

FLEXIBLE GROWTH RATES IN NESTLING WHITE-FRONTED BEE-EATERS: A POSSIBLE ADAPTATION TO SHORT-TERM FOOD SHORTAGE¹

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Abstract. Nestling White-fronted Bee-eaters (*Merops bullockoides*) in Kenya show an ability to slow their development rate in response to food stress and, more importantly, to recover from stress with resumption of normal development. Successful fledging occurred at ages ranging from 22–42 days. The magnitude of developmental slowing was greatest: (1) among the youngest nestlings in large broods, (2) in seasons of overall low food availability, and (3) in nests provisioned by breeding pairs alone (i.e., nests without helpers). We speculate that this ability to slow growth reduces a nestling's daily energy requirements and thereby increases its likelihood of surviving through short periods of severe food shortage.

Key words: Bee-eater; *Merops bullockoides*; growth rate; nestling development; retardation; food stress; environmental unpredictability.

INTRODUCTION

White-fronted Bee-eaters (*Merops bullockoides*) are common birds of the savannas of eastern and central Africa. They feed upon airborne insects which they obtain by flycatching from exposed perches. In the Rift Valley of Kenya and Tanzania this species generally breeds with either the long rains of March–May or the short rains of October–December (Wrege and Emlén, 1991). However, both the timing and the duration of rainfall are highly unpredictable in this area (Brown and Britton, 1980). So, too, is the magnitude of any “flush” in insect abundance associated with rainfall (Wrege and Emlén, *ibid*, Fig. 3). As a result, the availability of food is highly variable during the breeding season, and nestlings are frequently exposed to conditions of severe food shortage.

In a study of reproductive success and the sources of egg and nestling mortality in this species, Wrege and Emlén (1991) reported that nesting success was low, with only one nest in four producing an independent offspring (i.e., an offspring that survived to six months of age). We further reported that nestling starvation was the single largest source of pre-fledging mortality, claiming the lives of fully 48% of all hatchlings.

In the present paper we examine the possibility that nestlings can prolong their survival during periods of temporary food shortage by reducing energy expenditure channeled into growth. Specifically, we (1) describe the ability of nestlings to slow their rate of morphological development, (2) relate the magnitude of such slowing to food availability, and (3) speculate on the possible adaptive significance of labile nestling development schedules.

METHODS

The data presented here were collected as part of a larger study of the breeding biology of White-fronted Bee-eaters in Kenya. Background information on social organization and helping in this species can be found in Emlén (1990). Basic methods are described in Hegner and Emlén (1986), Emlén and Wrege (1988), and Wrege and Emlén (1991). Between 1977 and 1984, we closely monitored the success of over 500 nesting attempts. Bee-eaters excavate their nests 1–1.5 m deep in vertical cliff faces. We checked nests using a ripiascope that enabled us to directly view the contents inside (Demong and Emlén, 1975). Active nests were examined at intervals of three to five days throughout the nestling period. At each such check, a morphological description was made of all surviving nestlings.

Nestlings showed highly variable growth rates and frequently exhibited signs of morphological retardation. To analyze this quantitatively, we divided an index of retardation, defined as the

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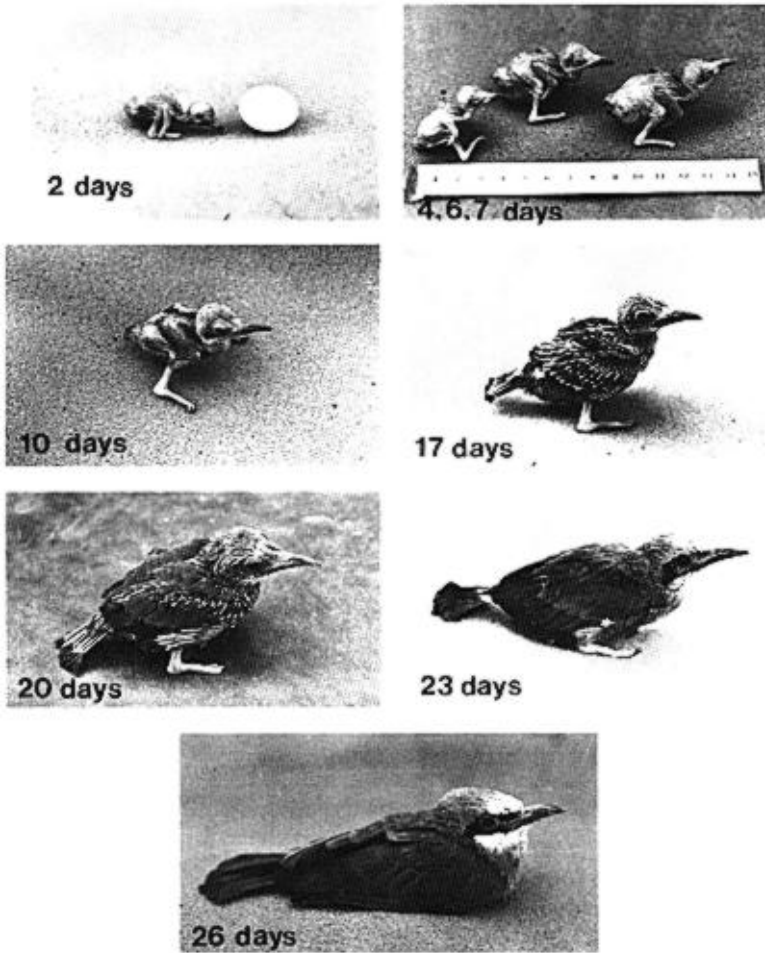


FIGURE 1. Growth and development of nestling White-fronted Bee-eaters. Comparison against these (and other) standardized photos allowed assignment of "morphological age."

difference between chronological (actual) age and morphological (or developmental) age. Morphological age was assigned by comparison to a standard set of photographs of the age-specific developmental sequence of well-fed nestlings. Nestlings used in constructing this sequence were from nests where the probability of food stress was minimal (e.g., oldest chicks in nests with at least three adults feeding). Figure 1 shows a sampling of this sequence. Note that our "standard" morphological age sequence represented rapid but not maximal growth; some nestlings exhibited a negative retardation index (see Fig. 2 below).

Well-fed nestlings completed their feather growth at 25 days of age and showed growth patterns remarkably similar to those described

by Fry (1972) for *Merops bullocki* (the sibling species of *M. bullockoides* from West Africa) and Koenig (1953) for captive reared *M. superciliosus*. A retardation index was assigned to each nestling when it reached the 22–25 day stage of morphological development. At this time the nestling was removed from its nest-chamber, ringed with a numbered aluminum band, marked with colored paint on its tail, weighed, measured, and returned to the nest.

After fledging, young continued to be provisioned by breeders and helpers for about six weeks. They molted into adult plumage at six months of age. All young remained with their parental group for at least nine months, at which time some individuals paired into other social groups (Hegner and Emlen, 1986). The survival

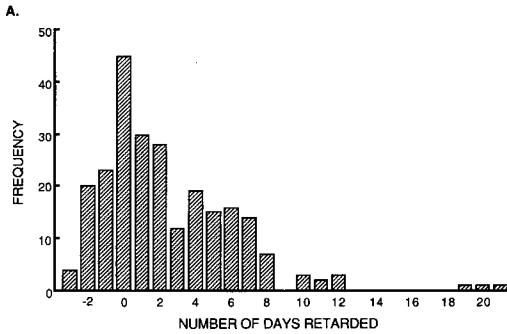


FIGURE 2. Frequency distribution of developmental retardation among pre-fledging White-fronted Bee-eater chicks. Retardation was scored as the difference between a nestling's chronological and morphological ages, measured when the nestling attained the morphological age of 22–25 days (see Fig. 1).

of fledglings to the age of independence (six months) was monitored by monthly censusing of family groups.

The abundance of aerial insects was measured through regular sampling using 3×5 m malaise nets. Food abundance was calculated as the average daily dry weight of insects caught during the median time of provisioning nestlings at the colony in question. Data were available for eight colony-seasons. (For full details of the insect sampling methodology, see Wrege and Emlen, 1991.)

RESULTS

The distribution of retardation values of 244 chicks that survived to the 22-day level of morphological development is shown in Figure 2. The considerable degree to which bee-eater nestlings can slow their development is evident. Beyond some level of retardation, nestlings succumb to starvation. Figure 2 grossly under-represents the *total* frequency of slowed development among nestlings because 48% of hatchlings starved before reaching the age for inclusion, and showed evidence of retarded growth before death.

Although most of the nestlings plotted in Figure 2 successfully left the nest chamber, we were able to determine the precise day of fledging for only 77 individuals. The distribution of their ages at fledging is shown in Figure 3. Taking 29 days as the normal fledging age for well-fed nestlings, fully one quarter of all surviving bee-eater chicks prolonged their development by more than 20% (delaying fledging by six or more days), while

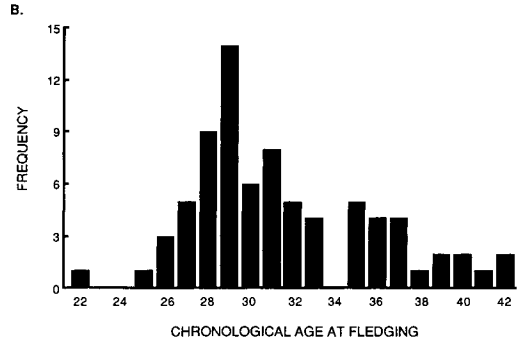


FIGURE 3. Frequency distribution of the chronological age at fledging for White-fronted Bee-eaters at Nakuru, Kenya.

10% extended their nestling period by more than 30% (fledging 10 or more days late). The twenty-day spread of fledging ages is considerably greater than that typical of most altricial avian species (Lack, 1968; Ricklefs, 1976, 1983; O'Connor, 1977, 1984).

We examined the relationship between slowed development and three separate measures of the amount of food available to nestlings: overall food abundance, nestling hatch order, and the presence of helpers. The magnitude of retardation was greatest in seasons of low food availability. In a multiple regression analysis controlling for the effect of number of nest attendants, the magnitude of retardation observed in both the oldest nestling (nestling 1) and the second oldest (nestling 2) was negatively correlated with insect abundance ($F_{\text{nestling 1 (3,153)}} = 6.43$, $F_{\text{nestling 2 (3,49)}} = 6.31$, both $P < 0.01$). The sample of surviving third oldest chicks was too small for analysis.

The severity of retardation also was related to hatch order. Because eggs hatch at approximately 24-hr intervals in White-fronted Bee-eaters, a size-graded hierarchy was present within virtually all broods (Wrege and Emlen, 1991). Direct observation at a nest excavated for filming purposes suggested that larger nestlings not only monopolized feedings but also directed aggressive attacks on their younger nest-mates. Competition for food therefore was predicted to be greatest for younger members of large broods. We examined the effect of hatch order on growth rate by comparing the retardation scores of older (i.e., nestling 1) versus younger nest-mates from all broods in which at least two young survived to scoring age (22–25 days of morphological de-

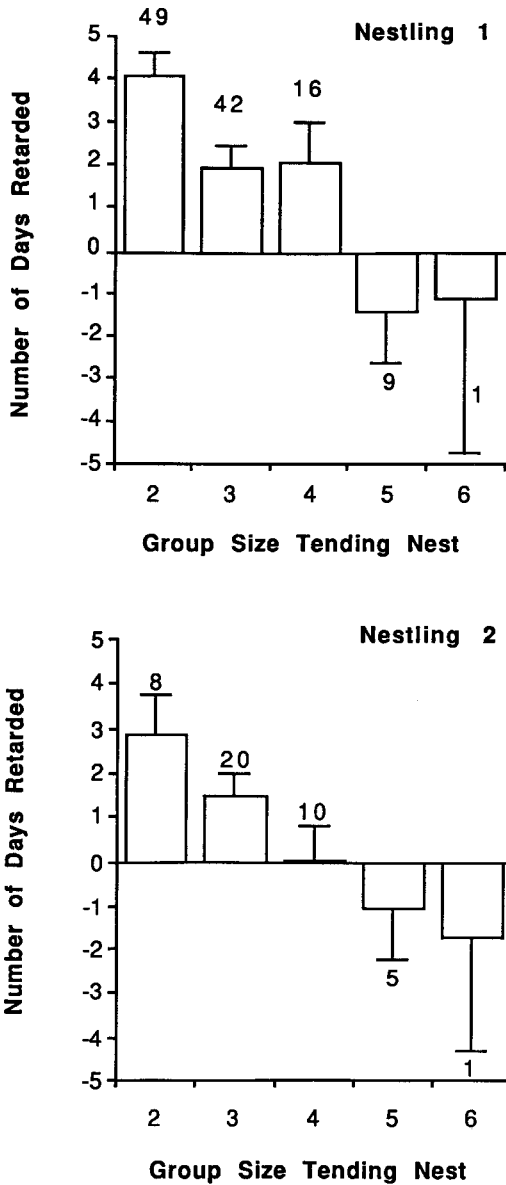


FIGURE 4. The influence of helpers in ameliorating the magnitude of retardation among nestling White-fronted Bee-eaters. (A) Adjusted mean retardation scores (\pm SE) for the oldest chick in each brood. (B) Similar scores for the second oldest chick of each brood. Sample sizes for the second oldest chicks are much smaller because many such chicks died of starvation prior to reaching the morphological age for inclusion.

velopment). Younger nestlings showed significantly greater retardation scores than their older siblings (paired *t*-test, $P < 0.01$).

Finally, the magnitude of developmental re-

tardation was reduced at nests being provisioned by helpers. Helpers in this species play a major role in the feeding of nestlings, bringing food at rates almost equivalent to those of breeders and resulting in a significant increase in the total provisioning rate to the nest (Emlen and Wrege, 1991). We examined the influence of helpers on nestling development using a multiple regression analysis that controlled for the effects of food abundance, brood size, and experience level of the breeding pair (Emlen and Wrege, 1991). The severity of retardation was progressively reduced with increasing numbers of helpers for both nestling 1 and nestling 2 ($F_{(1,111)} = 17.92$, and $F_{(1,43)} = 9.48$, respectively; both $P < 0.01$). This effect is shown graphically in Figure 4.

Many individual nestlings that showed delayed development seemingly recovered prior to fledging. No chicks left the nest until first reaching the morphological stage equivalent to 25 days (see Fig. 1). Individuals that grew more slowly simply delayed fledging until they had attained the same developmental stage as earlier departing individuals. This resulted in the wide range of fledging ages show in Figure 3.

Nestlings that delayed development, however, were typically lighter in weight and sometimes smaller in overall body size than their "normally" developing counterparts. Both pre-fledging weight and tail length (a measure of body size) were negatively correlated into the index of retardation (weight: $r^2 = 0.31$, $n = 136$, $P < 0.01$; tail length: $r^2 = 0.35$, $n = 136$, $P < 0.01$).

We therefore performed a logistic regression analysis of the effects of retardation, weight, and body size (tail length) on survival to six months of age. In addition to these variables, the models included covariates to control any effects of insect abundance, number of helpers at the nest, and breeder experience. We reported elsewhere that the retardation index alone (with covariates) was a significant predictor of post-fledging survival, with late fledging individuals suffering higher mortality (improvement chi-square statistic = 5.46, $P < 0.02$; Emlen and Wrege, 1991). However, when weight and tail length were incorporated, only tail length remained a significant predictor of post-fledging survival (improvement chi-square statistic = 12.52, $P < 0.01$; residual improvement chi square statistic for retardation index = 0.06, $P = 0.8$). Because the logit model is equivalent to a type IV model in regression, each predictor is evaluated after all

others have been entered. The implication is that small size, rather than slowed development per se, carries a survivorship cost. As is true for many avian species, individual bee-eaters that fledge at smaller than normal size suffer a higher probability of post-fledging mortality.

DISCUSSION

In most avian species, the time-course of nestling development is relatively fixed; periods of food shortage may lead to reduced weight gain, but behavioral, physiological, and morphological development continue at the species-typical rate (Lack, 1968; Ricklefs, 1968, 1983; O'Connor, 1984). White-fronted Bee-eaters depart from this pattern by exhibiting high intraspecific variability in post-natal development rate. Normal (well-fed) chicks attained the "pre-fledging" stage of morphological development at about 25 days of age. But other chicks took as long as 42 days to achieve the same stage. The coefficient of variation for nestling period (the time from hatching to fledging) was $CV = 13.73$.

The magnitude of developmental slowing was greatest in seasons of low food availability, among younger nestlings within a brood, and at nests without helpers. These findings indicate that delayed growth occurs in response to conditions of food shortage.

In a review of life history adaptations of breeding birds, O'Connor (1977) suggested that an ability of nestlings to temporarily suspend growth would be adaptive for species in which foraging conditions during nesting were not only unpredictable, but fluctuated over relatively *short time periods* (see also Ricklefs 1976). The ability of nestlings to delay further growth and to conserve energy would enable them to withstand temporary periods of food shortage. If conditions improved sufficiently rapidly, such nestlings could recover and fledge normally.

Both the seasonal ecology and the social behavior of White-fronted Bee-eaters are consistent with O'Connor's hypothesis. The seasonality of rainfall throughout much of East Africa is highly unpredictable (Brown and Britton, 1980) as is the day to day abundance of flying insects (Wrege and Emlen, 1991, Fig. 3). Short term shortages can be caused by prolonged periods of rainfall, cold temperatures, or strong winds. The amount of food provisioned to nestling bee-eaters depends not only upon the absolute abun-

dance of food in the environment, but also on the number of helpers provisioning the nest. This number can increase unexpectedly, causing a significant and immediate increase in food available to nestlings. Such helper supplementation occurs when individuals that start the season as breeders shift to become late-joining helpers at other active nests when their own initial breeding attempt fails (Emlen 1981, 1990). Such shifts are unpredictable, but they are not uncommon. One nest out of three gained extra helpers in this way. The social dynamics of this redirected helping provides an additional avenue for rapid recovery from short-term periods of food shortage in this species.

Flexible developmental rates of the type described here have been reported in several other altricial species including European Swifts, *Apus apus* (Koskimies 1948, 1950; Lack and Lack 1951), House Martins, *Delichon urbica* (Bryant 1975), and Mangrove Swallows, *Tachycineta albilinea* (Ricklefs 1976). Interestingly, all are aerial insectivores. The food supply of such species is notorious for its spatial patchiness, temporal unpredictability, and short-term responsiveness to local environmental conditions (e.g., Lack 1956, Emlen and Demong 1975, Brown 1988). Numerous authors have commented on the susceptibility of nestlings of aerial insectivores to periods of temporary food shortage.

Highly variable nestling periods also typify many pelagic seabirds, most notably several species of albatross (e.g., Lack 1968) and storm-petrel (summarized in Croxall et al. 1988). These species feed on ephemeral food supplies obtained at great distances from the nesting colonies (albatrosses on fish and squid, storm-petrels on surface invertebrates). Feeding conditions can deteriorate rapidly in times of inclement weather and nestlings are frequently forced to undergo fasting during periods of food shortage (e.g., Lack 1968, Boersma 1986). Further, feeding conditions can rapidly improve if environmental circumstances or the location of rich foraging patches changes. The distribution of reported instances of variable post-natal development rates thus accords quite well with the prediction of O'Connor (1977).

One might argue that the developmental flexibility observed in these species does not represent an adaptation but rather is a consequence of the pathology of near-starvation. Both adaptive and pathological explanations predict the

finding that retardation is more extreme under conditions of increased food stress.

Two lines of evidence bear on this distinction as it applies to *Merops bullockoides*. First, chicks not only survived, but attained full morphological development despite prolongation of the nestling period by as much as 50%. Such survival abilities are rare among altricial species and suggest a specialized strategy (Ricklefs 1983). Nearly half of all hatchlings, however, were unable to recover and succumbed to starvation.

Second, lability in morphological development is not a general phylogenetic feature of bee-eaters. It was not mentioned in Fry's (1984) review of the family Meropidae and was not observed in careful studies of nestling growth of two congeners, the Red-throated and European Bee-eater, *M. bullocki* and *M. apiaster* (Dyer 1979, Lessells and Avery 1989). In each of these species, breeding conditions are more predictable, and mean reproductive success much greater, than reported for White-fronted Bee-eaters at Nakuru (Fry 1972, 1984). Such interspecific comparison further suggests that the ability to opportunistically slow development is a specialized trait in *M. bullockoides*.

We therefore hypothesize that the ability of nestling White-fronted Bee-eaters to slow development and withstand morphological retardation represents an adaptation that enables them to reduce energy requirements over the short term, until increased food becomes available to complete development. If foraging conditions improve, or if additional adults join as helpers at the nest, developmentally retarded nestlings can recover and fledge successfully. The ability to slow development operates in combination with brood reduction (Wrege and Emlén, 1991) to provide flexibility in coping with an environment where provisioning rates fluctuate unpredictably over both short and long time intervals. The adjustment of development rate enhances the likelihood of survival if food shortages are temporary, while brood reduction ensures that mortality acts asymmetrically on the smallest nestling if food stress continues over the long term.

There is a strong need for additional quantitative data on both intra- and inter-specific variability in rates of nestling development. Although many studies have measured growth rates for weight, few have systematically measured morphological development or variability in

nestling period. We cannot rigorously test the adaptive hypothesis of variable nestling development schedules, or even determine where in the spectrum of species patterns the White-fronted Bee-eater falls, until more comparative data become available. We hope that the preliminary data presented in this report will stimulate other field workers to begin collecting these types of information.

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