OVERLAP OF BREEDING AND MOLTING SCHEDULES IN A COLLECTION OF AFRICAN BIRDS

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Many birds in northern temperate regions are known to have distinct and separate times of the year for breeding and for molt, but little information is available for tropical birds. Miller (1961) found a separation of molt and breeding in tropical *Zonotrichia capensis,* and he also described an inverse correlation in time between nesting activity and molt in an equatorial South American cloud forest (Miller 1963). Moreau (1936, 1950) reported overlap of molt and gonadal activity in less than 10 per cent of a sample of birds collected in equatorial Africa. Exceptions noted by Moreau were *Colius striatus* among the nonpasserines and *Turdoides jardinei* among the songbirds. These species had large gonads both in the breeding season and at the time of molt. In none of these studies was each of the instances of overlapping schedules discussed.

The degree of overlap of gonadal activity and molt in tropical birds is of interest mainly because, in temperate regions, the separation of these two events in the annual cycle is thought to indicate metabolic incompatability of synchronous molting and breeding. Both of these events increase the demands of birds on their energy resources. The separation in time suggests that birds are limited by the availability of food. Farner (1964) has noted that the scheduling of the events of the annual cycle may also reflect the dependence of each event on a different set of hormonal conditions, but such incompatabilities of physiological mechanisms are themselves likely products of selection for separation of the energy-consuming events of breeding and molting. In contrast to the temperate regions where these ideas have developed, tropical regions are sometimes regarded as stable in time with minimal seasonal fluctuations in the abundance of food. It might be thought that species not limited by food may therefore breed and molt at the same time of the year.

A collection of 1050 specimens of 190 species of birds was made from 1965 to 1967 as part of a field study in Africa. The collection has been divided between the U.S. National Museum, the University of Michigan Museum of Zoology, the University of California Museum of Vertebrate Zoology, and the University of Oklahoma Stovall Museum. No comprehensive systematic list of specimens is planned. Nearly all collecting was carried out during the local breeding seasons in each of the six countries visited (South Africa, Rhodesia, Botswana, Zambia, Malawi, and Kenya). The extent of molt was recorded for each bird at the time of its preparation as a specimen. About half of all birds collected were parasitic cuckoos, honey-guides, or parasitic finches, and most of the others were passerines; thus the sample does not provide a complete representative spectrum of species in which overlap of molt and breeding activity may occur. Within these limits, however, a list of the birds collected which did show overlap not only suggests certain species of interest for further field study, but also permits some general statements on the ecological conditions of overlap. Birds in the following list were in molt and had large gonads or other evidence of breeding activity. Names follow McLachlan and Liversidge (1957) for species found in southern Africa, and other species names follow Mackworth-Praed and Grant (1957). In parenthesis for some birds are the preferred names as used by White (1963, 1965).

LIST OF SPECIES

Gallinula choropus. A female Moorhen collected on 23 November 1965 was in light diffuse body molt in several tracts. Three yolky follicles larger than 4 mm in diameter indicated that the bird was about to lay.

Pterocles burchelli. Two adult Spotted Sandgrouse taken eight miles west of Maun, Botswana, on 23 April 1967 were in diffuse body molt. The male (4653) had testes 4 mm long, and the female (4654) had ovarian follicles slightly larger than 2 mm.

Streptopelia semitorquata. A male Red-eyed Turtle Dove on 30 November 1966 taken eight miles north of Cathcart, C. P., South Africa, had testes 12 mm long and was grow-

ing the innermost primary on each wing. No body molt was evident.

Cuculus canorus gularis. An adult female African Cuckoo (3897) taken at Hans Merensky Nature Reserve, Transvaal, South Africa, on 26 January 1966 with many regressed atretic or post-ovulatory follicles but with no yolky ovarian follicles larger than 3 mm, was in heavy body molt. A male (3990) was taken there on 18 March 1966 growing hundreds of body feathers in an irregular pattern; its testes were 3 mm. No other *C. c. gularis* were taken.

Cuculus cafer (*C. clamosus*). A female Black Cuckoo (4232) taken on 2 December 1966 on an aloe-acacia hillside eight miles north of Cathcart, C. P., South Africa, was in diffuse body molt. The largest ovarian follicle was 8 mm, and yellow structures which were either regressed atretic or post-ovulatory follicles were apparent. In contrast, five laying Black Cuckoos taken from October to January in this country showed no sign of molt. No molt was noted on 11 of the 15 males collected. One male (4343) in diffuse body molt taken on 19 January 1967 in open woodland 21 miles west of Marble Hall, Transvaal, South Africa, had testes 5 mm. The male was perched quietly and was preening on a limb only 3 ft from another male that was singing. Areas of growing feathers on the body were found on two other males taken in South Africa and Botswana with testes 5 mm long. All of the 14 males taken in the breeding season had testes ranging in length from 3 to 6 mm, a small size for a bird weighing 75 to 90 g. The other male (4020) was taken on 3 September 1966 in open woodland eight miles east of Mwinilunga, Zambia, and was in very worn plumage with many growing body feathers. This bird, perhaps a post-breeding male but one that sang frequently and came four times to a whistled imitation of his song, had testes of 4 mm.

Chrysococcyx klaas. A female Klaas Cuckoo taken on 22 October 1966 at Alexandria Forest, C. P., South Africa, was growing hundreds of body feathers. The bird (4159) had a soft, unshelled egg in the oviduct. Another female (3768) taken on 31 October 1965 from Committees Drift, C. P., South Africa, was laying and was replacing 20 rump feathers. A male *klaas* taken at Zambezi Rapids, Mwinilunga district, Zambia (4032), was molting body feathers on 7 September 1966; its testes were 4 mm and the bird was singing. The presence of a few barred juvenal feathers indicated that the bird was in its first year. Three other adults of this species taken in the breeding season showed no molt. A molting first-year male (4809) taken eight miles north of Cathcart, C. P., South Africa, on the Swart Kei River on 8 July 1967 had somewhat enlarged but yellow testes 3 mm. Testes of a breeding male in December were 5.8 and 5.7 mm; thus the testes of the molting males were relatively large.

Chrysococcyx caprius. Only four of 41 adult Diederik Cuckoos taken in the breeding season showed more than a few growing feathers. A non-laying female (4479) taken at Sabi Valley Experimental Station, Rhodesia, on 5 March 1967 had many body feathers in sheath. The largest ovarian follicle was 5 mm but no recent post-ovulatory follicles were found. Another non-laying female (3860) taken eight miles north of Cathcart, C. P., South Africa, on 19 December 1965 was molting hundreds of body feathers. Two laying females in this same region (3850, 4214) taken in November and December also were molting many body feathers.

Clamator glandarius. Two of the 23 adult Great Spotted Cuckoos taken had two generations of primaries in the wings. A first-year male (3840) taken eight miles north of Cathcart, C. P., South Africa, on 15 December 1965 had old primaries 6, 7, and 9, new primaries 1–5 and 10, and growing primaries 8. The bird had testes 7.0 and 6.4 mm. The other (4810) was taken on 9 July 1967 in the same area. The bird was in fresh adult plumage except for the old retained primaries number 4; the testes were 8 mm. This is the first winter record for the species in southern Africa. Testes of non-molting males taken in the breeding season ranged from 6 to 8 mm.

Friedmann (1948) noted the occurrence of interrupted wing molt in *C. glandarius* in museum specimens; he found it also in *C. levaillantii.* None of the 10 adult *C. levaillantii* taken in the present collection showed an interrupted molt.

Clamator jacobinus. A female (4395) taken on 5 February 1967 at Hans Merensky Nature Reserve, Transvaal, South Africa, had a large but atretic ovary. This was the only Jacobin Cuckoo of 60 adults taken which showed an interrupted wing molt. The bird was not molting at the time of collection, but two generations of primaries indicated an unresumed interruption in the previous molt. An interrupted molt has not previously been mentioned for this species (Friedmann 1948). Small areas of molting feathers were noted on the neck and back of three adult males (3793, 3847, 3853) in the breeding season.

Colius colius. A female White-backed Mousebird (4799) taken at Brits, Transvaal, on 29 June 1967 was in heavy body and wing molt. The bird was close to laying, as it had ovarian follicles of 7, 4, and 3 mm. It was taken from a group of six colies eating leaves in the garden of Magriet Ras.

Trachyphonus darnaudii. A male (4709) d'Arnaud's Barbet was taken 20 miles southwest of Sigor, West Pokot, Kenya, on 1 June 1967. It had testes 3 mm in length and was molting hundreds of body feathers.

Indicator variegatus. At Sigor, West Pokot, Kenya, a Scaly-throated Honey-guide was heard singing for several hours in a tall acacia tree on 4 June 1967. Testes of the bird (4721) measured 4 mm. Molt of the body feathers was accompanied by a wing molt which had been completed outward to primaries number 5 on each wing. The following morning it was replaced on the same call-site by another singing *I. variegatus.*

Indicator minor. An adult male Lesser Honey-guide (3964) was shot from a bee nest in a tree at Marble Hall Fisheries Station, Transvaal, South Africa, on 5 March 1966. The body was in heavy molt and two inner pairs of inner primaries (2 and 3) were growing. Testes were 3.2 and 2.7 mm, somewhat smaller than the common range of 4 to 5 mm in birds in the breeding season, but larger than in birds of a similar size in temperate regions in the non-breeding season. A female (3871) taken from a courting male at Brits, Transvaal, on 5 January 1966 in a drought situation had a yolky ovary partly destroyed by shot; the bird was growing about 300 feathers on the body. Twenty-eight additional adults taken in the breeding season showed no molt.

Geocolaptes olivaceus. A breeding pair of Ground Woodpeckers were shot at the nest hole eight miles north of Cathcart, C. P., South Africa, on 2 December 1966. Both were molting body feathers and an inner pair of primaries (pair number 1 in the male 4231, pair number 3 in the female 4238). Testes measured 14 × 8 mm, and the ovary was small but the brood patch wrinkled. Both had ants in the stomach.

Phyllastrephus fischeri. An adult male Fischer's Greenbul (4082) taken in riverine forest at Salujinga, Mwinilunga district, Zambia, on 14 September 1966 had testes 8 × 5 and 7 × 5 mm and was molting in all tracts. A female (4081) taken with the male was not molting and had a small ovary, a convoluted oviduct, and a bare belly. Both had insects (ants?) in the stomach.

Campephaga phoenicea. An adult female Black Cuckoo-shrike (3912) from Louw's Creek, Transvaal, on 31 January 1966 was molting hundreds of body feathers. The largest ovarian follicle was 3.5 mm. Feather sheaths apparently from the growing feathers and also stones and a yellow fluid were the stomach contents.

Coracina caesia. A female Gray Cuckoo-shrike (4187) taken at Alexandria Forest, C. P., South Africa, on 6 November 1966 had two fresh post-ovulatory follicles in the ovary and one of the corresponding yolks in the oviduct. As no yolked follicles remained in the ovary, the complete clutch was two eggs. The laying bird was growing hundreds of back feathers and also most of the rectrices.

Melaenornis edioloides. Sixteen miles east of Kisumu, Kenya, on 27 May 1967 a male East African Black Flycatcher (4694) was taken in heavy molt on the body, remiges, and rectrices. The testes were 2 and 3 mm.

Bubalornis albirostris. A male Buffalo Weaver (4600) in Maun, Botswana, on 16 April 1967 had testes 4 × 2 mm. The bird was in heavy molt of both the body and the flight feathers.

Petronia xanthosterna. An adult male Yellow-throated Sparrow (4744) taken at Olorgesailie, Kenya, on 12 June 1967 had testes 7 × 6 and 7 × 5 mm and was molting many body feathers. Twenty miles southwest of this locality a pair of these birds was seen feeding young in a nest hole on 16 May; thus the breeding season was at hand.

Sporopipes squamifrons. An adult female Scaly-feathered Finch (4354) was flushed from a nest containing three fresh eggs in open dry woodland 21 miles east of Marble Hall, Transvaal. The ovary showed four recent post-ovulatory follicles, and the fourth egg of the clutch was found in the oviduct. Body feathers, secondaries, and rectrices all showed a symmetrical pattern of molt. Another female, shot from a nest with a clutch of four incubated eggs on 25 January, was not molting; neither were three females and a male each shot from nests with eggs or young on 19 January in the same locality.

Amadina fasciata. A male Cut-throat Finch (4510) from Monkey Bay, Malawi, taken on 17 March 1967 was growing many feathers on the lower back and also was growing secondaries in a symmetrical pattern on the wings. The testes were 4 mm.

Lagonosticta jamesoni. (*L. rhodopareia jamesoni*). An adult male (4308) Jameson's Firefinch taken at Hans Merensky Nature Re-

serve, Transvaal, on 27 December 1967 had both testes 3 × 2 mm. The bird was molting many feathers on the head and back.

Hypocheras amauropteryx (*Vidua chalybeata*). A singing male taken at Maun, Botswana, on 17 April 1967 had testes 4.5 and 4 mm in length, but it was in incomplete breeding plumage as a result of the partial retention of dozens of brown feathers of the preceding non-breeding plumage. Several other males were taken in varying degrees of retention of the off-season plumage but with no growing feathers both in this species and in *V. "nigerrima."* A few male indigo-birds of these species also were taken in the weeks prior to the breeding season in late stages of the pre-nuptial molt and had partly enlarged testes. These birds as well as other parasitic viduines (*V. paradisea, V. macroura*) collected at the same stage of the annual cycle evidently molt and develop enlarged gonads from the minute size of the non-breeding season to the large size of breeding condition at the same time, in contrast to many northern temperate songbirds. The details of the ecology of the indigo-birds and other viduines will be expanded elsewhere.

DISCUSSION

The proportion of individuals in the collection of African birds which showed synchronous molt and gonadal or breeding activity was small. Only 41 birds of the total of 1050 specimens, in 24 of the 190 species, showed overlap. In addition the viduines mentioned but not listed were seen to undergo gonadal recrudescence and pre-nuptial molt at the same time in the same bird. The proportion of molting, breeding birds suggested by these figures is 3.8 per cent. Even this low figure is probably too high, because not all of the birds listed showed a clear-cut overlap of a seasonal, regular molt and breeding activity. The birds can be discussed in terms of four groups: interrupted molt, replacement molt, seasonal molt at a time of incomplete gonadal activity, and clearly defined overlap of breeding and molt. In several instances the data do not permit an unambiguous assignment.

Interrupted molt was observed in cuckoos of the genus *Clamator*. Only one individual was actually molting at the time of collection. The testes of this *C. glandarius* were no smaller than those of other males in the breeding season, and there appears to be no physiological incompatability of molt and breeding in the group. The absence of molt in other breeding individuals, however, points out that separate schedules for molt and breeding are commonly followed.

The "molt" recorded for several of the listed birds was in several cases probably no more than the replacement of feathers accidentally lost during the breeding season, and not a seasonal molt. All of the birds listed were growing many (usually hundreds) of body feathers. Birds for which adventitious replacement molt appears a plausible explanation of the growing feathers are: *Gallinula angulata,* all of the parasitic cuckoos except those discussed above, *Indicator minor* (no. 3871), *Campephaga phoenicea, Coracina caesia, Petronia xanthosterna,* and the estrildines *Amadina fasciata* and *Lagonosticta rhodopareia.*

In the cuckoos and the cuckoo-shrikes the high incidence of birds growing feathers in the breeding season is closely associated with the thin nature of the skin. The cuckoos with the thinnest skin and with the greatest tendency for feathers to be lost by the preparator in the skinning process are primarily the *Cuculus* species and secondarily *Chrysococcyx klaas.* These were the cuckoos in which more than 10 per cent of the birds had extensive tracts of growing body feathers in the breeding season. Cuckoos in general may also lose and replace body feathers as a result of attack by perceptive nesting host birds. It might be thought that since parasitic cuckoos do not require energy to feed their young, selection for separation of the events of molt and breeding might be reduced or even lost as a result of selection for a prolonged period of breeding to exploit more hosts. However, the parasitic cuckoos of southern Africa do not have a particularly long breeding season (McLachlan and Liversidge 1957; Benson et al. 1964). In addition, the other groups of parasitic birds in Africa, the honey-guides and the finches, did not show a corresponding overlap of breeding and molt. No striking adaptation of molt schedules that were directly related to brood parasitism was evident.

Several of the remaining species listed as overlapping in molt and breeding activity were perhaps not actually breeding but had incompletely developed or incompletely regressed gonads. This category may include *Pterocles burchelli,* the wintering *Chrysococcyx klaas, Trachyphonus darnaudii, Indicator minor* (no. 3964), *Melaenornis edioloides, Bubalornis albirostris, Petronia xanthosterna,* and the estrildines *Amadina fasciata* and *Lagonosticta rhodopareia.* The estrildines were taken early in their breeding seasons as indicated by the times of nesting listed in Mc-

Lachlan and Liversidge (1957) and in Benson et al. (1964). They were most likely developing large gonads in a late seasonal recrudescence synchronously with the later stages of a seasonal molt, as were the viduines. The size of the gonads of the other species in this category probably reflects a lesser amplitude of seasonal changes in gonad size than in such temperate region birds as *Zonotrichia leucophrys* (Blanchard 1941). The case for a relatively incomplete regression in some parasitic cuckoos in the non-breeding season is supported by the large testes of the wintering *Clamator glandarius* (4810) and also by the slightly larger-than-expected 3-mm testes of a molting, wintering European Cuckoo (*Cuculus canorus canorus*) taken on 21 December 1966 at Hans Merensky Nature Reserve, Transvaal.

The molt of both body feathers and flight feathers in *Geocolaptes olivaceus* and *Sporopipes squamifrons* at the time of nesting indicate a clear overlap of a patterned molt and breeding. Both of these birds and the laying *Gallinula chloropus*, which had an extensive body molt, were nesting late in their respective breeding seasons according to the dates of nesting given by McLachlan and Liversidge (1957). *Sporopipes squamifrons* is said by these authors to nest at any time of the year (although mainly from September to December). The apparent compatability of breeding and molt may permit the exploitation by breeding of a temporary, unseasonal rainfall in the arid habitat of this little finch.

The overlap of molt and breeding in *Colius colius* parallels the findings of Moreau et al. (1947) on an equatorial population of *Colius striatus*, a species which has little seasonal change in gonad size. Rowan (1967) has recently reported the occurrence of oviduct eggs in birds with wing molt in collections of all three species of *Colius* in South Africa. The overlap of molt and breeding in the mousebirds is noteworthy for indicating overlapping schedules outside of the tropics. The locality where the bird in the present study was taken is 25°40′ S, 27°40′ E. *C. colius* nests from August to November according to McLachlan and Liversidge (1957), thus the temporal modes of breeding and molt schedules are probably distinct in southern Africa.

The molting *Phyllastrephus fischeri* with large testes suggests that some bulbuls do not undergo a great seasonal variation in testis size. Richard Liversidge (pers. comm.) has found in another bulbul, *Pycnonotus capensis*, a minimum of seasonal variation at the southern tip of Africa. The *Streptopelia semitorquata* appeared to be initiating a molting season right in the middle of the breeding season. Additional field work is necessary to document the significance of gonadal activity with the timing of molt in the bulbuls and doves.

In the honey-guide *Indicator variegatus* sufficient field observations have been carried out to relate the overlap of gonadal activity and molt with the social system. Males of this species maintain call-sites throughout the year, although the birds are thought to restrict their breeding to a few months (Ranger 1955). Other species of honey-guides which Ranger and I have studied maintain call-sites during the breeding season. Probably the gonadal hormones produced by the testes in *I. variegatus* function to maintain the call-site behavior (singing and defense of the perch from other individuals) throughout the year. Testes of an adult male (4012) singing on a call-site in mid-winter on 30 June 1966 in Alexandria Forest, C. P., South Africa were 5.4 mm, no smaller than the range of testes (4 to 6 mm) of five singing adults taken from October to December in the breeding season in South Africa. The adaptive significance of large testes in this honey-guide is suggested not to be a prolonged period of breeding but a reflection of a hormonal control of aggressive behavior and the maintenance of social structure throughout the year.

The foregoing discussion of the instances of overlap indicates that the majority of African birds collected have separations in time of breeding and molting schedules. Most instances of overlap occurred either near the beginning or at the end of the breeding season. The general pattern of non-overlap suggests that similar demands on the energy requirements of breeding and molt operate in the tropics and in temperate regions. Although the tropics are sometimes regarded as fruitful, stable regions, Moreau (1966) has pointed out that rainfall and the abundance of food does vary greatly between the seasons throughout most of the African continent.

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