BREEDING SEASONALITY AND REPRODUCTIVE SUCCESS OF WHITE-FRONTED BEE-EATERS IN KENYA

PETER H. WREGE[1,2] AND STEPHEN T. EMLEN[1,2]

[1]Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 15853 USA, and
[2]National Museums of Kenya, Nairobi, Kenya

ABSTRACT.—White-fronted Bee-eaters (*Merops bullockoides*) at Nakuru, Kenya, reproduce in an environment where food supply for provisioning nestlings is unpredictable and generally scarce. With data from 8 yr of study on three populations of bee-eaters, we examined how these environmental conditions have influenced the timing of breeding and patterns of nesting success.

Breeding coincided with the general pattern of rainfall in the Rift Valley. Kenya experiences two rainy seasons per year, and individual bee-eaters bred with *either* the long *or* the short rains, but not both. Members of a given population bred colonially and quite synchronously, but members of adjacent populations were often out of phase with one another. As a result, the distribution of long- and short-rains breeding populations formed a spatial mosaic.

Reproductive success was highly variable but typically low. Mean ($\pm$SD) fledging success was 0.57 ± 0.83 young, and only one nest in four produced an independent offspring (6 months of age). Most prefledging mortality (88%) was due to egg losses and the starvation of young. Very little (7%) was attributable to predation. Social factors, primarily intraspecific nest parasitism, were responsible for nearly half of all egg losses, and represent an important cost of group living.

Starvation, the single most important source of prefledging mortality, claimed the lives of 48% of all hatchlings. Starvation was greatest at times of low food availability, in nests with large broods, and in nests tended by pairs without helpers.

Hatching was asynchronous. This enhanced the ability of older nestlings to monopolize limited food supplies, and resulted in the selective death of the smallest nestling first. Such brood reduction, coupled with the ability of nestlings to slow their development rate in response to food stress, is considered an adaptation for coping with the unpredictable variation in food supply commonly faced by these birds. *Received 17 August 1990, accepted 18 January 1991.*

EVOLUTIONARY processes act through variability in the lifetime reproductive output of individuals. An understanding of how selection has shaped the different components of life histories depends on knowledge of the sources of variability in reproductive success.

For 8 yr we have studied the social dynamics and reproductive success of individually marked White-fronted Bee-eaters (*Merops bullockoides*) in the central Rift Valley of Kenya. These birds are nonmigratory, cooperative breeders that live throughout the year in colonies of 25–400 individuals. Three populations were studied intensively, and known individuals were monitored continuously for 3–7 yr (depending on population). Helpers at the nest were a conspicuous feature of the social system, and we detailed their influence on measures of reproductive success elsewhere (Emlen and Wrege 1991).

In this paper we describe the salient features of resource availability and examine the timing of breeding as it relates to the annual pattern. We then provide reproductive success statistics, quantify sources of egg and nestling mortality, and discuss the influence of environmental conditions on reproductive output and the evolution of life history patterns.

METHODS

This study was conducted in Lake Nakuru National Park, Kenya. The bulk of our data come from 8 yr of concentrated study of 3 populations: Makalia (1977–1979), Badlands (1977–1978), and Baharini (1980–1984). A fourth population (Enderit) was monitored in 1977, and these data are included in analyses of seasonality and overall reproductive success. Additional data obtained from the Baharini population (1985–1986) as well as other populations in and around the national park are included in some analyses, as noted.

White-fronted Bee-eaters are colonial, roosting throughout the year, and breeding, in holes excavated 1–2 m into vertical earth banks or cliffs. These birds

feed almost exclusively on flying insects, and extended family groups (clans) defend foraging territories in savanna habitat surrounding the colony site (for a general description of the social structure and cooperative breeding behavior, see Emlen 1990). All adults were identified individually by permanent leg bands and plastic wing tags, and were sexed by laparotomy when in adult plumage.

MEASUREMENT OF REPRODUCTIVE SUCCESS

Behavioral observations.—Behavioral aspects of nesting phenology of the breeding colonies were observed daily (2–5 observation hours per colony). Information on nest activity and failure, as well as changes in the composition of groups tending specific nests, was obtained from such observations.

Nest checks.—We checked all active nests at regular intervals with a "ripariascope": a tube of adjustable length that contains lenses, lights, and a terminal mirror (Demong and Emlen 1975). During egg laying, nests were checked daily (Baharini population) or every second day (Makalia, Badlands, and Enderit populations). Checks usually began before the first egg, with supplemental checks whenever unusual behavior was suspected (e.g. intraspecific nest parasitism). Nest contents were monitored periodically throughout incubation but daily throughout the expected hatching period. Checks continued at intervals of 3–5 days to monitor the growth and fate of all nestlings. Before fledging, each surviving nestling was removed from its nest hole, banded with a numbered aluminum band, weighed, measured, and returned to the nest.

Nesting success.—Actual fledging from the nest was not always observed, primarily because the age at fledging varied from a norm of 28–30 days up to 42 days for individuals with slowed development (Emlen et al. in press). Although *chronological* age varied, all nestlings that successfully fledged first attained *morphological* age 25 (i.e. the stage of morphological development typically completed in 25 days by well-fed nestlings). We therefore used this morphological criterion as a standardized estimate of successful fledging.

Sources of egg and nestling mortality.—All losses were classifed to presumed cause of mortality according to the following criteria:

1. *Unhatched eggs*—eggs still present in the nest chamber when the oldest nestling was 5 days old (longest span for entire clutches to hatch was 4 days).
2. *Desertion*—eggs still present in the nest chamber when, before full-term incubation, the birds ceased incubation and roosting at that nest.
3. *Predation* (of eggs or young)—entire nest contents that disappeared between two successive checks separated by <6 days. Such losses were usually detected within 2 days. Hole-nesting limits likely

predators at Nakuru to snakes and mongooses, both of which are known to consume the entire nest contents in one visit. Madagascar Harrier Hawks (*Polyboroides radiatus*) and various small falcons might take single nestlings from hole entrances, but we rarely saw these predators at our study colonies.

4. *Other egg loss*—all losses of eggs not meeting the criteria above.
5. *Nestling starvation*—young that disappeared singly and for which there was prior evidence of morphological retardation of the individual (83% of cases) or of nestmates. Often we found the carcasses of such nestlings either in the nest chamber or discarded below the colony.
6. *Other nestling loss*—losses of nestlings not attributable to either starvation or predation.
7. *Horus Swifts*—occasionally Horus Swifts (*Apus horus*) actively took over bee-eater nest chambers by entering and pushing out eggs or killing nestlings by puncturing them with their claws.
8. *Catastrophic losses*—eggs or young lost to severe environmental conditions (e.g. flooding or cave-ins caused by heavy rains, rising stream levels, or both).

Fledgling survival to independence.—We calculated survivorship from fledging to independence for the Baharini population from monthly census data. Although fledglings reach adult foraging proficiency approximately 6 weeks after fledging (2.5 months of age), they remain with the family unit and do not molt into the definitive adult plumage until 6 months of age. We used the plumage criterion to define full independence. *Survivorship* was defined as the percentage of nestlings that reached morphological age 25 that were still alive at 6 months of age.

Data from the Makalia and Badlands populations were not used in survival analyses. From 1978–1979, nestlings were fitted with wing tags just before fledging, and we suspect that mortality was substantially higher on fledglings with tags than on those without (Emlen unpubl. obs.). Consequently, young from the Baharini population were not given wing tags until approximately 6 months of age.

ENVIRONMENTAL MONITORING

Insect availability was considered a possible predictor of reproductive success. Rainfall influenced insect abundance, and local weather conditions (hours of rain, strength of wind, etc.) affected both the flight activity of insects and the ability of bee-eaters to capture them. The availabilty of insects to foraging bee-eaters was therefore represented in analyses by variables of insect abundance, rainfall, and their interaction.

Rainfall.—Monthly total precipitation and number of days with >0.5 mm of rain were derived from daily precipitation data recorded at the national park head-

quarters, 3 km from the Baharini population (Fig. 1). There was no significant difference in the amount or pattern of rainfall collected at headquarters and at two sites near the southern study populations.

Insect abundance.—We monitored the abundance of flying insects, the primary food of White-fronted Bee-eaters, with a 3 × 5 m Malaise net (Malaise 1937, Marston 1965). Netting stations were established close to typical foraging territories in each of the three primary study populations. Stations were sampled monthly from 1978–1984 and biweekly from 1984–1986.

For each monthly or biweekly sample, daily sub-samples were collected on consecutive days until a minimum of three (maximum of six) subsamples were obtained under acceptable weather conditions. Un-acceptable weather conditions were (1) temperatures > 15% below the monthly average, or (2) steady winds >5 mph, or (3) rain. Each daily sampling period ran from 0800–1600. Samples were sorted to remove insects <5 mm in body length (smaller insects were rarely captured by the birds; Hegner 1981), oven-dried for 12–16 h at 80°C, then weighed to ±0.001 g. From these subsamples we calculated the mean daily biomass of insects per sampling period. In the following analyses, estimates of insect abundance for particular time intervals were calculated by integrating under the curve described by all sample means connected by straight line-segments.

STATISTICAL ANALYSES

We used SAS Statistical Software, version 5.1 (SAS 1985), for most statistical analyses. For logistic regression we used the PLR procedure, BMDP Statistical Software (1983).

RESULTS

BREEDING SEASONALITY

White-fronted Bee-eaters inhabit wooded savannah habitat across the entirety of central Africa, from the Democratic Republic of Congo and Angola in the west, through Kenya in the northeast, south to Mozambique and Natal (South Africa). This habitat, a mosaic of grasslands with scattered bush and open acacia woodland, is characterized by pronounced dry and rainy seasons. Throughout most of its range, there is one rainy season centered around October to December. But close to the equator in Kenya and Tanzania, the intertropical convergence causes two rainy periods each year, the "long rains" in March to May, and the "short rains" from October to December, with a pronounced dry season from June to September (Sinclair 1978; see Fig. 2b). The short rains of
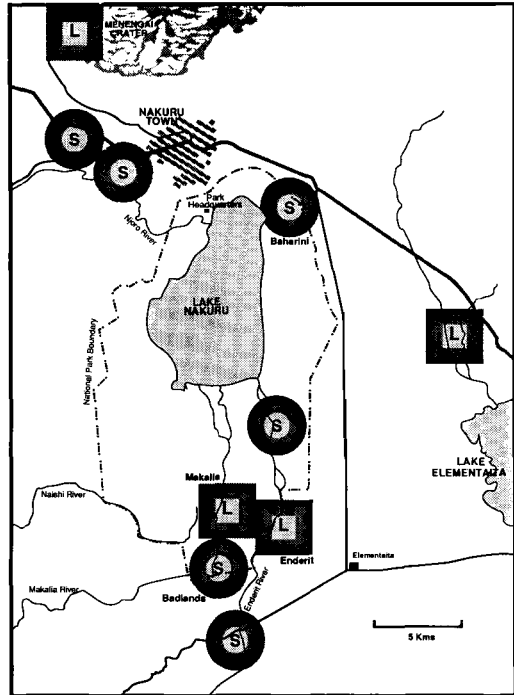

Fig. 1. The location of 10 *Merops bullockoides* populations in Lake Nakuru National Park, Kenya, and the surrounding area. Shaded circles = populations that breed during the short rains; shaded squares = those that breed during the long rains. The primary study populations were Baharini, Makalia, Badlands, and Enderit.

Kenya correspond to the single rainy season found elsewhere in the species' range.

Populations of White-fronted Bee-eaters near Nakuru have a single primary breeding season each year, roughly coinciding with either the long or the short rains. Interestingly, populations living within a few kilometers of one another may be timed to opposite seasons. Populations studied in the Nakuru area between 1977 and 1986 were either "long-rains" or "short-rains" breeders (Fig. 1). The mosaic nature of the distribution is apparent. The four populations studied most intensively, and for which we present data on reproductive success below, were Makalia, Badlands, and Enderit in the southern portion of the national park, and Baharini in the north.

In spite of the clear seasonality in breeding by populations near Nakuru, the rainfall pattern in this region differs from the Kenyan norm; when averaged over many years, it shows only
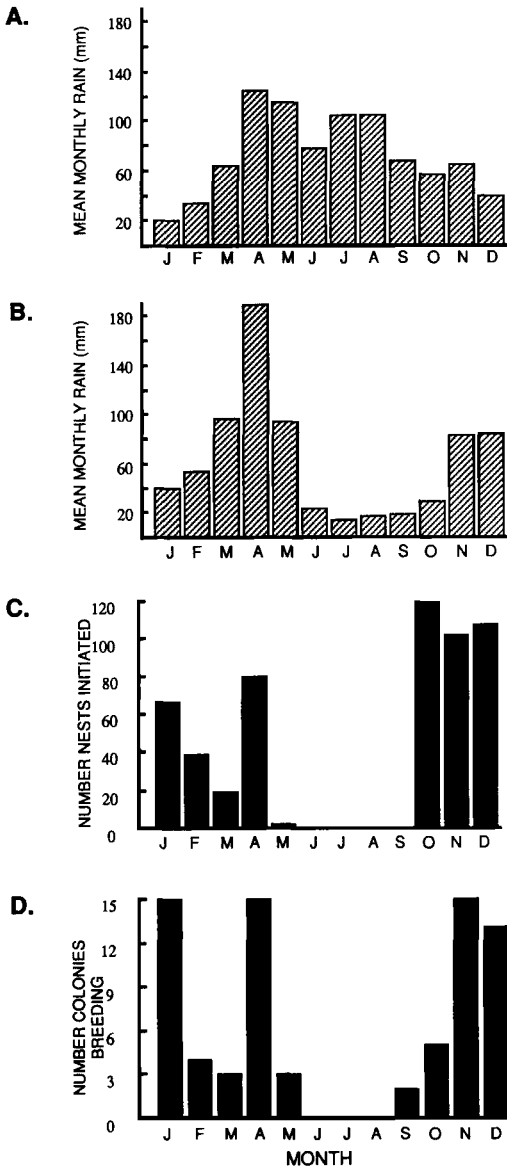
A.

B.

C.

D.

Fig. 2. Correlations between timing of breeding and rainfall in the Nakuru area, and a comparison with rainfall patterns elsewhere within the range of *Merops bullockoides*: (A) average monthly rainfall in Nakuru over 56 yr (*from* Brown and Britton 1980), (B) average monthly rainfall from Naivasha, Magadi, Arusha, and Moshi in the Rift Valley (Brown and Britton 1980), (C) frequency of nest initiation in the 4 study populations, 1977–1985, and (D) median date of egg laying for 15 populations within a 30-km radius of Nakuru National Park. Data from 1973, 1975–1986; the number of observations per population varies.

a single rainy period and lacks a well-defined dry period between June and September (Fig. 2a, data from Brown and Britton 1980). The bimodal pattern (Fig. 2b) is typical of the Rift Valley generally, and probably represents the pattern experienced by bee-eaters over most of their range in Kenya. Timing of breeding in the Nakuru area includes the *number of nests* initiated per month for all primary nestings of the four study populations (Fig. 2c) and the *number of colonies* (Fig. 2d) in the larger Nakuru area that initiated breeding in a given month (data from 1973 and 1975–1987). These comparisons suggest that the timing of breeding by the Nakuru bee-eater populations reflects the rainfall pattern found elsewhere in the species' range rather than the pattern found locally.

The mean monthly rainfall and insect abundance at our study site varied over a 9-yr period (Fig. 3). Rainfall was highly variable, both from month to month and between years. The influence of rainfall upon aerial insect abundance also varied. Generally, relative insect abundance tracked changes in rainfall with only a slight lag, a pattern most clearly seen for the years 1980 through 1985. The long-rains breeders (Makalia, Enderit) generally initiated nesting after Nakuru's annual dry period, whereas short-rains breeders initiated before the dry period (Fig. 3: bottom). Other than this very general pattern, however, neither insect abundance nor rainfall showed a consistent trend at the time of breeding.

On three occasions individuals of the Baharini population attempted to raise a second brood (Fig. 3: hatched blocks). This was not observed in the other populations and has been documented in only one other species of bee-eater (*Merops oreobates*; Fry 1984). We prefer to call this event *secondary nesting* because participants included not only previously successful pairs (the usual definition of second brooding) but also unsuccessful pairs and individuals that had been helpers in the primary nesting. Although clutches lost early in incubation were sometimes replaced immediately, such losses were rare (see below). Nests that failed later in the cycle were not usually replaced. Secondary nesting was more or less synchronized in the colony as a whole; pairs that failed relatively early waited until several weeks after successful pairs fledged young from the primary attempt. In 1981 and 1982, secondary nesting followed largely successful primary nesting, whereas in
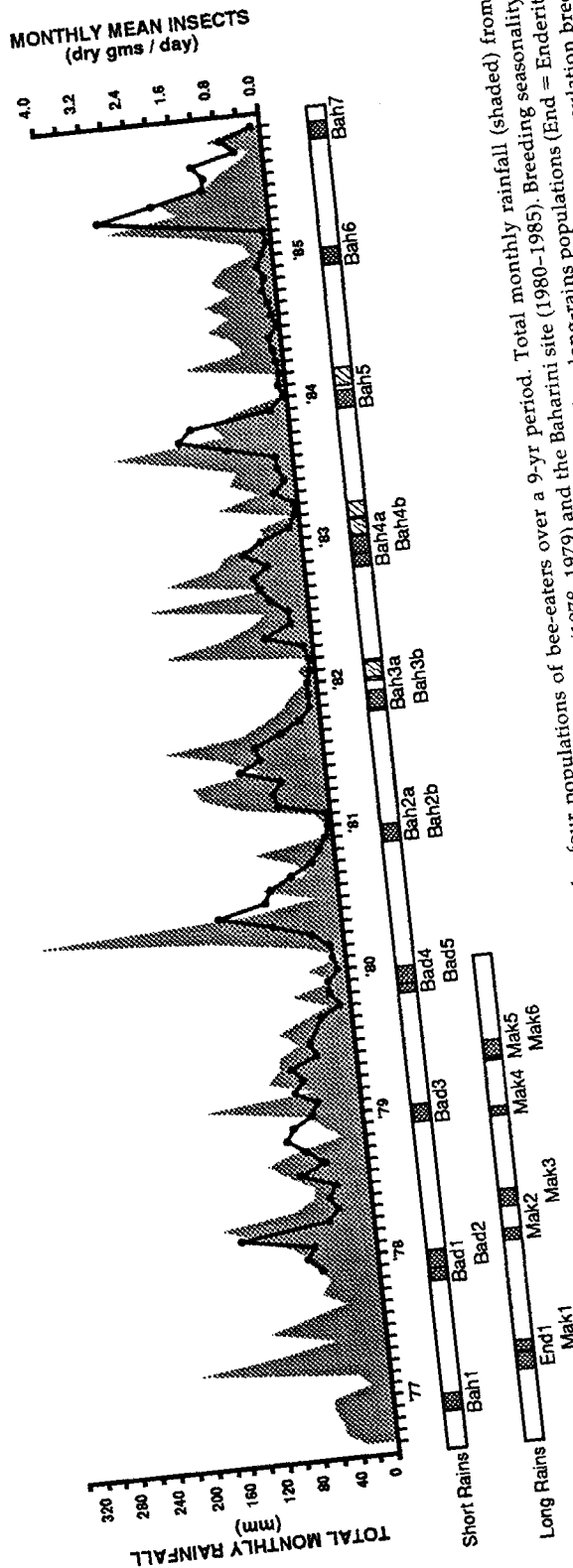
Fig. 3. Seasonality of insect abundance, rainfall, and breeding by four populations of bee-eaters over a 9-yr period. Total monthly rainfall (shaded) from records at the headquarters sampling station; insect abundance (curve) from the Makalia site (1978–1979) and the Baharini site (1980–1985). Breeding seasonality is shown in the bottom segment: short-rains populations (Bad = Badlands, Bah = Baharini) are indicated in the upper bar, long-rains populations (End = Enderit, Mak = Makalia) are along the lower bar. Numerals indicate sequential breeding seasons of each population, with an *a* or *b* to indicate that the population bred as two subpopulations in two different colonies. Shaded blocks represent the duration of the breeding season, from median laying date to median fledging date. Hatched blocks represent secondary nesting attempts (second brooding) by the Baharini population. The Baharini population was not sampled in 1978–1980.

TABLE 1. Reproductive success ($\bar{x} \pm$ SD) for four populations of White-fronted Bee-eaters in Nakuru, Kenya. Baharini and Badlands populations bred with the short rains; the Makalia and Enderet populations bred with the long rains. Samples include all nests with accurate data for the phase of reproduction; sample sizes are in parentheses.

	Clutch size	No. hatched	No. fledged	% nests successful
	Baharini			
1980	2.60 ± 0.74 (53)	1.70 ± 1.23 (46)	0.82 ± 0.82 (51)	61.1 (54)
1981	3.16 ± 1.75 (44)	2.32 ± 1.04 (31)	0.80 ± 0.84 (45)	57.7 (52)
1982	2.62 ± 0.82 (34)	2.06 ± 1.15 (36)	1.20 ± 0.99 (35)	72.5 (40)
1983	2.00 ± 0.71 (25)	1.08 ± 1.15 (25)	0.28 ± 0.46 (25)	38.2 (34)
1984	2.91 ± 1.61 (22)	2.24 ± 1.34 (21)	0.80 ± 0.77 (20)	71.4 (28)
Total	2.70 ± 0.82 (178)	1.89 ± 1.23 (161)	0.81 ± 0.85 (176)	60.1 (208)
	Badlands			
1977	2.91 ± 0.73 (23)	2.70 ± 0.70 (23)	1.50 ± 1.14 (32)	79.4 (34)
1978	2.64 ± 0.58 (22)	1.95 ± 1.05 (20)	0.65 ± 0.75 (20)	50.0 (20)
Total	2.78 ± 0.67 (45)	2.35 ± 0.95 (43)	1.17 ± 1.08 (52)	68.5 (54)
	Makalia			
1977	2.62 ± 0.89 (37)	1.03 ± 1.30 (38)	0.03 ± 0.16 (39)	02.6 (39)
1978	2.68 ± 0.69 (85)	1.95 ± 1.22 (84)	0.31 ± 0.62 (86)	23.0 (87)
1979	2.43 ± 0.80 (42)	1.86 ± 1.23 (44)	0.26 ± 0.57 (46)	19.6 (46)
Total1	2.60 ± 0.77 (164)	1.45 ± 1.34 (166)	0.23 ± 0.55 (171)	17.4 (172)
Total2[a]	2.59 ± 0.77 (159)	1.62 ± 1.31 (141)	0.45 ± 0.69 (88)	33.7 (89)
	Enderit			
1977	2.50 ± 0.76 (26)	2.00 ± 1.05 (21)	0.27 ± 0.60 (40)	20.0 (40)
1977[a]	2.50 ± 0.76 (26)	2.00 ± 1.05 (21)	0.37 ± 0.67 (30)	26.7 (30)
	Baharini secondary nestings			
1981	2.29 ± 0.76 (7)	0.80 ± 1.30 (5)	0.00 ± 0.00 (7)	12.5 (34)
1982	2.50 ± 0.62 (34)	1.91 ± 1.01 (33)	0.74 ± 0.95 (35)	47.2 (36)
1983	2.17 ± 0.58 (12)	1.00 ± 1.28 (12)	0.08 ± 1.28 (13)	07.7 (13)
Total	2.40 ± 0.63 (53)	1.58 ± 1.18 (50)	0.49 ± 0.84 (55)	33.3 (57)

[a] Without catastrophic losses.

1983 fledging success in the primary breeding was extremely low.

GENERAL PATTERN OF REPRODUCTIVE SUCCESS

Breeding in each population was characterized by high variance and low success (Table 1). Nests initiated during the short rains (Baharini and Badlands populations) averaged 0.89 fledged young, while nests from the long-rains populations (Makalia, Enderit) averaged 0.24 fledglings. The long-rains (but *not* the short-rains) populations suffered high catastrophic losses due to flooding of the river systems along whose banks the colonies were located. When we excluded these losses for purposes of comparison, average nesting success in the long-rains populations was 0.43 fledged young, still considerably lower than the average for short-rains populations. Although secondary nestings in Baharini involved few nests, they ap-

pear to have lower mean success rates than nests in the corresponding primary breeding seasons.

Pooling all data, fewer than half of the breeding attempts succeeded in fledging young (41% of 531 nests), and the overall mean (± SD) number of chicks fledging was 0.57 ± 0.83. When catastrophic losses are omitted, 50% of 438 nests were successful, and the mean number of chicks fledging was 0.70 ± 0.87. Of these fledglings, 58% survived to reach independence (6 months of age). The cumulative probability of survival to each major stage of development is shown in Fig. 4.

SOURCES OF VARIATION IN REPRODUCTIVE SUCCESS

High variability occurred in both hatching and fledging success between years and populations (Table 1). An understanding of this variation begins with an examination of the deter-

minants of clutch size and the subsequent sources of egg and nestling mortality.

Clutch size.—Mean clutch size, averaged across all populations, was 2.62 eggs, and it varied significantly between years (ANOVA: $F_{year} = 6.54$, df $= 9/409$, $P \ll 0.01$). Long-rains and short-rains populations did not differ significantly ($t = 1.04$, df $= 348$, $P > 0.3$), but clutches laid during the secondary nestings in Baharini were significantly smaller than those of primary nestings ($t = 2.59$, df $= 238$, $P < 0.02$).

Several factors might contribute to clutch size variability: (1) the condition or quality of the breeding female, (2) the availability of resources necessary to produce eggs, (3) the presence of helpers at the nest (which allofeed the breeding female), (4) the time of laying within the season, and (5) the anticipated future availability of food for feeding nestlings (Klomp 1970, Cody 1971, O'Connor 1984). To examine clutch-size variation, we used a multiple ANCOVA model that included variables representing each of these factors. The first was represented by female identity and age; the second by insect availability in the month of laying, as well as averaged over the 3 months before laying; the third by group size at the time of laying; the fourth by date of laying relative to the median for that season; and the fifth by insect availability during the nestling period. The analysis was limited to Baharini females for whom we had data on a minimum of three clutches from three different years ($n = 33$ females).

Clutch size was correlated significantly with insect availability at and before laying, but not with female quality, group size, date of laying, or insect abundance during the nestling period. Two measures affecting insect availability (insect abundance in the month before laying, and rainfall over the 3-month period before laying) accounted for 16% of the variation in clutch size ($F_{insects} = 10.67$, df $= 1/76$, $P \ll 0.01$; $F_{rain} = 13.75$, df $= 1/76$, $P \ll 0.01$). The correlation with insect abundance was negative. This indicates that clutch sizes were actually smaller in years with higher insect densities. The biological significance of this correlation is unclear. Most of the variation in clutch size (32%) was attributed to characteristics of the individual breeding females ($F_{female} = 1.48$, df $= 32/76$, $P = 0.08$); however, we were not able to identify any particular characteristic (age, breeding experience, time with current mate) that was responsible for the
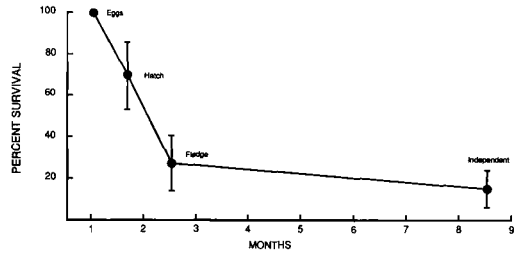

Fig. 4. Cumulative transition probabilities from egg laying to independence. Probability of survival through each breeding phase, from eggs to fledging, was calculated from all populations and all years. Survival from fledging to 6 months of age was estimated from Baharini primary nesting data only. Bars indicate the standard error of cumulative probabilities, calculated for each population-year.

correlation, and repeatability of clutch size within females was low ($r = 0.12$).

Sources of egg and nestling mortality.—All noncatastrophic sources of prefledging mortality are diagramed in Fig. 5. Nests lost to flooding were excluded to facilitate interpopulation comparison. The two largest causes of mortality were egg losses and starvation of nestlings. Predation on eggs and young was of only minor importance to White-fronted Bee-eaters. These patterns were consistent in most years and in all populations.

Of all eggs laid, 28% never hatched. This accounted for 40% of all prefledging losses. At least 18% of these losses were due to the active removal of eggs by bee-eaters. Removed eggs frequently were found under the Baharini and Badlands colonies, which confirmed that predation was not involved in such losses. Similar confirmation was not available for many Makalia colonies because they were located over water. This may partly explain the higher value for egg predation in Makalia (Fig. 5), because entire clutches removed by bee-eaters would erroneously be assigned to predation unless the eggs were actually found below the colony.

Intensive behavioral observations and frequent nest checks at the Baharini primary nesting colonies allowed us to examine in detail the causes behind this high rate of egg loss. Social factors accounted for nearly half (48%) of all egg losses (Table 2). The single largest source was intraspecific nest parasitism (24% of egg losses). Females parasitizing nests sometimes tossed out a host egg before laying their own, and parasitically laid eggs often failed to hatch
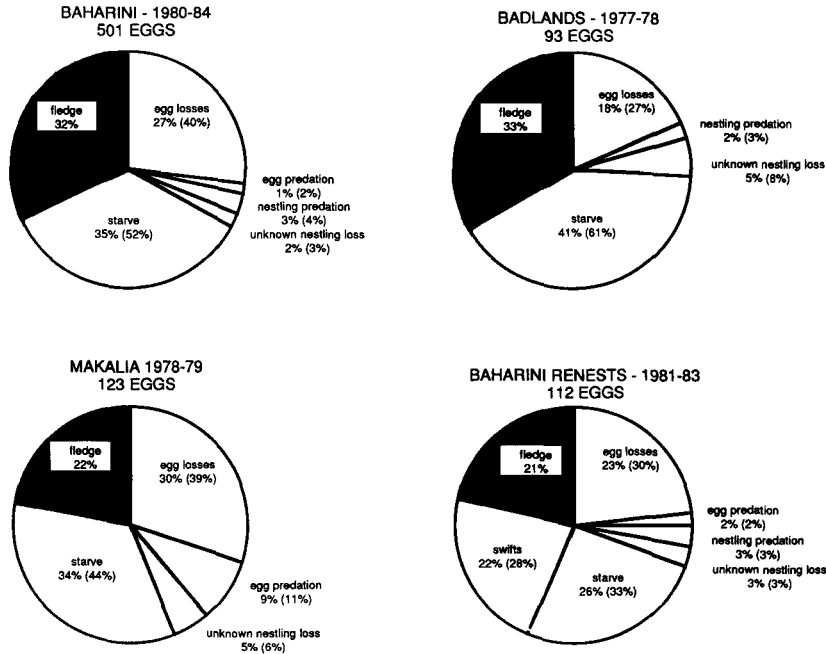
Fig. 5. The causes of egg and nestling mortality in three populations of bee-eaters. All primary nestings are pooled for each population (all secondary nestings are pooled in the relevant plot for Baharini). Each sector of the diagram represents the percentage of all eggs laid that were lost to a particular mortality source. The percentage of all losses attributed to each source is indicated in parentheses. Makalia population colonies that suffered the loss of virtually all eggs during flooding were omitted.

because they were laid after the host clutch had been completed. More frequently eggs were tossed out by the host female herself. Parasitic eggs laid before the host's own first egg were removed by the host female (Emlen and Wrege 1986). On four occasions breeding females removed their entire clutches shortly after attempted or successful parasitism, presumably because they detected the parasitism in some way (n = 12 eggs in Table 2).

Competition between two females over the same mate or for the same nest hole, and the sudden loss of a mate through conscription (when a breeder is socially harassed into abandoning its mate to help at the nest of close kin; Emlen 1981, Emlen et al. unpubl. obs.), together accounted for an additional 15% of egg losses.

The single largest source of prefledging mortality was nestling starvation. Starvation accounted for 48% of all noncatastrophic losses and was a conspicuous aspect of bee-eater reproduction in every population in every year; 48% of all hatchlings starved before they reached fledging age. Although modal clutch size was 3 eggs, in three-quarters (76%) of all nests ei-

ther a single young fledged or none at all; and only 4% of nests with young had 3 young successfully fledge (n = 322 nests).

Five lines of evidence indicate that what we have called starvation did indeed result from the inability of the breeders (plus any helpers) to sufficiently provision nestlings. First, most nestlings showed signs of retarded development before they were found dead or disappeared from the nest.

Second, starvation losses followed a consistent pattern in which the smallest nestling in the brood died first. Nestlings hatched asynchronously (at approximate 24-h intervals). Consequently, chicks within a brood were clearly differentiated by size and morphological development within 3 or 4 days. We assume that the size hierarchy at this early age reflects the hatching sequence. A similar pattern was reported for the Red-throated Bee-eater (*Merops bullocki*) by Dyer (1979). He found that under conditions of food stress, asymmetries in the weight of asynchronously hatched broodmates increased with increasing age, and mortality also followed the sequence of youngest first. In the

TABLE 2. Causes of egg mortality during primary nestings of the Baharini population. All egg losses that could be attributed to some particular source of mortality are included (17 eggs lost to unknown causes are omitted).

Cause of egg loss	No. of eggs	% egg losses
Socially induced losses		
Parasitism	35	24.3
Mate competition/hole takeover	12	8.3
Conscription[a]	9	6.3
Other social causes	13	9.0
Nonsocial losses		
Desertion after breeder death	26	18.1
Other desertion	4	2.8
Sterile eggs	19	13.2
Predation	10	6.9
Single egg losses[b]	16	11.1
Total[c]	144	100.0

[a] Conscription is when a nesting attempt is abandoned by one breeder to become a helper at another nest, usually of close kin. Typically such conscription is preceded by social harassment from an older member of the clan.

[b] Single eggs that disappeared during the incubation period were probably removed by the breeders and/or helpers. These eggs were frequently found under the nesting colony.

[c] The total sample of eggs included in this analysis and resulting percentages differ from Figure 5 because (a) losses due to unknown causes are omitted here, and (b) Figure 5 includes only nests with completely accurate data on both clutch size and fledging success.

Baharini population, 100% of starvation losses in broods with multiple young took the smallest nestling. For the oldest nestling, the early establishment of a hierarchy in size and mobility may be a direct advantage in competition with siblings for access to food. In 1987, we dug an underground observation pit from which we could directly view an active nesting chamber (for technique, see Fry 1972). Limited observation of nestling interactions and adult feeding behavior showed extreme aggression by the oldest nestling toward its smaller siblings, including vigorous pecking and violent shaking while holding the neck. Food items brought by adults were monopolized by the oldest nestling, to the point that younger siblings eventually ceased begging until the oldest was satiated (S. King pers. comm.). (This behavior is visible in the BBC video, "The Bee Team," A. Fothergill, producer.)

Third, starvation losses increased with brood size. If each nestling can monopolize food resources when in competition with siblings lower in the age/size hierarchy, the probability of death by starvation should increase with an in-
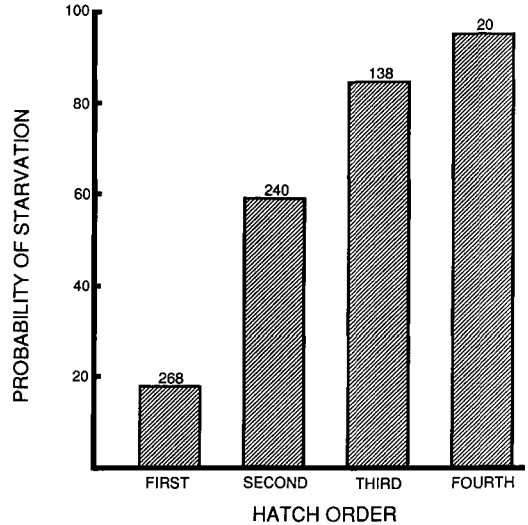

Fig. 6. The probability of starvation as a function of competition from older nestmates. Pooled data are from primary nestings of the four study populations. Above each bar is the number of nests that included a nestling hatching first, second, third, or fourth (i.e. the second bar includes all nests with ≥2 nestlings, but not nests that hatched only one young).

crease in the number of older nestmates (Fig. 6). The first-hatched chick had an overwhelming competitive advantage over its broodmates. First-hatched chicks suffered a 19% probability of starving before fledging. The likelihood of starvation increased to an overwhelming 84% and 95% for chicks with 2 and 3 older nestmates, respectively.

Fourth, starvation losses were reduced when helpers were present (Emlen and Wrege 1991). Helpers play full roles in provisioning nestlings and bring food to nestlings at 78% the rate of the breeders. When the influences of food availability and the quality of the breeders were controlled statistically, helper number was a highly significant predictor of both starvation rate ($F = 17.92$, df $= 1/126$, $P < 0.01$) and fledging success ($F = 32.46$, df $= 1/178$, $P \ll 0.01$) (Emlen and Wrege 1991).

Finally, the frequency of starvation loss was related to food availability. In a regression model with group size and brood size as covariates, insect availability (estimated by three variables, see Methods) was a significant predictor of starvation ($F_{insects} = 7.45$, df $= 3/253$, $P \ll 0.01$). For all brood sizes, the frequency of starvation in years of low insect availability was higher than in years of high food availability.

Predation-related losses of eggs and nestlings were very low (7%) in all populations. The low predation rate was presumably due to the bee-eater's habit of excavating their nests 1–1.5 m deep into vertical cliffs and river banks. The principal (and infrequent) predators were snakes (Boomslang, *Dispholidus typus*; Egg Eating Snake, *Dasypeltis scaber*; Spitting Cobra, *Naja* sp.; Rock Python, *Python sebae*) and mongooses (Egyptian, *Herpestes ichneumon*; Slender, *H. sanguineus*; Eastern Dwarf, *Helogale undulata*). All had difficulty gaining access to nests, but all consumed the entire nest contents when they did so.

DISCUSSION

BREEDING SEASONALITY

White-fronted Bee-eaters in Kenya inhabit an unpredictable environment in which there generally are two rainy seasons per year, the long rains in March–May and the short rains of October–December (Brown and Britton 1980). In the Nakuru area, breeding by each population of *Merops bullockoides* roughly coincides with either one of these two rainy periods. Long-rains breeding populations are interspersed with short-rains breeding populations, creating a spatial mosaic of the two types (Fig. 1). This separation into contiguous but "out-of-synchrony" breeding populations is unusual among vertebrates and, to our knowledge, has been reported only for Hyraxes (class Mammalia, Order Hyracoidea) living on isolated kopjes in the Serengeti plains of Tanzania (Hoeck 1982).

In spite of periodicity reflecting the rainy seasons, nesting did not appear to be proximally tied to local environmental cues. Several lines of evidence supported this conclusion. First, nest initiations did not correlate with any obvious patterns of local rainfall or insect abundance (Fig. 3). Second, different long-rains (or short-rains) populations residing within a few kilometers of one another (and therefore presumably experiencing similar environmental conditions) often initiated breeding weeks or even months apart. Third, short-rains breeders in Nakuru began nesting during October–December despite the absence of the increase in rainfall typically experienced elsewhere in the Rift Valley (Figs. 2 and 3). In addition, breeding was sometimes offset even within subsections of the same population. From 1980 to 1982, the Baharini population subdivided to breed at two different colony sites; median dates of egg laying between the two subpopulations differed by as much as 4 weeks (Fig. 3).

Dittami and Gwinner's (1985, Dittami pers. comm.) work on several passerine species in Kenya's Rift Valley provides a possible mechanistic explanation for why White-fronted Bee-eater populations cannot breed with both rainy seasons or easily shift from one season to the other in successive years. They suggest that breeding initiation does not depend on environmental cues per se, but rather on the occurrence of "permissive" environmental conditions following a fairly rigidly programmed annual molt (see also Fogden 1972, Fogden and Fogden 1979, Stiles 1980). The result may be a somewhat flexible onset of breeding from year to year, depending on whether sufficiently harsh environmental conditions inhibit nesting once the molt cycle is completed and breeding is physiologically possible. In the absence of inhibitory environmental conditions, timing of breeding may be influenced more by social stimulation or the carry-over effect of timing the previous season (Snow and Snow 1964, Fogden and Fogden 1979).

White-fronted Bee-eaters initiated a complete molt once annually, beginning ca. 4 months after the onset of breeding. Opportunistic records of molt suggest that its timing was relatively fixed and synchronous within populations; short-rains breeders began molt in March–April, while long-rains breeders did not begin molt until July–August. Annual molt cycles that are timed more rigidly than breeding initiation have been reported for a number of tropical species (Snow and Snow 1964, Fogden 1972, Stiles and Wolf 1974, Dittami and Gwinner 1985). If the molt cycle of White-fronted Bee-eaters is of sufficient duration, each population would be physiologically incapable of breeding in the "alternate" season. This still leaves unanswered the question of how certain populations come to cycle on April breedings, while neighboring populations cycle on October–December breedings.

SOURCES OF EGG AND NESTLING MORTALITY

Nesting success was generally low among the populations of White-fronted Bee-eaters at Nakuru. Averaging the data from 14 population-seasons (including second nestings), we found only 41% of 531 nests from which young

fledged. Average (±SD) productivity was 0.57 ± 0.83 fledglings per nesting attempt. Incorporating the 42% mortality that occurs between fledging and attainment of independence at 6 months of age, we found only 1 nest in 4 produced a surviving independent juvenile.

The two long-rains populations (Makalia and Enderit) nested in colonies along rivers and lost a major proportion of nests to floods. The potential for flooding may have been exacerbated by deforestation of the watershed (C. van-Someren pers. comm.). However, rapid changes of water level and seasonal flooding are typical of most savannah river systems. Although such catastrophic loss was not characteristic of the short-rains populations in our study, major losses to colony cave-ins, subterranean safari ants (*Doryus* sp.), and Horus Swifts were occasionally observed at the colonies of peripheral populations. We do not know whether such losses are a consistent, though infrequent, characteristic of bee-eater nesting mortality, or are characteristic only of certain populations with vulnerable nesting sites.

In all populations, the primary causes of low reproductive success were high rates of egg loss and nestling starvation. Nest predation was negligible, only 2–9% of the eggs laid in any colony. Similar low rates of egg and nestling predation have been reported from Red-throated Bee-eaters in Nigeria (5%, Fry 1984) and Carmine Bee-eaters (*Merops nubicus*) in Zimbabwe (11%, Emlen and Demong unpubl. data). Low predation rates are typical of hole-nesting species in general (Nice 1957, Lack 1968, Ricklefs 1969), and cooperative breeders are no exception (e.g. Koenig and Mumme 1987, Lennartz et al. 1987).

Nearly one-half of the egg loss was socially induced. This is of special interest because it documents a cost of group living. Brown (1987) noted that, among cooperative breeders, such behavior has only been reported from species exhibiting plural breeding (those in which two or more females may breed within the same social group). These are precisely the situations in which competition among potential breeders would be expected.

In Acorn Woodpeckers (*Melanerpes formicivorus*) and Groove-billed Anis (*Crotophaga sulcirostris*), joint-nesting females routinely toss one another's eggs out of the nest (Mumme et al. 1983, Vehrencamp 1977). Koenig and Mumme (1987) found that egg losses were high among

Acorn Woodpeckers (56% of all nesting mortality) and that 26% of such losses were due to egg destruction by competing females. Among anis, Vehrencamp and her co-workers reported that 19% of eggs laid were lost due to egg tossing (Vehrencamp et al. 1988).

In the present study, 28% of eggs were lost before hatching, half of them due to various forms of social competition (Table 2). The most common causes were associated with intraspecific nest parasitism, because both host and parasite tend to remove eggs from parasitized nests. White-fronted Bee-eaters are both colonial and cooperative breeders. Colonial nesting facilitates opportunities for nest parasitism by unrelated females. Cooperative breeding provides further opportunities for *kin-parasitism*, in which the perpetrator is an integrated female member of the same clan, most frequently a daughter, who adds to the parental clutch an egg of her own that she then helps to rear (Emlen and Wrege 1986). Because kin-parasitism was difficult to detect, some of the egg losses attributed to other sources of mortality may have been, in actuality, due to this cause. If true, the importance of socially induced egg losses would be even greater than reported.

The largest single source of prefledging mortality was starvation. Starvation losses were highest when food availability was low and the number of adults provisioning the nest was small. Further, the nestlings at greatest risk of starvation were the youngest members of large broods, because hatching was asynchronous and produced a size hierarchy among broodmates that enabled the largest siblings to monopolize food brought to the nest. Clearly, White-fronted Bee-eaters at Nakuru frequently had difficulty obtaining sufficient food to provision their nestlings. An astonishing 48% of all hatchlings starved before reaching fledging age. Food stress of this magnitude has not previously been described for any other species of cooperatively breeding bird.

ADAPTATIONS TO A VARIABLE ENVIRONMENT

Various features of avian reproductive biology have been interpreted as adaptations to maximize the number of young that can be reared under a given set of environmental conditions. Three features, in particular, involve specializations to cope with conditions of food shortage: adjustments of clutch size relative to

food availability, brood reduction, and slower growth rates of young (e.g. Lack and Lack 1951; Lack 1968; Ricklefs 1965, 1968, 1973, 1976; O'Connor 1977). Two features of the nestling food supply, its predictability at the time of egg laying and its stability during the nestling period, are important determinants of the most appropriate response to food stress (O'Connor 1977). *Adjustments of clutch size* will be adaptive when conditions before or at the time of egg laying accurately predict conditions during the time of provisioning nestlings (Perrins 1965, Cody 1966). A female could then lay the number of eggs that she and her mate (and any helpers) could raise optimally at predicted food levels. If food levels at the time of provisioning cannot be predicted during or before egg laying, clutch size should not be adjusted. Instead, females are expected to lay the clutch size appropriate to good years, but to have a means of adjusting brood size downward if conditions deteriorate (Ricklefs 1965, O'Connor 1977). *Brood reduction* refers to the situation where nestlings develop a size-graded hierarchy of competitive ability such that the effects of food shortage impact asymmetrically on the smallest (i.e. the youngest) member of the brood (Lack 1954, Ricklefs 1965). Under harsh conditions, such chicks starve. The brood size is brought into line with food supplies without seriously jeopardizing the survival probabilities of the older chicks. The third strategy, that of slowed nestling development rates, is predicted to occur when conditions during the nestling period are not only unpredictable but also variable over relatively short time periods (Ricklefs 1976, Howe 1976). The ability of nestlings to retard further growth and to conserve energy would enable them to withstand temporary periods of food shortage. If conditions improved with sufficient speed, such nestlings could recover and fledge normally. The ability to alter the rate of morphological development within the nestling period is seen as distinct from the overall slow development that characterizes many tropical frugivores and oceanic seabirds. O'Connor (1977) formalized the dependence of these strategies on the predictability of food resources, expanded the set of relevant predictions for each, and tested them with data from three representative species of birds. We examined the three specializations as they apply to White-fronted Bee-eaters.

Adjustments of clutch size.—White-fronted Bee-eaters fledged only a small fraction (27%) of the eggs laid. Significant year-to-year variation in clutch size was attributable to factors relating to food availability during laying. Clutch size was *not* correlated with insect availability during the nestling phase. Regardless of what cue females might use at the time of laying to predict food resources following hatching, the hypothesis of clutch-size adjustment predicts a correlation with future insect abundance. No such correlation was observed.

When faced with high but variable starvation losses across years, bee-eaters in Nakuru showed no food-related adjustments in clutch size. The reason for this presumably lies in the unpredictability of feeding conditions. At egg laying, bee-eaters are unable to predict how much food will be available between hatching and fledging of young. Changes in two factors, one environmental and one social, might improve feeding conditions following the completion of the clutch. First, large fluctuations occur in actual insect abundance (Fig. 3). Laying a relatively fixed clutch would allow the breeders to take advantage of any improvement in food conditions that might occur; in the absence of such improvement, rapid brood reduction can still be achieved by other means (see below).

Second, the flexible helper structure of White-fronted Bee-eaters can increase the number of provisioners. The number of adults tending a nest often increased as the breeding season progressed, mostly due to nesting failure by some breeders who subsequently "redirected" their efforts to ongoing nests of close kin (Emlen and Wrege 1988). Nearly 20% of nests gained late-joining helpers in this manner. The presence of helpers leads to an increased feeding rate and dramatically increased nestling survival (Emlen and Wrege 1991). The possibility of gaining additional late helpers provides a social parallel to the improvement of environmental conditions. In both cases the specter of food stress on the nestlings is reduced. In both cases, premature reduction of the initial clutch could lead to decrease rather than an increase in the number of young ultimately fledged.

Brood reduction.—Whereas it is relatively inexpensive to tend an extra egg throughout incubation, the cost of maintaining an extra nestling during its development is much higher. Lack (1954) was the first to suggest that asynchronous hatching was an adaptation to food stress because it led to the development of sibling hierarchies among nestmates which, in turn, facilitated brood reduction to match food

availability. Asynchronous hatching may also stagger the period when the greatest food demands are made on adult provisioners (Hussell 1972, Bryant 1978; but see Lessells and Avery 1989). Since their inception, these ideas have been applied in a large number of avian studies (see Clark and Wilson 1981). Recent models, however, demonstrate that predation pressure can also lead to asynchronous hatching (e.g. Clark and Wilson 1981, Magrath 1988). These hypotheses are not mutually exclusive, but teasing apart their relative importance is difficult.

Such a detailed examination of the selective factors underlying asynchronous hatching was beyond the scope of this study. But tropical bee-eaters appear to be good candidates for Lack's brood-reduction hypothesis. In six tropical species for which incubation and hatching synchrony data are known, all appear to begin partial incubation with the first egg, and successive eggs hatch at approximate 24-h intervals (Dyer 1979, Fry 1984, this study). Predation rates are extremely low in all species studied and are similar on both eggs and nestlings (3% each for White-fronted Bee-eaters; see also Dyer 1979, Fry 1984). Yet partial brood loss (i.e. presumed starvation) claims the lives of 48% of all hatchling White-fronted Bee-eaters, 28% of hatchling Carmine Bee-eaters, and 17% of hatchling Red-throated Bee-eaters (Dyer 1979, this study). The European Bee-eater (*Merops apiaster*), a Palearctic breeder, has been studied extensively in southern France and also exhibits asynchronous hatching, with 21–30% of hatchlings lost to starvation (Lessells and Avery 1989).

Whatever the selective pressures that maintain asynchronous hatching in bee-eaters, one effect was that nestlings were quickly sorted into a hierarchy of size and development, such that the oldest (i.e. largest) could monopolize available food when it was limiting. In our study, all starvation losses in broods with >1 nestling acted first on the smallest nestling, and the likelihood of any given nestling starving increased dramatically with the number of older siblings in the nest (Fig. 6). Dyer (1983) also reported that 95% of brood reduction in Red-throated Bee-eaters and 100% in Carmine Bee-eaters were of the youngest nestling, and that most reduction occurred in large broods. Lessells and Avery (1989) describe a similar increased probability that the youngest nestlings die first in European Bee-eaters.

White-fronted Bee-eater nestlings also show highly variable development rates that enable them to survive temporary periods of food deprivation (Emlen et al. in press). Normal (well-fed) chicks attain the prefledging stage of morphological development ca. 25 days of age. But others take as long as 42 days to achieve the same stage. As a result, different nestlings fledged at very different ages. We argue elsewhere (Emlen et al. in press) that the ability to slow development and withstand morphological retardation is an important adaptation, which enables nestlings to reduce energy requirements over the short term, until environmental or social conditions improve.

White-fronted Bee-eaters fit nicely into the predictive framework outlined by O'Connor (1977). Breeding females did not adjust clutch size to future feeding conditions. Instead they laid a modal clutch that was considerably larger than the number of young that could be reared in most years. Consequently, large scale brood reduction was commonplace. Asynchronous hatching of the clutch and rapid development of a size hierarchy among nestmates facilitated a patterned reduction of broods such that the youngest was the first to starve. Committing available resources to chicks preferentially by age results in the least amount of energy lost with the death of each subsequent nestling, and increases the probability of survival for at least some of the brood (Lack 1954). Finally, nestlings exhibit an ability to slow development during periods of food shortage. If foraging conditions improve, or if additional adults join as helpers at the nest, retarded nestlings can recover and fledge successfully.

This suite of features matches those hypothesized to be adaptive for avian species in areas where food levels fluctuate unpredictably during the breeding season, producing frequent but temporary times of food shortage (Howe 1976, Ricklefs 1976, O'Connor 1977). These are precisely the conditions in the Rift Valley area of East Africa.

LITERATURE CITED

BMDP. 1983. BMDP statistical software. Berkeley, Univ. California Press.

BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton, Princeton Univ. Press.

BROWN, L. H., & P. L. BRITTON. 1980. The breeding season of East African birds. Nairobi, East Africa Nat. Hist. Soc.

BRYANT, D. M. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. Ibis 120: 16–26.

CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Q. Rev. Biol. 56: 253–277.

CODY, M. L. 1966. A general theory of clutch size. Evolution 20: 174–184.

———. 1971. Ecological aspects of reproduction. Pp. 461–512 *in* Avian biology, vol. 1 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

DEMONG, N. J., & S. T. EMLEN. 1975. An optical scope for examining nest contents of tunnel-nesting birds. Wilson Bull. 87: 550–551.

DITTAMI, J. P., & E. GWINNER. 1985. Annual cycles in the African Stonechat and their relationship to environmental factors. J. Zool. (London) 207: 357–370.

DYER, M. 1979. The adaptive significance of co-operative breeding in the Red-throated Bee-eater *Merops bulocki* (Vieillot) and other bee-eaters (Aves: Meropidae). Ph.D. dissertation, Aberdeen, Univ. Aberdeen.

———. 1983. Effect of nest helpers on growth of Red-throated Bee-eaters. Ostrich 54: 43–46.

EMLEN, S. T. 1981. Altruism, kinship, and reciprocity in the White-fronted Bee-eater. Pp. 217–230 *in* Natural selection and social behavior (R. D. Alexander, and D. Tinkle, Eds.). London, Chiron Press.

———. 1990. The White-fronted Bee-eater: helping in a colonially nesting species. Pp. 489–526 *in* Cooperative breeding in birds: long-term studies of ecology and behavior (P. Stacey and W. Koenig, Eds.). Cambridge, Cambridge Univ. Press.

———, & P. H. WREGE. 1986. Forced copulations and intra-specific parasitism: two costs of social living in the White-fronted Bee-eater. Ethology 72: 2–29.

———, & ———. 1988. The role of kinship in helping decisions among White-fronted Bee-eaters. Behav. Ecol. Sociobiol. 23: 305–315.

———, & ———. 1991. Breeding biology of White-fronted Bee-eaters at Nakuru: the influence of helpers on breeder fitness. J. Anim. Ecol. 60: 309–326.

———, ———, N. J. DEMONG, & R. E. HEGNER. 1991. Flexible growth rates in nestling White-fronted Bee-eaters: a possible adaptation to short-term food shortage. Condor 93. In press.

FOGDEN, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307–343.

———, & P. M. FOGDEN. 1979. The role of fat and protein reserves in the annual cycle of the Gray-backed Camaroptera in Uganda. J. Zool. London 189: 233–258.

FRY, C. H. 1972. The social organization of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. Ibis 114: 1–14.

———. 1984. The Bee-eaters. Vermillion, Buteo Books.

HEGNER, R. E. 1981. Territoriality, foraging behavior, and breeding energetics of the White-fronted Bee-eater in Kenya. Ph.D. dissertation, Ithaca, New York, Cornell University.

HOECK, H. N. 1982. Population dynamics, dispersal and genetic isolation in two species of hyrax (*Heterohyrax brucei* and *Procavia johnstoni*) on habitat islands in the Serengeti. Z. Tierpsychol. 59: 177–210.

HOWE, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. Ecology 57: 1195–1207.

HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317–364.

KLOMP, H. 1970. The determination of clutch size in birds. Ardea 58: 1–124.

KOENIG, W. D., & R. L. MUMME. 1987. Population ecology of the cooperatively breeding Acorn Woodpecker. Monogr. Popul. Biol., no. 24 (R. M. May, Ed.). Princeton, Princeton Univ. Press.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, Clarendon Press.

———. 1968. Ecological adaptations for breeding in birds. London, Methuen.

———, & E. LACK. 1951. The breeding biology of the swift *Apus apus*. Ibis 93: 501–546.

LENNARTZ, M. R., R. G. HOOPER, & R. F. HARLOW. 1987. Sociality and cooperative breeding in Red-cockaded Woodpeckers, *Picoides borealis*. Behav. Ecol. Sociobiol. 20: 77–88.

LESSELLS, C. M., & M. I. AVERY. 1989. Hatching asynchrony in European Bee-eaters *Merops apiaster*. J. Anim. Ecol. 58: 815–835.

MAGRATH, R. D. 1988. Hatching asynchrony in altricial birds: nest failure and adult survival. Am. Nat. 131: 893–900.

MALAISE, R. 1937. A new insect trap. Entomol. Tidskr. 58: 148–160.

MARSTON, N. 1965. Recent modifications in the design of Malaise traps, with a summary of the insects represented in the collections. J. Kansas Entomol. Soc. 38: 154–162.

MUMME, R. L., W. D. KOENIG, & F. A. PITELKA. 1983. Reproductive competition in the communal Acorn Woodpecker: sisters destroy each other's eggs. Nature 306: 583–584.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74: 305–321.

O'CONNOR, R. J. 1977. Growth strategies in nestling passerines. Living Bird 16: 209–238.

———. 1984. The growth and development of birds. New York, Wiley & Sons.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34: 601–647.

RICKLEFS, R. E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505–510.

———. 1968. Patterns of growth in birds. Ibis 110: 419–451.

———. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9: 1–48.

———. 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177–201.

———. 1976. Growth rates of birds in the humid new world tropics. Ibis. 118: 179–207.

SAS INSTITUTE, INC. 1985. SAS users guide: statistics, version 5.0. Cary, North Carolina, SAS Institute.

SINCLAIR, A. R. E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. Ibis 120: 480–498.

SNOW, D. W., & B. K. SNOW. 1964. Breeding seasons and annual cycles of Trinidad land-birds. Zoologica 49: 1–39.

STILES, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. Ibis 122: 322–343.

———, & L. L. WOLF. 1974. A possible circannual molt rhythm in a tropical hummingbird. Am. Nat. 108: 341–354.

VEHRENCAMP, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. Science 197: 403–405.

———, R. R. KOFORD, & B. S. BOWEN. 1988. The effect of breeding-unit size on fitness components in Groove-billed Anis. Pp. 291–304 *in* Reproductive success: studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, Ed.). Chicago, Univ. Chicago Press.