Flexible Helper Structure as an Ecological Adaptation in the Pied Kingfisher (*Ceryle rudis rudis* L.)

Heinz-Ulrich Reyer

Max-Planck-Institut für Verhaltensphysiologie, D-8131 Seewiesen, Federal Republic of Germany

Summary. The pied kingfisher has two types of helpers at the nest: primary ones, helping their own parents, and secondary ones, helping birds other than parents. Primary helpers are always accepted by breeding pairs, secondary helpers only in poor environmental conditions where the time and energy budget of parents is not sufficient for rearing the offspring alone. Under these conditions, helpers increase the breeding success of pairs (Tables 2 and 3) by providing additional food for the young (Table 4). Thus the flexible helper structure can be seen as an ecological adaptation. It is argued that – originating from a skewed sex ratio and breeding in colonies – this adaptation evolved through the combined effects of individual and kin selection.

Introduction

Helpers at the nest, as defined by Skutch (1961), have been reported to date in over 150 bird species (Grimes, 1976; Rowley, 1976; Woolfenden, 1976; Zahavi, 1976). The few features shared by most cooperative breeders are easily outnumbered by the diversities. Consequently the adaptive significance of such cooperative (communal) breeding is poorly understood and the driving forces in the evolution of helping are controversial. Some scientists favor individual selection, others favor kin selection (Brown, 1974, 1978; M. Dyer and C.H. Fry, unpublished work; Emlen, 1978, 1980; Fry, 1977; J.D. Ligon, unpublished work; Ligon and Ligon, 1978; Ricklefs, 1975; Woolfenden, 1975, 1978; Woolfenden and Fitzpatrick, 1978).

This controversy seems to arise partly from existing species-specific differences, and partly from the lack of data regarding the effects of helping on inclusive fitness, both for breeders and helpers. Moreover, satisfactory correlations between social structure and environment – a prerequisite for understanding the adaptive significance and evolution of behavior – are lacking. Most investigators of cooperative breeding did not pay enough attention to ecological parameters. With a few exceptions (Brown and Balda, 1977; Vehrencamp, 1978), habitat qualities have either been ignored totally, or the categories employed in ecological investigations have been relatively crude (Gaston and Perrins, 1975). We cannot expect to discover any satisfactory correlation between social structure and environment, however, as long as we continue to classify the distribution of animals and their food merely as either stable or unpredictable; habitats merely as desert, savannah, bushland, forest, or marsh; and food no more precisely than as grain, fruit, nectar, or insects (for summaries see Emlen, 1978; Fry, 1977; Grimes, 1976; Woolfenden, 1976).

The present and a following paper will show that finer measurement of ecological parameters can reveal relationships between helper structure and environment, even for different populations of the same species. These relationships, which are not biased by species-specific differences, can be interpreted in terms of ecological adaptation. They also can help to assess the importance of individual and kin selection in the evolution of cooperative breeding.

Materials and Methods

Two breeding populations of the pied kingfisher (*Ceryle rudis rudis* L.) in Kenya (East Africa) were compared, one (20–30 pairs) at the Winam Gulf of Lake Victoria (34°18′ E, 0°21′ S), the other (15–20 pairs) at the southern end of Lake Naivasha (36°42′ E, 0°21′ S). Most of the birds in these two colonies had been mistnetted and were individually color-ringed or wing-tagged. Some casual observations in a colony of over 50 pairs at Lake Simbi (34°38′ E, 0°21′ S) were also recorded. These investigations are part of our continuing studies, commenced in 1975, on the ecology and the behavior of various East African kingfisher species (Alcedinidae).

Results

General Remarks on the Biology of the Pied Kingfisher

Within their East African range, pied kingfishers inhabit many lakes and rivers and are particularly frequent in the marginal regions of the big freshwater lakes. They live almost exclusively on fish. To catch their prey, they fly over the water searching, sometimes hovering above the surface, and plunge swiftly when they see a fish. They swallow small fish while in the air, and continue searching. Bigger fish are carried to perches on the shore and battered before being swallowed. Direct dives from such perches were rarely observed in the areas investigated.

Outside the breeding season, pied kingfishers can be seen singly, in pairs, or in small groups along the whole shore area. In the evening, they congregate at communal roosting sites. During this time of the year, considerable local movements may be undertaken; these can carry individuals over hundreds over kilometers (Backhurst, 1974). In the breeding season, the birds usually concentrate at rivers, canals, road embankments, and other places having sandy or clay banks, not too far from the lake. Here 20, 50, 100 or more birds excavate nesting holes. In this way, breeding colonies are formed. The average distances between adjacent nesting holes were 5.2 m at L. Victoria and 1.6 m at L. Naivasha. Both are well above the possible minimum (0.5 m) found in the pied kingfisher and in other colonial breeders such as bee eaters. Therefore – and because suitable, unused nesting places were in the vicinity of both colonies – the carrying capacity of the habitat was probably not exhausted in respect to nesting sites. It was not exhausted in respect to food either. All members of the colony hunted in the same area over the lake and did not defend individual fishing grounds. Only in the vicinity of the nesting holes did ♂♂ and ♀♀ behave territorially.

The sexes can be distinguished by plumage differences: ♀♀ have only one broad, interrupted chestband; ♂♂ have in addition a second narrower, uninterrupted band. This is more pronounced and even in older ♂♂ than in yearling ♂♂. The ♂♂ and ♀♀ take turns incubating the eggs from which the blind, naked young emerge after 18 days. From the first day, they are fed with fish brought from the lake mainly by the ♂, and possible helpers; later, when brooding declines, the ♀ joins increasingly in feeding the young. Nestlings are fully fledged after about 26 days and can fish for themselves roughly 14 days later, but stay with their parents for several months. Sexual maturity can be reached within the first year.

Hand-reared yearling pied kingfishers bred successfully in our aviaries, their first clutch containing five eggs from which four young hatched. These figures do not differ from those which we found in older breeders. Further information on the biology of the pied kingfisher is given by Douthwaite (1970, 1973, 1976, 1978), Sugg (1974), and Migongo (1978).

Comparison of Two Colonies

Sex Ratio and Population Structure

In both study areas there was a significant surplus of ♂♂. At Lake Victoria, ♂♂ outnumbered ♀♀ by 1.8:1 (107 ♂♂, 61 ♀♀; $P < 0.01$, χ^2 test), at Lake Naivasha by 1.7:1 (33 ♂♂, 19 ♀♀; $P < 0.05$). These figures are based on counting both ringed and unringed birds. For the same L. Victoria colony, Sugg (1974) obtained a figure of 2:1, both in 1971 and 1972. Similar sex ratios ranging from 1.5 to 2.5 have been reported by Douthwaite (1973, 1978) for breeding and non-breeding populations in Uganda and Zambia. Only one of his counts, made at a roost, resulted in an even sex ratio. All these data taken together suggest that in populations of adult pied kingfishers, there are 1.8 as many ♂♂ as ♀♀ (1074 ♂♂, 610 ♀♀; $P < 0.001$). Among the young, however, an even sex ratio seems to exist. Out of 40 nestlings and fledglings which were sexed either by laparatomy of by hand-rearing them to maturity, 21 were ♂♂, 19 ♀♀ (1.1:1).

One reason for the later-occurring skew toward a surplus of ♂♂ probably lies in a higher mortality rate of breeding ♀♀. Incubating and brooding at night fall to the ♀ exclusively, and even by day the ♀ performs the greater part of these activities. Consequently it is more endangered if nesting holes cave in or are flooded, as well as by nest predators such as the monitor lizard (Varanus niloticus), cobras (Naja spec.), and the ichneumon (Herpestes spec.) (Douthwaite, 1970, 1978). All four breeders which disappeared during our study were ♀♀, and though this toll on breeding ♀♀ was low in our colonies (6%), it may be much higher in other colonies where predation rates of more than 40% have been found (Douthwaite, 1978).

A second reason for the skeward sex ratio may be a higher mortality rate of juvenile ♀♀. In contrast to yearling ♂♂, yearling ♀♀ do not apparently return to their natal colonies (Table 1). A stronger dispersal of ♀♀ has also been observed in other bird species. It has been suggested that on their routes into distant, unknown areas, ♀♀ might be endangered more than ♂♂ remaining in familiar areas (e.g., Zahavi, 1974; Woolfenden and Fitzpatrick, 1978). This phenome-

Table 1. Recaptures and resightings of juvenile and adult pied kingfishers, ringed in the same colony at L. Victoria the previous year. Data from 1976 to 1979 pooled. Juvenile birds were nestlings when ringed, adults were ringed as $\geq$ yearlings. The data ca. 32 ♂♂ and ca. 31 ♀♀ are based on the assumption of a sex ratio approximately equal to 1 (see. p.220)

		No. marked	No. recaptured + resighted	%
Juveniles	♂♂	ca. 32	10	31
	♀♀	ca. 31	0	0
	Total	63	10	16
Adults	♂♂	72	25	35
	♀♀	48	12	25
	Total	120	37	31

Table 2. Number of pairs with and without helpers in two pied kingfisher colonies. The difference is significant $(P < 0.005)$ when in both colonies only the categories *pairs without helpers* and *pairs with helpers* are considered (χ^2 test). No difference is made between primary and secondary helpers

No. of breeding pairs with	L. Victoria	L. Naivasha
No helpers	14	13
1 Helper	19	5
2 Helpers	7	0
3 Helpers	1	0
> 3 Helpers	0	0
Total	41	18

non may prevent inbreeding depressions (Greenwood et al., 1978).

Recapture and resighting data of ringed birds at L. Victoria showed that only 25% of adult ♀♀ and 35% of adult ♂♂ return in the following year to the same breeding colony (Table 1).

At L. Naivasha, the figure was 35% for each sex (six out of 17). The results in the two colonies, however, cannot be compared with each other since the Naivasha figure might be biased twofold: (a) the sample size is small, and (b) though the birds congregated in the colony the year after ringing them, no breeding activity was possible since the risen water level had swamped the nesting banks. Nevertheless, the rate of return seems to be low for both colonies, and seems to be fairly consistent from year to year. This follows for L. Victoria from comparing our own data, collected from 1977 to 1979, with those of Sugg (1974), who worked in the same colony in 1971 and 1972. He obtained return rates of 20% for ♀♀ and 30% for ♂♂. With his and our data pooled, the difference between the sexes just reaches significance $(P = 0.05; \chi^2$ test). This difference seems to be at least partly a consequence of the different mortalities in breeding ♀♀ and ♂♂ (p. 220). The low return rates in both sexes may result from a generally high rate of mortality, also found in other kingfisher species (McClure, 1974). It also may result from movements between the various colonies. We checked 123 pied kingfishers in three neighboring colonies which were 2, 4, and 9.5 km away from the L. Victoria study area. Though not a single ringed bird was found, there are indications for dispersal of adult pied kingfishers:

1) Outside the breeding season, considerable local movements are frequent.

2) In 1978 and 1979, unknown pairs appeared in the L. Victoria colony, and known pairs left without breeding.

3) Despite poor reproductive success, the colonies on the Entebbe peninsula (Uganda) have increased in the last years, which suggests that many breeders are immigrants from more successful colonies (Douthwaite, 1978).

Helper Structure

Although helpers at the nest were found in both colonies, their frequencies were different, both per pair and per colony. At L. Naivasha, no pair had more than one helper and only 28% of all pairs were assisted when feeding nestlings. At L. Victoria, as many as three helpers per pair did occur and 66% of all pairs were assisted (Table 2). In both colonies, and in others, all helpers were male $(n = 60)$.

However, the numerical difference between the two colonies did not exist at the beginning of the breeding season. During nest-digging, courtship, egg-laying, and incubating, 67% of all L. Victoria pairs had no helpers either $(n = 52)$. This is similar to the L. Naivasha figure.

Primary Helpers. The other pairs which had helpers during these initial periods had already arrived with them in the colony. Such helpers which accompany pairs from the very beginning of the breeding season are termed 'primary helpers' in this paper.

During the excavating, courtship, and egg-laying periods, primary helpers feed the ♂ of the pair, support it in feeding the ♀ (both by feeding the ♀ directly and via the ♂), and help the pair ward off rivals from the nesting site. After the eggs are laid, helpers participate in driving off nest predators, and later in feeding the young. Tunneling, copulating, incubating of eggs, and brooding of young were not observed in primary helpers.

To date, 17 primary helpers have been recorded at L. Victoria, and five at L. Naivasha. For ten of

the 17 L. Victoria birds, the descent is known from ringing. They all were yearling sons of at least one of the breeders which they now accompanied. Three further unringed ♂♂ were identified as yearlings by their fainter chest patterning; two of them helped pairs each with one mate having bred successfully the year before. The third ♂ helped at a nesting site where young had fledged in the previous year. As those breeding pairs which return to the same colony also return to precisely the same nesting site, this last bird, too, probably was helping his own parents. In the remaining four cases, there were no indications either for or against a relationship between pairs and their helpers.

Only observations from 1977 are available for the colony at L. Naivasha, as the water level had risen in 1978 and 1979 and swamped the nesting banks. Therefore nothing is known about the relatedness between the five primary helpers and the breeders. But according to their faint chest bands, all five were yearling ♂♂.

From all the evidence, we may assume that primary helpers are the sons of least one pair member. The two colonies do not seem to differ with respect to this helper type. The relative frequencies of pairs with primary helpers were similar for both colonies: 33% for L. Victoria and 28% for L. Naivasha. And with one exception in which a pair had two primary helpers at L. Victoria, the number per pair was one in both areas.

Secondary Helpers. The difference between the two colonies arose 3–4 days after the young had hatched. Then a second helper type appeared, apparently being attracted by the nestlings' intensive begging cries. These 'secondary helpers' flew through the colony, fish in beak, landed in the vicinity of various nesting holes, and waited. Later they approached the entrance repeatedly and also tried to feed the adult ♀ belonging to the respective hole. In both colonies, they were initially repelled, particularly by the ♂ of the pair, But if persistent at L. Victoria, a helper was accepted after 2–4 days and was allowed to remain at the nest, where he participated in feeding the young and warding off nest predators.

At L. Naivasha, however, expulsion continued throughout the nesting period. None of the nine surplus ♂♂ which showed feeding tendencies as accepted. Thus, in contrast to L. Victoria, secondary helpers were not observed at L. Naivasha, This difference accounts for the different frequencies of assisted and unassisted pairs in the two colonies (Table 2).

Secondary helpers can be recruited from single surplus ♂♂ as well as from ♂♂ of those pairs and groups whose own breeding attempts have failed ear-

lier. This is demonstrated by the following examples from L. Victoria.

1) A year-old ♂ attached himself to a neighboring pair feeding young, after his father and his father's new ♀ had left the colony, abandoning an uncompleted nesting hole.

2) Three pairs discontinued tunneling, two after coming up against obstacles, one after losing part of their nest in a landslip. Each ♂ acted as a secondary helper at a neighbor's nesting hole. The ♀♀ stayed with their mates, but did not join in helping.

3) A year-old ♂ flew back and forth through the colony with his father, after his mother had fallen victim to a nest predator. Both ♂♂ were seen with fish in their beaks outside various holes; at one of these, the son was eventually tolerated by the pair, while his father was chased away.

4) Several ♂♂ which had obviously arrived in the colony singly, flew through it repeatedly carrying fish. They tried to feed the young at various holes. At least five of these ♂♂ functioned later as helpers at one hole or another.

To date, 19 secondary helpers have been recorded at L. Victoria. The status for 7 of them is unknown. The other 12 were certainly not the yearling sons of the pairs which they joined, and the rings gave no evidence for any other close genetic relatedness between them and the breeders. Whether this means that they helped unrelated birds will be discussed later (p. 226).

Prolonged chasing away of potential secondary helpers, which was the rule at L. Naivasha, was observed at L. Victoria in only two cases. Both cases involved breeding pairs which had only two nestlings from the very beginning. Normally, 4–5 young hatched in each colony.

These two pairs had not accepted secondary helpers until their young were 12 days old, which was unusual at L. Victoria. Then two young of similar age were added to each clutch with the result that both pairs had one secondary helper each within three days. This suggests that the parents' decision to accept secondary helpers depends on the number of young they have to rear and can rear. The results further suggest that pairs at L. Victoria need more helpers than their L. Naivasha counterparts to achieve a similar breeding success.

Breeding Success and Feeding Rates

This last hypothesis is strengthened by a comparison of the breeding success in the two colonies (Table 3). Average clutch size and hatching rates were the same in the two colonies, and also within the colonies for

Table 3. Clutch size, number of hatched, and number of fledged young for pairs with and without helpers in two breeding colonies. $\bar{x}$ = mean, SD = standard deviation, n = sample size. Values per bird are given *in brackets*, values per nest *without brackets*. For significance of differences, see the text

	L. Victoria			L. Naivasha		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Clutch size	4.9	0.6	22	5.0	0.6	8
Young hatched	4.6	0.5	14	4.5	0.7	2
Young fledged						
No helpers	1.8 (0.9)	0.6	14	3.7 (1.9)	0.9	9
1 Helper	3.6 (1.2)	0.5	12	4.3 (1.4)	0.5	4
2 Helpers	4.7 (1.2)	1.0	6	—	—	—

Fig. 1. Number of fish eaten by five nestlings of different weight. The *letters below the bars* indicate the individuals, and the *numbers* show the respective weight at the beginning of the experiment. For further details, see the text

pairs with and without helpers. Nevertheless, the breeding success of individual pairs, expressed in the number of their fledging young, varied clearly. At L. Victoria, only 39% of hatched birds survived to fledging when cared for exclusively by parents, as opposed to 78% when fed additionally by one helper, and 100% when two helpers assisted. The improvement with each additional helper is significant in all cases ($P < 0.001$, $P < 0.01$, and $P < 0.025$; Mann-Whitney U-test, one-tailed). Even on a per-adult-bird basis, groups with one and two helpers are more successful than pairs without helpers ($P < 0.01$ and $P < 0.05$). But on this basis, there is no difference between the success of pairs with one and those with two helpers.

At L. Naivasha, pairs without helpers succeeded in raising as many as 80% of their hatched young, which is double the number raised by their counterparts at L. Victoria ($P < 0.001$) and almost the same number as in pairs with one helper at L. Victoria. Probably due to the small sample, no significant improvement of breeding success was recorded at L. Naivasha if there was one helper. On a per-bird basis, assisted pairs were even less successful than unassisted ones ($P < 0.05$). Probably because of the same small sample, no difference was found between the success of pairs with one helper at L. Naivasha and those at L. Victoria ($P < 0.2$).

Regular counts and weight measurements of nestlings have shown that at L. Victoria many offspring of pairs without helpers starve. Fourteen 9- to 12-day-old young from nests without helpers weighed between
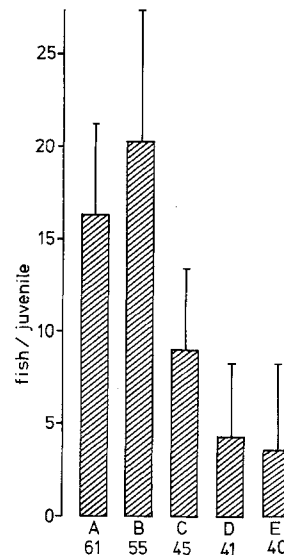
27 and 93 g, and 12 comparable young from nests with one helper weighed between 53 and 88 g. The average weights of the heaviest birds in these two groups did not differ significantly ($\bar{x}$ = 74 and 76 g), but the average weight of the smallest young was lower in nests without helpers ($\bar{x}_0$ = 36 g, n = 7) than in nests with one helper ($\bar{x}_H$ = 57 g, n = 6; $P < 0.01$, U-test, two-tailed). The smallest nestlings usually died, probably because their stronger siblings snatched most of the food. This was confirmed by the following experiment.

At the age of about ten days, five nestlings of different weights were placed in an artificial nest-chamber. The chamber had only one circular opening of 5 cm in diameter. The birds were individually color-marked at the tips of their bills. On three consecutive days, they were given less fish than they need at this age and the fish were only fed to that nestling which put out his head through the opening. The experiment clearly showed that heavier birds pushed the lighter ones aside and received most of the food (Fig. 1).

At L. Naivasha, the offspring from nests with helpers and without helpers weighed the same at equivalent stages of growth. These results suggest that at L. Victoria helpers are necessary to prevent a food deficit in the young, whereas at L. Naivasha they are not. Indeed, at L. Victoria, from about the fourth to the tenth day after hatching, pairs with helpers provide more fish per offspring than those without ($P < 0.02$; U-test, two-tailed; Table 4), and pairs without helpers do not meet the energy requirements of

Table 4. Average number of fish/offspring × h fetched by pairs with and without helpers to nests with 3–6 young which were 4–12 days old. All observations were made for a 5-h period from 0730 to 1230 h. Each mean $\bar{x}$ is based on observation of at least 41 fish and 15 h at three nests, at most 142 and 55 h at 11 nests. SD = standard deviation, n = sample size. For significance of differences, see the text

	Breeding pairs					
	Without helpers			With helpers		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n
L. Victoria	0.57	0.13	9	1.03	0.32	11
L. Naivasha	0.84	0.15	4	0.86	0.27	3

their young (H.-U. Reyer, in preparation). At L. Naivasha, however, pairs with helpers fetch approximately the same number of fish as those without (Table 4) and both groups meet the energy requirements of their young at all ages.

Ecological Conditions. These differences in feeding rates and reproductive successes can be explained with the different ecological conditions which exist in the two colonies.

1) At L. Victoria, 56% of the fish fed to the 4- to 12-day-old young were *Engraulicypris argenteus* (Cyprinidae) ($n=128$). The remaining 44% consisted of various *Haplochromis* species (Cichlidae). At L. Naivasha, *Tilapia leucosticta, T. zillii* (Cichlidae), and *Micropterus salmonides* (Centrarchidae) were fed to the nestlings. For comparable length, all Cichlid fishes and *Micropterus* are very similar in their caloric values, but because of its slender body an *Engraulicypris* of the same length yields less energy than the other species (H.-U. Reyer, in preparation). To compensate for that, the adults at L. Victoria have to feed more fish to their young than do the adults at L. Naivasha.

2) The mean wind speed at L. Victoria in the observation months May–September is consistently higher than at L. Naivasha (Chipeta, 1976). At L. Victoria, the wind sweeps from across the lake by day, roughening the surface and forming breakers which disturb the sand and muddy the waters along the shore. The pied kingfishers have to fly far out to fish and only 24% of their dives are successful ($n=107$). Catching a fish takes an average 13.0 min of flying and hovering over the lake ($n=22$). At L. Naivasha, the wind comes from the land, and there is a beach zone of calm, relatively clear water protected by a papyrus belt. Here the pied kingfishers are more successful (79% of 52 dives) than at L. Victoria ($P<0.001$; χ^2 test), and catching a fish takes

less time (5.9 min, $n=26$; $P<0.0002$, U-test, two-tailed).

3) At L. Victoria, the distance from the colony to its fishing grounds is about 500–700 m, about double the L. Naivasha distance.

4) Contrary to L. Naivasha, the L. Victoria colony is in an area thickly populated by humans. Throughout the day, people come down to the river for various activities. Adult birds, arriving with a fish, are often disturbed and have to wait several minutes until they can feed it to the nestlings.

These environmental differences mean that L. Victoria pied kingfishers must expend considerably more time and energy on fishing and on raising young than their counterparts at L. Naivasha (H.-U. Reyer, in preparation), but there are probably scarcely any differences among birds within a colony, as members all hunt in the same area.

Discussion

Cooperative breeding in the pied kingfisher is characterized by a flexible helper structure, which is adapted to the particular environmental conditions in that potential helpers, available because of a general $\male\male$ surplus, are recruited more in unfavorable (L. Victoria) than in favorable conditions (L. Naivasha). Thereby the breeding success improved especially under poor conditions, making the total number of fledglings/pair similar for both the colonies investigated (L. Victoria, 3.2; L. Naivasha, 3.9). With one exception, in neither colony were more helpers found per pair than were necessary for the maximal possible breeding success. The number of helpers is apparently determined by the breeding pairs which, in unfavorable conditions, accept secondary, probably unrelated helpers as well as primary, related helpers, but bar the secondary helpers in favorable conditions. Even individual pairs switched their behavior from one strategy to the other when conditions were experimentally changed (p. 222). Accessibility and quality of food, the distance between the colony and its fishing grounds, as well as the frequency of disturbance by people proved to be the decisive environmental factors in the study areas. For the birds, these factors result in more favorable or less favorable time and energy budgets, which make the breeding success of pairs without helpers, pairs with one helper, and pairs with two helpers roughly predictable (H-U. Reyer, in preparation).

Occasional observations at Lake Simbi confirm that with decreasing quality of the biotope, the number of helpers per pair increases. In this colony, the pied kingfishers are exposed to similar conditions

as at L. Victoria, but their expenditure of time and energy must be greater still, as the fishing grounds are at least 1.5–2.0 km away. The breeders in this colony seem to have adapted to the conditions by recruiting three or more helpers.

This adaptability to the environment is, of course, limited by the sex ratio. At L. Victoria, 34% of the pairs probably had no helpers because all the available ♂♂ were 'booked up.' If several pairs have three or more helpers, as at L. Simbi and in other colonies (Douthwaite, 1978), this must either be at the expense of other pairs, or else the surplus of ♂♂ must be greater still. The latter was the case in a colony in Uganda (2.3:1; Douthwaite, 1973). Investigations to clarify whether a relationship exists between the inclemency of an environment and the surplus of ♂♂ have been started.

From the results mentioned above, it becomes evident that the number of helpers per pair in the pied kingfisher is an *adaptation to* and not a *consequence of* differences in the quality of the environment. Some authors have indeed thought it a consequence, since in some species with all-purpose territories, a positive correlation exists between territory size and quality and helper number (Brown and Balda, 1977; Gaston and Perrins, 1975; J.D. Ligon, unpublished work; Parry, 1973; Woolfenden, 1975; Zahavi, 1976). A negative correlation as found in the pied kingfisher also seems to exist in the colonial white-fronted bee eater (*Merops bullockoides*) (Emlen, 1980). Thus the difference perhaps reflects a difference between territorial and colonial species. There are numerous other differences between pied kingfishers and most cooperative breeders. In addition to the defense of all-purpose territories, most species show many other characteristics of *K* selection: delayed breeding (or even maturity), low fecundity, high survival rate, sendentariness, diminished dispersal, and almost no migration. Most of these features are considered to be adaptations to the strong competition in stable environments whose carrying capacity in respect to food, territory, or nesting sites is reached or nearly reached. The result is a slow population turnover and a wide generation overlap (Brown, 1974, 1975; Emlen, 1978; Fry, 1977; Pianka, 1978; Woolfenden, 1976). For pied kingfishers, hardly any of these features apply (see p. 220, 221), and they show more characteristics of *r* selection than all other known cooperative breeders among birds.

Because of these numerous differences, it cannot be expected that the evolution of cooperative breeding in the pied kingfisher can be explained with the same 'ecological saturation' model which has been proposed for *K*-selected species with all-purpose territories (Brown, 1974; Fry, 1977; Selander, 1964). Emlen

(1978, 1980) came to the same conclusion recently for the white-fronted bee eater (*M. bullockoides*) which, along with other bee eaters (Fry, 1972, 1977; M. Dyer and C.H. Fry, unpublished work), shows many similarities with the pied kingfisher.

As already suggested by Brown (1974), it seems more likely that the crucial factors spurring the development of cooperative breeding in the pied kingfisher are the skewed sex ratio and breeding in colonies. A ratio of 1.7 or 1.8 ♂♂ per ♀ means that only 55%–59% of all ♂♂ have a chance of mating. The others either can wait until next breeding season, or help rear the young produced by others. Selection will decide for the latter course if the birds' inclusive fitness (Hamilton, 1964) is increased thereby. Opportunities for such help are numerous in breeding colonies.

The increase in inclusive fitness through helping is obvious for the primary helpers: by improving the survival rate of related birds, a primary helper at L. Victoria raises his inclusive fitness by about 0.9 or 0.45 genetic equivalents when he rears full or half-siblings, respectively. For L. Naivasha, the values are 0.3 and 0.15, if the breeding success figures given in Table 3 are confirmed. These calculations are based on the formulae given by Brown (1978) and Emlen (1978). The calculations assume one helper son per pair in both colonies and the number of fledged young given in Table 3. Because of this and other simplifications (see Brown, 1978; Emlen, 1978; J.D. Ligon, unpublished work; Woolfenden, 1975), the values should be regarded not as precise, but only as rough estimates in comparison with the yearlings' chances of rearing their own young. These changes are probably almost zero. The high ♂♂ surplus will affect yearling ♂♂ in particular. They probably cannot successfully compete with older, more experienced ♂♂, and consequently will have little or no chance to win a mate and reproduce. Since this ♂♂ surplus seems to be a feature of the species as a whole, dispersing to other colonies would not improve the reproductive prospects. Therefore the genetic equivalents mentioned should be the highest attainable for yearling primary helpers in the two colonies. Since this improvement of inclusive fitness results from raising relatives, kin selection (Maynard Smith, 1964) must be held responsible for the evolution of this helper type (see also Maynard Smith and Ridpath, 1972; Brown, 1974).

For secondary helpers, the benefit of helping is more difficult to assess. The ringing gave no evidence for any close genetic relatedness between secondary helpers and breeders. It could be argued, however, that this relatedness was not detected because the birds had hatched before the study had commenced four years ago. But then, how could one explain that

the secondary helpers 'applied' to various pairs, remaining where they were tolerated first? Moreover, the yearly population turnover is about 65% for ♂♂ and 75% for ♀♀. Thus the probability of finding a close relative after 3–4 years is very low. Yet, at least in those cases in which secondary helpers joined neighboring pairs, relatedness cannot be excluded, particularly when we consider site attachment (p.222).

It also could be argued that, due to inbreeding, the average relatedness between all members of the colony is fairly high. Again, the high population turnover plus the probably existing immigration from other colonies (p. 221) makes this unlikely. In an effective population size of 20–30 ♂♂, an annual immigration rate of 65% (making good mortality and immigration losses) would result in an average relatedness of less than 0.01 (calculated according to Brown, 1974).

From all the evidence, we may assume that most secondary helpers probably are not closely related to the breeders and their young. Therefore it seems unlikely that kin selection was the driving force in the evolution of this helper type. Various authors have suggested and summarized the possibilities by which helping can improve the helpers' individual fitness, and some regard individual selection as the main force behind the evolution of cooperative breeding (Brosset, 1978; Brown, 1974, 1978; Emlen, 1978, 1980; J.D. Ligon, unpublished work; Ligon and Ligon, 1978; Ricklefs, 1975; Selander, 1964; Woolfenden and Fitzpatrick, 1978; Zahavi, 1974, 1976).

According to our present, scarce data, secondary helpers may increase their own reproductive success in two ways:

1) Pied kingfishers which return to the same colony the next year usually are the earliest to feed young, tend to have more secondary helpers than birds breeding late (12 vs 7), and consequently have more young. Thus a secondary helper may gain knowledge of a colony in one year, which improves his future reproductive success via early breeding, and recruiting of secondary helpers.

2) In 1979, one ♂ bred with a ♀ which he had 'served' as a secondary helper in 1978. This also had yielded him a primary helper since the two were accompanied by one of the ♀'s yearling sons. The ♀'s previous mate was still alive and mated with a new ♀. Thus, secondary helpers may improve their future reproductive success by taking over ♀♀ and recruiting primary helpers from the young they have helped to rear.

The last observation suggests that the secondary helpers are at the same time potential competitors for the scarce ♀♀. Thus they may decrease the breeding ♂♂'s inclusive fitness. This hypothesis is confirmed by the observation that it is mainly the male mates which attack candidate helper ♂♂ (p.222). The secondary helpers should be accepted only when this disadvantage of losing inclusive fitness is more than compensated for by the helpers' contribution to reproductive success. Since the effect of helpers on reproductive success differs markedly between L. Victoria and L. Naivasha (Table 3), this competition hypothesis can explain the different treatments of secondary helpers in the two colonies. It also can explain why usually there were no more helpers per pair than were necessary for the maximal possible breeding success, and why breeders do not accept secondary helpers if they have only a few young to rear (p.222). These cases illustrate that there is a breeder–secondary helper conflict which can shift with ecological conditions (Emlen, 1978).

One explanation of the greater tolerance shown by pairs toward primary, related helpers in both colonies could be that related helpers represent less competition for ♀♀. In many animal species, familiarity with other members of the family and/or stable hierarchies either are assumed or have been proved to be mechanisms preventing such possibly incestuous matings (Bischof, 1972; Ligon and Ligon, 1978; Maynard Smith, 1964; Parry, 1973; Woolfenden and Fitzpatrick, 1978; Zahavi, 1976).

In this case, the taking over of ♀♀, one of the possible benefits from helping for secondary helpers, would not apply for primary helpers. This does not mean, however, primary helpers gain no individual advantages from cooperative breeding. The gain of experience and the recruiting of helpers mentioned above may hold for them as well. On the other hand, the finding that primary related helpers have individual benefits is not sufficient for assuming that individual selection has been the driving force in the evolution of cooperative breeding. When, for socioecological reasons, birds are deprived of the chance to breed, and when they also profit from their helping activities, their altruism is certainly in question (J.D. Ligon, unpublished work), but this is no argument against kin selection. As long as the conditions relatedness and increased breeding success are fulfilled, helping behavior cannot help but being kin selected.

The described helper structure in the pied kingfisher is an example showing that both individual and kinship components of natural selection must have been at work in the evolution of cooperative breeding in this species. Perhaps kin selection was more important in evolving primary helpers, and individual selection in evolving secondary helpers. In order to estimate the relative importance of these two components, it is not sufficient to know the advantages of breeders and helpers in terms of inclusive fitness;

the relative frequencies of both helper types must also be known. In the two colonies investigated, the total numbers of primary, related helpers (22) and secondary, probably unrelated helpers (19) were similar. According to preliminary investigations in other colonies, the L. Victoria system with both types of helpers seems to be more representative for the species as a whole than the L. Naivasha system with primary helpers only.

By comparing the inclusive fitness of primary, probably more kin-selected helpers with that of secondary, probably more individually selected helpers, I hope it will be possible one day to express the contributions of individual and kin selection in terms of genetic equivalents.

References

Backhurst, G.C.: East African ringing report 1972–1973. J. East Afr. Nat. Hist. Soc. Nat. Mus. **146**, 1–9 (1974)

Bischof, N.: Inzuchtbarrieren in Säugetiersozietäten. Homo **23**, 330–351 (1972)

Brosset, A.: Social organization and nest-building in the forest weaver birds of the genus *Malimbus* (Ploceinae). Ibis **120**, 27–37 (1978)

Brown, J.L.: Alternate routes to sociality in jays – with a theory for the evolution of altruism and communal breeding. Am. Zool. **14**, 63–80 (1974)

Brown, J.L.: The evolution of behaviour. New York: Norton 1975

Brown, J.L.: Avian communal breeding systems. Annu. Rev. Ecol. Syst. **9**, 123–155 (1978)

Brown, J.L., Balda, R.P.: The relationship of habitat quality to group size in Hall's babbler (*Pomatostomus halli*). Condor **79**, 312–320 (1977)

Chipeta, G.B.: A study of wind power availability in Kenya. M.S. thesis, University of Nairobi (1976)

Douthwaite, R.J.: Some aspects of the biology of the lesser pied kingfisher *Ceryle rudis* Linn. Ph.D. thesis, Makerere College, University of East Africa (1970)

Douthwaite, R.J.: Pied kingfisher *Ceryle rudis* populations. Ostrich **44**, 89–94 (1973)

Douthwaite, R.J.: Fishing techniques and foods of the pied kingfisher on Lake Victoria in Uganda. Ostrich **47**, 153–160 (1976)

Douthwaite, R.J.: Breeding biology of the pied kingfisher on Lake Victoria. J. East Afr. Nat. Hist. Nat. Mus. **31**, 1–12 (1978)

Emlen, S.T.: The evolution of co-operative breeding in birds. In: Behavioural ecology. Krebs, J.R., Davies, N.B. (eds.), pp. 245–281. Oxford, London, Edinburgh: Blackwell 1978

Emlen, S.T.: Altruism, kinship, and reciprocity in the white-fronted bee-eater. In: Natural selection and social behaviour. Alexander, R.D., Tinkle, D. (eds.). New York: Chiron Press (in press) 1980

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

Fry, C.H.: The evolutionary significance of co-operative breeding in birds. In: Evolutionary ecology. Stonehouse, B., Perrins, C.M. (eds.), pp. 127–136. London: Macmillan 1977

Gaston, A.J., Perrins, C.: The relationship of habitat to group size in the genus *Turdoides*. Emu **74** [Suppl.], 309 (1975)

Greenwood, P.J., Harvey, P.H., Perrins, C.M.: Inbreeding and dispersal in the great tit. Nature **271**, 52–54 (1978)

Grimes, L.G.: The occurrence of co-operative breeding in African birds. Ostrich **47**, 1–15 (1976)

Hamilton, W.D.: The genetical theory of social behaviour. I., II. J. Theor. Biol. **7**, 1–52 (1964)

Ligon, J.D., Ligon, S.H.: Communal breeding in green wood-hoopoes as a case for reciprocity. Nature **276**, 296–298 (1978)

McClure, H.E.: Migration and survival of the birds of Asia. Bangkok 1974

Maynard Smith, J.: Group selection and kin selection. Nature **201**, 1145–1147 (1964)

Maynard Smith, J., Ridpath, M.G.: Wife sharing in the Tasmanian native hen, *Tribonyx mortierii*: A case of kin selection? Am. Nat. **106**, 447–452 (1972)

Migongo, E.W.K.: Environmental factors affecting the distribution of malachite and pied kingfishers in Lake Nakuru National Park. M.S. thesis, University of Nairobi (1978)

Parry, V.: The auxiliary social system and its effect on territory and breeding in kookaburras. Emu **73**, 81–100 (1973)

Pianka, E.R.: Evolutionary ecology. New York: Harper and Row 1978

Ricklefs, R.E.: The evolution of co-operative breeding in birds. Ibis **117**, 531–534 (1975)

Rowley, I.: Co-operative breeding in Australian birds. Proc. XVI Int. Ornithol. Congr. (Canberra, Australia). Frith, H.J., Calaby, J.H. (eds.), pp. 657–666. Canberra: Australian Academy of Science 1976

Selander, R.K.: Speciation in wrens of the genus *Campylorhynchus*. Univ. Calif. Berkeley Publ. Zool. **74**, 1–224 (1964)

Skutch, A.F.: Helpers among birds. Condor **63**, 198–226 (1961)

Sugg, M.S.: Mensural and moult data from a breeding colony of pied kingfishers. Ostrich **45**, 227–234 (1974)

Vehrencamp, S.L.: The adaptive significance of communal nesting in groove-billed anis *Crotophaga sulcirostris*. Behav. Ecol. Sociobiol. **4**, 1–33 (1978)

Woolfenden, G.E.: Florida scrub jay helpers at the nest. Auk **92**, 1–15 (1975)

Woolfenden, G.E.: Co-operative breeding in American birds. Proc. XVI Int. Ornithol. Congr. (Canberra, Australia). Frith, H.J., Calaby, J.H. (eds.), pp. 674–684. Canberra: Australian Academy of Science 1976

Woolfenden, G.E.: Growth and survival of young Florida scrub jays. Wilson Bull. **90**, 1–18 (1978)

Woolfenden, G.E., Fitzpatrick, J.W.: The inheritance of territory in group-breeding birds. BioScience **28**, 104–108 (1978)

Zahavi, A.: Communal nesting by the Arabian babbler. Ibis **116**, 84–87 (1974)

Zahavi, A.: Co-operative nesting in Eurasian birds. Proc. XVI Int. Ornithol. Congr. (Canberra, Australia). Frith, H.J., Calaby, J.H. (eds.), pp. 685–693. Canberra: Australian Academy of Science 1976