsson *et al*. 1985, Bensch *et al*. 1990, this study) and different patterns of interrupted moult (Aidley & Wilkinson 1987, Jenni & Winkler 1994). The Common Whitethroat is a widespread species, and the selective forces might differ between the north and the south, as well as between the west and the east parts of its breeding range.

This mixture of moult patterns could be explained as an intermediate step in the adaptive process of attaining a complete pre-breeding moult. Recovery data from this study hint that the populations studied originate from middle or eastern Europe, and it might be plausible that the extensive moult in winter quarters observed in this study is to be presumed if there is a general trend from complete post-breeding moult to complete pre-breeding moult in a west to east scale. In the eastern parts of the species' European breeding range, from east Poland, western Siberia, Hungary, Rumania and eastern Bulgaria and eastwards, it occurs in the *volgensis* subspecies (Cramp 1992) and from Turkey, Levant, Caucasus, Transcaucasia and Iran in the *icterops* subspecies (Cramp 1992), both exhibiting complete pre-breeding moult (Cramp 1992, Svensson 1992).

This paper is based on data collected for a master thesis in biology, written at the department of Animal Ecology in Uppsala, Sweden. We are grateful to Mats Björklund and Ben Sheldon for providing laboratory facilities and support. We would like to thank the staff of the Lake Chad Bird Migration Project, especially Christian Hjort, Franz Bairlein, Phil Hall, Stephen Rumsey, Fernando Spina. Special thanks go to A.P. Leventis who gave logistical and financial support. Finally, we would like to thank Staffan Bensch and Thord Fransson for valuable comments on the manuscript. The Swedish participants were funded through a grant from the Hasselblad foundation to Ottenby Bird Observatory. This paper constitutes report no. 170 from Ottenby Bird Observatory.

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Received 26 April 2000; revision accepted 20 August 2001