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BREEDING BIOLOGY OF THE PIED KINGFISHER *CERYLE RUDIS* ON LAKE VICTORIA

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ABSTRACT

Pied Kingfisher colonies on the northern shore of Lake Victoria are mainly in borrow pits and ditches within 1 km of the lake. Two colonies were studied in detail from October 1967 to November 1969. Eggs were laid in every month of the year but most breeding activity occurred between April and October. Groups of birds displayed in the air and then on the ground before burrowing began. One in five burrows was completed taking on average 26 days to excavate. The final lengths of nesting burrows ranged from 80-250 cm and was inversely related to the hardness of the ground. Eggs were laid on consecutive days; the most frequent clutch size was five. Incubation, mainly by the female, began before the clutch was complete and took 18 days. 'Courtship' feeding began during excavation of the burrow and ended during incubation. Additional males sometimes fed the mated male during incubation. Both sexes fed the young but most feeding visits were by males; several males fed the chicks at some burrows. Most chicks fledged 24 or 25 days after hatching. Colonies on the Entebbe peninsula have increased in size this century, and now include some of the largest recorded, but few young were reared during this study suggesting they are maintained by immigration.

INTRODUCTION

The Pied Kingfisher is a conspicuous bird beside many areas of fresh water in Africa often nesting colonially in eroding river banks. No detailed account of its breeding biology has been published but between October 1967 and November 1969 I made frequent visits to two colonies on the Entebbe peninsula, on the northern shore of Lake Victoria, to study this aspect.

The lake, like most other East African lakes, lacks naturally exposed cliffs along its shore suitable for kingfisher colonies. Most colonies are located in Man-made features, such as borrow pits and roadside ditches within one kilometre of the shore, but one found near Lake Wamala may have over three kilometres from open water. Burrows at the study colony at Kazi, some 16 km south-east of Kampala, were mostly dug in shallow roadside ditches within 200 m of the lake but a few holes were also found in a bank, cleared of bushes, on the shore. The burrows in the colony at Kisi, 30 km south-east of Kampala, were mainly dug into the sides of four small sand pits, 50 m from the shore, but other burrows were scattered in the flat grasslands in the hinterland and in a low grassy bank above the shore.

The climate of the northern shore of Lake Victoria is warm and humid. Monthly mean temperatures vary from 20.5°C in July to 22°C in March. Rain falls in every month but March to May and late October to early December are particularly wet. The annual rainfall at Entebbe averages 1580 mm. The lake rises and falls by about 0.5 m over the year, with water levels usually at their highest in June and lowest in November. The lake shore is typified by rocky, thicket-clad headlands and deep, sheltered inlets ending in papyrus swamp and swamp forest. Between head-

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land and swamp the shore is usually sandy and overhung with thickets of *Mimosa pigra* L. and *Triumphetta macrophylla* K. Schum. Patches of forest fringe the shore but most has been felled and replaced by a mosaic of thicket-covered termitaria and open *Loudetia* grassland which is maintained by slashing, burning and grazing by stock.

METHODS

The colony at Kazi was normally visited two or three times each week when breeding was in progress and at least twice a week at other times. The colony at Kisi was visited once or twice each month; other colonies were visited infrequently.

At each visit to Kazi and Kisi small numbered stakes were placed outside new burrows and a rough sketch map of the colony was drawn. The length of each burrow was measured with a steel tape measure, and signs of use or disuse were recorded. The presence of birds, or their tracks, and freshly excavated soil indicate use, whereas cobwebs and loose fallen soil in the entrance suggest disuse.

Most burrows at Kazi and Kisi were close to the surface and shafts could be dug to examine the nest contents. The shaft was sunk beyond the nest chamber to reduce the danger of roof falls; the hole was resealed with pieces of softboard, turf and soil-filled polythene bags.

RESULTS

The breeding season

Eggs were laid in every month of the year but breeding at the colonies on the Entebbe peninsula fluctuated seasonally (Fig. 1). Most burrows were dug some distance from the shore; digging activity became widespread in late March and April and reached a peak in June. First broods fledged in late June and July. Renewed interest in the colonies towards the end of August was seldom sustained and most were deserted by the end of October. Sometimes however breeding continued locally: in 1968, for example, the number of active 'Long Burrows' (see below) at Kazi did not decline until November and the last broods fledged at the end of December.

Sugg (1974) made similar observations at a colony in the Kavirondo Gulf of Lake Victoria. Most birds bred between May and November; digging activity was greatest in May, June and July and the first juveniles were seen in June. Breeding at the northern end of Lake Victoria therefore occurs mainly in the long dry season.

A few pairs did not fit this pattern, nesting on the shore whenever water levels were falling (Fig. 2) i.e. usually between June and November and sometimes between January and March. Elsewhere in Africa, birds nesting along river banks do so mainly as water levels are falling. On the lower Kafue in Zambia, and Boro, near Maun in Botswana, most birds began to breed as the river banks were exposed in July, but they had finished in October, well before levels began to rise again. However, in both areas, some digging occurred in February; on the Boro it ended when the river bank became flooded suggesting breeding was interrupted by a lack of suitable nesting sites (personal observations). In West Africa, breeding along the Niger and Benue rivers begins in October, soon after water levels have begun to drop (Bannermann 1951).

Nuptial displays

Interest in the colonies on the Entebbe peninsula resumed in January when groups of three or four birds, calling noisily, were occasionally seen chasing one another over the site. In March the chasing parties became more frequent and larger, often containing six to eight birds, and they began to land in the colony area. At Kazi they were most evident in 1968 in late March and early April and late June and early July, and in 1969 in late May and from late June to mid July. Males outnumbered females in the groups as they did in the population overall (Douthwaite 1973).

During the excavation of nesting burrows, groups similar in size and composition to the airborne chasing parties displayed on the ground in areas of short grass or bare earth. Both sexes displayed: the displaying bird adopted an upright posture and with wings half extended (Fig. 3) turned about within the group giving the 'threat call' (Table 1). The display lasted a few seconds

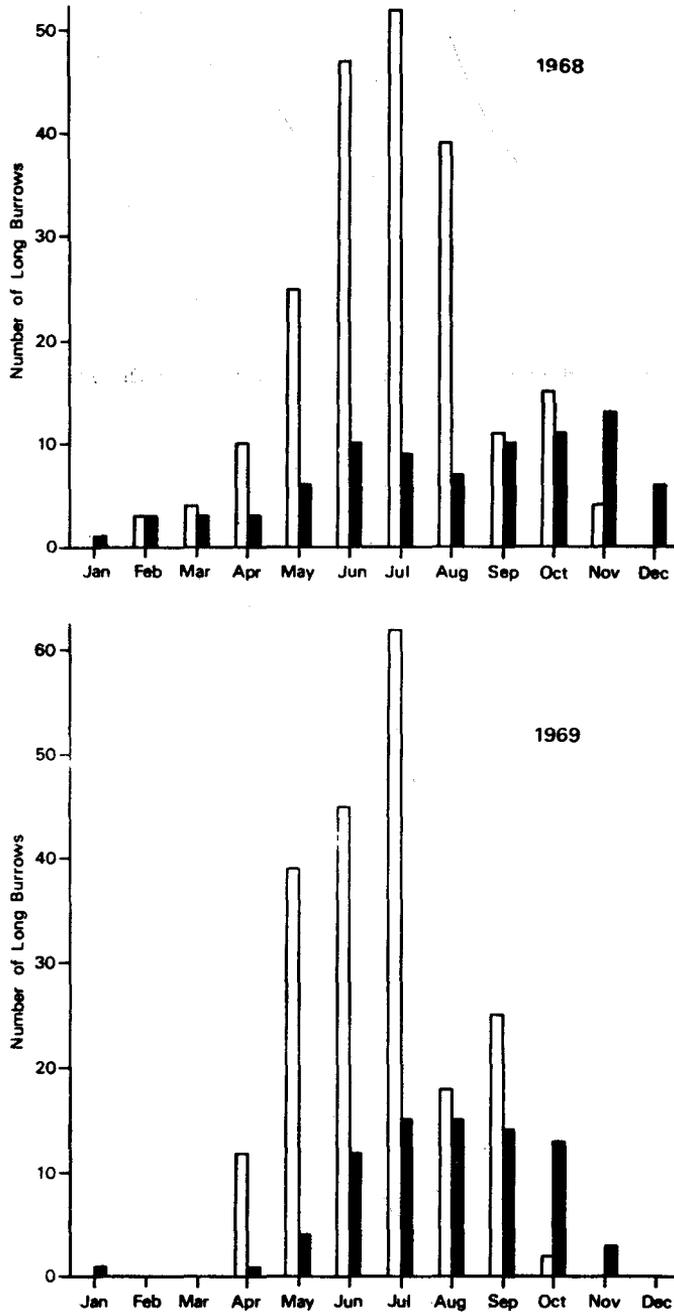


Fig. 1.
The number of active Long Burrows at Kisi (open columns) and Kazi (solid columns) during the first week of each month, 1968-69.

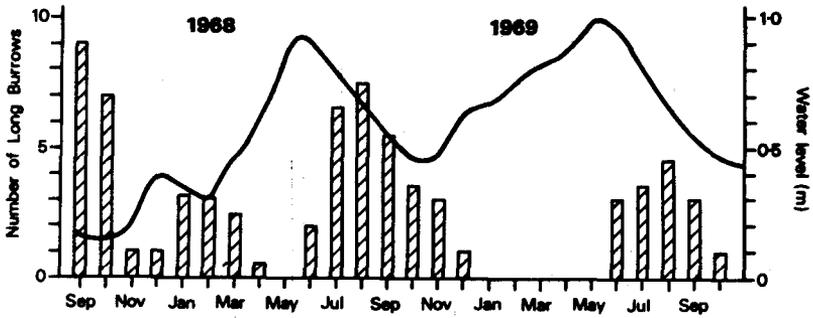


Fig. 2.
The lake level at Entebbe, and number of active Long Burrows on the shoreline in the first week of each month, 1968-69.

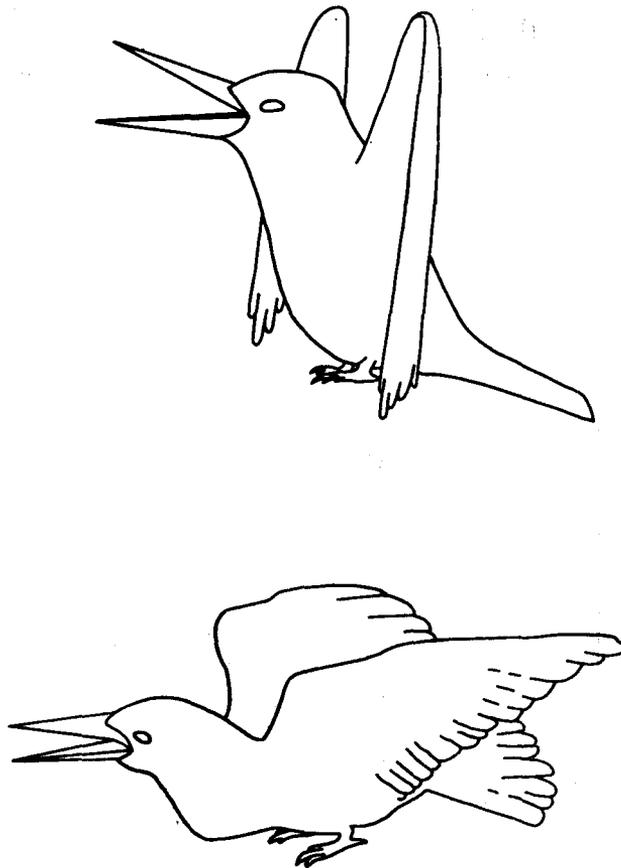


Fig. 3.
Display postures: in the ground display group (Top) and 'threat' (from a photograph).

but was usually repeated several times. When directed towards a particular bird the latter responded either with a similar display or with the 'appeasement call' (Table 1). Displays usually ended without physical contact but beak snapping, brief wing grasping and, rarely, serious fighting sometimes developed particularly towards the end of the breeding season.

The burrow

Centres of activity within the colony were superseded by new ones as the breeding season progressed. Despite a high rate of nest failure there appeared to be no competition for sites which had been used successfully earlier in the season.

Digging was intermittent at first and the pair often broke off to join a ground display group or to dig elsewhere. Gradually the efficiency and intensity of digging increased and a nesting burrow was dug. Soil, loosened by stabbing with opened mandibles, was kicked backwards down the burrow to form a mound 20-40 cm from the opening.

Table 1. Calls of the Pied Kingfisher.

Call	Description	Age	Situation	Function
<i>scare</i>	Grating; repeated	Chick 1-2 days old	Hunger	—
<i>choop</i>	High-pitched; repeated	Somewhat older chicks than above	Hunger	—
<i>cherr erk</i>	Loud, penetrating and continuous. First syllable produced on exhalation, second on inhalation	From a few days after hatching to a few days after fledging	Immediately before feeding	Begging
<i>werk . . . werk . . . werk. werkwerkerkerk. erk or sooip . . . sooip . . . sooip sooipsooipipipipip kittle te ker</i>	Loud, rising to a crescendo, then subsiding Repeated every 1-2 seconds	From 33 days old From 17 days old	In response to the threat call. Also given after the departure call by perched birds Given in flight by a departing bird; also by perched birds closely approached by others, and then followed by the appeasement call	Appeasement Departure-contact
<i>quick or quick ick</i>	High-pitched, repeated irregularly	From fledging	Potential danger	Warning
<i>pip weep or pitcheck</i>	Repeated at about 5 second intervals	From about 10 days after fledging	Given by perched birds as another flies past	Contact
<i>jerp</i>	Low-pitched; repeated	From about two weeks after fledging	On seeing a predator; made esp. by parents of well-grown broods	Anxiety
<i>chickerkerker</i>	High; staccato; repeated irregularly	On assuming adult plumage (i.e. 6 months old)	Given by birds defending nest sites and perches or during display in the ground display groups (Fig. 3)	Threat
<i>shreeur</i>	Shrill; repeated. Given by the male only	—	During copulation	

Burrow length was inversely related to the hardness of the ground. Holes were comparatively long in the uncemented sands at Kisi, intermediate in length at Kazi and comparatively short in the hard red earth at Myanzi (Fig. 4).

There were three kinds of burrow. Most were short, ending without a nest chamber. At Kazi most 'Short Burrows' were less than 50 cm long and were abandoned after an average use of four days. They were quickly eroded at Kisi. Many were dug by poorly co-ordinated pairs in their initial burrowing attempts, while others were 'cock nests' and dug by unmated males. A few were abandoned because the sites proved unsuitable. Only one in five burrows dug at Kazi was completed. These 'Long Burrows' ended in a nest chamber; at Kazi and Kisi they were never less than 120 cm long but at Myanzi some may have measured only 80 cm. The longest burrow found was 250 cm long. The nest chamber is unlined, but during incubation and the nestling period it becomes littered with fish bones. Initially the chamber measures about 45 cm long, 24 cm wide and 15 cm high but it becomes wider and lower as the nestling dig soil from the walls for sanitation. At Kazi 'Long Burrows' were occupied for an average of 49 days, and some were re-used in subsequent breeding attempts. A few burrows were abandoned at the point where excavation of the nest chamber would normally begin and were therefore intermediate in length. Most were probably dug by pairs immediately after breeding failure.

The initiation and completion of burrows usually occurred between my visits to Kazi; initiation was therefore assumed to have occurred mid-way between the date on which the burrow was first recorded and the date of the preceding visit; a similar assumption was made for the date

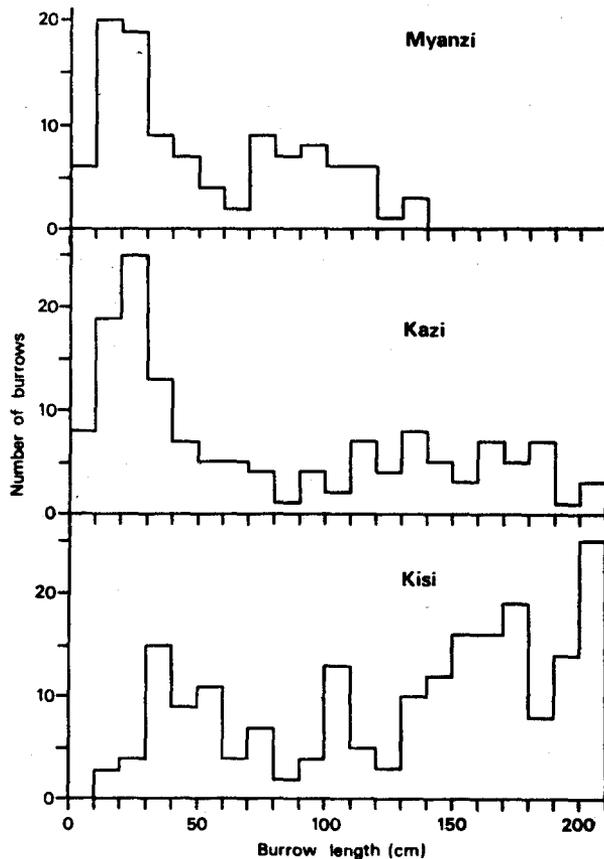


Fig. 4.

Burrow lengths in hard red earth (Myanzi), sandy loam (Kazi) and uncemented sands (Kisi).

of completion. The estimated average time taken to complete 66 'Long Burrows' at Kazi was 26 days, and varied from 11 days to 11 weeks. Construction time did not vary seasonally except in March and April when burrows were often temporarily abandoned—a tendency also noted by Jackson (1938); nor was construction time related to the hardness of the ground or the final length of the burrow.

Courtship feeding, laying and incubation

Courtship feeding began during excavation of the burrow and ended during incubation. Immediately before, and during laying females became very passive, seldom flying except to take food from the male. Laying usually occurred soon after the burrow was completed, the estimated average interval for 20 burrows being three days. The eggs, which were laid on consecutive days, were porcelain white at first but soon became earth-stained. Their minimum, mean and maximum dimensions were: length ($n=133$) 26.0-29.2-31.9 mm; diameter ($n=133$) 21.5-23.5-25.2 mm; weight ($n=34$) 6.7-8.2-10.4 g. In length and diameter they were almost identical to those measured in southern Africa (Roberts 1961). The most frequent clutch size was five (Table 2).

Incubation usually began before the clutch was complete. Both sexes incubated, but females were noted on 22 (70%) of the 31 occasions incubating birds were identified. Hatching in eight clutches was complete, but in another seven one egg failed to hatch. The first chick emerged up to three days before the last, but 18 days elapsed between the laying of the last egg and hatching of the last chick. Empty egg shells were carried outside and often dropped close to the burrow entrance.

Table 2. Clutch size in Uganda.

Number of eggs	1	2	3	4	5	6	7
Number of clutches	1	1	4	7	22	10	1

Inter-male feeding

During laying and incubation the male spent much time on the ground outside the burrow entrance. Newcomers were usually threatened and the intruder would give the 'appeasement call' and retreat. Sometimes however an intruder male, holding a fish head-outermost, approached the mated male. The latter usually seized the fish and a struggle began which ended with the mated male taking the fish and eating it. The intruder then departed. Occasionally the mated male refused the fish, but then responded with the 'appeasement', and not 'the threat, call'. Inter-male feeding was observed throughout the year, sometimes well away from any colony, but it occurred most frequently outside burrows containing incubating females. Only once was an intruder male seen to feed a mated female: it occurred immediately after a changeover at the nest when the mated male had disappeared inside. The fish was exchanged with the usual struggle.

Co-operative feeding of the young

Both sexes fed the nestling but of 96 feeding visits observed at different burrows 69 (72%) were made by males. Pairs were assisted by helper males which varied in number between burrows. At one, 14 visits by males were observed but none by females, and four, possibly five different males were involved. At another, the ratio of male to female visits was 4:5 and there was no sign of helpers. Female helpers assisting the pair were not seen.

At least one helper was seen feeding a group of recent fledglings on the Kafue river in Zambia (H. Black, pers. comm.).

Defence of the colony

Snakes, Striped Ground Squirrels *Xerus erythropus*, a Great Grey Mongoose *Herpestes ichneumon* and Monitor Lizard *Varanus niloticus* were mobbed by two or three birds when they entered the colony. Snakes and squirrels were driven off but the Great Grey Mongoose and Monitor Lizard paid little attention to the diving birds. Dogs and men entering the colony elicited a display flight in which birds giving the 'warning call' circled slowly, alternating three or four rapid and exaggerated wing beats with glides.

Growth and development of the young bird

Changes in digestion and diet; food consumption and weight in hand-reared birds, with age, have been described elsewhere (Douthwaite 1976). The growth in weight of wild nestlings is illustrated in Figure 5. Vocal development is outlined in Table 1.

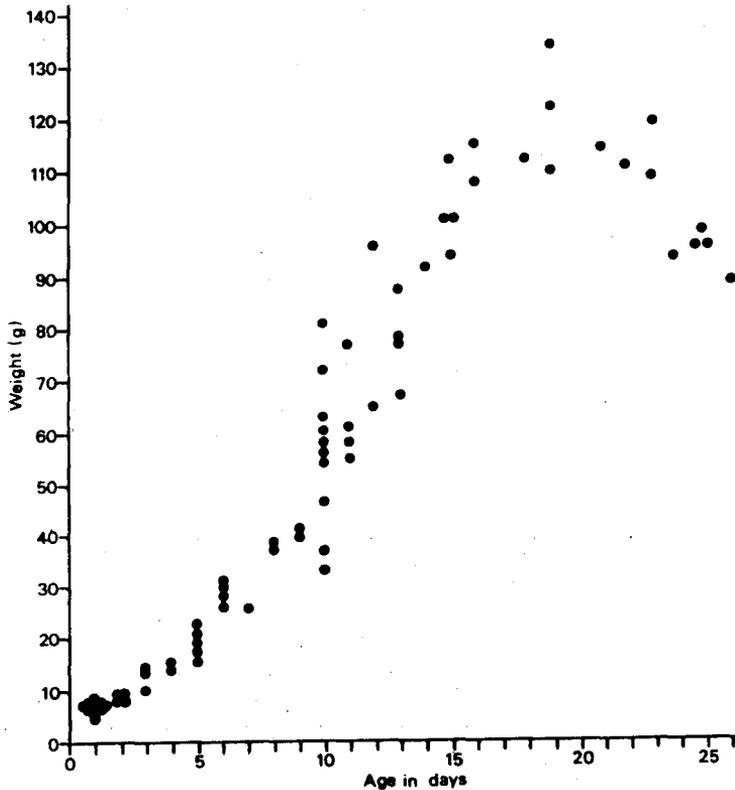


Fig. 5.
Weights of wild nestlings of known ages.

At hatching the chick is naked. The feather tracts of the scapulars, rectrices, remiges, nape and crown darken by the fourth day and the remainder, except on the belly and around the cloaca, by the sixth; at seven days old they are in pin. The feathers around the cloaca and on the belly are in pin three days before fledging but their growth is not completed until after fledging. The remiges and rectrices erupt at 11-13 days old; their rates of growth decline progressively and the wings and tail reach asymptotic lengths of about 138 mm and 78 mm at six weeks. Growth is uninterrupted by fledging, which occurs at about 124 mm and 69 mm respectively (Fig. 6). The scapulars and wing and tail coverts are fully grown at about 15 days.

The eyes begin to open at five days and the lids are well parted at nine days. The nictitating membrane begins to function in the next two days. The mandibles continue to grow for three or four months: at hatching the upper is shorter than the lower, but at fledging it is slightly longer. By the time growth is completed they are equal in length, straight, and sharply pointed.

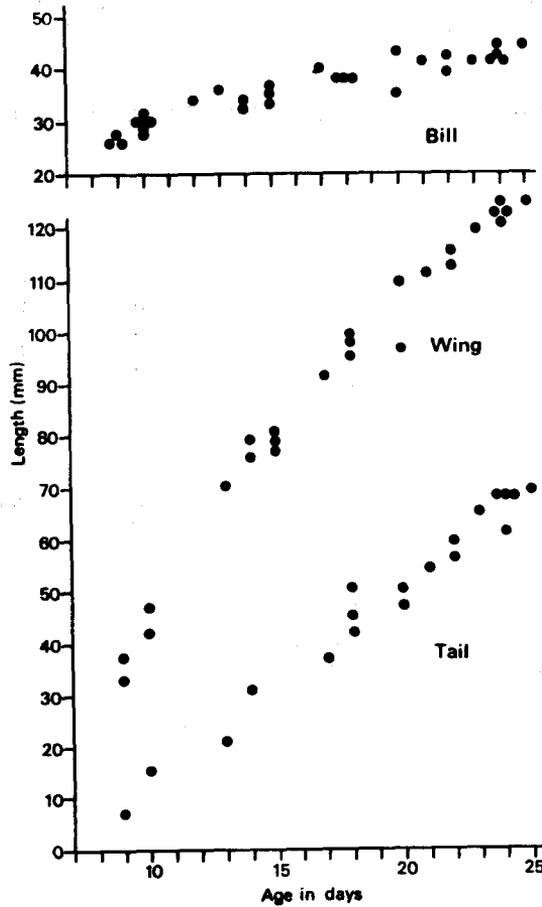


Fig. 6.

Lengths of bills, wings and tails of wild nestlings of known ages.

Most chicks fledged 24 or 25 days after hatching. Two which fledged at 27 and 29 days old were from a brood heavily infested with Tropical Fowl Mite *Ornithorhysus bursa* (Table 3).

The fledgling is usually fed in the air, often after a chase, but it returns to a perch before swallowing the food. Within three days it is shaking and battering the fish and within two weeks it is diving into the water probably in pursuit of food. Juveniles are fed by adults for at least a month after fledging, but a colour-ringed juvenile was apparently independent at two months. Young Eastern Belted Kingfishers *Megaceryle alcyon* become independent more quickly, diving into the water on the third day, catching fish on the seventh or eighth, becoming self-sufficient within two weeks and dispersing within the month (Salyer & Lagler 1946, White 1953).

Table 3. Duration of the nesting period.

Duration in days	23	24	25	26	27	28	29
Number of chicks	1	7	5		1		1

Breeding success

At Kazi at least 17 ± 1 pairs attempted to breed in 1968 and 19 ± 1 pairs in 1969. Success in the two years was similar and data have been combined (Table 4).

Table 4. Breeding success at Kazi in 1968 and 1969, with causes of failure.

	Clutches	Broods	Total
Number starting	66	30	—
Losses due to:			
Predation by snakes	0	1	1
Predation by ants	0	1	1
Unidentified predators	3	5	8
Flooding of burrows	0	2	2
Excavation of sand by Man	2	1	3
Trampling of burrows by cattle	5	1	6
Desertion	2	0	2
Irregular incubation	9	0	9
This study	8	4	12
Unknown causes	7	2	9
Number failing	36(55%)	17(57%)	53(80%)
Number succeeding	30	13	

A total of 105 'Long Burrows' were dug but at least 39 (37%) were abandoned before laying began. For the rest, failure could be divided more or less equally between site factors, predation, parental behaviour and interference from this study. Sand extraction, trampling by cattle and flooding (i.e. site factors) caused the loss of 11 nests. At least 10 others were destroyed by predators. One brood was eaten by Safari Ants *Dorylus nigricans*, and another by a 1.9 m long Black-necked Cobra *Naja melanoleuca*, which also killed both parents. Snakes probably took most of the other eight clutches or broods which disappeared and were probably also responsible for some of the failures due to unknown causes. Eleven clutches were lost from parental factors—desertion for no apparent reason, renewal of digging activity during incubation, and infertility. Usually the pairs involved had made unsuccessful attempts to breed earlier. Loss due to this study occurred mainly in 1969 when someone opened the inspection shafts of eight burrows and fed the nest contents to his dog. Only 13 broods, containing about 58 young, fledged successfully.

At Kisi nests were destroyed by sand extraction, trampling by cattle and predation. Snakes probably took some broods but the most serious predator was the Marsh Mongoose *Atilax paludinosus* which dug open burrows at night and ate the contents, which sometimes included adult kingfishers. In Table 5 the number opened each month is compared with the number of 'Long Burrows' in use in the sand pits at the beginning of the month. The proportion of nests predated would have been higher than indicated since eggs were never laid in some burrows, but only those with eggs or young were opened. Additionally, some 'Long Burrows' would have been recorded more than once. Burrows scattered in the grassland near the sand pits suffered less predation from Marsh Mongooses, only two (4%) of the 51 'Long Burrows' found in 1968 and one (2%) of the 47 'Long Burrows' found in 1969 being opened.

The juvenile plumage persists for six months after fledging yet few juveniles were seen amongst the population on the Entebbe peninsula (Table 6). In October 1968, 115 birds were counted in a communal roost near the colony at Kazi; about half came from the colony, the other birds being non-breeders or from other colonies. At the time 21 nestlings had fledged from burrows at Kazi. Assuming the sample age count at the roost (Table 6) was representative, and that all the juveniles present had originated from the colony at Kazi, 15 (71%) of the original 21 had disappeared. There was no evidence of birds roosting elsewhere nor of age-specific movements. If juveniles from other colonies were also using the roost the post-fledging mortality had been even greater. Many fledglings were probably taken by Marsh Harriers *Circus ranivorus* which regularly patrolled kingfisher colonies during the breeding season.

Table 5. Predation of nesting burrows at Kisi by Marsh Mongooses.

	1968		1969	
	Number of Long burrows	Number predated in following month	Number of Long burrows	Number predated in following month
January	0	0	0	0
February	3	0	0	0
March	4	4	0	0
April	8	1	7	1
May	17	0	27	13
June	32	3	29	21
July	40	3	31	14
August	28	0	6	2
September	8	3	18	0
October	10	5	0	0
November	3	1	0	0
December	1	0	0	0
Total	154	20(13%)	118	51(43%)

Table 6. The proportion of juveniles in sample counts.

Locality	Date	Total count	Number of juveniles (%)
Kazi roost	October 1968	62	4.8
Kazi roost	November 1968-February 1969	316	3.2
Entebbe	November 1969	50	2.0
Kazinga Channel	November 1967	33	18.2

DISCUSSION

Co-operative breeding is widespread amongst birds in Africa and Grimes (1976) summarised knowledge of its occurrence in 52 species of 30 families. Within the Alcedinidae the behaviour is known only in the Pied Kingfisher, the sole colonial species, but in another coraciiform family, the Meropidae, it occurs in three colonial species, the Carmine Bee-eater *Merops nubicus*, White-nubicus, White-throated Bee-eater *M. albicollis* and Red-throated Bee-eater *M. bulocki* (Fry 1972). As in the Pied Kingfisher, Fry (1972) found that males predominate in the populations of all three species, and as the helper sex. In the Red-throated Bee-eater male helpers feed the nestlings and fledglings, but unlike Pied Kingfisher helpers they also assist with burrow excavation and incubation; in addition they sometimes feed and copulate with the female but do not feed the mated male. Fry (1972) found that multiple breeding units of Red-throated Bee-eaters produced more progeny per nest than did pairs alone, suggesting helpers are of value to breeding pairs. However the benefits of co-operative breeding to helpers are less obvious unless, by so doing, their chances of mating successfully are increased. Copulation between helper males and paired females was observed in Red-throated Bee-eaters but not in Pied Kingfishers; the advantages of co-operative breeding in the latter species are obscure and will only be understood through observation of individually marked birds.

The functional significance of other aspects of the Pied Kingfisher's behaviour also needs clarification. Pairing probably takes place in the airborne chasing parties as a similar display, which White (1953) suggested served as courtship, occurs in the Eastern Belted Kingfisher. Relationships between the pair and helper males may be established in the ground display groups for neither this display nor helper males are reported for the Eastern Belted Kingfisher. Inter-male

feeding during incubation, by reinforcing the dominance of the mated male over potential helpers, may reduce the aggression of the mated male so that the helpers are allowed to enter the burrow to feed the chicks.

Despite their lack of success the colonies on the Entebbe peninsula are amongst the largest recorded. Indeed, there is evidence that the population has increased in the last 60 years (see Jackson 1938). One explanation for the paradox, which would explain why colonial nesting persists in the face of repeated failure, is that most of the population are immigrants from more successful colonies. The recovery of a Pied Kingfisher on Lake Kyoga ringed 760 km to the north at Gambela in Ethiopia (Backhurst 1974) shows that birds are capable of extensive movement and are therefore likely to be found attempting to breed in areas where the food supply is abundant but safe nesting sites are scarce.

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