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ASPECTS OF THE BREEDING BIOLOGY OF CARMINE AND LITTLE
BEE-EATERS AT ZARIA, NIGERIA

by Michael Dyer

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Of the 14 Meropidae found in West Africa, only one, the Red-throated Bee-eater *Merops bullocki*, has been studied in any detail (Fry 1972, 1973; Dyer 1983). For most species a little is known of habitat, breeding season, migration and diet (see references in Fry 1973), but because of their hole-nesting habit, few data are available on perinatal biology, i.e. incubation period, nestling growth and development, nestling mortality and fledging success. During an intensive study of the perinatal biology of *M. bullocki* at Zaria, (11°03'N, 07°42'E), northern Nigeria, I had the opportunity to study also Carmine and Little Bee-eaters *M. nubicus* and *M. pusillus*. This paper outlines some previously unrecorded aspects of the breeding biology of these two bee-eaters.

STUDY AREA AND METHODS

The study was undertaken from 25 April to 12 June 1976 and from 19 May to 17 June 1980, on the River Galma 5 km southeast of Zaria. Vegetation consisted mainly of a uniformly dense growth of 1-2 m high *Mimosa pygma* edging a heavily grazed and cultivated floodplain with a mosaic of degraded thorny shrubs (*Acacia*, *Balanites*, *Dicrostachys*, *Ziziphus*) and scattered trees (*Parkia clappertoniana*, *Khaya senegalensis*, *Mangifera indica*).

In both years a colony of *M. nubicus*, estimated to contain 400 breeding pairs, nested in the south bank of the river. In 1976 data on clutch size, hatching success, brood reduction and nestling growth were obtained from 17 nests by constructing an observation trench (Fry 1972) behind a 7-m long section of the colony. Due to limited time available in 1980, observations on *M. nubicus* were made only between 29 May and 3 June, and confined to recording food items brought to nestlings by adults. Insects carried in adults' bills were identified as to Order, occasionally Family, with a 20 x telescope from a hide situated 10 m from the colony. A 20 sq. m area of steeply sloping cliff, on which provisioning adults settled before entering their nests, was scanned every 10 min over five 1-h observation periods, to identify insects held in the birds' bills.

Pairs of *M. pusillus* nested every 50 m or so along the banks of the Galma, and entry into their nests was facilitated by excavating a small hole (Dyer & Crick 1983) behind each of them. 12 nests were studied in 1976, and two in 1980. All were opened before the onset of egg-laying (whereas *M. nubicus* clutches were already completed when nest-chambers were first examined). Thus I could determine the *M. pusillus* incubation period by marking individual eggs.

Nests of both species were visited daily to record the fate of clutches, determine hatching periods, weigh nestlings, and document nestling

mortality. Weights were taken with either a 50-g or 100-g Pesola spring balance.

RESULTS AND DISCUSSION

Clutch size and incubation period

For *M. pusillus* eight clutches of 4 and six of 5 were recorded (mean, 4.4); for *M. nubicus* eight completed clutches of 2 and seven of 3 were found (mean, 2.5). Clutches of 2 have not previously been documented for *M. nubicus*, yet they comprised nearly half the sample.

In asynchronously hatching clutches like those of bee-eaters, it is difficult to determine the incubation period unless the day of laying and hatching of each egg in the clutch is recorded. By marking eggs, the incubation period of *M. pusillus* was found to be 22 ± 1 days. However, McLachlan & Liversidge (1978) give its period in South Africa as 28-29 days, a remarkable difference if correct.

Hatching asynchrony and brood reduction

Asynchronous hatching of eggs in bee-eater clutches yields nestlings of different ages. In *M. bullocki*, for example, eggs hatch at approximately 24 h intervals (Fry 1972, Dyer 1983), so that a 3-egg clutch hatches over a 2-day period. Asynchronous hatching provides a mechanism by which competitive differences arise amongst siblings, so that if food becomes limiting, parents may selectively starve younger and weaker siblings and bring the number of young they can adequately nourish into line with available food resources (O'Connor 1978). This is known as 'brood reduction'.

M. pusillus eggs at Zaria hatched on average at less than 24 h intervals (Table 1). In 10 clutches the first and second eggs laid hatched on the same day, indicating that incubation began after the second egg was deposited. The general trend in clutches of *M. pusillus* is that of increased hatching intervals between later-laid eggs, a pattern found to a much more marked degree in the Australian Bee-eater *M. ornatus* (Dyer & Gartshore, in prep.). By contrast, eggs in *M. nubicus* clutches hatched on average at two-day intervals, so that a clutch of 3 took a day longer to hatch than a 5-egg clutch of *M. pusillus* (Table 1).

Hatching success was 98% for *M. pusillus* and 86% for *M. nubicus*. Only one *M. pusillus* egg did not hatch - the fifth in a clutch of 5. Single *M. nubicus* eggs in three c/3 clutches and two c/2 clutches failed to hatch. In one of the latter, the nestling that emerged was severely deformed: it lacked eyes, its mandibles were crossed, and feet and toes were badly deformed.

Starvation mortality through brood reduction was not recorded in any *M. pusillus* nests. But in one brood of four, the third-hatched nestling suddenly died of no apparent cause, at age 12 days. I believe that brood reduction does occur sometimes in *M. pusillus*, but perhaps only when food

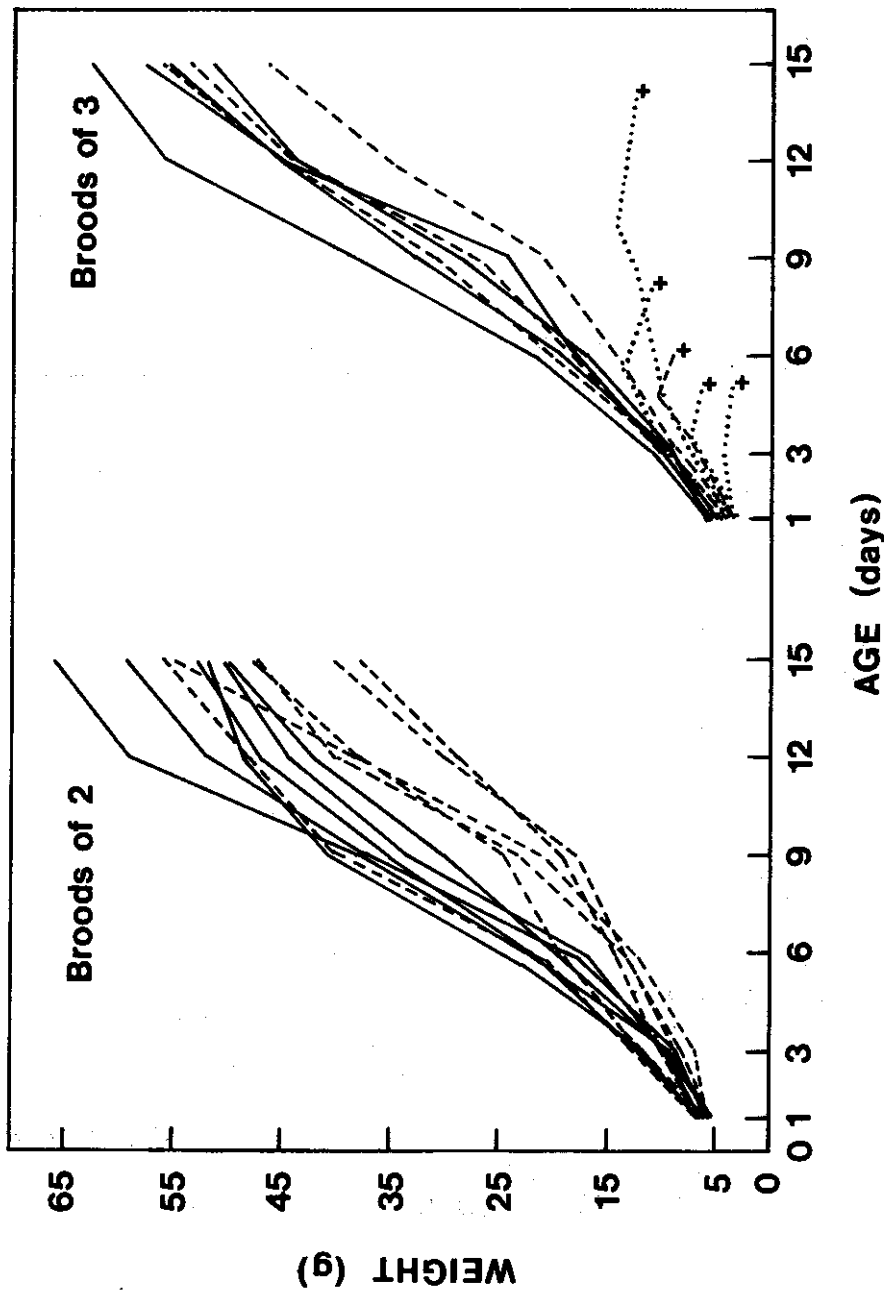


Figure 1. Growth to age 15 days of six broods of 2 and four broods of 3 *M. nubicus*. 1st-hatched nestling—; 2nd-hatched—; 3rd-hatched—; died +.

Table 1 Intervals (mean days \pm S.D.) between hatching of successive eggs, and overall hatching periods in clutches of *M. nubicus* and *M. pusillus*

	Clutch size	Egg 1 & 2	Egg 2 & 3	Egg 3 & 4	Egg 4 & 5	Overall hatching period (days)
<i>M. nubicus</i>	2	2.0 \pm 0.0	-	-	-	2.0
	3	1.8 \pm 0.1	2.2 \pm 0.1	-	-	4.0
<i>M. pusillus</i>	4	0.1 \pm 0.1	0.8 \pm 0.1	1.0 \pm 0.1	-	2.9
	5	0.1 \pm 0.1	0.9 \pm 0.1	1.0 \pm 0.1	1.1 \pm 0.1	3.1

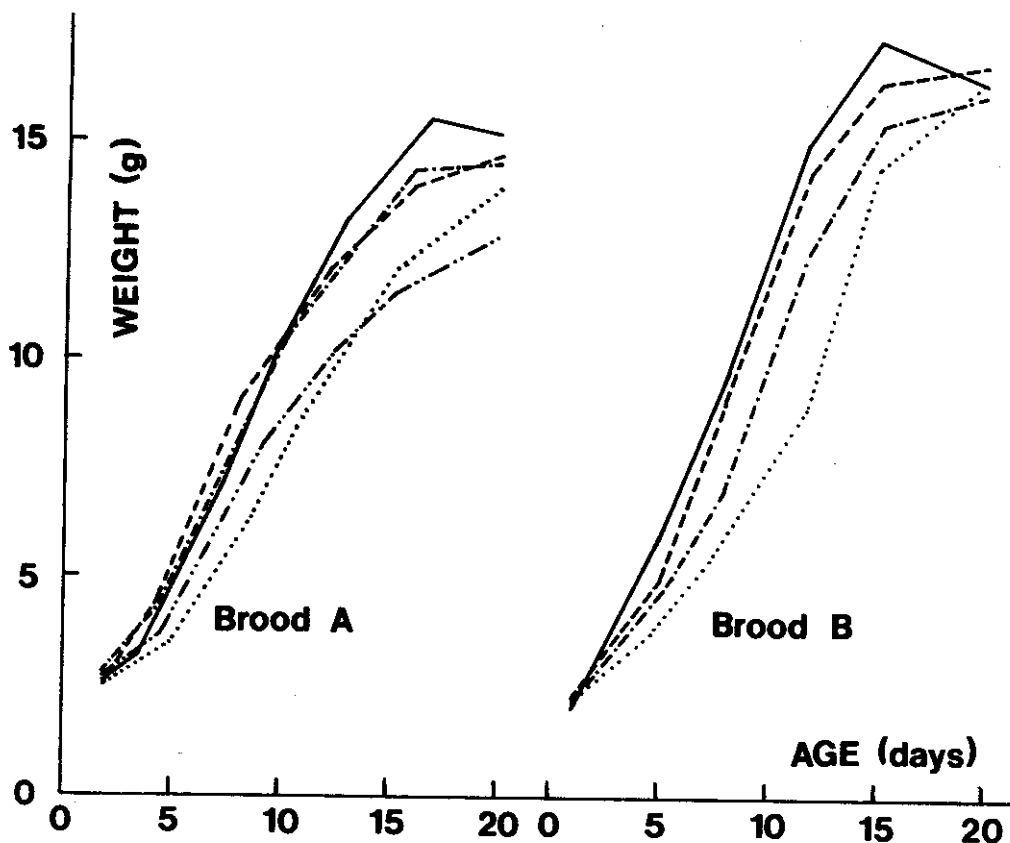


Figure 2 Growth of two broods of *M. pusillus*, Brood A with 5 young, Brood B with 4. 1st-hatched nestling—; 2nd-hatched----; 3rd-hatched-.-.-.; 4th-hatched.....; 5th-hatched-.-.-.-.

is scarce after heavy and continual early wet-season storms, or in late and enduring periods of 'harmattan'. By contrast, brood reduction was found in all six *M. nubicus* broods initially containing three young: in five the third-hatched nestling died, and in the sixth only the oldest nestling survived. Normally brood reduction occurred by the time the oldest sibling was six days old; by then a difference in weight of as much as 25 g existed between the eldest and youngest siblings. In one brood, the third-hatched nestling survived until day 13. All broods of two were reared successfully.

In *M. pusillus* large clutches, and the 24 h egg-hatching interval, may represent one end of a continuum of brood reduction strategies in bee-eaters. Small clutches and long egg-hatching intervals, as found in *M. nubicus*, may represent the other end. The small *M. pusillus* (14 g) presumably exploits a diverse and abundant source of small-bodied insects, and pairs of adults can raise large broods most of the time. However, asynchronous hatching, even to a small degree, gives parents an option for brood reduction when conditions dictate it. *M. nubicus* (51 g) may be somewhat of a specialist on orthopterans and other large insects (Fry 1984) that could be patchy in distribution and abundance. Thus, with unpredictable food resources, brood reduction would commonly occur, to facilitate which, a long hatching interval has evolved.

Nestling growth and behaviour

The growth of *M. nubicus* and *M. pusillus* is similar to that of *M. bullocki* (Dyer 1983) - a typical sigmoid curve characterised by nestling weights exceeding those of adults. In *M. nubicus* (Fig. 1) the heaviest nestling was 67.1 g, and they generally attained weights 20% in excess of adult weight. Due to the two-day hatching interval, divergence in nestling growth was conspicuous, with early-hatched siblings growing faster and heavier than later-hatched ones. Daily increments in weight were initially 3-4 g, and increased to 8.0 g by day 8. The greatest daily weight gain recorded was 9.6 g. In broods of 3, the four day difference in hatching between oldest and youngest nestlings resulted in deaths of the latter (Fig. 1). Even in broods of 2, growth of the younger nestling lagged considerably behind that of the older. For example, by day 9, 1st-hatched nestlings were 68% of adult weight when 2nd-hatched ones were only 50%.

Fig. 2 shows the growth of a brood of 5 (Brood A) and of 4 (Brood B) *M. pusillus*. Neither has much divergence in individual growth rates. Greater weights were attained in B than in A.

The nestling period of *M. pusillus* was 23 ± 1 days. During this time nestlings generally remained confined to the nest-chamber. Occasionally when the brood was close to fledging, one or two nestlings would shuffle down the nest-tunnel to be fed, but none were ever observed being fed at the nest-entrance.

It was difficult to ascertain the nestling period of *M. nubicus* because of the propensity of older nestlings to leave the nest prematurely when nest-chambers were opened to extract nestlings for weighing. Prematurely-

departed nestlings sometimes returned to the nest-chamber for up to four days after a one- or two-day absence. By and large, young remained in the nest at least 23 days before attempting to fly. Compared to *M. bullocki* and *M. pusillus*, *M. nubicus* nestlings were very active and mobile in the nest-chamber. At 12-15 days they often moved down the nest-tunnel and mandibulated discarded insects on the chamber floor. Fully-feathered siblings took turns to be fed at the tunnel entrance, protruding head and foreparts out into the open. (I once counted 141 protruding nestlings waiting to be fed.) If two adjacent nests were close enough, nestlings would 'fence' bills with each other and show other aggressive behaviour. When Black Kites *Milvus migrans* passed close to the nesting cliff-face, nestlings quickly retreated down their tunnels.

Food of nestling Carmine Bee-eaters

35 counts of insect food items were made, 7 in each of five 1-hour observation period. The maximum number of insects recorded on each count ranged from 11 to 32. Not all insects could be identified; some were either too small and/or too badly battered. Insects (N=586) of eight orders were identified. Numerically, the most important of these were Orthoptera, Hymenoptera and Odonata, accounting for 447 insects or 80% of the total (Fig. 3). In an analysis of the diet of adult *M. nubicus* Fry (1973) found comparatively few orthopterans; they comprised <10% of nestling food. Those values may have been depressed by large numbers of termites and flying ants in the analysis, but Fry (*loc. cit.*) considered that by weight orthopterans comprised 50% of the diet.

M. nubicus is highly opportunistic when feeding nestlings, taking in large numbers whatever prey may be temporarily abundant (Fry 1984). That may account for the large representation of odonates in the Zaria sample (Odonata were not recorded in the adult diet by Fry, 1973). Acridid grasshoppers totalled 39% of all insects fed to nestlings. Large numbers of venomous Hymenoptera were also recorded. Most bees and wasps could not be identified, but I suspected that most of the 109 indeterminate insects in Fig. 3 were honey-bees *Apis mellifera*.

When foraging, adult Carmine Bee-eaters generally confined their activities to within 2-3 km of the colony, but I once tracked an adult from a car, flying with food directly towards the colony 8 km away. *M. pusillus* on the other hand foraged within 150 m of their nests. There appeared to be no defence of feeding territories between adjacent pairs.

Fledgling behaviour

Fledglings were easily recognised in the field (Fig. 4). In the few cases I was able to observe, fledging occurred synchronously within broods of *M. pusillus* but asynchronously in *M. nubicus* broods. For example, all five nestlings from a brood of Little Bee-eaters left the nest within 2-3 hours of each other, but two nestling Carmine Bee-eaters fledged over a 3-day period.

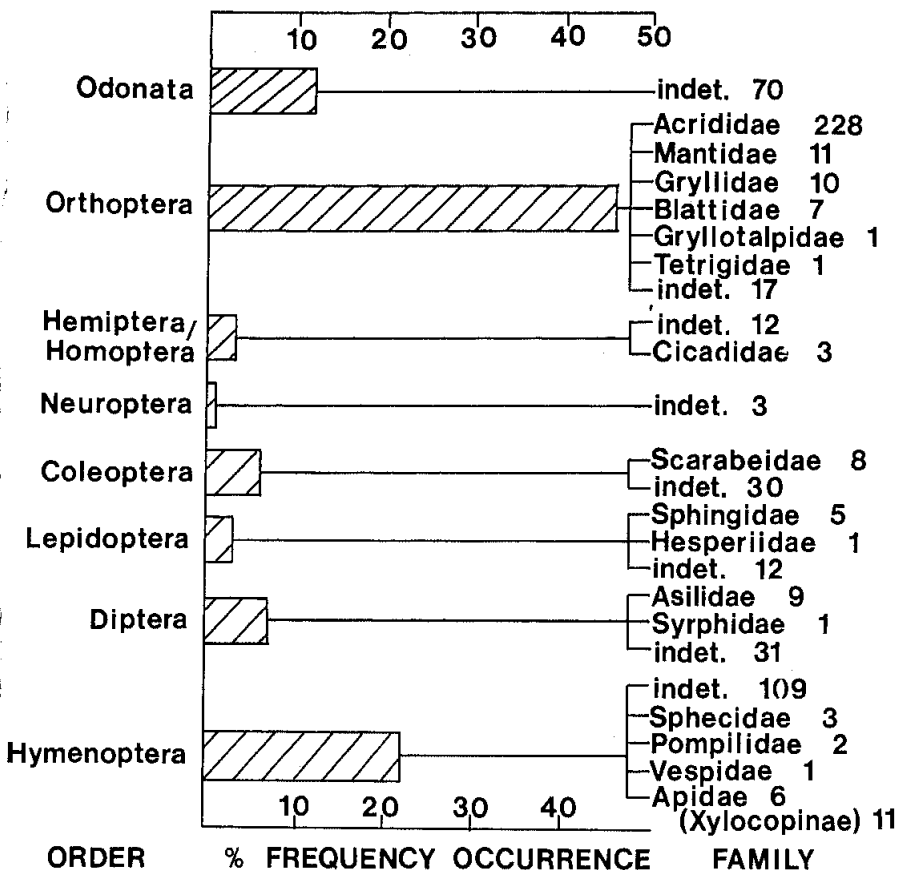


Figure 3 Nestling diet of *M. nubicus* at Zaria. Numbers following insect Family name indicate total individuals counted. Indet. = indeterminate.



Figure 4 Adult (on right) and fledgling *M. nubicus*.

There were notable specific differences in behaviour. *M. pusillus* fledglings perched for long periods on small bushes or grass stems near the nest, and only occasionally made short, inexpert flights from perch to perch as they were fed. *M. nubicus* fledglings were capable of sustained flight immediately upon leaving the nest, and flew with considerable skill continuously for several minutes in company with their parents. Often a fledgling followed its parents back to the nest preceding it into the tunnel, and presumably competing with its unfledged sibling for the insect being delivered. Returning fledglings sometimes stayed in the nest for over an hour. Once both nestlings had fledged, adults and young quickly left the area and were not seen again.

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