SEASONALITY OF BREEDING AND MOULT IN FOREST AND SAVANNA BIRDS IN NORTHERN CONGO

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Studies of annual cycles of land birds in equatorial regions are still relatively few, in Africa (Moreau 1950 ; Brown & Britton, 1980 ; Brosset & Erard, 1986), as elsewhere (e.g. Fogden, 1972). Whereas Fogden, in the wet forest environment of Sarawak, found that breeding and moult activities were strongly seasonal, Moreau's review concluded that forest birds of the African lowlands seemed to breed over protracted and rather indefinite periods. His analysis was based mainly on data published by Bates (1908) for southern Cameroon, and by Chapin (1932) for the Zaire basin. However, to a large extent both of these authors used gonad activity as an indication of breeding, and in the case of male birds, this method is unreliable (cf. Moreau 1936 ; Snow & Snow, 1964) ; neither Bates nor Chapin gave any sample sizes. Chapin's data were also pooled from a large area with differing rainfall regimes. For East Africa, the compilation by Brown & Britton (1980) shows prolonged breeding activities, but records are lumped for different altitudes and different years, thus obscuring the possible effects of temperature gradients and annual variation in rainfall. In a synthesis of breeding records from western Cameroon by Serle (1981), a little further away from the Equator, only highland birds appeared to be strongly seasonal (in avoiding the main rains). Breeding records from the lowlands apparently showed a lack of seasonality in many bird families, but are lumped from a great number of years and several localities. In Central Africa, the only extensive study to date at a single locality is that of Brosset & Erard (1986) over a period of 20 years at M'Passa in north-east Gabon. The authors examined c. 1600 nests in that time, and their results, although published only in part (Brosset, 1981 ; Brosset & Erard, *op. cit.* ; Brosset, 1990 ; Erard, 1990), clearly demonstrate the existence of marked breeding seasonality, with a peak of laying for many species observed in the months of December to February, in the short dry season.

This paper examines breeding and moult data obtained during 13 months of residence in the Odzala National Park of northern Congo. This site is only 220 km east of M'Passa, at the same latitude, and subject also to a bimodal rainfall regime. Yet there are marked differences in breeding seasonality between the bird populations of the two areas, and these are discussed below. Some data on moult are analysed in the context of similar studies elsewhere in the Tropics (e.g. Dowsett & Dowsett-Lemaire, 1984). Nomenclature follows Dowsett & Forbes-Watson (1993).

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STUDY AREA

Odzala N.P. is situated at the north-western limit of the Congo basin ; most of the area is a plateau at 500-600 m alt. slightly dissected by river valleys at an altitude of 350-450 m. The study was conducted in the southern half of the park (0° 30' N, 14° 50' E), where the vegetation consists of a forest-savanna mosaic.

THE ENVIRONMENT

The savannas of Odzala are at the northern limit of the grassy plateau of the middle Congo and consist of wooded grassland (often with 25-30 % of arboreal cover) with rather few tree species — mainly *Hymenocardia acida*. Despite recent anti-poaching measures, large expanses are still burnt at each of the two dry seasons. Fresh herbaceous regrowth is rapid, and the foliage of burnt trees regenerates after a few weeks. Precipitation brings about important emergences of flying termites, which are especially spectacular in the early rains of late August and September, but they continue to appear throughout the rainy seasons, and also during the occasional storms in the « dry » seasons.

The plateau grasslands are dotted about locally with patches of evergreen thicket — the first stage of forest regeneration. Over 90 % of the forests are on dry sandy soils and are extremely heterogeneous in tree species composition ; the canopy (30-40 m high) is often rather open, with a dense understorey of monocotyledon herbs 2-3 m high, mainly Marantaceae. Several species of emergents or other tall trees are briefly deciduous in either or both of the two dry seasons. Along streams and in depressions, swamp forests have a more uniform structure, usually a closed canopy with more open understorey.

As a consequence of the large tree species diversity in forests, aseasonal fruiting of some species (e.g. *Ficus* spp.) or multi-annual fruiting of others (especially edge species), some small fruits are available all year round. In open-canopy dryland forest, the dry seasons have a more drastic influence on the environment than in the closed-canopy swamp forest : the epiphytic vegetation and leaf litter dry more quickly, more tree species lose their leaves. Feeding activities of army ants are greatly reduced in dryland forest during the dry spells, much less so in swamp forest. Dambos (i.e. water-logged meadows) often line gallery forests ; a few small marshes and salt-pans complete the range of habitats (for further details, see Dowsett-Lemaire, 1996, 1997a and b).

CLIMATE

Weather data were not collected in the park before our arrival ; monthly totals of rainfall and mean temperatures were the following during the study :

		J	F	M	A	M	J	J	A	S	O	N	D
rain (mm)	(1994)	105	108	57	159	290	47	3	98	184	241	209	11
	(1995)	33	89	180									
temp. (°C)	(1994)	26.2	27.5	27.5	27.1	25.7	25.0	24.5	24.5	25.4	25.7	25.9	26.0
	(1995)	26.2	25.6	26.4									

In 1994 the total rainfall was 1 512 mm. The main rains lasted three months, from the end of August to the end of November, but the short rains only five weeks — 380 mm fell from 29 April to 3 June. The secondary dry season of December-January to March-April is often referred to as the « short dry season » (e.g. by Brosset & Erard, 1986) but appears slightly longer here than the main dry season of June to August. It can shift by several weeks from one year to the next : December 1993 had been very wet, and the dry season extended from January to April 1994. In contrast, in 1994-95, the secondary dry season started and finished more than a month earlier, from the end of November to the middle of March.

Minimum temperatures remained virtually constant throughout the year, being comprised every month between 18-23 °C. The monthly variations of means are due to higher maxima in the secondary dry season, often between 34-38 °C in 1994 and 33-36 °C in 1995. These figures reflect the situation in open savanna near the edge of forest, but temperatures are likely to be high also in the many forest clearings exposed to sunlight — and these do not benefit from savanna breezes.

METHODS

I was resident in Odzala from late December 1993 to 7 April 1995, except 8 May to 2 August 1994. Data on moult and a large proportion of those on breeding were obtained by examining birds in the hand during mistnetting operations ; 250 m of nets were erected at two different forest sites for three days each month of January to April, August-September and November-December 1994. The avifauna of evergreen thickets was sampled with 144 m of mistnets for four days in August and October 1994, and that of bush savanna with 200 m of nets for five days in April, with a brief control in January 1995. A few savanna birds were also caught in thickets in August and October, and near our house in November-December. The airfield was prospected monthly from March-April and August-December for the selective capture of nightjars (Caprimulgidae) with a torch and butterfly net. Finally, 100 m of mistnets caught some dambo birds (pipits and *Cisticola* warblers) in February 1994. In all, 856 birds of 114 species were caught and ringed, and there were in addition 150 retraps, up to 11 months after first capture. By far the three most numerous species captured were the Yellow-whiskered Greenbul *Andropadus latirostris* in forest (n = 82 ringed), Little Greenbul *A. virens* and Olive Sunbird *Nectarinia olivacea* in forest and thicket (n = 80 and 65 respectively). All birds caught were aged if possible and examined for moult and presence of an active brood-patch. In small land birds a brood patch remains « active » for about a month, being fat and wrinkled during incubation and gradually less fat during the feeding of nestlings. At about the time the young leave the nest, it becomes smooth. The month of laying cannot be extrapolated precisely from a smooth brood patch ; in the case of 15 females *Andropadus virens* and *A. latirostris* caught with smooth brood patches in August (the only two species showing so much past breeding activity at that time), records were backdated to June and July laying. These females had not yet started moult and some *A. virens* were caught with a fledgling. It is possible a few had laid as far back as May, but a fairly large April sample of 44 birds showed that breeding had barely started then.

Breeding records also came from observations of occupied nests or nests being built (except in species with protracted nest-building such as *Malimbus*

spp.), dependent fledglings, mating, females of *Batis* and *Dyaphorophyia* spp. actively fed by their males (a certain sign of incubation : Erard, 1990 ; pers. obs.).

Moult of primary remiges was scored from 0 to 50, as is usual (cf. Ginn & Melville, 1983) ; moult of other plumage still occurring after completion of the primary moult was also noted.

RESULTS

Breeding records

A total of 345 dated breeding records from 129 species are presented in Tables I (birds of forest and thicket), II (savanna and dambo) and III (marsh and water edge). All records but five (provided by A. Cruickshank) are my own. In addition, the weaver *Ploceus nigerrimus,* a semi-commensal species feeding in savanna, thickets and edges of swamp forest, laid in January-February, September, November-December (at seven colonies). In the colonial species of *Gymnobucco* barbets (Table I), the different pairs of a colony breed in synchrony and however many breeding records come from such a colony, they are counted as one.

TABLE I

Breeding seasonality (i.e. number of clutches laid each month) in forest and thicket species.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Gypohierax angolensis										1		
Guttera plumifera	1								1	1		
Turtur tympanistria								1				
T. brehmeri	1								1			
Cuculus solitarius								1	1	1	1	1
C. clamosus									1		2	
Cercococcyx olivinus									1	1		
Caprimulgus batesi	1											
Merops breweri							1					
M. gularis												1
Phoeniculus castaneiceps	1											
Tockus hartlaubi											1	
T. fasciatus										2		
Gymnobucco peli		1						1				
G. bonapartei		1						1	1			
Pogoniulus scolopaceus									1			
P. bilineatus								2				
P. subsulphureus		1										
Camphethera nivosa								3				
Mesopicos elliotii							1					
Andropadus virens				1		6	3	3	1	1		

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
A. gracilis												1
A. latirostris				1		3	3	4	1	1		
Chlorocichla simplex								1				
Phyllastrephus icterinus							1	1			1	1
P. xavieri									1			
P. albigularis								1			1	
Bleda syndactyla								2		2	1	
B. eximia							1	1	1	2	1	
Criniger chloronotus										1		
C. olivaceus								1				
Neocossyphus rufus												1
Stizorhina fraseri									1			
Alethe diademata							1				2	1
A. poliocephala								1				
Stiphrornis erythrothorax									1	1		
Sheppardia cyornithopsis	2											1
Cossypha niveicapilla								2	1			
Bathmocercus rufus												1
Sylvietta virens									1	1		
Hylia prasina											1	
Apalis rufogularis											1	
Camaroptera chloronota								3	2			2
Fraseria ocreata										1		
F. cinerascens											1	
Muscicapa infuscata			1									
Megabyas flammulatus		1									1	
Bias musicus			1							1		
Batis minulla	1			1					1			
Dyaphorophyia concreta									1		1	
D. castanea									4		3	
Terpsiphone viridis									1			
T. rufocinerea								1				1
Erythrocercus mccallii			1									
Illadopsis rufipennis								2				
I. cleaveri										1	1	
Parus funereus									1	1		
Anthoscopus flavifrons									1			
Anthreptes fraseri										1	1	1
A. aurantium									1			
A. rectirostris									1			
A. collaris								1	1		1	1
Nectarinia seimundi					1							1
N. olivacea	1	1	1	1				1	1	1	1	1
N. verticalis						1						
N. cyanolaema							1			1		
N. chloropygia	1								2		1	
N. johannae	1											
N. superba				1						1		
Nicator vireo										1		
Dicrurus atripennis											1	
D. adsimilis			1									

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Malimbus cassini									1		1	
M. erythrogaster												1
Parmoptila woodhousei								1				
Nigrita canicapilla	1								1	1	1	
N. luteifrons					1		1					
N. bicolor								1	1			
Lagonosticta rubricata	1											
Total (n = 190)	**12**	**5**	**5**	**5**	**2**	**10**	**13**	**36**	**35**	**25**	**26**	**16**

Many forest birds, especially those of the understorey, are essentially active in the month preceding, and during, the long rains (Table I) : 122 of 190 records (64 %) fall in the months of August to November. Marked exceptions to this pattern include the two common *Andropadus* bulbuls (*A. virens* and *latirostris*) with a mixed fruit-insect diet, which breed 2-3 months ahead of the insectivorous bulbuls of the forest interior (*Bleda, Criniger, Phyllastrephus* spp.). Several sunbirds *Nectarinia* spp. may also show a different cycle, but samples are very small ; breeding is probably continuous in *Nectarinia olivacea* at the level of the population — only a small proportion of females caught each month is breeding. Some flycatchers with laying records in January-April are species of thickets (*Batis minulla, Bias musicus*), forest edge (*Bias*) or open canopy (*Muscicapa infuscata, Megabyas flammulatus*) and clearings (*Erythrocercus mccallii*), whereas *Dyaphorophyia* species of the forest interior breed in September-November.

Savanna birds are even more strongly seasonal with 93 of 133 records (70 %) falling from August to October (Table II). This time of year is especially favoured by grassland birds (e.g. *Cisticola* and *Prinia* spp.) ; the only two dry-season (August) records of *C. brachypterus* come from the edge of a moist dambo whereas all 11 records from wooded grassland are from the long rains. The February record of a *Prinia subflava* is also from a dambo. *Anthus pallidiventris* breeds only on very short grassland, usually that regrowing after a dry-season bush fire ; the November record (in the rains) comes from the short grass of the airstrip. *Macronyx croceus,* on the other hand, nests in unburnt grassland, and records extend from the long rains to the secondary dry season. The February records of *Mirafra rufocinnamomea* and *Erythropygia leucophrys,* two ground-feeders, come from recently burnt savanna. Otherwise, most of the January-April records concern species of woodland, feeding in and around small trees (*Pycnonotus barbatus, Bradornis pallidus, Batis minor, Anthoscopus caroli, Nectarinia cuprea*) : all of these were found to breed then in patches of savanna that had been burnt a month or two previously and which were experiencing a new flush of leaves.

TABLE II

Breeding seasonality (i.e. number of clutches laid each month) in species of wooded grassland and dambo.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Milvus migrans									1	1		
Francolinus afer								1	1			
Streptopelia semitorquata										1	1	
Centropus senegalensis										1		
Caprimulgus natalensis	1		1									
Colius striatus										1		
Ceyx pictus								1			1	
Merops variegatus							1	1	1			
Mirafra rufocinnamomea		2							2			
Psalidoprocne pristoptera				1					1			
Riparia cincta								1	3	2		
Hirundo semirufa									1			
Anthus pallidiventris			1				1	2			1	1
Macronyx croceus	1	1	1	1					2	2	2	2
Pycnonotus barbatus	1	1	1					2		1		
Neolestes torquatus								1				
Erythropygia leucophrys		1					1	4	5	1		1
Myrmecocichla nigra								1				
Schoenicola brevirostris											1	
Eremomela icteropygialis									1	1		
Cisticola brunnescens									2			
C. juncidis										1		
C. natalensis									1	1		
C. brachypterus								2	6	4	1	
C. galactotes										1		1
Prinia subflava		1								1	1	
P. leucopogon									1	2		
Camaroptera brachyura									2	3		
Bradornis pallidus		1		1				1		1		
Myioparus plumbeus								1				
Batis minor		1	1					1		1		
Parus leucomelas								1				
Anthoscopus caroli			1									
Nectarinia cuprea	1		1					1	6	1		
Lanius collaris									1	1		
Ploceus superciliosus							1	1	1			
Euplectes macrourus										2		
Estrilda paludicola											1	
E. melpoda										3		
Total (n = 133)	**4**	**8**	**7**	**3**			**4**	**22**	**38**	**33**	**9**	**5**

Birds of water habitats (Table III) seem to show two trends, although data are few. Most of those that breed in marshes do so when the water level is high (e.g. *Tachybaptus ruficollis, Amaurornis flavirostris*) ; the November record of *Actophilornis africanus* is from a seasonal marsh with highest water level then, the August record is from a permanent swamp. On the other hand, species nesting in river banks (*Alcedo quadribrachys*), on seasonally uncovered rocks (*Glareola nuchalis*), or trunks in river beds do so when water levels are lowest. For *Muscicapa cassini,* there are breeding records for both dry seasons ; field observations for the period June-August are too limited to ascertain whether the *Glareola* and *Hirundo* also breed at that time. The March record of *Cisticola anonymus* is from *Mimosa* bush in seasonally flooded marsh which had by then reached its lowest water level.

TABLE III

Breeding seasonality (i.e. number of clutches laid each month) in species nesting on the edge of water and in marshes.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tachybaptus ruficollis											1	
Tigriornis leucolophus										1		
Scopus umbretta												2
Amaurornis flavirostris										1		
Actophilornis africanus								1			1	
Glareola nuchalis	2											
Alcedo quadribrachys		1										
Hirundo nigrita												1
Cisticola anonymus			1									
Muscicapa cassini	2	3					2	1				1
Nectarinia reichenbachii												1
Total (n = 22)	**4**	**4**	**1**				**2**	**2**		**2**	**2**	**5**

MOULT RECORDS

Seasonality of moult

As for breeding, it would be more instructive to show the number of birds starting moult each month, but the duration of moult is still not well known in many species, and backdating to start of moult from advanced scores would be too approximate. Dependent or very fresh-plumaged juveniles have been excluded from consideration.

Monthly totals of moulting birds from forest and thicket are shown in Table IV. *Andropadus virens* shows a well-marked moulting season from August to November, following the breeding months of May or June to August. The relatively low moulting scores (2-18, mean = 10) of the 11 birds examined in mid

and late August indicate that most would have started moult in that month rather than July. Two of the four birds handled in September had just completed primary moult and were still replacing secondaries. Moult starts at least two months later in *A. latirostris,* and from moult scores in the nine December birds (2-34, mean = 16), most would have carried on moulting into January or February 1995, a pattern not resembling that of January 1994, when 17 of 18 birds caught had already completed moult.

TABLE IV

Number of forest and thicket birds in primary moult each month; followed by number of individuals not moulting.

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Turtur tympanistria								0;5		2;2	0;1	0;1
T. brehmeri	0;1	0;1										
Alcedo leucogaster	0;1		1;0									
Ceyx lecontei								0;1	0;2			
Halcyon badia		0;1									0;1	
H. malimbica								0;1				
Pogoniulus scolopaceus								0;1		1;3		
P. bilineatus				0;4				0;1				
P. subsulphureus				0;2				0;2				
P. atroflavus	0;1								0;1			
Indicator maculatus								0;2	0;7			1;3
I. exilis	1;0											
I. willcocksi												0;1
Campethera nivosa	1;2	0;1		0;1				0;2	0;2			
C. caroli	0;1		1;0									
Mesopicos elliotii		0;1										
Smithornis sharpei		1;0										
Andropadus virens	0;15	0;1	0;3	0;13				11;13	0;4	7;1	5;2	2;7
A. gracilis								0;5		1;2		
A. curvirostris	0;2		0;2	0;1								
A. latirostris	1;17		1;8	2;29				0;17	0;5		2;1	9;3
Chlorocichla simplex								1;2				
Phyllastrephus icterinus	2;3	2;1	3;0					0;6			1;5	
P. xavieri	1;1								0;2			
P. albigularis	0;2			2;1					0;1			0;1
Bleda syndactyla	2;2	1;0						0;1	0;3		0;1	0;1
B. eximia	2;8	1;0	0;1	1;1				0;5	0;7		0;1	0;1
Criniger chloronotus		2;0	2;1								1;0	
C. calurus	2;1	1;0										
C. olivaceus	1;0		0;1					0;1				
Neocossyphus rufus			0;1						0;1			
N. poensis				2;0								
Stizorhina fraseri				1;1				0;2				0;1
Alethe diademata	1;5	2;0	2;0	0;1				0;4	0;5		0;4	0;3
A. poliocephala	1;0	2;5	0;4					0;9			2;2	
Stiphrornis erythrothorax	0;5			0;2					0;3		1;1	
Sheppardia cyornithopsis	0;2	0;2	0;1					0;1			0;1	

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cossypha niveicapilla								0;8		1;2		
Sylvietta virens				1;1				1;2		1;0		
S. denti	0;1											
Hylia prasina	1;3		0;2	0;1				0;2			0;1	0;4
Camaroptera supercili-aris										0;1		
C. chloronota	0;6	1;1	0;2	1;1				0;4	0;8			0;4
Fraseria cinerascens		0;1	1;0					0;1				
Batis minulla										0;1		
Dyaphorophyia concreta	0;1		1;1								1;1	
D. castanea	0;1			0;1						0;3		1;0
Elminia nigromitrata	0;1	1;1	0;1								0;1	
Trochocercus nitens		1;0										
Terpsiphone viridis	0;1							1;0		0;1		
T. rufocinerea	0;1	0;1	0;1					0;1	0;1		0;1	0;2
T. rufiventer	1;0	0;1										
Illadopsis fulvescens	1;1			0;4					0;4			0;1
I. rufipennis	3;1	6;2	3;1					0;2				
I. cleaveri	0;2	3;0	2;0	1;2				0;1	1;2		1;2	0;1
Anthreptes fraseri	1;0											
A. rectirostris											0;1	
A. collaris								1;1		1;2		
Nectarinia olivacea	1;10	0;3	0;6	4;4				4;9	0;11	5;4	0;14	0;1
N. verticalis								2;3		0;1		
N. chloropygia								0;1		1;0		
N. johannae								1;0				
Malaconotus cruentus									0;1			
Nicator vireo	0;1								0;2			0;1
Dicrurus atripennis		0;1										
Parmoptila woodhousei			0;1									
Nigrita canicapilla			0;1									
Spermophaga haematina	0;6	0;1		0;2				1;1	1;5			

January to March-April is the main moulting season of a number of species of the forest interior, including several bulbuls of the genera *Phyllastrephus, Bleda* and *Criniger, Alethe* thrushes, flycatchers and babblers. This pattern, although based on small samples, is further confirmed by the observation of birds having just completed primary moult (thus counting as non-moulting birds in Table IV) but still moulting secondaries, body plumage and/or tail feathers : this is the case of a *Bleda eximia, Criniger olivaceus,* two *Alethe poliocephala,* and an *Elminia nigromitrata* all examined in late March, and of two *Stiphronis erythrothorax* and one *Hylia prasina* caught in April.

We have no direct data for *Sheppardia cyornithopsis,* but a female who was breeding in January-February was retrapped in fresh plumage in August when she was sexually inactive, having moulted in the intervening period of March to July. For several sunbirds, species of forest edges, canopy or thickets, and a seed-eater (*Spermophaga*) there are moult records for August-October. In *Nectarinia olivacea,* with breeding records in most months, moult of different individuals is very scattered, with records in August, October, January and April ; one bird, having

just completed primary moult in August, would have replaced most feathers in June-July, and another, having just finished in January, would have done so in November-December.

The main netting session in savanna was carried out on 4-8 April 1994, with 90 birds of African species caught. Their state of plumage is given in Table V. This includes 63 adults (and unaged *Erythropygia leucophrys*) of 21 species : most of these are moulting (19) or have recently completed moult (35) ; very few are in worn plumage (one *Pycnonotus barbatus,* two of 10 *Erythropygia leucophrys,* one pair of *Bradornis pallidus,* two of 11 *Nectarinia cuprea*). Of 27 aged first-year birds, most seem to be moulting in line with the adults. Among a dozen adult birds caught in January 1995, active moult was recorded in *Merops variegatus, Cisticola natalensis* and *brachypterus, Camaroptera brachyura,* while a pair of *Eremomela icteropygialis* was in worn plumage, and a *Ceyx pictus* and an *Erythropygia leucophrys* had just completed moult.

TABLE V

State of plumage of 90 savanna birds examined in the hand from 4-8 April 1994. « Moulting » refers to primary moult; « fresh » means recently moulted

Species	Numbers caught, with age and plumage characters
Ceyx pictus	1 ad. slightly worn, 2 imm. fresh
Riparia cincta	3 ad. moulting, 1 imm. moulting
Hirundo semirufa	3 ad. fresh & 1 moulting, 3 imm. moulting
Anthus pallidiventris	1 imm. fresh & 4 moulting
Pycnonotus barbatus	1 ad. worn & 2 moulting
Neolestes torquatus	1 ad sl. worn
Erythropygia leucophrys	7 FG fresh, 2 worn & 1 moulting
Eremomela icteropygialis	1 ad. fresh & 1 sl. worn
Cisticola brunnescens	3 ad. fresh & 1 moulting, 6 imm. fresh & 2 moulting
C. natalensis	1 ad. fresh & 1 moulting
C. brachypterus	3 ad. fresh, 4 imm. fresh & 1 moulting
C. lateralis	1 ad. fresh
Prinia subflava	3 ad. moulting
P. leucopogon	1 ad. fresh
Camaroptera brachyura	1 ad. fresh & 1 moulting
Bradornis pallidus	2 ad. worn
Myioparus plumbeus	3 ad. moulting
Batis minor	1 subad. fresh & 1 worn
Nectarinia cuprea	8 ad. fresh & 2 worn, 1 imm. fresh
Estrilda paludicola	1 ad. moulting
E. melpoda	3 ad. fresh & 1 moulting
E. astrild	1 ad. slightly worn
Lonchura cucullata	2 ad. moulting

Ceyx pictus, Pycnonotus barbatus and *Batis minor* (all adults) were also mistnetted in other months, in thickets : some individuals of the *Ceyx* were

moulting in August, October, November and December, and some *Pycnonotus* also in August and October ; one *Batis minor* was moulting in August and another in October. Of a sample of eight *Anthus pallidiventris* caught in a dambo in February, none of four adults and four immatures was moulting ; an immature *Cisticola brunnescens* was in moult, but none of eight adults, nor any of 10 *C. eximius.* A *Caprimulgus natalensis* was moulting in March, and a *C. climacurus* in October.

The duration of moult

Based on retraps of individuals, the following data are available. Three *Illadopsis rufipennis* caught on 1 February with primary moult scores of 16, 17 and 21, were retrapped together on 28 March with scores of 43, 42 and 46 respectively. Most passerines show a linear progression of moult (cf. Fogden, 1972 ; Ginn & Melville, 1983 ; Dowsett & Dowsett-Lemaire, 1984), and assuming this to be the case for the *Illadopsis,* we can estimate a total of 102 to 111 days for the completion of primary moult. A *Caprimulgus climacurus* female had not yet started moult on 31 August, but was retrapped on 31 October with a moult score of 43, thus primary moult may have been completed in less than 70 days. A *Ceyx pictus* showing a score of 2 on 18 October and retrapped on 28 January in completely new plumage would have moulted in less than 75 days. One *Bleda eximia* and one *Hylia prasina* caught in January in worn plumage and retrapped in April in very fresh plumage had moulted in less than three months. The fastest rate was achieved by three *Alethe poliocephala* caught in worn plumage on 1 February and retrapped in very fresh plumage (one still growing body feathers) on 29 and 30 March : thus primary moult was completed in less than two months.

Moult of immatures in relation to adults

It is not always possible to age birds, as in several species adults retain pale gapes (e.g. *Phyllastrephus* spp., *Erythropygia leucophrys, Sylvietta virens, Camaroptera chloronata*). In the sociable *Illadopsis* babblers (*I. fulvescens* and *rufipennis*) all members of a group except the breeding pair retain pale gapes, although most of them must be over a year old ; in *I. rufipennis* at least (I have no data for *I. fulvescens*), these subadults moult in synchrony with the full adults. In other species where first-year birds can be distinguished, the proportion of immatures in a population seems extremely low : for example all 17 *Alethe poliocephala* mistnetted were adult, only one of 20 *Bleda eximia* was a juvenile, and 10 of 65 *Nectarinia olivacea* ; seven immature *Alethe diademata* caught for 13 adults was an exceptional figure.

The few moult data for immature birds seem to indicate, as for subadult *Illadopsis rufipennis,* that they replace feathers at the same time as the adults. On 28 March an immature *Criniger chloronotus* had a moult score of 48, the adult female caught with it had a score of 45 and the male (also in the same net) had just finished. All five immature *Nectarinia olivacea* caught moulting were replacing feathers in the same months (April, August and October) as several adults. Three immature *Andropadus virens* were moulting in August, October and November alongside several adults. A young *Bleda eximia* born in December and first ringed in January was already moulting in the following March-April (with a score of 33 on 23 April) ; its father had just started moult in mid-January, but not its mother who was still feeding it. Of savanna species, moult seems to progress in much the

same way in immature and adult *Riparia cincta, Hirundo semirufa, Cisticola brunnescens* and *brachypterus* (Table V) — the only species for which we have comparative data.

Development of moult in members of pairs

In several species, members of the same pair caught or retrapped together when moult was in progress often showed different scores between male and female, as follows : *Phyllastrephus xavieri* (a male had a primary score of 25, its female had not yet started), *P. albigularis* (male scored 42, female 10), *Bleda syndactyla* (male scored 3, female was worn), *Bleda eximia* (male scored 5, female was worn, with dependent juvenile), *Criniger chloronotus* (male had finished, female scored 45), *Sylvietta virens* (male had finished, female scored 19), *Dyaphorophyia concreta* (male had finished, female scored 11), *Illadopsis cleaveri* (male scored 18, female 17), *Anthreptes collaris* (in one pair, male scored 13, female was worn ; in another pair, male scored 42, female was worn, with juvenile), *Nectarinia verticalis* (male scored 14, female was worn, with independent juvenile). In all 12 pairs but one (*Illadopsis cleaveri*), the male was more advanced than his female. The delay in the start of moult in females could be of the order of 1-2 months in some species. Several pairs were still accompanied by dependent or independent juveniles, showing that moult follows breeding without delay, at least in males.

Overlap of breeding and moult

In species caught in some numbers and with well-defined moulting seasons (in particular *Andropadus virens* and *latirostris*) there is little overlap between breeding and moult periods as a whole, which are mainly consecutive. In *Nectarinia olivacea,* breeding and moult records are rather spread out, but not one of the females caught when actively breeding was in moult. An overlap of the two activities was recorded in only two females, both bulbuls : an *Andropadus virens* and a *Pycnonotus barbatus* with primary moult scores of 10 and 13 had fat and wrinkled brood patches characteristic of early incubation. They were both caught in thickets in August just before the onset of the main rains.

Observations on vocal activity

Vocal activity of forest and savanna birds was monitored quantitatively from August 1994 to January 1995, and general observations made also in the months of February to May. Full details will appear elsewhere ; a few short comments here can serve to illustrate the relationship between vocal activity and annual cycles of breeding and moult.

Many forest birds remain moderately vocal throughout the year ; however, most cuckoos, both trogons *Apaloderma* spp. and some raptors (especially *Accipiter tachiro*) reduce their vocal output considerably for several months, from February to May (in 1994), and some did so earlier in 1994-95. I have no data for June, but by mid-July 1994 all cuckoos but one (*Cercococcyx olivinus*) were again in full song (R.J. Dowsett, pers. comm.). The secondary dry season started several weeks earlier in 1994-95 than in the previous year (see above), and several species stopped calling earlier : for example Lyre-tailed Honeyguide *Melichneutes robus-*

tus virtually stopped displaying from the end of October (whereas they were still active in December 1993-January 1994) ; *Cercococcyx olivinus* called daily from the end of August to the end of November (but in 1993-94 they were still singing regularly in January and stopped only on 7 February). In several savanna species, especially *Prinia* and *Cisticola* spp. and a cuckoo (*Cuculus gularis*), singing output is strongly linked to the main rains : in 1994 these species called from the last week of August to the end of October (*C. gularis*) or of November (*Prinia* and *Cisticola*), but in 1993-94 some birds were still calling in December-January. Thus for a number of forest and savanna species the end of the main rains signals the end of vocal and breeding activities.

On the other hand, some arboreal savanna birds such as *Batis minor* (with scattered breeding records) produce songs in all months. *Nectarinia cuprea* stopped singing and abandoned their territories in October-November 1994 for 2-3 months following breeding. It is likely that most moult took place then (since the majority of birds caught in early April were in fresh plumage) ; by January, and especially in February, singing was resumed and territories re-occupied, though this did not lead to another peak of breeding activity.

A few species stop calling for only a month or two : for example *Andropadus latirostris* were silent in January-February 1994 (a period of sexual rest following moult) ; later in 1994 there was a decrease of vocal output mainly in November, during moult.

DISCUSSION

Breeding seasonality

Breeding in the equatorial forest-savanna mosaic of Odzala N.P. appears strongly seasonal for both forest and savanna birds, with most breeding records concentrated in the long rains and (except for birds of dry grassland) also in the month preceding them. These results are in agreement with Brosset & Erard's (1986) findings that forest birds from nearby north-east Gabon also display markedly seasonal breeding, but the peak of activity at M'Passa is recorded several months later, during the secondary dry season. Brosset & Erard also showed that, in two years of their 20-year study with abnormal rainfall regimes, birds could shift their breeding activities by several months. However, from rainfall records taken elsewhere in the Mbomo district of Odzala (Hecketsweiler *et al.*, 1991) and those published for Makokou near M'Passa (in Brosset & Erard, 1986), the rainfall patterns experienced at Odzala in 1994 fall in the norm. Moreover, I was present in the field in two successive dry seasons of January-March, and the pattern of reduced breeding activities noted in 1994 was repeated in 1995. Monthly totals of breeding records may even be slightly biased towards an over-representation of data for January-March from the time spent in the field overall.

How can the difference in timing of breeding be explained between two localities only 220 km from each other ? Brosset (1990 : 269) interpreted the advantages of the December-March dry season as being « food production following the rain, (combined) with metabolic comfort of the brooding birds due to sunny weather and the cessation of the heavy rains ». Differences in forest structure may provide the answer. Odzala is situated in a mosaic of forest and

savanna, at the northern limit of the vast grassland savanna of middle Congo, and the forests have not yet reached a state of climax (Dowsett-Lemaire, 1996) : the canopy is very broken up and the high temperatures of the secondary dry season, combined with the lack of prolonged rain, rapidly dessicate the understorey, and no doubt impose more stress on the environment of this type of forest than in the closed-canopy primary forest of north-east Gabon. Only the swamp forests, limited to small galleries and depressions, have a closed canopy and retain some moisture at ground levels : army ants continue to hunt actively in swamp forest throughout the months of December to March, whereas they are hard to find in dryland forest at that time. The November-December breeding records of the ant-dependent *Alethe diademata* come from swamp forest, as do also those of *Sheppardia cyornithopsis* for December-January — a species indeed confined to swamp forest in Odzala.

At M'Passa, both *Andropadus virens* and *latirostris* breed in phase with the bulk of forest species, i.e. most clutches of *A. virens* are laid in January-February, and all of those of *A. latirostris* from late December to early April, except in abnormal rainfall years (Brosset & Erard, 1986 ; Brosset, 1990). Surprisingly, in 1994 at Odzala these bulbuls started to breed several months before the majority of forest insectivores, including bulbuls of the genera *Bleda, Criniger* and *Phyllastrephus*. I suspect they had done so in 1993 as well, as by January 1994 they had already completed moult, months ahead of the other species. We do not know enough about the diets of these birds (apart from the fact that they eat large quantities of small fruit in addition to insects) to seek an explanation. In the forests of Malawi, I also noted that *Andropadus* bulbuls (also with mixed diets) start breeding one or two months before insectivorous *Phyllastrephus* bulbuls (Dowsett-Lemaire, 1989).

My data on water-edge birds breeding in the dry season when water levels are lowest conform broadly with those of Brosset & Erard (1986) and Erard (1990), except that these authors never obtained any breeding evidence for *Muscicapa cassini* in the cool dry season of June-August. In many parts of Gabon, and also southern Congo (pers. obs.), this dry season is characterized by an abundance of cloudy days, but this is not so in Odzala where sunshine is the rule, at least in July-August. This may explain why *M. cassini* can breed at that time, as well as other species in thickets, forest and savanna.

Breeding activities of savanna species are more concentrated in time, which is to be expected in an environment more strongly influenced by the variation in rainfall. Nearly all instances of nests started outside the main rains occurred in recently burnt savannas experiencing a new grass and leaf flush : thus it is likely that breeding activities would be even more focused on the long rains in the absence of human interference with the environment. There is almost no natural savanna in north-east Gabon, and we have no comparative data from elsewhere in Central Africa. In East Africa, savanna birds, and especially grassland species, breed mainly in the longer rainy season of the two (Beesley, 1973 ; Brown & Britton, 1980).

Brosset & Erard (1986) suggested that rainfall *per se* could act as a proximate factor in inducing the start of breeding. But at Odzala many species, especially in forest, start breeding before the onset of the rains, and in savanna some species breed outside the rains in recently burnt bush. In forest, deciduous trees come into leaf again before the onset of the rains. An increase in food supply, linked to a flush of green vegetation, seems a more likely proximate factor. We know too little

about birds' diet to say more than this. As for the end of breeding, that may be decided by the start of the moult, another energy-demanding activity that has to be completed before the lean season (cf. Snow & Snow, 1964 ; Fogden, 1972 ; Dowsett & Dowsett-Lemaire, 1984)

MOULT

Moult of flight feathers appears to be directly consecutive to breeding, and this pattern also holds true elsewhere in the Tropics (Snow & Snow, 1964 ; Fogden, 1972 ; Diamond, 1974 ; Dowsett & Dowsett-Lemaire, 1984 ; Erard, 1990). Erard made the remarkable observation that in several species of flycatchers, pairs that had started building nests late in the season abruptly stopped and began to moult their flight feathers. The fact that in several pairs of birds still accompanied by a dependent or full-grown juvenile, moult had already started in the males, also indicates that moult follows breeding without delay ; presumably females cannot start so soon because of their heavier investment in breeding duties. Dowsett & Dowsett-Lemaire (1984) made similar observations on a male White-chested Alethe *Alethe fuelleborni* starting moult before its mate, and this sexual shift in the start of moult is also known for some Palaearctic passerines in which males are less involved in the feeding of the young (Ginn & Melville, 1983). Whether young birds all have a complete moult in their first year (as seems to be the case in places, e.g. Fogden (1972) but not others, e.g. Dowsett & Dowsett-Lemaire (1984)) cannot be ascertained from my limited data, but quite a few young birds do so, in many different genera (*Riparia, Hirundo, Andropadus, Criniger, Bleda, Cisticola, Illadopsis, Nectarinia*) and at the same time as the adults.

These various observations strongly suggest, as had already been argued by Snow & Snow (1964) and others, that the timing for the start of moult is strongly imprinted in the endogenous annual cycle of birds and may be the main factor determining the end of breeding.

In the montane forests of Malawi, moult is completed before the start of the cold dry winter ; in Gabon, flycatchers moult mainly from March to May, during the second rainy season (Erard, 1990), and the main period of inactivity of these and other species is the cool dry season of June-August (Brosset & Erard, 1986 ; Brosset, 1990). As at Odzala breeding and moult take place at least three months earlier than in Gabon, it would seem the lean season corresponds to the short rainy season of April-May and early dry season that follows, with, as already mentioned above, the exception of *Andropadus virens* and *latirostris* active when other species are resting.

With consecutive seasons of breeding and moult, an overlap between the two activities in an individual can be no more than exceptional, and was found in only one female of two bulbul species, in a thicket environment. Brosset & Erard (1986) handled more than four times the number of birds that I did and found evidence of overlap in only one generalist species *Nicator chloris*. We found no evidence of overlap in montane forest birds in Malawi, based on a sample of c. 2000 birds examined (Dowsett & Dowsett-Lemaire, 1984), nor did various authors working elsewhere in tropical or equatorial forest (Snow & Snow, 1964 ; Fogden, 1972 ; Diamond, 1974). A breeding-moult overlap is recorded mainly in birds of more seasonal habitats than tropical forest, or with unpredictable rainfall (Payne, 1972).

Some of the few examples of breeding-moult overlap in tropical forest birds cited by Foster (1975) were shown to be invalid (Dowsett & Dowsett-Lemaire, 1984 : 104).

The maximum duration of moult is known for only a few species, where it appears rather short : less than two months in three *Alethe poliocephala,* less than 70-90 days in four other species, while three *Illadopsis rufipennis* moulted in just over 100 days. Whereas many Palaearctic passerines moulting before they leave their breeding quarters can do so in barely two months (Ginn & Melville, 1983), tropical species often take longer, in the region of 3-4 months (Dowsett & Dowsett-Lemaire, 1984) or 4-5 months (Fogden, 1972).

The differences observed in the timing of the annual cycles of birds at Odzala and M'Passa stress the danger of lumping records from even neighbouring sites in reviews on this subject.

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SUMMARY

The study was conducted in Odzala N.P., a forest-savanna mosaïc close to the Equator (0° 30' N) and subject to a bimodal rainfall regime. Breeding data assembled over 13 months show a peak of laying activities in August-November in forest birds (especially insectivores of the forest interior) and in August-October in savanna species, thus during the main rains (September-November) and the month preceding them. Exceptions to this pattern include species of forest edge and open canopy, water-edge birds preferring the low water levels of the dry seasons, and a few individuals of some savanna species nesting during the new flush of vegetation following dry-season bush fires. A comparison with the intensive study of Brosset & Erard (1986) in neighbouring north-east Gabon shows important differences for forest species, probably attributable to differences in forest structure and micro-climate.

Primary moult is consecutive to breeding and is centred around December-April for many species. It is known to last less than two or three months in several species. An overlap in breeding and moult seems exceptional as it was found in only two individual bulbuls. The few data available suggest that first-year birds have a complete moult at the same time as the adults. In several pairs caught together, the male was in a more advanced state of moult than its mate. It seems likely that the timing for the start of moult is strongly imprinted in the endogenous annual cycle of birds and may be the main factor determining the end of breeding.

RÉSUMÉ

L'étude a eu lieu au P.N. d'Odzala, une région de mosaïques forêt-savane proche de l'équateur (0° 30' N) et sujette à un régime de pluies biannuel. Basées

sur 13 mois d'observations, les données de nidification montrent un pic des activités de ponte en août-novembre chez les espèces forestières (surtout les oiseaux insectivores du sous-bois) et en août-octobre chez les espèces de savane, soit pendant la saison principale des pluies (septembre-novembre) et le mois qui la précède. Les exceptions à ce schéma comprennent des espèces de la lisière forestière et voûte ouverte, les oiseaux ripicoles qui nichent en période de basses eaux, et quelques individus de certaines espèces savanicoles qui nichent aussi en saison sèche, pendant la repousse de végétation provoquée par des feux de brousse. Une comparaison avec l'étude de Brosset & Erard (1986) dans la région limitrophe du nord-est du Gabon montre d'importantes différences de saisonalité pour les espèces forestières, et l'explication la plus probable réside dans les différences de structure de la végétation forestière (et donc du micro-climat) observées entre ces deux régions.

La mue primaire suit directement la nidification et est centrée sur les mois de décembre-avril pour beaucoup d'espèces. On sait (par les reprises du baguage) qu'elle ne dure pas plus de deux ou trois mois chez plusieurs espèces. Un chevauchement entre les activités de nidification et de mue semble exceptionnel puisqu'il n'a été constaté que chez deux individus (Pycnonotidés). Les quelques données disponibles suggèrent que les oiseaux de première année ont une mue complète en même temps que les adultes. Chez plusieurs couples capturés ensemble, le mâle était à un stade de mue plus avancé que la femelle. Il est probable que le moment où doit débuter la mue est déterminé dans le cycle annuel endogène des oiseaux et pourrait aussi être le facteur principal provoquant la fin des activités reproductrices.

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