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# The moult of Barred Warblers *Sylvia nisoria* in Kenya—evidence for a split wing-moult pattern initiated during the birds' first winter*

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The moult of Barred Warblers *Sylvia nisoria* was studied during three winter seasons in southeastern Kenya at a southward passage site (Ngulia) and a wintering site (Mtito Andei). Most Barred Warblers migrating through Ngulia in November had yet to commence winter moult. These birds probably moulted subsequently in winter in northern Tanzania. In December, birds were found in heavy moult at Mtito Andei, and some of these birds were known to stay throughout the winter. By contrast, most birds reaching southeastern Kenya from late December onwards had already completed part or all of their winter moult, presumably at stopover sites in northern and eastern Kenya or in Ethiopia. Thus, winter moult in Barred Warblers takes place mainly in late November and December, either just before or soon after the final leg of autumn migration. In general, first-year birds renewed all tertials and tail feathers, about three to five secondaries per wing and commonly also the outer one to four large primaries per wing. Adults renewed all tertials and tail feathers, almost all secondaries and only occasionally an outer primary. The replacement of relatively fresh juvenile secondaries during the birds' first winter implies that the split moult pattern of this species (secondaries, tertials and tail moulted in winter; primaries and tertials in summer) is endogenously controlled.

In several passerine species where adults normally have a complete moult on the breeding grounds, some individuals leave a few secondaries unmoulted before autumn migration (e.g. Hyytiä & Vikberg 1973, Mead & Watmough 1976, Swann & Baillie 1979, Norman 1991). This is often interpreted as a result of birds being late in breeding the preceding summer and therefore having to interrupt their moult prematurely to avoid a delayed autumn migration.

Recent studies of moult in the Barred Warbler *Sylvia nisoria* have revealed an unusual strategy, in which adults embark on autumn migration with most or all secondaries unmoulted (Fracasso 1985, Hasselquist *et al.* 1988, Nissling *et al.* 1989, Nikolaus & Pearson 1991). Examination of birds on Swedish breeding grounds led Hasselquist *et al.* (1988) to conclude that this species moults primaries, tertials and central tail feathers in summer but the secondaries, together with a varying number of tertials and tail feathers, in winter. Of particular interest was the finding that young birds replace a number of secondaries during their first winter. The retention of old secondaries by Barred Warblers in autumn cannot therefore be accounted for by the proximate (time-stress) explanation referred to alone.

Since information on Barred Warbler moult in Africa was limited (e.g. Witherby *et al.* 1943, Williamson 1968, Pearson 1978), Hasselquist *et al.* (1988) were obliged to draw conclusions on winter moult from differences in feather wear of birds arriving back at their breeding grounds. Here we present moult data for the species collected during three winter seasons in Kenya. We can confirm the general strategy outlined above and can now describe in more detail the year-round moult schedule of this species.

## STUDY SITES AND METHODS

Barred Warblers were studied at two nearby sites in southeastern Kenya in the boreal winters (November–March) of 1989/90, 1990/91 and 1991/92. Birds were caught at Ngulia

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**Table 1.** *Progress of winter moult in Barred Warblers in Kenya. The average number of new (moulted the same winter season) and growing flight feathers of first-year birds and adults caught at Ngulia and Mtito Andei in different months. Data from 1989/90, 1990/91 and 1991/92 are combined. Values are for left wing and the whole tail. Sample sizes (n) for adults at Mtito Andei include the retraps listed in Table 2*

| Age group | Feather tract | Moult status | Ngulia | | Mtito Andei | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Nov | Dec | Nov | Dec | Jan | Feb/Mar |
| First-year birds | Secondaries | New | 0 | 0 | | 1 | 2.3 | 3.9 |
| | (per wing) | Growing | 0 | 0 | | 5 | 0.7 | 0.1 |
| | Tertials | New | 0 | 0.6 | | 1 | 2.3 | 3.0 |
| | (per wing) | Growing | 0.3 | 0.3 | | 2 | 0 | 0 |
| | Primaries | New | 0 | 0 | | 0 | 1.3 | 2.0 |
| | (per wing) | Growing | 0 | 0 | | 2 | 0 | 0 |
| | Tail feathers | New | 0.1 | 0.7 | | 0 | 7.0 | 11.8 |
| | | Growing | 0.8 | 0.7 | | 12 | 1.0 | 0 |
| | *n* | | 29 | 18 | 0 | 1 | 3 | 10 |
| Adults | Secondaries | New | 0.2 | 2.4 | 0 | 1.4 | 4.1 | 4.9 |
| | (per wing) | Growing | 0.1 | 0.4 | 1.0 | 2.4 | 0.3 | 0.2 |
| | Tertials | New | 0 | 0.8 | 0 | 0.7 | 2.0 | 2.9 |
| | (per wing) | Growing | 0.1 | 0.2 | 0.5 | 1.1 | 0.4 | 0 |
| | Primaries | New | 0 | 0 | 0 | 0 | 0.1 | 0.3 |
| | (per wing) | Growing | 0 | 0 | 0 | 0.1 | 0 | 0 |
| | Tail feathers | New | 0.2 | 4.8 | 0 | 3.4 | 8.6 | 11.1 |
| | | Growing | 1.8 | 1.2 | 6.0 | 4.4 | 0.7 | 0.4 |
| | *n* | | 47 | 18 | 2 | 11 | 12 | 16 |

Lodge (3°00'S, 38°13'E) in Tsavo West National Park and near Mtito Andei (2°41'S, 38°08'E), a small town 35 km to the north.

At Ngulia, thousands of birds, mainly Palaearctic passerines, have been caught for ringing on southward migration (October–January) each year since 1972 (see Pearson & Backhurst 1976, Backhurst & Pearson 1984, 1992, for details of trapping and locality). Barred Warblers occur from late October to early January with a peak passage from mid-November to early December (Backhurst & Pearson 1984). The moult state of Barred Warblers was examined during routine trapping 23 November–9 December 1989, 15–28 November and 14–22 December 1990, and 29 November–16 December 1991. Birds were trapped at night when attracted in mist to the bright lights of the lodge and also on mornings when large numbers of migrants had landed. Almost all birds that land at Ngulia leave by the following night, and it was assumed that Barred Warblers caught here were on active migration. They were probably in the final stage of southward migration, since the species is not known to winter regularly south of northern Tanzania (Moreau 1972, Pearson *et al.* 1988).

The Mtito Andei site was located *c.* 5 km east of the town in dense bushland (for definition of this vegetation category, see Pratt & Gwynn 1977) dominated by *Commiphora, Grewia, Premna* and *Acacia*, mostly 2–3 m high, with a few emergent trees, including baobabs *Adansonia digitata* and *Acacia tortilis*, and a well-developed herbaceous underlayer. In both winter seasons, the area came into leaf with the onset of the rains in mid-November and was thick and luxuriant during December and January. The density of Barred Warblers in March and December 1990 was estimated from counting calling birds along a 1-km transect.

Trapping was carried out on 31 days between 5 November 1989 and 25 March 1990, on 18 days between 27 November 1990 and 22 January 1991, and on 9 and 17 November 1991. Between 60 and 150 m of mist-net were in use each morning and late afternoon. The trapping effort was distributed as follows: November, 9 days; December, 19 days; January, 10 days; February, 5 days; March, 8 days.

Birds were aged and sexed using eye colour and plumage characteristics (Svensson 1984, Hasselquist *et al.* 1988) and were separated into first-year birds and adults. "First-year" is equivalent to the Euring-codes 3 and 5 (before and after 1 January, respectively), while "adult" equals Euring-codes 4 and 6.

At both sites, the state of the 12 tail feathers and of the nine large primaries, six secondaries, and three tertials of the left wing was routinely examined. We refer to these feather tracts collectively as the "flight feathers". Feathers were classified as J (juvenile), O (old—moulted the summer before last, *c.* 18 months before), X (moulted the previous winter), S (moulted the previous summer) and N (new-grown the same winter season). In late winter it became difficult to separate O, X and S feathers, and these were then all classified as G (as opposed to N). Actively growing feathers

scored 1–4 points and new feathers 5 points (Ginn & Melville 1983).

Primaries (P) were numbered 1 to 9 descendantly, while secondaries (S, 1–6) and tertials (T, 1–3) were numbers ascendantly. Tail feathers (R) were numbered from the central (1) to the outermost (6) feather. In many birds, moult of body feathers and wing coverts was also recorded.

## RESULTS

Out of 159 Barred Warblers examined, 112 were caught at Ngulia (47 first-year birds and 65 adults) and 47 at Mtito Andei (14 first-year birds and 33 adults). Numbers of birds examined from each month at the two sites are shown in Table 1. At Mtito Andei, birds were heard as early as 8 November, but relatively few were caught during November–December. Full wintering numbers appeared to build up during January. The average trapping rate was 0.2 birds per day in November, 0.6 birds per day in December, 1.5 birds per day in January, 1.4 birds per day in February and 2.6 birds per day in March. About 3.4 Barred Warblers per ha were estimated present in the Mtito bush during March 1990, but only 0.9 birds per ha in December 1990.

### Moult in first-year birds

First-year birds at Ngulia in November–December had not begun to moult to any significant extent. They still retained most of their juvenile flight feathers (Table 1, Fig. 1). Only one bird had started secondary moult (S1 growing) and none was caught with moulting primaries. About 60%, though, were growing single tail feathers and/or tertials. The only extensively moulting first-year bird trapped by us was the single December bird at Mtito Andei (on 20 Dec.). This bird had T3 and S1 new, while T1–2, S2–5, all tail feathers and the two outermost primaries (P8–9) were growing.

By contrast, first-year birds caught at Mtito Andei during January–March seemed to have essentially finished winter moult, and none had more than two growing flight feathers (left wing and tail taken together). Ten February–March birds had moulted all their tertials and on average 3.9 secondaries (range 1–6) and 2.0 outer primaries per wing (range 0–4), as well as 11.8 tail feathers (range 10–12). These figures probably give a good indication of the extent of winter moult in first-year Barred Warblers.

The secondary most often renewed was S6 (the innermost). The primaries moulted were the 1–4 outermost (with one exception, a bird which had renewed P1 as well as P8–9). We could not determine whether these primaries were moulted ascendantly or descendantly, and the only bird with growing feathers had P8–9 in pins of equal length. Most first-year birds moulted the alula in winter, and all moulted the upperwing-coverts and the body feathers. This took place mainly in December–January, but growing body feathers were noted commonly up to late March.

One first-year bird caught for the first time at Mtito Andei on 20 February was retrapped twice (Table 2). When first caught, it had all tertials, all tail feathers and S6 and P9 new, but all other secondaries and primaries were juvenile. On 9 March, S5 and the left R5 were growing, and on 23 March these feathers were fully grown.

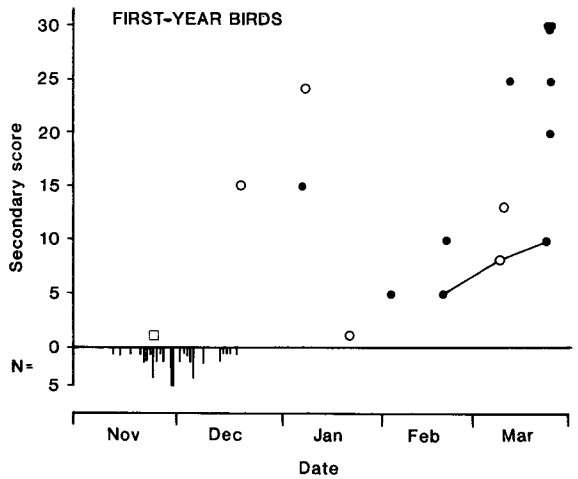


**Figure 1.** Moult status of secondaries (secondary score of left wing) in first-year Barred Warblers trapped at Ngulia (squares) and Mtito Andei (circles) in Kenya in the winters 1989/90, 1990/91 and 1991/92. The three seasons are combined. Open symbols refer to actively moulting birds while filled symbols refer to birds not in active moult. Lines connect individuals retrapped within the same winter season. Only the first trapping occasion is shown for retraps that did not change secondary score between catches. Birds that had not yet commenced winter moult of secondaries are indicated by bars below the line for secondary score zero.

### Moult in adults

Fourty-two adults caught at Ngulia, the last on 4 December, had yet to commence winter wing-moult, and 27 of them had not started tail-moult either. In these birds it was possible to determine which flight feathers had been moulted in the breeding quarters the preceding summer. The summer moult always included all primaries and on average 2.4 secondaries per wing (range 0–6), 2.9 tertials per wing (range 2–3) and 4.9 tail feathers (range 0–12). The secondary most often moulted was S1; 67% of the birds had moulted this feather, whereas only 24% had moulted S6. Four birds had not fully replaced their tertials; all retained the small T3. All birds except two had replaced at least one (and most of them both) of the central tail feathers. The incidence of summer moult decreased from the centre of the tail outwards, and R5 and R6 had been replace by only 25% of the birds.

At Ngulia, 44% of the adults passing in November had started to moult a few tail feathers, but only 18% had started to moult one or two secondaries and tertials. However, most December birds were well into winter moult, and some seemed to have completed it. It was noticeable, though, that in December the birds migrating through Ngulia had on average far fewer growing flight feathers (average 1.8 ± 2.6

**Table 2.** *Moult status of flight feathers in Barred Warblers retrapped between, or within, the winter seasons of 1989/90 and 1990/91 at Mtito Andei, Kenya. J = juvenile feather (from the nest), S = feather moulted the preceding summer, X = feather moulted the preceding winter, G = either S or X, 1–4 = growing feathers, N = new feather, — = not recorded. The numbers of primaries of a certain stage, starting from P1, are shown as indices. For further explanations, see text*

| | | | Tertials | Secondaries | Primaries | Tail feathers |
|---|---|---|---|---|---|---|
| Individual | Date | Age[1] | 321 | 654321 | 1–9 | 654321123456 |
| Between seasons | | | | | | |
| A35668 | 19 Dec 89 | Ad | NNN | NNNNNS | $S^9$ | NNN1NNNNSNSS |
| | 1 Jan 91 | | 111 | 11SSS1 | $S^9$ | SSSX111XSSSS |
| A35919 | 8 Jan 90 | Ad | GNN | NNNNNN | $S^9$ | NNNNNNNNNNNN |
| | 21 Feb 90 | | NNN | NNNNNN | $S^9$ | NNNNNNNNNNNN |
| | 12 Dec 90 | | NSS | NXXXSX | $S^9$ | 1N41SSSNNN44 |
| Within seasons | | | | | | |
| A35949 | 20 Feb 90 | Juv | NNN | NJJJJJ | $J^8$, N | NNNNNNNNNNNN |
| | 9 Mar 90 | | NNN | N3JJJJ | $J^8$, N | NNNNNNNNNN2N |
| | 23 Mar 90 | | NNN | NNJJJJ | $J^8$, N | NNNNNNNNNNNN |
| A35620 | 29 Nov 89 | Ad | S1S | SSSSSS | $S^9$ | XXXXXSS1XXXX |
| | 12 Mar 90 | | NNN | NNNNNN | $S^9$ | NNNNNNNNNNNN |
| A35645 | 17 Dec 89 | Ad | NN3 | N41344 | $S^9$ | SNNS133NNNNS |
| | 8 Jan 90 | | NNN | NNNNNN | $S^9$ | NNNNNNNNNNNN |
| A35652 | 17 Dec 89 | Ad | 133 | X1X113 | $S^9$ | 444441N4S444 |
| | 7 Jan 90 | | NNN | 4GNNNN | $S^9$ | NNNNNN4NNNNN |
| A35927 | 8 Jan 90 | Ad | GGN | NGNNNG | $S^4$, N, $S^4$ | NNNNNGNNNNGN |
| | 4 Feb 90 | | GGN | NGNNNG | $S^4$, N, $S^4$ | — |
| A35950 | 20 Feb 90 | Ad | NNN | 1N1GGG | $S^9$ | NNNNNNNNNNNN |
| | 11 Mar 90 | | NNN | NN44GG | $S^9$ | N1NN4NNNNNNN |

[1] Ad = adult; Juv = juvenile.

s.d., $n$ = 18; left wing and whole tail taken together) than the adults at the Mtito Andei wintering site (5.9 ± 7.9 s.d., $n$ = 11; Mann-Whitney $U$-test, $U$ = 161, $P$ = 0.005; see Table 1, Fig. 2).

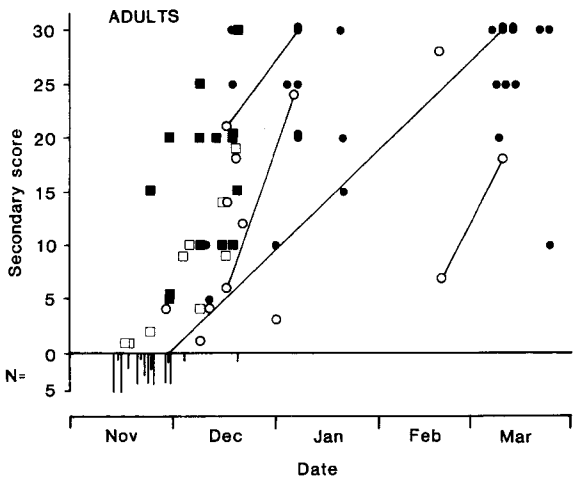


**Figure 2.** Moult status of secondaries in adult Barred Warblers trapped at Ngulia (squares) and Mtito Andei (circles) in Kenya in the winters 1989/90, 1990/91 and 1991/92. Symbols and data treatment as in Figure 1.

The main period of flight feather moult at Mtito Andei was late November and December (Table 1, Fig. 2). One particularly heavily moulting female on 20 December had all tertials, all secondaries and seven tail feathers growing simultaneously. Five other birds had 3–5 secondaries per wing, 1–3 tertials per wing, and up to 10 tail feathers in growth. The earliest bird at this site with an apparently complete winter moult was caught on 19 December. The last extensively moulting individual was caught on 1 January (Table 2), and only the occasional replacement of secondaries and tail feathers was noted from mid-January. Any secondaries not moulted were usually the outer ones. With a few exceptions, birds moulted their secondaries convergently, that is, the first secondaries to be shed were the inner- and outermost, with two moult centres moving towards the middle of the tract (see, for example, individuals A35645 and A35668 in Table 2). New outer primaries (1–3 per wing) were noted in only three out of 16 birds. As in first-year birds, body feathers and upperwing-coverts were moulted together with the flight feathers, and some body feathers were still growing in February–March. To judge from February–March birds, which had probably finished moult (Table 1), adult Barred Warblers typically replaced all tertials and tail feathers and almost all secondaries in winter.

At Mtito Andei, two birds ringed as adults the first season were retrapped the next, while five adults were retrapped

at least once within the same season (Table 2). Of particular interest were two birds that moulted individual tail feathers twice within the same winter.

## DISCUSSION

### Location of the East African moulting grounds

Barred Warblers are known to winter in only a limited area of eastern Africa, in northern and eastern Kenya, northeastern Tanzania and probably southern Ethiopia (Moreau 1972, Pearson 1978). Most of the Barred Warblers at Ngulia in November had hardly begun their winter moult. These birds had presumably travelled quickly south from stopover sites in Ethiopia (Pearson *et al.* 1988) and they presumably moulted in northeastern Tanzania later in winter. The birds caught at Mtito Andei during November–December (predominantly adults) were moulting and at least some remained to winter there. Thus, early Ngulia passage birds and the first local, wintering arrivals would seem not to begin moult until they had completed migration.

By contrast, most adults at Ngulia in December, and both adults and first-year birds arriving at Mtito Andei from January onwards, appeared to have completed most or all of their winter moult elsewhere. They may have moulted further north in Kenya, but this would have had to be rapid since the species is not common there until mid-November (D.J. Pearson, pers. obs.). Alternatively, they might have moulted during an October–November stopover in Ethiopia, but such moult has not yet been noted in birds caught there in autumn (J.S. Ash, *in litt.*). In conclusion, Barred Warblers conduct their winter moult either just before or shortly after the last leg of their southward migration.

### Annual moult pattern

Hasselquist *et al.* (1988) concluded that the winter moult of the Barred Warbler involved most of the secondaries but only a few tail feathers and tertials. Because of the fresh appearance of some feathers of breeding birds in Sweden in June and July, together with information on caged first-year birds (Berthold 1987), they suggested that this moult occurred shortly before spring migration.

The present Kenyan study confirms in detail the earlier conclusions on primary and secondary moult but shows that the winter moult of tail and tertials is typically complete in both adults and first-year birds. It also reveals that the main winter moult period is earlier than originally supposed, during November–December. Whereas the secondaries moulted in winter fade slowly, the tertials and tail feathers (especially the central ones) wear quickly and appear bleached by the time birds are back on the breeding grounds. Hasselquist *et al.* (1988) therefore assumed that many tertials and tail feathers had not been moulted in winter. Some of the tertials and tail feathers recorded in Sweden as fresh (=winter moulted) were, however, probably single feathers remoulted in late winter. Some feathers may be moulted twice in one winter season, as retrapped birds have shown, though whether this is an adaptive strategy or the result of accidental loss is not clear.

Using data from both summer and winter quarters (Hasselquist *et al.* 1988, this study), we can summarize the year-round pattern of flight feather moult in the Barred Warbler (Fig. 3). During their first winter, mainly in November–December, young birds moult all tertials and tail feathers, about half their secondaries (especially the innermost) and often their outer primaries. On their breeding grounds, between late June and late August, first-summer birds moult all primaries and tertials, as well as the central tail feathers and the odd (usually outer) secondary. In Africa, during November–December (January), adults renew all tertials and tail feathers and most of (sometimes all) their secondaries but seldom any primaries. Moult in later breeding seasons is similar to the first summer moult.

Thus, Barred Warblers divide their moult over the year, so that primaries, secondaries and most tail feathers are moulted once, whereas tertials and centre tail feathers are moulted twice. In their first year, outer primaries may also be moulted twice. A biannual moult of tertials and centre tail feathers is easily explained considering the heavy exposure and wear these feathers receive. Moult of outer primaries during the first winter presumably improves flight performance for the demanding northward migration. If not moulted in winter, these feathers are distinctly more worn by spring in first-year birds than in adults. This strategy of replacing outer primaries before a long spring migration is also found in first-year, but not adult, Indigo Buntings *Passerina cyanea* (Rowher 1986) and is well known in first-year northern waders that winter in or south of the tropics (e.g. Prater *et al.* 1977). A similar behaviour is adopted by adult River Warblers *Locustella fluviatilis* before embarking on a late autumn migration from northeastern to southern Africa (Pearson & Backhurst 1983).

The seasonally divided moult pattern of the Barred Warblers clearly begins in the birds' first winter, with the renewal of several secondaries. Accordingly, when birds leave their breeding grounds the following summer these feathers are still quite new, and it is not because of shortage of time that particular season that they remain unmoulted (cf. Hyytiä & Vikberg 1973, Mead & Watmough 1976, Swann & Baillie 1979, Norman 1991). The relative freshness of the juvenile secondaries replaced in winter argues against wear as a cause for their moult. Instead, it is reasonable to assume that its initiation is endogenously controlled.

The ultimate causes for a split moult in the Barred Warbler remain to be established. Hasselquist *et al.* (1988) suggested that, by renewing some secondaries in winter, first-year birds are able to complete moult faster the following summer and so leave for Africa earlier. Various ecological factors might favour an early departure from the breeding grounds. For example, it may be important to avoid intra- or interspecific competition on autumn stopover sites (cf. Rappole & Warner 1976, Carpenter *et al.* 1983, Moore & Yong 1991), to reach

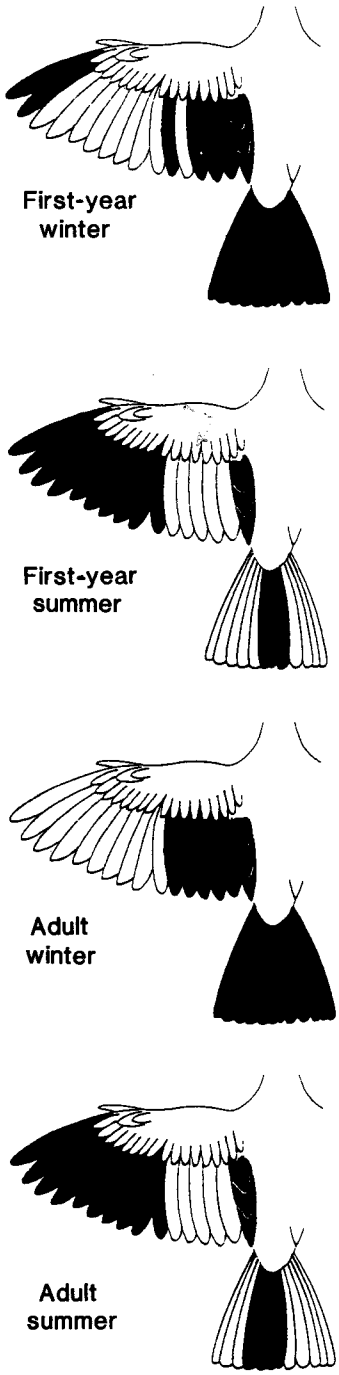


**Figure 3.** A schematic presentation of the annual pattern of flight feather moult in the Barred Warbler, from the winter moult of first-year birds to the summer moult of adults. 'First-year summer' refers to second calendar year birds (Euring code 5). The moult of one wing and the whole tail is shown. Shaded feathers are moulted in the respective season. Data on summer moult are from Hasselquist *et al.* (1988).

abundant stopover food resources in time (Bibby & Green 1981) or to arrive early at the wintering grounds to secure good territories (Price 1981). Although we could not definitely establish that Barred Warblers at Mtito held winter territories, frequent calling and chasing behaviour, especially close to dawn and dusk, were indicative of territorial behaviour (cf. Price 1981, Kelsey 1989).

Observations on autumn passage in northern Sudan revealed a similar split moult strategy in some other passerine migrants (Nikolaus & Pearson 1991). Thus, adults of Orphean Warbler *Sylvia hortensis* (see also Berthold & Querner 1982), Ortolan Bunting *Emberiza hortulana*, Masked Shrike *Lanius nubicus* and Woodchat Shrike *L. senator* commonly moult all primaries in summer but few or no secondaries. However, the details of winter moult and its extent in first-year birds are not yet known in these other species. Interspecific comparisons may well help to reveal the adaptive value of these split moult patterns.

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