

BREEDING AND MOULT CYCLES OF SOME MONTANE FOREST BIRDS IN SOUTH-CENTRAL AFRICA

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The breeding seasons of forest birds in tropical Africa have received quite a lot of attention, reviews covering large parts of the continent being by Chapin (1932), Moreau (1950), Benson (1963) and Brown & Britton (1980), among others. However, the data used by these authors were of necessity gathered over a number of years, and often from diverse places. If breeding seasons are flexible in relation to climatic differences between years, then the seasonality apparent from lumping all years greatly exceeds that in any one year. Brown & Britton (1980) attempted to relate breeding seasons to regional climate in East Africa, but even so their regions have been criticized as being still too heterogenous (Diamond, 1981), and their resulting sample sizes are very small. Even when analysis is confined to the forests of a limited area, as in Tanzania (Moreau, 1950 ; Beesley, 1973) and Cameroon (Serle, 1981), the small samples for each species, gathered over several years as a rule, greatly limit the conclusions that may be drawn.

Moreover, none of these studies successfully relates the breeding cycle to that of moult, although Moreau (1936) and Moreau *et al.* (1947) attempted to with the limited moult data available to them. Yet it has become clear from several studies elsewhere in the tropics that the timing of moult is of considerable importance, possibly even determining to a great extent the time available for breeding (Snow & Snow, 1964 ; Fogden, 1972 ; Diamond, 1974). Consequently, we paid particular attention to the relationship between breeding and moult in the forest birds of the Nyika Plateau, in south-central Africa, during a residence spanning three consecutive breeding seasons. This paper analyses more than 1000 egg-laying records and moult data from more than 2000 birds handled.

Nomenclature follows Benson *et al.* (1971), as amended by Dowsett & Dowsett-Lemaire (1980).

STUDY AREA AND METHODS

The Nyika Plateau lies between 10 and 11° S, mostly in Malawi with a salient of territory in Zambia, and is within the boundaries of National Parks in both countries. The Plateau consists of extensive rolling grasslands, mostly

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between 2000 and 2500 m alt., scattered about with small patches of evergreen forest. A detailed account of the area and the forest habitat is given in Dowsett-Lemaire (in press a). Our main study area was on the gentle south-western slopes, on both sides of the international border. All ringing activities (mostly by R.J.D.) and most field observations (mainly by F.D.-L.) were undertaken in Chowo Forest (90 ha, the largest on the western Nyika) and nearby small patches (in Zovochipolo), all lying between 2100 and 2225 m. The forests there have a tall canopy (20-25 m) with emergent trees and numerous lianas; they belong to the « Submontane » type of forest as defined by Chapman & White (1970).

We were resident on the Plateau from late October 1979 to March 1982; the periods when we were both absent cover August 1980 and May - July 1981. Breeding records were backdated to the month of laying and come from a variety of sources: mistnetted females in a laying condition or with an early brood patch, occupied nests (especially sought for hole-nesting species that can be watched at a distance without being disturbed), and above all observations of dependent young (often of individually colour-ringed parents). The period of post-fledging dependence in many small passerines is about a month. It soon appeared that an active search for low nests led to an increase in predation (Dowsett-Lemaire, in press c) and so this method was quickly abandoned. In two species, behavioural data could also be used. In the White-tailed Crested Flycatcher *Elminia albonotata*, females beg and are fed by the males at the onset of breeding. In the Cape Batis *Batis capensis*, females beg vigorously throughout incubation, but much less after the young hatch. Besides Chowo Forest and 80 patches in Zovochipolo (0.12 — 12 ha), visits were also paid to some lower - and higher - altitude forests, between 1925 and 2450 m (see Dowsett-Lemaire, in press a).

TABLE I

Monthly samples of adult birds of 11 common forest species examined in the hand for moult on the Nyika Plateau.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
<i>Andropadus tephrolaemus</i>	20	29	10	4	0	29	16	6	15	29	33	33	224
<i>Alethe fuelleborni</i>	11	21	9	0	0	9	0	0	6	19	30	44	149
<i>Cossypha anomala</i>	18	3	3	1	0	10	2	1	14	19	31	29	131
<i>Cossypha caffra</i>	15	1	2	0	0	0	2	4	3	9	8	35	79
<i>Pogonocichla stellata</i> ¹	88	18	8	0	0	11	6	0	27	107	155	200	620
<i>Turdus olivaceus</i>	13	1	0	0	0	5	0	0	1	10	10	5	45
<i>Apalis thoracica</i>	13	5	9	2	0	2	2	2	15	16	21	22	109
<i>Batis capensis</i>	11	11	5	0	0	20	4	3	15	18	37	42	166
<i>Elminia albonotata</i>	7	5	3	1	0	6	1	3	8	20	14	17	85
<i>Nectarinia mediocris</i>	17	23	8	5	0	7	8	4	4	18	20	43	157
<i>Zosterops senegalensis</i>	22	29	13	4	0	39	0	0	43	74	95	65	384
Totals	235	146	70	17	0	138	41	23	151	339	454	535	2149
%	11	7	3	1	0	6	2	1	7	16	21	25	100

1. Includes birds in first-year dress (3-15 months old).

Mist-netting was carried out in 11 small patches in Zovochipolo (from 0.16 to 1.2 ha in size, with a total of 7.3 ha) and in a 25 - ha portion of Chowo Forest. All birds caught were colour-ringed, weighed, measured and examined for moult and visible fat deposits, and whenever possible were sexed by cloacal examination (Dowsett, 1983 a). Monthly samples of the 11 main species captured and examined for moult are given in Table I. 82 % of these handlings relate to the main study period 1979 - 1982, previous visits to the area being only between October and early January, and of short duration.

ENVIRONMENTAL CONDITIONS

Monthly variations in temperature are shown in Table II. There is a definite cool season lasting mostly from May to August, whereas the hottest months are usually October and November. There is little variation overall, either inside forest or outside, during the « summer » (November - April) which coincides with the rainy season. Chilinda is 100 m higher than our main study area, and as the temperatures there are taken in an open situation, they are likely to be more variable than inside forest, with higher maxima and lower minima.

TABLE II

Temperature data (°C) from : Chilinda, Nyika National Park Headquarters at 2300 m a.s.l. (outside forest), and Zovochipolo at 2220 m (inside forest).

	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
Chilinda												
Years recorded	14	15	14	13	13	13	13	13	13	13	14	15
Mean maximum	19	21	21	20	19	20	19	18	18	17	17	17
Mean minimum	8	10	11	11	11	11	11	11	7	4	5	6
Zovochipolo												
1981-82												
Mean maximum	20	20	21	19	18	18	18	18	-	-	-	18
Mean minimum	10	12	13	12	12	12	12	10	-	-	-	9

Rainfall is strongly seasonal, though there is a good deal of variation in the timing of the start of the single rainy season (Fig. 1) and there may be dry spells of up to two weeks in the middle of it. Total figures for the three study seasons were 1881, 1314 and 1394 mm, a mean of 1530 mm. The first storms of each year, in October - November, always induce spectacular insect emergences in open situations up to the edge of forest patches, whereas inside forest they induce a flush of vegetation growth on the ground as well as on trunks (epiphytes).

Before the start of the rains however, insect activity inside forest has already increased as a result of two main factors. A few of the trees and large woody creepers are briefly deciduous, and foliage regrowth starts before the rains in most of them — from August to October. In our main study area, 20 common species are affected in this way, and the new foliage is immedia-

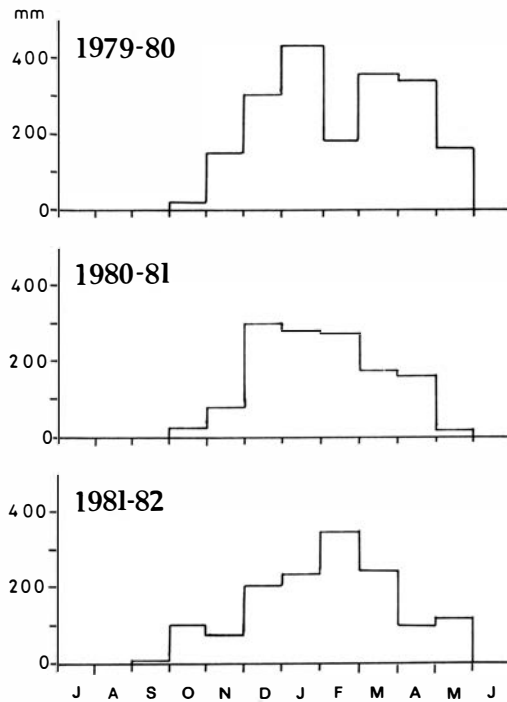


Figure 1. — Total rainfall (mm) recorded per month in the study area (Zovochipolo).

tely attacked by insect larvae. Moreover, Acanthaceae herbs and subshrubs, which dominate the undergrowth along streams and in some openings, flower from July to September - October and attract swarms of tiny insects then — mostly Hymenoptera and Diptera.

Subjectively, insect abundance seems highest in the second half of the dry season and the first half of the rains. Observations and mist-netting show that, by late December or early January, many of the commonest species (e.g. Mountain Bulbul *Andropadus tephrolaemus*, Starred Robin *Pogonocichla stellata*, Bar-throated Apalis *Apalis thoracica* and all Muscicapidae) move to feed higher in the mid-stratum, canopy and on the forest edge. Because of this wide vertical range of feeding in many species, conventional methods of insect sampling (at ground level) were not considered worthwhile.

Details of the periodicity of fruiting will be published later (Dowsett-Lemaire, in prep.). In brief, species of edible fruits are almost twice as abundant from late August to November as at other times of year.

BREEDING SEASONS

Except for the two *Nectarinia* sunbirds and, perhaps, the Red-faced Crimsonwing *Cryptospiza reichenovii*, the breeding activities of the Nyika forest birds are concentrated at the end of the dry season and at the beginning of the rains (Table III). For 14 species with over 20 breeding records, 90 % or

more of these are within a period of two to four months. There is no indication here that breeding seasons, as claimed by Kunkel (1974) for equatorial and tropical forest birds, are very extended. For this part of Africa, Kunkel referred to data in Benson (1963), of which he said that « for most of the bird species the nests recorded during any one month hardly ever account for more than 20 % of the year's total ». This statement is largely untrue, even where (Tables 1 and 6) Benson has presented the records per families and not as a rule per species. In any case, care is needed in trying to interpret records lumped for several species, or records collected from many localities over many years — as was also done by Moreau (1950) and Brown & Britton (1980). In the 14 species with over 20 records in Table III, there are at least two months with over 20 % of records.

TABLE III

Breeding seasons of forest birds on the Nyika Plateau : number of clutches started each month, 1979-1982 (3 seasons).

		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Totals
Columbidae	<u>Columba arquatrix</u>						3	1						4
	<u>Turtur tympanistria</u>				1	2								3
	<u>Aplopelia larvata</u>				1			2	3					6
Musophagidae	<u>Tauraco livingstonii</u>					1	2							3
Trogonidae	<u>Apaloderma vittatum</u>						3	1						4
Bucerotidae	<u>Tockus albeterminatus</u>				2									2
Capitonidae	<u>Pogoniulus leucomystax</u>					3	54	18	2					77
Indicatoridae	<u>Indicator variegatus</u>				2	1								3
Picidae	<u>Dendropicos griseocephalus</u>			9	15	8								32
Timaliidae	<u>Alcippe abyssinica</u>						4	2						6
Pycnonotidae	<u>Andropadus tephrolaemus</u>				7	21	16	4						48
	<u>Phyllastrephus flavostriatus</u>						2	2	1					5
Turdidae	<u>Alethe fuelleborni</u>						2	19	8	4				33
	<u>Cossypha anomala</u>							22	20	6				48
	<u>C. caffra</u>						4	9	9	3				25
	<u>Pogonocichla stellata</u>					5	64	120	63	6				258
	<u>Sheppardia sharpei</u>						5	1	1					7
	<u>Turdus olivaceus</u>					3	12	7	1					23
	<u>T. gurneyi</u>							1	1					2
Sylviidae	<u>Bradypterus mariae</u>							2	7	3				12
	<u>B. cinnamomeus</u>							3	9	2	1			15
	<u>Chloropeta similis</u>								1	5	4			10
	<u>Apalis thoracica</u>					1	13	15	5	5	1			40
	<u>A. chapini</u>						1	1	2					4
Muscicapidae	<u>Muscicapa adusta</u>					1	3	1	1					6
	<u>Batis capensis</u>					31	49	37	40	8	3			168
	<u>Elminia albonotata</u>					2	11	20	15	1				49
Malaconotidae	<u>Dryocopus cubla</u>				2									2
	<u>Laniarius fuelleborni</u>						1	1	2	2				6
Sturnidae	<u>Onychognathus walleri</u>				2	10	11	3						26
	<u>Cinnyricinclus leucogaster</u>						4							4
Nectariniidae	<u>Nectarinia verticalis</u>								1	1	2		1	5
	<u>N. mediocris</u>	1	6	7	10	4	1						1	30
Zosteropidae	<u>Zosterops senegalensis</u>					7	46	19	3					75
Estrildidae	<u>Cryptospiza reichenovii</u>			1	1	1								3
Totals		1	7	17	41	102	311	311	193	48	11	0	2	1044
		<1	<1	2	4	10	30	30	19	5	1	0	<1	

The bias introduced by the lumping of records from different localities is illustrated for *Pogonocichla stellata* in Fig. 2 f : these records are from various localities in Malawi excluding the Nyika (Benson & Benson, 1977), and show a rather misleading picture. Whether January laying is important elsewhere is not known, but certainly December is under-represented. Fig. 2 d also shows how the timing of short visits to an area (in this case most visits were at the end of the year) can put a false emphasis on a particular month (December), as opposed to the results of our three seasons of residence which clearly show the preponderance of November records. There is also an annual variation in the timing of egg-laying (Fig. 2 a-c), which for *Pogonocichla* at least can be best explained by the annual variations in breeding success. The species was most successful in 1979-1980 (Dowsett-Lemaire, in press c) when few re-layings were necessary, and least successful in 1981-1982 when we find the highest proportion of December - January records (mostly re-layings).

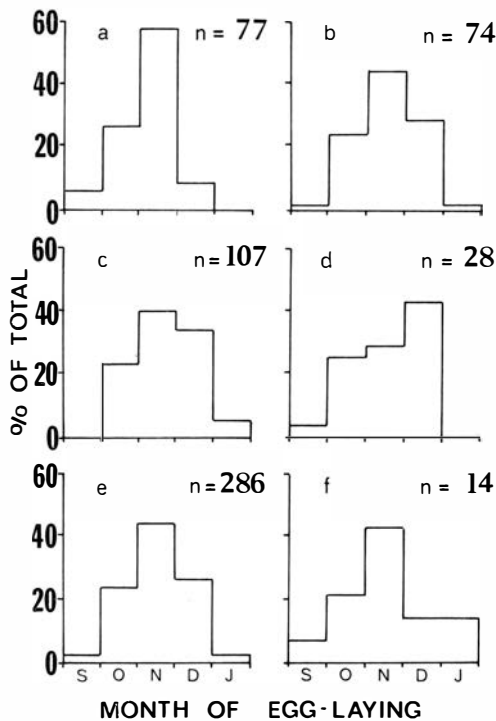


Figure 2. — *Pogonocichla stellata* breeding seasons, as shown by histograms of egg-laying records per month : (a — e) Nyika Plateau (a = 1979-1980 ; b = 1980-1981 ; c = 1981-1982 ; d = pre-1979 ; e = total all years) ; (f) elsewhere in Malawi.

Not surprisingly the short breeding seasons observed are associated with single-broodedness. Exceptionally, in 1980, three pairs of Moustached Green Tinkerbird *Pogoniulus leucomystax* apparently raised a second brood — these account for the two December layings (Table III) and one in late November.

In 1980-1981, the favourite Loranthaceae berries consumed by these birds and fed to nestlings (*Englerina inaequilatera*) continued to fruit later than in other years ; in 1981 fruiting ended in December. Only one pair of one other species (Waller's Red-winged Starling *Onychognathus walleri*) was known to make an attempt at a second nesting (Dowsett-Lemaire, 1983 a).

Species with a pure fruit diet (Rameron Pigeon *Columba arquatrix*, Green Loerie *Tauraco livingstonii*), those in which fruit is at least important (*Pogoniulus leucomystax*, *Andropadus tephrolaemus*, Yellow White-eye *Zosterops senegalensis*) and the ground doves which eat many seeds of fallen fruits all breed during the peak of fruit availability. The differences in diet between the ground-feeding Tambourine Dove *Turtur tympanistria* and the larger Cinnamon Dove *Aplopelia larvata* are not well-known, but their respective seasons seem distinct. Although the actual records are few (Table III), our impression is reinforced by the very different patterns in vocal activity : the last songs of *Turtur tympanistria* are normally heard in October whereas *Aplopelia larvata* is most vocal in November and December.

Cryptospiza reichenovii is the only grass-seed eater, but it also consumes small insects. Forest grasses mature between March - April and November ; the breeding season of *Cryptospiza* seems limited to the second half of that period, possibly because small insects (particularly those attracted to the thickets of flowering Acanthaceae) are more abundant then. Although back-dated records are few (Table III), we had more than a dozen records of singing males and alarm-calling pairs (some obviously with young) from August to October.

The two species of *Nectarinia*, the Green-headed Sunbird *N. verticalis* and the Eastern Double-collared Sunbird *N. mediocris*, are active at different seasons (Table III), though the reasons for this are not understood. In the case of *N. mediocris* there is a slight peak of nectar flowers in the dry season (around July, Dowsett-Lemaire, in prep.), but probably of more importance is the fact that the greater number of forest edge shrubs (e.g. *Buddleia*, *Gnidia*, *Hypericum*, *Kotschyia*) flower in the dry season and attract many small insects on which these sunbirds feed. The same applies to the undergrowth vegetation.

It is difficult to discuss the habits of insectivorous species without knowing more about their specific diet. Generally, it appears that species that sally and snatch off bark and foliage and/or flycatch start to breed earlier than the foliage gleaners proper, i.e. before the beginning of the rains (for example *Pogonocichla* and the three Muscicapidae, as opposed to most Sylviidae and Fülleborn's Black Boubou *Laniarius fülleborni*). In the Turdidae that feed on or near the ground (e.g. the Olive-flanked Robin *Cossypha anomala*), moist conditions are obviously important. The White-chested Alethe *Alethe fülleborni* is a specialized ant-follower (cf. Dowsett-Lemaire, in press a) and army ants are much more active in the rains than in the dry season. The few breeding records coupled with many of singing birds indicate that the Orange Thrush *Turdus gurneyi* is active in the rains, in contrast to the Mountain Thrush *T. olivaceus* ; data on the differences in diet are needed to understand this limited overlap.

The Scaly-throated Honeyguide *Indicator variegatus* parasitizes the nests of Olive Woodpeckers *Dendropicos griseocephalus* (Dowsett-Lemaire, 1983 b, in press b). The latter feed on insect larvae under the bark, and these are

probably more accessible in the warmer second half of the dry season, before the emergences of imagoes in the rains.

Even though rainfall is strongly seasonal on the Nyika, it is unlikely to be the « Zeitgeber » stimulating breeding in most species (cf. Stiles, 1980) ; in any case, the majority of birds start breeding before the onset of the rains. Although experimental evidence is lacking, it seems more likely that the proximate factors for most species are the actual increases in food availability — e.g. for frugivores, the increase in the number of fruiting plant species in August - September.

It is clear from Table III and from the above discussion that any attempt to generalize about forest breeding seasons must be a simplification, possibly of limited value in view of the varied and special requirements of each species. However, the preponderance of breeding records for the late dry season and early rains is striking, and is in accord with some studies elsewhere.

In Africa, avoidance of the heavy rains for breeding has been reported for forest birds from montane Cameroon (Serle, 1981) and southwards from Tanzania (Moreau, 1950). Moreau's generalization that most forest birds begin to breed before the rains set in, and have nearly all finished by the time they are half over, probably holds good for much of highland Africa in which there is a single rainy season. The conclusion of Brown & Britton (1980) in East Africa, that insectivorous forest passerines « which breed in relatively-cold montane forests usually prefer the dry season » is in need of confirmation.

Elsewhere in the tropics studies of breeding seasons have been mainly from areas with two more-or-less distinct rainy seasons (Snow & Snow, 1964 ; Diamond, 1974) or with more rain over a much longer period than on the Nyika (Fogden, 1972). In Jamaica (Diamond, 1974), as in Africa (Moreau, 1950), the main heavy rains appear to be avoided by most species. In Trinidad (Snow & Snow, 1964), most breeding appears to be over by the middle of the main wet season, although the nesting seasons of some species cover a large part of the year (e.g. two *Turdus* species). But in Sarawak (Fogden, 1972), there seems to be a gradual increase in breeding activity with the increase in rain, peaking just after the main rains. Local differences in peak food availability doubtless influence breeding seasons, but the period of moult may also determine the end of breeding in some situations.

Finally, evidence for more than one brood (coupled with extended breeding seasons) in tropical forest birds is so far limited (Snow & Snow, 1963 ; Willis, 1974).

THE MOULT CYCLE

Adult and post-juvenile moults

Of the 43 species that regularly breed in the study area forests, we have observations of active moult of the remiges in 29. All of these appear to be post-nuptial moults. For most species a moult of remiges and rectrices is undertaken only by adults, juvenile birds of about 3 months of age moulting only the body feathers. This is proven in the ten following passerines : *Andropadus tephrolaemus*, *Alethe fuelleborni*, *Cossypha anomala*, *Pogonocichla stellata*, *Turdus olivaceus*, *Apalis thoracica*, *Batis capensis*, *Elminia albonotata*,

Black-fronted Bush Shrike *Malaconotus multicolor* and *Nectarinia mediocris*. In two nonpasserines, however, juveniles do have a complete moult (including remiges) at the same time as adults, namely *Turtur tympanistria* and Bar-tailed Trogon *Apaloderma vittatum*. It is likely to be also the case in one passerine, *Zosterops senegalensis* : although some individuals are not moulting during the period that most of the population is, the numbers involved are probably too small for these to be all the juveniles. There are no retraps of definitely-aged juveniles to confirm that they do moult completely.

In the two species for which the most complete data are available, the unmoulted juvenile wing is shorter than that of the adult. First-year *Pogonocichla stellata* retrapped as adults had increased wing-lengths on their first full moult (at about 15 months of age) by 3 - 4 mm or 4 - 5 % (n = 26). This species has a distinctive olive yearling plumage, quite unlike that of the monochromatic adults, but in *Alethe fuelleborni* the shorterwinged juveniles are otherwise inseparable from adults. They could, in fact, be confused with the adult females (smaller than males), at least outside the breeding seasons when inactive females no longer exhibit a brood patch. Consequently, in this and other species in which the juvenile remiges are not moulted during the first year, the use of differences in wing-lengths to sex individual birds is not recommended (Dowsett, 1983 a).

In most species first-year birds essentially resemble adults in plumage, the only notable exceptions (apart from *Pogonocichla* already mentioned) being *Apaloderma vittatum* and *Batis capensis*, both of which have a female-like yearling dress. In a few species first-year birds may retain some of the distinctive juvenile wing coverts (e.g. *Cossypha anomala*, *Turdus olivaceus* and *Elminia albonotata*), although the lesser and median coverts at least are usually moulted.

That there is only a partial moult by most juveniles is in contrast to the situation in the lowland forests of Sarawak, where Fogden (1972) reported that juveniles of all the species examined, both passerine and non-passerine, had a complete moult at the same time as adults. Fogden suggested that this might be because all the juvenile plumage was basically of poor quality, grown quickly to reduce the amount of time spent in the nest (when young are most vulnerable to predation). The Nyika is more like the temperate regions, where post-juvenile moults are usually confined to the contour plumage (Snow, 1967). Perhaps this is a result of pronounced seasonality of climate in these areas precluding an energy-consuming complete moult at the time when juveniles are newly independent. Fogden (1972) did not mention the length of nestling periods in Sarawak, but in Africa the 13.5 - 15.5 days in *Pogonocichla stellata* (Oatley, 1982 b) is little more than the 12 days reported for the comparable European Robin *Erithacus rubecula* (Lack, 1965). In any case, the moderate nest predation rates recorded for *Pogonocichla* and other species on the Nyika (Dowsett-Lemaire, in press c) would not be expected to favour especially short nestling periods ; the resulting quality of the juvenile plumage may be good enough for a complete moult to be unnecessary the first year.

In no species are there ever more than 3 or 4 primaries in each wing (excluding the outer primary) less than full grown at any time. In some non-passerines, the sequence of primary replacement is not strictly descendent but often irregular. Otherwise, moult of the various body tracts and flight feathers normally follows the same sequence in most species. For example, there is

a significant relationship between the timing of primary and secondary moult in *Pogonocichla stellata*, when moult scores are compared ($r = 0.93$, $n = 19$). Moult of the first secondaries in that and most other species does not usually start until the equivalent of about three primaries has been replaced. Tail moult may not start until much later — in the case of *Pogonocichla stellata* about six weeks after the start of primary moult. Body moult usually starts slightly before the remiges, and is the last to be completed.

Because of this general synchronization, it is possible to use primary moult score as an index of the progress of moult as a whole. The outermost primary is small in all the passerines considered here, and so for practical purposes the maximum primary score is 45, based on nine primaries. As pointed out by Evans (1966), where a linear relationship exists between primary moult score and date (as discussed below), this implies that each primary feather takes the same time to grow, irrespective of its length. Evans found this to be true in the Lesser Redpoll *Carduelis flammea*.

Duration of moult

In most of those species for which we have sufficiently large samples for any one year, there is a significant correlation between progress of moult (primary moult score) and date (e.g. Figs 3 - 5). Results for some species are shown in Table IV, where all the correlations are highly significant ($P < 0.001$). We have computed the regression lines to determine an approximate duration of individual moult, following Pimm (1976) in considering moult score rather than time the dependent variable. We have used data only from actively moulting birds, i.e. with primary scores of 1 - 44. Where several scores exist for an individual captured more than once in a season, we have taken the last score available. For each species, the annual regression line has been compared to the slopes of lines provided by multiple retraps of individual birds : this usually produced good agreement (e.g. Fig. 3), with the exception of a single *Pogonocichla stellata* in 1979-1980, whose slope suggested a period some 30 % longer than the regression line mean.

This mean was also compared to the figures for maximum moult duration provided by the many individuals caught just before or just after moult but only once during it, and which could not therefore be used directly. In no case did the regression line mean exceed these maxima.

Table IV details the mean duration of individual moult for six forest species, using those years in which the best correlation was obtained between primary score and date. For three additional species, which produced poorer correlation, there is good evidence for moult duration from retraps : Yellow-streaked Bulbul *Phyllastrephus flavostriatus* 145 days (mean weights : male 31.8 g, female 25.2 g), *Elminia albonotata* 105 days (mean weight 9.2 g) and *Zosterops senegalensis* 85 days (mean weight 10.9 g). For only two of these species have estimates of moult duration been made previously, *ca* 90 days in *Phyllastrephus flavostriatus* in Tanzania (Moreau *et al.*, 1947) and *ca* 42 - 56 days in *Pogonocichla stellata* in South Africa (Oatley, 1982 a). Both underestimates show the need for a sufficiently large sample of individually-marked moulting birds in such a study. The range of 83 - 145 days recorded in the Nyika forest passerines is similar to results obtained elsewhere in the tropics (Snow & Snow, 1964 ; Fogden, 1972 ; Diamond, 1974 ; Snow, 1976) and is

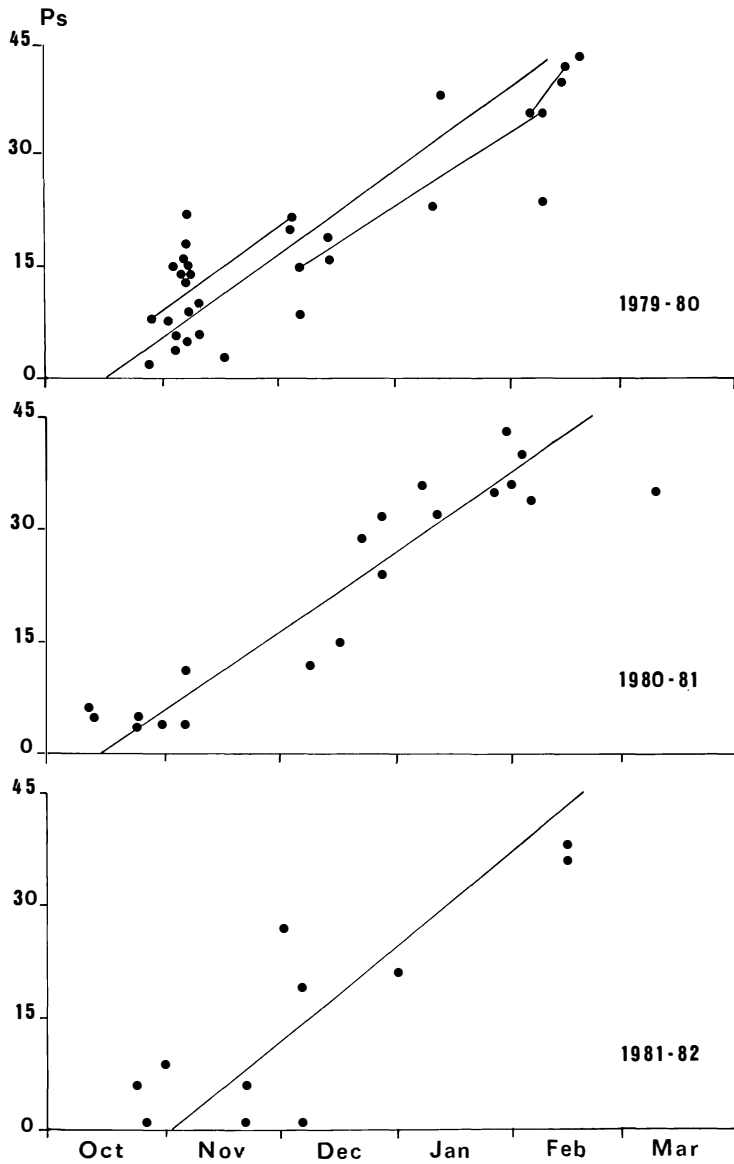


Figure 3. — Primary moulting score (Ps) in *Andropadus tephrolaemus*. Regression lines are shown for each season; in 1979-1980, three lines also connect retraps of individuals.

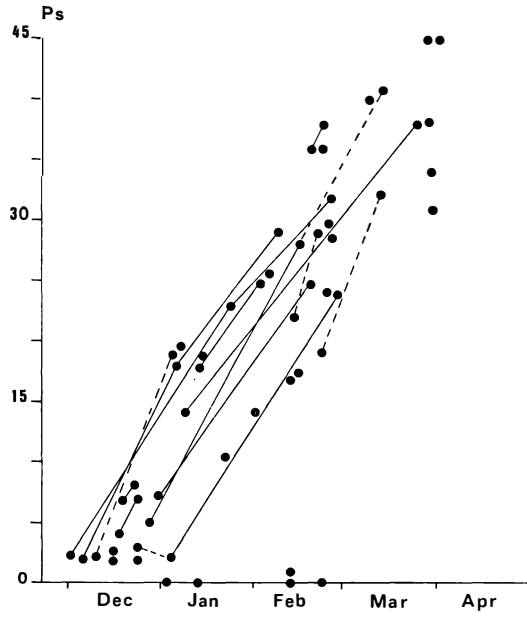


Figure 4. — Primary moult score (Ps) in *Alethe fuelleborni*. Solid lines connect same-season retraps, broken lines later-season retraps.

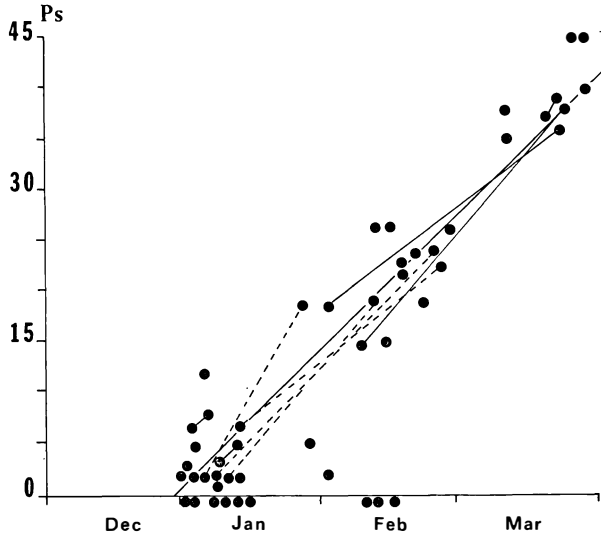


Figure 5. — Primary moult score (Ps) in *Pogonocichla stellata*. Solid lines connect same-season retraps and show the regression line, broken lines later-season retraps.

TABLE IV

The mean duration of individual moult in some forest birds on the Nyika Plateau.

Species	Mean weight (g)	Year	n ¹	Mean duration of moult (days)	Correlation ²
<u>Andropadus tephrolaemus</u>	37.6	1980-81	20	131	$\bar{r} = 0.93$
<u>Alethe fuelleborni</u>	49.4	1979-80	17	126	0.86
<u>Pogonocichla stellata</u>	18.6	1979-80	23	100	0.96
<u>Apalis thoracica</u>	12.1	1979-80	14	83	0.90
<u>Batis capensis</u>	12.8	1979-80	14	105	0.83
<u>Nectarinia mediocris</u>	8.3	1980	13	96	0.85

1. n = number of individual adults moulting remiges

2. Correlation between date and primary moult score

in striking contrast to the shorter periods known for temperate region species (Fogden, 1972).

In the six species dealt with in Table IV in addition to *Phyllastrephus*, *Elminia* and *Zosterops*, there appears to be no strongly significant correlation between mean body weight and individual moult duration ($r = 0.75$, $P = 0.02$). However, in those five species in Table IV which complete moult just before the cold weather (i.e. excluding *Nectarinia mediocris*) there is a rather stronger correlation between moult duration and the mean date on which moult started ($r = -0.95$, $P < 0.02$). That is to say, those species that start moulting latest have the shortest individual moult durations. This, if proven by further investigation, would provide strong support for the idea that moult needs to be completed by a certain time, possibly to avoid the cold weather, the « lean season » (Ward, 1969 ; Fogden, 1972) when feeding is probably difficult. Multiple regression analysis of these preliminary data suggests that the mean date on which moult starts may account for as much as 90 % of the variation in moult duration. However, these data are too few to be more than a pointer to further investigation.

Fig. 3 suggests that *Andropadus tephrolaemus* were able to speed up their moult after a late start in 1981-1982, as was claimed for some of the data presented by Fogden (1972). However, comparison of the three regression lines (using F in an analysis of variance) shows there to be no significant difference between the three years ($F = 0.84$, $P > 0.05$). Further data would be needed to prove that an increase in the rate of moult can occur, but the variation in the mean figures for this one species over three years (110 - 131 days) does imply some flexibility. Fogden (1972) suggested that, in lowland Sarawak, most species time their moult to avoid the lean season, individuals starting late even speeding up (although the evidence for this appeared to be limited). On the other hand, the existence of an endogenous mechanism predetermining the start of moult — in order to have it completed before the lean season — had been suggested by Snow & Snow (1964) for the Trinidad forest birds.

Timing of moult

All but two of the 24 passerine species studied moult between October and April, the exceptions being two sunbirds : the few data for *Nectarinia verticalis* suggest they moult between June and September, while *Nectarinia mediocris* starts as early as July. Fig. 6 compares the timing of moult with that of breeding in those 11 forest species for which we have most data.

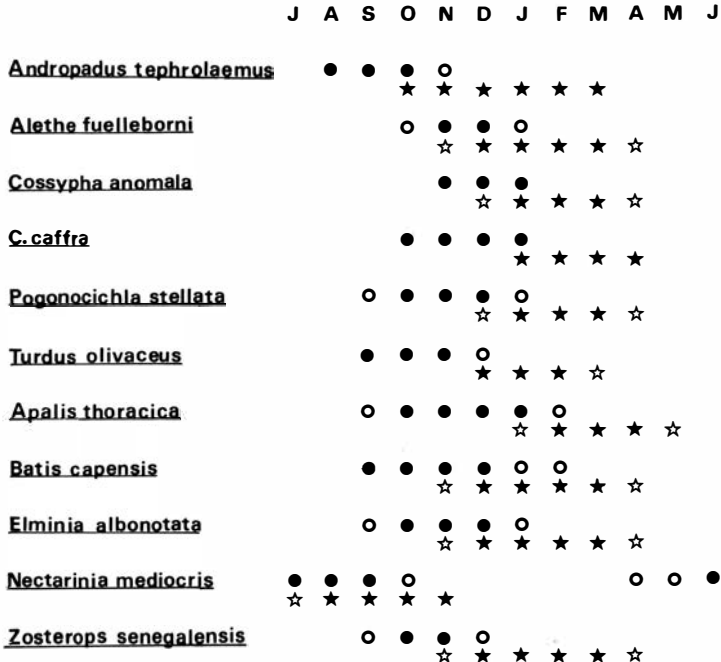


Figure 6. — The timing of moult (stars) is shown in relation to egg-laying (dots - circles) in some forest birds on the Nyika Plateau. Open symbols denote months with fewer than 10 % birds breeding/moulting. The pattern of the end of moult in some species rarely or not caught in April - May (cf. Table I) is inferred from regression lines.

Of the birds that moult mainly during the rains, the first to start (in October) is *Andropadus tephrolaemus*, with at least nine other species starting during November. Commencement of moult is not necessarily related directly to the start of breeding : for example, the first *Pogonocichla stellata* regularly begin to replace the first remiges and body feathers in the last few days of December, which is some time after some other forest Turdidae which start breeding later (e.g. *Alethe fuelleborni*). We have few data for the start of moult in any non-passerines, and in these moult duration may be protracted, judging by the results of Fogden (1972).

We have evidence of out-of-season moult in only one species on the Nyika : two *Zosterops senegalensis* were in active moult, only half advanced, in mid-June, more than two months after the rest of the population had finished. The many others handled at that time had no more than a few body

feathers still in moult. We have no other evidence of delayed or arrested moult, and in most species there were no known adults that did not moult each year. Fogden (1972), on the other hand, found that individuals of many species (including passerines such as bulbuls, babblers and flycatchers) did not necessarily moult each year.

In spite of the close correlation in the start of moult by most individuals, there were some that evidently started moult very late (Figs 3 - 5). These were invariably adults (mostly females, although there may have been some capture bias) which had dependent young to a late date. In *Pogonocichla stellata* no fewer than 10 females had still not started moult after 10 January, but there was not room to plot them all in Fig. 5. One of these had started replacing primaries by 1 February, when its juveniles were independent. No second broods were recorded in any of these passerines, and late broods were presumably all from replacement clutches. In such cases, delayed moult affected both male and female : for example, a pair of *Alethe juelleborni* were caught on 12 February, the female not yet moulting, the male just starting (Fig. 4). Fogden (1972) also found in Sarawak that adults with late broods could delay moult. Unfortunately we have no evidence from the Nyika of the duration of moult in such birds, whether they speed up to avoid the lean season (as suggested by Fogden) or whether they arrest moult then, and complete it later.

Annual variation in the start of moult was proven in a few individuals. In *Andropadus tephrolaemus*, for example, one female started 51 days after the mean date in 1979-1980, but only 21 days after the next year. Another started moult one day in advance of the mean in 1980-1981, but 19 days after the mean the next year. Presumably such variation is a direct result of the date on which any young reared become independent.

The start of moult by the majority of the population varies less each year. For example, there was less than one day's difference in the mean date moult started in *Pogonocichla stellata* in 1979-1980 and 1980-1981, and in *Andropadus tephrolaemus* a difference of only 1.5 days between those two years. For *Pogonocichla*, this consistency is especially striking, in two years which saw very different weather conditions, breeding success (Dowsett-Lemaire, in press c) and timing of breeding. However, in *Andropadus* moult started 18 days later on average in 1981-1982, although it finished at much the same time (Fig. 3). Interestingly, this last breeding season was a very poor one for *Andropadus*, with very few young reared (Dowsett-Lemaire, in press c). Snow & Snow (1964) showed there was much variation in the start of moult each year in Trinidad in some individual manakins (up to 26 days in successive years and up to 78 days over five years), although in other species there was less variation (e.g. two to 14 days' difference in successive years). Fogden (1972) reported that the timing of moult in Sarawak was similar during two years in most of the species studied, with the exception of some bulbuls *Pycnonotus* spp. which started moult some 2 - 3 months earlier in a season in which most had abandoned breeding attempts early on. Such extreme flexibility in the start of moult probably does not exist in Nyika species, judging by our observations over three seasons.

THE RELATIONSHIP BETWEEN MOULT AND BREEDING

Although Fig. 6 shows an overlap between breeding and moult in all species overall, we have little evidence of such an overlap in any individual passerine, among hundreds of moulting or breeding individuals examined. In *Pogonocichla stellata* for instance, no adult known to be still feeding young in January - February ($n = 21$) had begun to moult remiges. Only one female with dependent fledglings had a few body feathers in pin (in February). Conversely, individual case-histories show that birds which commence moult early either did not breed or completed the raising of a brood in the earlier part of the nesting season. Thus in *Alethe fuelleborni* a male that started wing moult as early as the first week of December was unmated, and a pair that began in the course of December had just been deserted by their independent young (fledged early, in November).

There is however occasionally an overlap between male gonad activity and primary moult in its earliest stages, based on males which still have prominent cloacal protuberances — but these did not seem to be still in charge of a family. The period during which males are sexually active is quite long : for example, individual male *Pogonocichla* can be active from mid-September to early January.

Fogden (1972) also found a lack of overlap between breeding and moult in forest birds in Sarawak. In the tropics and elsewhere the majority of birds have moulting schedules that do not overlap with breeding activities (Payne, 1972). The number of species where an overlap has been reported is, however, not negligible and now approaches 300 (Payne, *in litt.*), 200 more than was known by 1972. But these figures may be too high in so far as the evidence for some species is only circumstantial, i.e. comes from individuals moulting within the species's breeding season but not proven to be actually nesting themselves. In any case, the overlap of moult and breeding is recorded mostly for birds from habitats other than tropical forests (Payne, 1972). In a review covering the tropics, Foster (1975 a) found evidence of breeding females actively moulting remiges for rather few species, and no more than two were forest passerines (both Neotropical, the Barred Woodcreeper *Dendrocolaptes certhia* and the Blue-grey Tanager *Thraupis episcopus*). In the case of the latter, D.W. Snow (*pers comm.*) considers the date unusual, suggesting the female had in fact finished breeding. The Neotropical data relating to forest passerine birds are no more extensive than those from Africa, referred to by Foster (1975 a). A female Grey Cuckoo-shrike *Coracina caesia* with eggs in South Africa was growing many back feathers and most rectrices (Payne, 1969), which suggests it may have had an accident (a suggestion with which R.B. Payne, *in litt.*, is in agreement). Foster (1975 a) quoted Britton (1972) as showing moult-breeding overlap in the Yellow-whiskered Bulbul *Andropadus latirostris* (in Kakamega, western Kenya), but in fact this species has a protracted breeding season (Brown & Britton, 1980), and Britton (1972) claimed no evidence for overlap in any individual bird.

Moreau *et al.* (1947) had criticized the assumption that moult in tropical forest birds starts only after breeding, but their contrary evidence involved only male specimens whose testes contained free spermatozoa.

Foster (1975 b) suggested that tropical birds could increase substantially the length of their reproductive period and thus the potential number of

young produced, by moulting and breeding simultaneously. We have no evidence that such overlap is other than marginal in any of the Nyika forest passerines, whose breeding is strictly limited by seasonal factors. As pointed out by Keast (1968), an overlap between breeding and moult would be most advantageous in highly unpredictable habitats, not those such as tropical montane forests in which there is fairly regular seasonality, and time for only one brood.

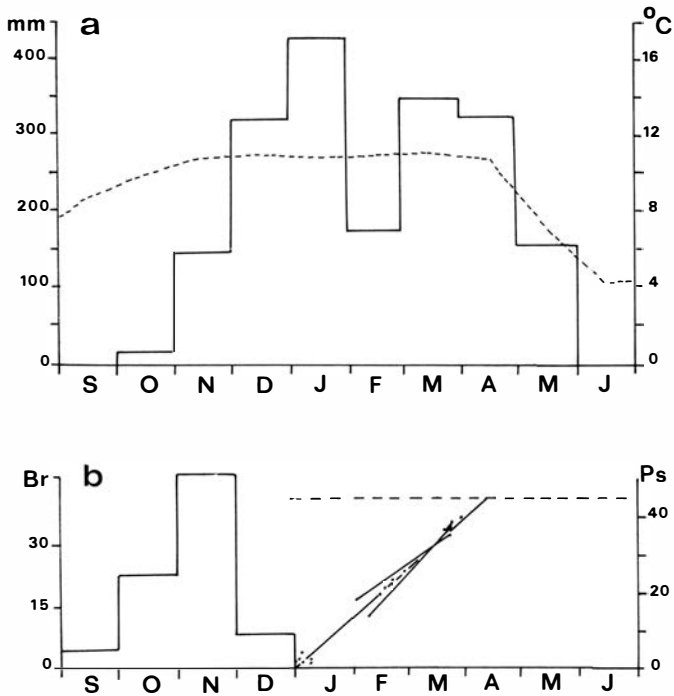


Figure 7. — Breeding and moult in adult *Pogonocichla stellata* in 1979-1980, related to rainfall and minimum temperatures : (a) histogram of rainfall (mm) in the study area, mean minimum temperatures (°C) at Chilinda ; (b) monthly egg-laying records (Br, n = 77), graph of primary moult score (Ps) including retraps and regression lines.

Fig. 7 summarizes this strict seasonality, as shown by a typical species (*Pogonocichla stellata*) in a good season (1979-1980). Although necessarily a simplification, this shows well certain important features of the annual cycle in this passerine, such as the start of some breeding in advance of the rains, the preponderance of the single broods being from eggs laid in November. Breeding stops and moult starts essentially at the end of December (although in some years replacement layings may continue into early January). The regression line and retraps show moult finishing during April, at which time there is still considerable rain. However, in this and most other species breeding during the rains, moult is ended before the marked drop in minimum temperatures that occurs in late April or early May, the prelude to the winter « lean season ». Food for insectivorous species is likely to be hard to obtain at this time, and indeed in one species (*Pogonocichla stellata*) a large propor-

tion of the population — mostly females, immatures and non-territorial males — leave the study area for warmer, lower levels in winter (Dowsett, in prep.).

SEASONAL VARIATIONS IN BODY WEIGHT

In the course of the annual cycle of breeding and moult, an individual bird's weight varies considerably in response to the changing demands made upon it. During the year, the weight of an individual female *Pogonocichla stellata*, for example, will increase by up to 45 % of its minimum weight. Even in males of that species, increases of more than 20 % are not unusual (e.g. Fig. 8). In *Pogonocichla* (and most other passerine species in the Nyika forests) daily weight variation is only about 6.5 % (Dowsett, 1983 b).

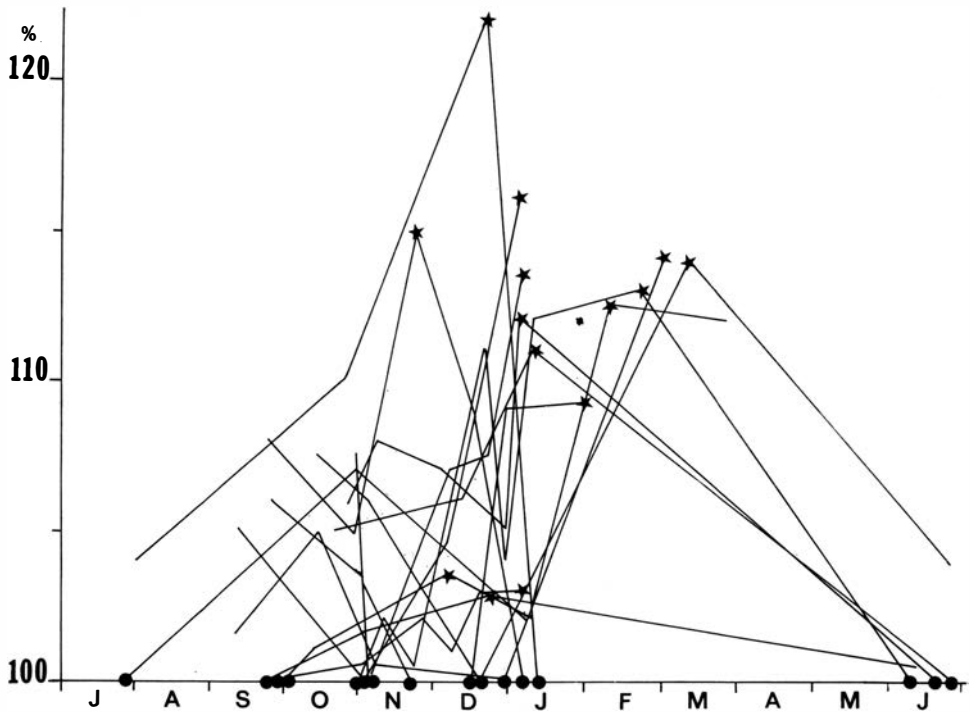


Figure 8. — Seasonal weight variations in individual adult male *Pogonocichla stellata*. Weights are shown as percentage of the minimum weight recorded for each individual. Solid lines join retrap weights for each individual, with a star representing its maximum and a dot its minimum.

Because of these seasonal changes, it is important to know the sex and breeding condition of the individuals comprising a sample of body weights. In all the species handled in the present study, mean weights of the population as a whole do not always satisfactorily reflect seasonal changes in the individual, owing to the different stages reached in the annual cycle, even in

species that have a very circumscribed breeding season. For example, the adult male *Pogonocichla* sample means plotted in Fig. 9 do show the high weights reached during moult (February - March), but at other seasons conclusions cannot be drawn, especially where sample sizes are small.

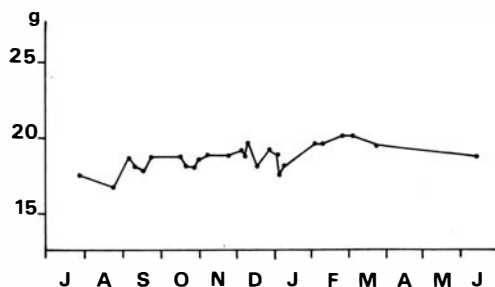


Figure 9. — Mean weights (g) of samples of adult male *Pogonocichla stellata* caught during each netting session. Sample sizes range from 1 (Aug.) to 39 (Nov.), mean 10 (n = 26). Mean weights are plotted against the median date of each sample.

Consequently, we have analysed only weights of individual birds caught in at least four different months of the year (preferably during both breeding and moult). In all species females are heaviest when containing eggs, and males also often attain their highest weights just before breeding (Fig. 8). Minimum weights in adults are reached almost invariably while they are feeding juveniles.

Interestingly, in some species at least, weights may be high in all but the earliest stages of moult. We have evidence of this in at least the following seven diverse species : the non-passerine *Apaloderma vittatum*, and the passerines *Andropadus tephrolaemus*, *Phyllastrephus flavostriatus*, *Alethe juelleborni*, *Cossypha anomala*, *Pogonocichla stellata* (first-year birds as well as adults) and *Bradypterus mariae*. This suggests that the lengthy period of moult may not be especially demanding of energy. Rather few weights are available for the winter months, but some individuals of a number of species (though by no means all) do reach minimum or near minimum weights then.

In Sarawak, Fogden (1972) found that peak weights were reached just before breeding (although he did not apparently distinguish laying females), and declined thereafter, with no resurgence. However, an increase of weight during moult has been reported in other studies. Oatley (1982 a) found that weights of *Pogonocichla stellata* in South Africa appeared to be high during the period of moult. Snow & Snow (1963 b) reported that the males of some species in Trinidad showed a tendency to increase weight during moult, and mentioned significant gains in two manakins *Pipra erythrocephala* and *Manacus manacus*. An increase in body weight at that time is recorded for many other species, and reflects increases in lean dry weight, fat, water content of the growing feathers and in blood volume (Payne, 1972). Britton (1972) did however report weight loss in moulting Black-eyed Bulbuls *Pycnonotus barbatus* in Kenya, with a significant inverse correlation between moult score and individual body weight.

The rather clear pattern of seasonal weight variation found among Nyika passerines accords well with data obtained on visible fat deposits in the furcula (tracheal pit). Except for *Apalis thoracica*, *Zosterops senegalensis* and *Cryptospiza reichenovii*, most species rarely had individuals showing fat deposits at any season. However, where there were significant deposits in adults (i.e. levels of 2 - 4 on a scale of 0 - 4), this was in all species almost invariably just before breeding or during the winter, and sometimes during moult. For example, mean fat levels in *Zosterops senegalensis* peaked in September (1.5 ± 0.99 , $n = 18$), June (1.9 ± 0.97 , $n = 39$) and February (1.4 ± 0.97 , $n = 10$). In that species, as in others, minimum levels were when young were still dependent — in the case of *Zosterops* in December : 0.5 ± 0.78 , $n = 17$. The differences between this December sample and those for the three peak months are all highly significant (Student's t-test, $P < 0.001$). Other studies have also shown that the level of furcula fat can be a good reflection of body weight (e.g. Dowsett-Lemaire & Collette, 1980).

« Winter fattening » was reported for several Jamaican birds by Diamond (1974). On the Nyika it seems likely that some individuals manage to deposit fat in the lean season, presumably as a safeguard against possible shortages in food supply later. If this is the case, then the pattern of weight and fat deposit variations in these forest birds would seem to lend support to the hypothesis that the dry winter months, with their low minimum temperatures, are a time of potential food shortages, and that this might preclude the extra energy requirements of moult then.

SUMMARY

The authors studied breeding and moult in the montane forest birds of the Nyika Plateau (Malawi - Zambia) for three successive years (1979-1982). This paper analyses more than 1000 egg-laying records and moult data from more than 2000 birds handled. With the exception of two species (*Nectarinia* spp.), breeding activities are concentrated at the end of the dry season and at the beginning of the single rainy season (Table III, Fig. 1). The short breeding seasons (two to four months in most species) are associated with single-broodedness; the start of breeding is likely to be influenced by an increase in food supply.

In most species a complete moult is undertaken only by adults, independent juveniles replacing only the body feathers. Primary (remiges) moult score can be used as an index of the progress of moult as a whole, and is correlated with date (Figs 3 - 5). Regression lines agree with data from retraps of individual birds. In nine forest passerines the mean duration of individual moult ranges between 83 and 145 days. All but two (*Nectarinia* spp.) of the 24 passerine species studied moult in the summer months (October - April), and there is some evidence that those species that start moulting latest in the summer have the shortest individual moult durations. Moult immediately follows breeding (Figs 6 and 7), but there is no evidence of overlap between the two activities in any individual bird.

In most species individual weights are high at the beginning of breeding (laying females of course are heaviest), low when feeding young, and high

again when moulting (e.g. in *Pogonocichla stellata*, Fig. 8). Though data for the cool dry season are few, there is evidence of « winter fattening » in at least some species.

RESUME

La nidification et la mue des oiseaux des forêts de montagne du Plateau du Nyika (Malawi - Zambie) ont été étudiées pendant trois années consécutives (1979-1982). Cet article analyse plus de 1 000 données de pontes, et plus de 2 000 captures au filet pour la mue. Chez toutes les espèces sauf deux (*Nectarinia* spp.), les activités de nidification se concentrent à la fin de la saison sèche et au début de l'unique saison pluvieuse (Tableau III, Fig. 1). Une seule nichée est élevée pendant ces courtes saisons de reproduction (deux à quatre mois chez la plupart des espèces) ; le début de la nidification est probablement influencé par une augmentation de l'abondance des ressources alimentaires.

Chez la plupart des espèces, seuls les adultes effectuent une mue complète, tandis que les jeunes (indépendants) ne remplacent que les tectrices. Le taux de remplacement des rémiges primaires reflète la progression de la mue en général, et on observe une corrélation linéaire entre ce taux et la date (Figs 3 - 5). Les lignes de régression et les reprises d'individus donnent une durée moyenne de mue individuelle variant de 83 à 145 jours chez 9 espèces de passereaux. Toutes sauf deux (*Nectarinia* spp.) des 24 espèces de passereaux étudiées muent pendant l'été (octobre - avril), et les espèces qui commencent la mue tard en été la complètent apparemment plus vite que celles qui commencent tôt. Les oiseaux muent immédiatement après la nidification (Figs 6 et 7) ; un chevauchement entre les deux activités n'a été observé chez aucun individu.

Les poids des oiseaux sont en général élevés au début de la reproduction (surtout les femelles en ponte) ; ils baissent pendant le nourrissage des jeunes, et remontent pendant la mue (cf. *Pogonocichla stellata*, Fig. 8). Certains oiseaux s'engraissent en saison sèche froide, mais les données pour cette époque sont peu nombreuses.

ACKNOWLEDGMENTS

Fieldwork was supported by grants from the South African Nature Foundation and the Frank M. Chapman Memorial Fund (Dowsett) ; and by a grant « Chargé de Recherches » from the Fonds National de la Recherche Scientifique in Belgium, travel funds from the National Geographic Society, and grant 2.4560.75 from the Fonds Belge de la Recherche fondamentale collective, through the Laboratory of Ethology (Prof. J.-C. Ruwet), Liège University (Dowsett-Lemaire). Dowsett's studies of *Pogonocichla* are from a thesis which fulfilled part of the requirements of an M.Sc. thesis at the University of Natal, supervised by Prof. G.L. Maclean. We are grateful to staff of the National Parks Services of Malawi and Zambia for help in various ways. We thank Dr. A.W. Diamond and Prof. R.B. Payne for helpful criticism of the manuscript, and Dr. D.W. Snow for commenting on certain points.

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