INVESTMENT AND RELATEDNESS: A COST/BENEFIT ANALYSIS OF BREEDING AND HELPING IN THE PIED KINGFISHER (*CERYLE RUDIS*)

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Abstract. Helping at the nest in birds is often termed altruism. However, so far, no study has ever demonstrated high costs to a helper's own lifetime reproductive success (=direct fitness), nor its compensation through benefits from relatives other than its own offspring (=indirect fitness). In this paper on pied kingfishers (*Ceryle rudis*) the relationship between investment, relatedness and inclusive fitness (expressed in terms of genetic equivalents) is investigated for breeding males, and males that help either relatives (=primary helpers) or strangers (=secondary helpers). With respect to guarding nests against predators and feeding young, primary helpers invest as much as breeders, but secondary helpers contribute significantly less. These differences in status and investment (measured in energy expenditure) affect the birds' future to such an extent that primary helpers have a lower chance of surviving and mating than secondary helpers. However, their costs in direct fitness are compensated by pronounced benefits to indirect fitness, resulting from improved survival of siblings and parents. An attempt is made to calculate the inclusive fitness of birds following different strategies over a 2-year period. It is concluded that (a) breeding is superior to helping and helping superior to doing nothing and (b) that kin-selection must be invoked to explain why surplus males choose the more costly primary helper strategy instead of the cheaper secondary helper strategy. Alternative explanations, including group selection, parental manipulation and reciprocity, are discussed.

Current evolutionary theory predicts that, in order to maximize its inclusive fitness, an animal should adjust its investment in offspring relative to expected benefits minus expected costs (Trivers 1972; Dawkins & Carlisle 1976; Boucher 1977; Maynard-Smith 1977). Following Trivers (1972), parental and alloparental 'investment' is defined here as any behaviour that increases the chances of survival of existing offspring at the costs of the parents' or helpers' ability to invest in future offspring. Although terms like 'effort' or 'expenditure' would have been more appropriate in this paper to describe the empirical observed matter, I have decided to employ the more widely-used term 'investment'. This seems justified as this paper provides evidence that indeed the 'effort' has a negative effect on future reproductive success.

Costs and benefits of reproductive behaviour can result from an individual's own reproduction (=direct fitness) and from the reproduction of relatives other than its own offspring (=indirect fitness; Hamilton 1964; Brown & Brown 1981). With respect to direct fitness, empirical support for the above prediction comes mainly from parental defence, which increases as the number of young and their reproductive value increases, and as the reproductive value of the mother decreases (Milinski 1978; Robertson & Bierman 1979; Tallamy 1982), although in some cases this relationship may be more difficult (Weatherhead 1979; Curio 1980). With respect to indirect fitness the benefit to an individual depends, among other factors, on the coefficient of its relatedness (r) to the young it rears. Thus, under certain circumstances, a positive correlation between investment and relatedness might be predicted (Weigel 1981).

Cooperatively breeding species, in which helpers invest in kin other than their own offspring, have sometimes been used to test this prediction. However, the result is ambiguous. For some mammals it has been shown that the intensity of help increases with increasing relatedness (Yamada 1963; Sherman 1977, 1981; Armitage & Johns 1982), but for birds little more than correlations between the number of helpers and relatedness has been demonstrated (Woolfenden 1981; for reviews see Brown 1978, *in press*; Emlen 1978; Harvey et al. 1980; Vehrencamp 1979; Riedman 1982). But mere correlations do not prove that enhanced indirect fitness is responsible for the evolution and maintenance of helping behaviour. Association and assistance between close kin could as well be a by-product or secondary result of benefits arising from improved direct fitness (Vehrencamp 1979; Koenig & Pitelka 1981). This suspicion is justified, in

particular, if animals invest in unrelated off-spring, a situation that seems to occur more frequently than previously suspected (Balda & Balda 1978; Stacey 1979; Ligon 1981; Power 1981; Zahavi 1981).

In some of these cases unrelated helpers contributed even more than related ones. Besides the fact that feeding rates may be influenced by age and number of nestlings, weather and other factors (Brown et al. 1978), there is increasing evidence that investment is not so much a function of relatedness but rather a function of sex, age, and status (Rowley 1978, 1981; Stallcup & Woolfenden 1978; Ligon 1981). These in turn seem to affect the helper's own reproductive success, e.g. through shared paternity and egg-ownership (Dow 1977; Vehrencamp 1977; Stacey 1979; Joste et al. 1982) and when helping improves experience, survival, territory inheritance, and recruitment of own helpers (Brown 1978; Ligon & Ligon 1978; Rood 1978; Stallcup & Woolfenden 1978; Woolfenden & Fitzpatrick 1978; Taborsky 1984). The more important such personal advantages become the more will the effect of relatedness be blurred (for overviews see Brown 1978, in press; Emlen 1978).

Most authors currently argue, therefore, that the direct component of inclusive fitness may be of equal or even greater importance for the evolution of helping behaviour than the indirect component. The few attempts to quantify the relative proportions of these two components support this, at least for birds and mammals (Markl 1980; Vehrencamp 1979; Brown & Brown 1981; Emlen 1981, 1982a; Koenig & Pitelka 1981; Rowley 1981; Woolfenden 1981; Reyer 1982a). However, even demonstrating a relatively high benefit in indirect fitness would not justify speaking of 'altruism' or making only kin selection responsible for the evolution of helping, unless one shows that (a) the benefit arises from helping per se and (b) its costs reduce the helper's direct fitness (Power 1981; Brown, in press). So far, this has not been demonstrated for any cooperatively breeding bird and there is no good evidence for altruism (Brown 1978; Koenig & Pitelka 1981).

In this paper I test the consequences of helping on direct and indirect fitness and the importance of kin selection for colonial pied kingfishers from Lake Victoria, Kenya. For two reasons this species seems particularly suited for such a test. (1) Its time- and energy-consuming hunting behaviour (flying, hovering, diving) involves high costs for any helping bird; the benefits are also high, however, as the survival of young depends strongly on the number of adults feeding them. (2) The existence of two distinct categories of helpers (primary = related and secondary = unrelated) allows separation of individual from kin benefits.

Methods and Results

Study site, general methods, general biology and differences in helper structure between populations in relation to ecology have been described elsewhere (Reyer 1980, 1982b).

Date and Mode of Association between Breeders and Two Types of Helpers

Primary helpers are with the breeding pairs from the very beginning of the breeding season, whereas potential secondary helpers — although present as well — are not tolerated before the young have hatched. This is the criterion for defining the two categories. With 47 primary helpers and 48 secondary helpers recorded so far, the two types seem to be equally frequent at Lake Victoria.

From the very beginning primary helpers restrict their assistance to one pair only, e.g. helper A to pair 1, helper B to pair 2 (Fig. 1). But secondary helpers, such as C, initially approach various pairs, e.g. pairs 3, 6 and 7. And one pair, such as 6, may be visited by several different potential helpers, e.g. C, E and F. During their attempts to join various pairs the secondary helpers are initially repelled, particularly by the males of the breeding pairs. But if persistent, they are ultimately accepted at one hole or another 3–7 days after the young have hatched, e.g. C at 7 and E at 6. Thereafter they restrict their activities to this particular pair. They switch to another pair only if breeding is unsuccessful, as do primary helpers if their parents fail to raise further offspring.
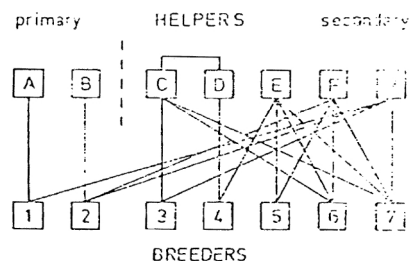

Fig. 1. Schematic representation of associations between helpers (A–F) and breeding pairs (1–7) at the beginning of a breeding season. ? = unmarked bird. Secondary helpers C and D are bracketed to indicate that they are brothers joining different pairs.

After the young had hatched there was never more than one primary helper per pair, but up to four secondary helpers were found, sometimes in addition to the primary helper.

Relatedness between Helpers and Nestlings

Through colour-banding over 8 years the descent of 24 primary helpers and 27 secondary helpers could be established. Primary helpers proved to be the 1–3-year-old sons of at least one bird from the breeding pair they assisted (Table I). This means they invested in full- or half-siblings. There were only two exceptions to this: at each of two nests, one yearling whose parents were no longer there assisted the secondary helper (now a breeder) that had helped raise him the year before. The average coefficient of genetic relationship between primary helpers and nestlings (r_{ph}) was 0.32 (SD $= 0.16$, $n = 24$). Similar values have been calculated for other birds (Gaston 1978a; Rowley 1981; for fish helpers see Taborsky & Limberger 1981).

Secondary helpers, on the other hand, approached various pairs and apparently remained where they were first tolerated. None of the 27 secondary helpers was the son of any breeder he joined and in most cases his parents were not even in the colony (Table I). Also the colour-banding showed no evidence for any other close genetic relatedness, down to the level of 1/8. Of course it could be argued that relatedness of all colony members is fairly high, due to inbreeding. In fact, one condition that would favour inbreeding, namely little migration between colonies, seems to be fulfilled, at least in adult pied kingfishers.

The extent of migration was estimated by two different methods.

(1) In 1979 and 1982 a total of 351 adult pied kingfishers were checked in three neighbouring colonies lying 2, 4 and 9.5 km away from the main study area at Lake Victoria. Only one female marked as an adult in one colony moved to the nearest other colony. This very limited

extent of colony change under natural conditions was supported by observations under 'experimental' conditions at Lake Naivasha (Kenya). Here three males and four females had been ringed in 1981 in a small colony where no breeding was possible in the subsequent year as the banks had been fortified. In 1982 two of these males and three of the females appeared in a new, artificially-created colony some 1.5 km away from the former one. Allowing for mortality this probably represented the total remaining marked population. Thus, even when birds are forced to move they seem to choose the nearest alternative, so it is unlikely that at Lake Victoria a significant proportion of birds had moved to colonies lying farther than 9.5 km from the main study site. This allows the use of return rates as a measure of survival. (2) Regular counts in our study colony at Lake Victoria suggested great year-to-year stability of the population with 36, 34, 37 and 37 males ($\bar{x} = 36$) and 27, 26, 30 and 26 females ($\bar{x} = 27$) in 1980, 1981, 1982 and 1983 respectively. Because of this stability, plus seasonal reproduction, and the known age of several marked birds, mean adult survival of males could be calculated from the number of breeding adults surviving into the next year ($n = 26$), divided by the number of their surviving male yearlings plus adults ($n = 50$; see Vehrencamp 1978). The resulting figure is 52.0%, similar to the fraction of male breeders returning the year after ringing (60.5%, Table III). Thus adult male mortality seems to be compensated by juvenile males from the same colony.

For females the above method of calculating survival could not be used as juvenile females, in contrast to juvenile males, do not return to their natal area (Reyer 1980). Consequently adult female mortality must be compensated completely by juvenile females immigrating from other colonies. This, plus the fact that incestuous matings were never observed (see below), renders inbreeding an insignificant factor. Therefore the average inbreeding coefficient (F) of 0.023, calculated for other colonial species (Barrowclough 1980) was applied to pied kingfishers. Using the formula $r = 2F/(1 + F)$ (Brown 1974) the average coefficient of genetic relationship between a secondary helper and a random individual he helps to rear (r_{sh}) is 0.05. This is about six times lower than the r_{ph} of 0.32 between primary helpers and nestlings.

The above values of r_{ph} and r_{sh} hold only if helpers do not father any of the nestlings they rear. As pied kingfisher copulations are preceded

Table I. Frequency Distribution of Primary and Secondary Helpers in Relation to Presence of Parents

	Present:			
	Both parents	Father only	Mother only	No parent
Primary helper	9	9	4	2
Secondary helper	0	4	0	23

by shrill, repeated calls and frequently occur in the open, they are easier to detect than in many other bird species, including cooperative breeders. From observing 53 copulations between identified individuals I have no indication that females copulate with helpers. Without any exception they were mounted by their respective mates. In only one case did a primary helper attempt to mount his stepmother but he was rejected. Chances of mating for secondary helpers may be even lower because breeding males did not tolerate them in the vicinity of their females and nests until the young had hatched. Although these observations do not rule out any genetic contribution by helpers I consider its probability small enough to be disregarded.

Contribution of Breeders and Helpers to Brood-care

Because of their early association with breeders, primary helpers engage in some activities that are not open to secondary helpers; among these are chasing away competitors for nest-sites and the regular feeding of male and female breeders prior to egg-laying (Reyer 1980). In addition to these qualitative differences, quantitative differences in nest-guarding and food contribution occur once the young have hatched.

Nest-guarding. Guarding the nest against predators such as snakes (*Naja* sp.), monitor lizards (*Varanus niloticus*) and the ichneumon (*Herpestes* sp.) is an important activity in pied kingfisher broodcare (see also Douthwaite 1978). Attacks on such predators could rarely be observed directly; even when this was possible the confusion caused by several birds whirling around made it difficult to tell which individuals contributed most. Therefore the following less direct measure of nest-guarding had to be used. After feeding a fish to a nestling, adult birds usually remain near the nest-hole for some time, watching the colony from a prominent perch. The time between leaving the nest and departing for the lake was defined as nest-guarding. Figure 2a shows that, according to this measure, secondary helpers invest less than all other birds, whereas there is no significant difference between male breeders, female breeders and primary helpers.

This result is paralleled by one from an experimental situation. In order to measure the energy expenditure of feeding adults (see Discussion), some breeders and helpers were caught in the late afternoon, measured and weighed, injected

with doubly-labelled water, blood sampled and then released about 1.5 h after catching. The day following this procedure all five primary helpers and 10 out of 12 breeders resumed feeding nestlings, but only 1 out of 5 secondary helpers did so. The differences between secondary and primary helpers and between secondary helpers and breeders are significant (both $P < 0.027$; two-tailed Fisher exact probability test). Thus secondary helpers do not only spend less time in guarding, they also seem to take fewer risks than parents and primary helpers.

Food contribution. Feeding of 11–20-day-old nestlings was monitored from 0630 to 1830 hours with respect to number, type and size of fish taken into the nest by individually marked birds. Of all food items 67.8% ($n = 410$) were comprised of Cichlid fish such as *Haplochromis* and *Tilapia*, 27.3% of *Engraulicypris argenteus* (Cyprinidae) and 4.9% of Nile perch (*Lates*, Centropomidae), catfishes (Siluridae) and unidentified species. Fish intended for feeding young are always carried parallel to the beak, head foremost. This allows calculation of actual fish size from photographs of birds with known beak length:

$$SL = \frac{BL \cdot F_\text{p}}{B_\text{p}} \qquad (1)$$

Here SL is the standard fish length (mm), BL the actual beak length, F_p and B_p are the pictured lengths of fish and beak. Because of differences in body shape Cichlids and *Engraulicypris* of the same length do not yield the same metabolic energy. Sizes were therefore converted into kcal by establishing a regression between SL and dry weight and by measuring the energy content per g dry weight through bomb calorimetry. Results are shown in Table II.

Based on these results, the average energy content/fish taken to the nestlings was calculated for each feeding adult separately. By multiplying this value by the total number of fish that the particular individual took in to the nest/day his total energy contribution was calculated for that day. Because of deviations from a normal distribution, the means and 95% confidence limits were calculated after log-transformation of these data, and then retransformed into a linear scale. The same method of calculation was used for all other means and confidence limits given in this paper.

Results are shown in Fig. 2b, c, d. There is no significant difference between the contributions of

a) nest-guarding (min)

b) fish / ad x day
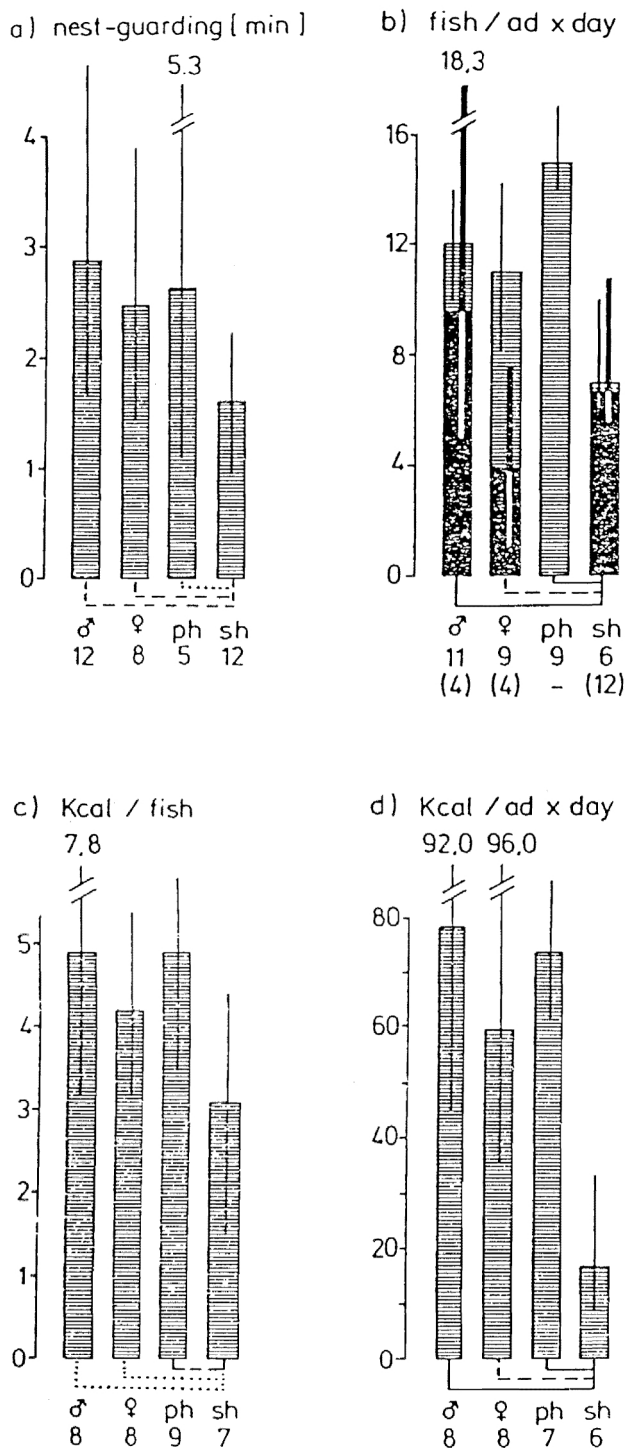
c) Kcal / fish

d) Kcal / ad x day

Fig. 2. Investment of breeders (♂, ♀), primary helpers (ph) and secondary helpers (sh) in (a) nest-guarding (b) feeding with respect to number of fish/day, (c) energy content/ fish and (d) total energy/day. Shaded bars and thin vertical lines: pairs with two or less than two helpers; black bars and thick lines: pairs with more than two helpers. Bars represent means, vertical lines 95% confidence limits. Bars are connected by horizontal lines if the difference between them is significant (continuous

breeders and primary helpers, whether we look at number of fish (Fig. 2b), energy content/ fish (Fig. 2c) or total energy/day (Fig. 2d). Secondary helpers, however, contribute less. Differences are more pronounced for number of fish and total energy/day than for energy/fish. But even a small size difference can have marked effects on the time and energy expenditure of feeding birds.

This was shown by comparing the duration of feeding trips in relation to prey type. Based on the results from radio-tracking, absence from the nest of ≤ 30 min was considered a feeding trip for all individuals except secondary helpers, who apparently do not hunt at their maximum capacity. Average durations of feeding trips were calculated separately for each individual and for each of the two main prey types. Then these mean durations were averaged over all individuals (except secondary helpers).

The results showed that for feeding one cichlid, birds spend about 45% more time in flying and hovering than for feeding one Engraulicypris, including transport to the colony (Fig. 3a). This probably results from differences in the biology of these fishes, with Engraulicypris occurring in schools near the surface and cichlids living less clumped and in deeper water (Fryer & Iles 1972). Figure 3b shows the mean ratios between Engraulicypris and cichlids fed by breeders and helpers. A ratio of 1 would indicate equal numbers of both prey types; the lower the ratio, the lower is the relative number of Engraulicypris. As such ratios can be biased when sample sizes are small, individuals with low feeding frequencies/day were pooled until the total number of fish/day was 10 or more.

No significant difference was found between prey type ratios of breeders and primary helpers. But secondary helpers fed relatively more Engraulicypris than females did, and a similar trend emerged when they were compared with male breeders and primary helpers. If breeders and primary helpers are pooled the difference from secondary helpers is significant ($P < 0.01$, U-test, two-tailed). Thus secondary helpers not only feed fewer fish than breeders and primary helpers (Fig. 2b), they also feed relatively more small Engraulicypris than big cichlids (Figs

Table II. Relationship between Standard Length (SL, mm), Dry Weight (W_d in g) and Energy Content (kcal/g W_d) for Cichlid Fishes and *Engraulicypris argenteus* from Lake Victoria

Prey type	Dry weight	r	n	Energy content		
				$\bar{x}$	SD	n
Cichlidae	log $W_d = 0.026 \cdot SL - 1.461$	0.99	95	4.515	0.054	3
Engraulicypris argenteus	log $W_d = 0.037 \cdot SL - 2.320$	0.98	52	4.768	0.145	3

The regression for *Engraulicypris* was recalculated from Douthwaite (1976): $r =$ Pearson correlation coefficient.

2c, 3b). This means an additional reduction in the time spent flying and hovering (Fig. 3a) and consequently a lower energy expenditure (see Discussion).

The above results are based on data from breeding pairs with up to two helpers. At nests with primary helpers the average number of young was 4.3 (SD = 0.9) with an average age of 15.8 days (SD = 3.0). At nests with secondary helpers the values were almost identical with 4.5 nestlings (SD = 0.8) and 15.0 days of age (SD = 5.1). Thus the low feeding contribution of secondary helpers cannot be attributed to lower energy requirements of nestlings (see Royama 1966; Brown et al. 1978; Tinbergen 1981).

Four birds can bring enough food to guarantee the survival of all young hatching from a normal clutch of five (Reyer 1980, 1982b). Therefore in groups with three and more helpers a lowering of the individual burden is to be expected. For this I have no data on average fish size and total kcal per adult per day. But as far as number of fish is concerned the female is the first one to profit from additional feeders. If results in Fig. 2b (shaded areas) are compared with results from four groups with three to four secondary helpers each (and no primary helpers), there is little difference in the contributions of male breeders and secondary helpers (Fig. 2b, black areas), but the females' contribution decreases significantly (P = 0.05, U-test, one-tailed). Similar observations have been reported for other species with a surplus of males (Rowley 1981). This supports the prediction that with a skewed sex ratio, reduction of investment is favoured in the rarer sex (Maynard-Smith 1977).

The Effect of Feeding Young on Survival

Based on Fig. 2b, the energy expenditure for males of different status in one year was ranked

from high to low. This was then compared with the proportion of birds returning to the same colony the following year (Table III), which, with hardly any emigration, is a reliable measure of survival (see above). For males there is a significant negative correlation, indicating that higher investment indeed leads to lower survival ($r_s = 0.900$, $P = 0.05$, Spearman rank correlation, one-tailed). For females this seems true only if those birds that raised offspring with not more than one helper are compared with those not having bred at all. But survival of breeding females with two or more helpers is not only higher than that of females with not more than one helper, which is to be expected because of the reduction in number of feeding trips (Fig. 2b, black area), it is even higher than that of non-breeding females ($\chi^2 = 4.072$, $P = 0.044$). This
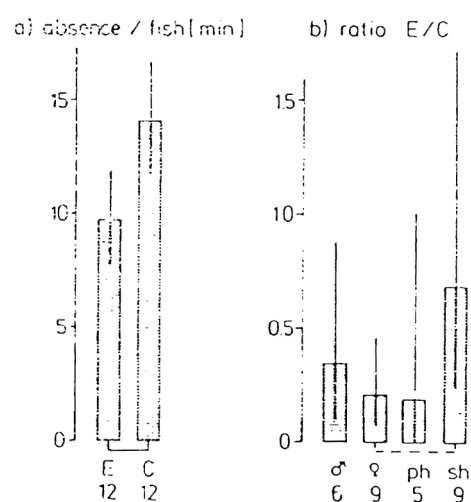

Fig. 3. (a) Time absent from the colony (min) per *Engraulicypris* (E) and cichlid (C) fed to nestlings. (b) Ratios of *Engraulicypris*/cichlid fed to nestlings by breeders (♂, ♀), primary helpers (ph) and secondary helpers (sh). For further explanation, sample sizes and significances see legend to Fig. 2.

Table III. Percentage of Males and Females Returning to the Same Colony in Relation to their Former Status and Energy Expenditure

| | Primary helpers | Breeders with: | | Secondary helpers | Non-feeding birds |
		≤ 1 helper ($\bar{x}=0.55$)	≥ 2 helpers ($\bar{x}=2.21$)		
Rank	1	2	3	4	5
Males	47.4 (19)	58.6 (29)	64.3 (14)	73.1 (26)	70.1 (77)
Females	—	44.8 (29)	85.7 (14)	—	56.7 (60)

Numbers in parentheses are sample sizes. Numbers 1–5 are ranks of energy expenditure from high to low. $\bar{x}$ refers to the average number of helpers in the respective category.

surprising result can probably be explained by the fact that in larger breeding groups females regularly beg fish from secondary helpers. One female for whom an almost complete time budget over 2 days is available was provided with more fish than she took into the nest. This is likely to improve body condition and survival.

The Effect of Age and Helping on Future Direct Fitness

The two different helper strategies do not only lead to different mortality rates (Table III) but also to differences among the surviving helpers in their own future reproductive success. Table IV shows that in the year following helping 89.5% of the surviving secondary helpers were mated, but only 33.3% of the primary helpers were.

Table IV. Number (and Proportion) of Primary Helpers, Secondary Helpers and Mated Males in Relation to their Status during the Previous Season

| Previous season | Following season | | | |
| | Mated | Helper | | Total |
		Primary	Secondary	
1. Primary helper	3 (0.33)	3 (0.33)	3 (0.33)	9
2. Secondary helper	17 (0.89)	0 (0)	2 (0.11)	19
3. Mated males	61 (0.98)	0 (0)	1 (0.02)	62
Comparison	1/2	1/3	2/3	
	<0.01	<0.001	NS	

Differences between categories 1–3 were tested with Fisher's exact probability test (two-tailed) after pooling columns 2 and 3.

To test whether this difference is mainly a result of age (with primary helpers usually being younger than secondary helpers, Reyer 1980) or a result of helping or both, I compared younger versus older helpers and feeding versus non-feeding potential helpers. Non-feeding primary helpers can occur when their parents and several other pairs fail to breed (e.g. in very dry years when the soil is too hard for digging nest-holes). Non-feeding potential secondary helpers mainly resulted from the experimental interference described in the section on nest-guarding.

The results (Table V) suggest that in primary helpers age may be a determinant of mating chances whereas the act of helping is not. For secondary helpers the reverse seems to be true: no age effect could be found but birds that had helped showed a tendency to be more successful than birds that had not. Thus, con-

Table V. Number of Surviving Primary and Secondary Helpers Mated in the Following Season in Relation to (a) Age and (b) Helping

| | Primary helper | | Secondary helper | |
	Mated	Not mated	Mated	Not mated
(a) In relation to age				
≤ 2 year	4	8	4	2
>2 year	5	2	10	2
P	0.131		NS	
(b) In relation to helping				
Helping	3	6	17	2
No helping	4	8	3	3
P	NS		0.069	

Sample sizes in (a) are not necessarily identical to those in (b) or those in Tables III and IV as yearling males cannot only be aged when ringed at birth but also by their plumage (Reyer 1980). Probabilities are derived from one-tailed Fisher tests.

trary to primary helpers, the act of helping seems to improve a secondary helper's chance of getting a mate.

This is supported by the following observations: out of the 17 former secondary helpers, seven took over the female they had helped the year before. In three of these seven cases the previous mate of the female was still alive and in one case without a new mate. Whether the males had been dislodged by their former helpers or whether the pairs had separated voluntarily is not known. But once I actually observed at the end of the breeding season a heavy and prolonged fight between a breeder and his secondary helper. In all seven cases of female take-over and in eight other instances the breeding site within the colony was also taken over by the former secondary helper.

These differences in mating chances between the two types of helper may result partly from age differences and partly from incest-avoiding mechanisms which prevent primary helpers from mating with their mothers. In the only two cases in which a primary helper took over the female he had helped the year before, this was his stepmother.

From the combined data on survival rates (Table III) and chances of getting a mate (Table IV) it follows that, with respect to own future reproductive success, being a secondary helper is a much better strategy than being a primary one ($\chi^2 = 10.936$, $P < 0.001$).

The Effect of Helping on Indirect and Inclusive Fitness

At Lake Victoria helping markedly improved the reproductive success. Table VI shows the average number of helpers and fledged young (in total and per feeding adult) broken down into four categories; pairs without helpers, with primary helpers only, with secondary helpers only and with primary plus secondary helpers. From these figures I calculated the average number of fledglings/pair (N) in relation to a bird's status:

$$N = \frac{N_i \cdot n_i + N_j \cdot n_j}{n_i + n_j} \qquad (2)$$

Here n_i and n_j are the numbers of cases in two of the four categories of Table VIa and N_i and N_j are the average numbers of young fledging in the respective categories (Table VIb). If, for example, a potential primary helper does help his parents, he can either be the only one (see above), which would yield a reproductive success of $N_i = 3.57$ ($n_i = 11$), or he could feed together with one or more secondary helpers which would result in $N_j = 4.57$ fledglings ($n_j = 10$), the maximum possible number (Reyer 1980). If he does not help his parents, these could either end up without helpers ($N_i = 1.82$, $n_i = 19$) or with secondary helpers only ($N_j = 3.71$, $n_j = 11$).

The resulting figures for N are given in Table VII for primary and secondary helpers together with the coefficients of relatedness already calculated, the average number of helpers, H, (Table VIa) and the probability, q, of being a primary or secondary helper. Assuming that a yearling male can adopt the strategy he chooses, $q = 1$ in the first year; in subsequent years q is the product of survival rate (Table III) and the probability of the respective status (Tables IV and V). Table VII also shows the values for direct (D) and indirect fitness (I) resulting from the different strategies. They are expressed in

Table VI. Average Number of Helpers (a) and Fledglings (b, c) per Nest for Pairs with Different Types of Helpers or No Helpers

	No helpers	Primary helpers only	Secondary helpers only	Primary + secondary helpers
(a) No. helpers per nest				
$\bar{x}$	0	1.00	1.45	1.00	1.20
SD	0	0	0.69	0	0.63
N	19	11	11	10	10
(b) No. fledglings per nest				
$\bar{x}$	1.82	3.57	3.71	4.57
SD	0.60	0.53	0.76	0.98
N	18	7	7	7
(c) No. fledglings per feeding adult and nest				
	0.91	1.19	1.08	1.09

Data include those published in Reyer (1980).

Table VII. Direct (D), Indirect (I) and Inclusive Fitness (W) of Primary Helpers, Secondary Helpers, First-year Breeders, and Delayers during their First Year, Second Year and First and Second Years Combined

Year	Code*	Probability of status (q†)	Average no. of fledglings/nest‡			Average no. of helpers§ ($\bar{H}$)	Coefficient of relatedness** (r or r')	Gain in fitness††		
			with help (N_2 or N'_2)	without help (N_1 or N'_1)	With breeding (N_0)			Direct (D)	Indirect (I or i)	Inclusive (W)
Primary helper										
1	a	1.00	4.05	2.51	—	1.00	0.32	0	0.49	0.49
2	a	0.16	4.05	2.51	—	1.00	0.21	0	0.05	0.05
2	b	0.16	4.12	2.46	—	1.33	0.05	0	0.01	0.01
2	c	0.16	—	—	2.51	—	0.50	0.20	0	0.20
2	d	—	3.48	3.14	—	—	0.21 (0.16)	0	0.23	0.23
							Total:	0.20	0.78	0.98
Secondary helper										
1	b	1.00	4.12	2.46	—	1.33	0.05	0	0.06	0.06
2	c	0.65	—	—	2.51	—	0.50	0.82	0	0.82
2	d	—	3.48	3.14	—	—	0.05 (0.05)	0	0.02	0.02
							Total:	0.82	0.08	0.90
First-year breeder										
1	c	1.00	—	—	1.88	—	0.50	0.94	0	0.94
2	c	0.46	—	—	2.95	—	0.50	0.68	0	0.68
							Total:	1.62	0	1.62
Delayer		0.23	—	—	2.51	—	0.50	0.29	0	0.29

*Code: a = primary helper; b = secondary helper; c = breeder; d = long term effect on recipients of help.

†q = probability of becoming a primary helper, secondary helper or breeder.

‡N = average number of fledglings/nest with help (N_2), without help (N_1) and as parent (N_0); N' = average number of fledglings/nest for a breeding pair that has been helped the year before (N'_2) or not (N'_1).

§$\bar{H}$ = average number of helpers/breeding pair: 1.33 is the mean number of secondary helpers averaged over pairs with primary plus secondary helpers and pairs with secondary helpers only (from Table VI).

**r = coefficient of relatedness between a bird and the young he rears; r' = coefficient of relatedness between a bird and the young of a breeding pair if he helped that pair the year before (e.g. 0.21) or not (e.g. 0.16).

††D = gain in direct fitness; I, i = gain in indirect fitness; W = gain in inclusive fitness.

For further explanation see text.

terms of genetic equivalents and were calculated from the following formulas (modified from Brown 1975):

direct fitness: $D = q \cdot N_0 \cdot r$ (3a)

indirect fitness: $I = q \cdot \dfrac{N_2 - N_1}{\bar{H}} \cdot r$ (3b)

Equation (3b) describes the helper's immediate effect on its indirect fitness through improving the breeders' reproductive output during the year of help. But its help has also a long term effect on its own survival, options and success in subsequent years. From Table VII it follows that a bird starting as a primary helper has an equal chance of (but different expected fitness gains from) becoming a primary helper (code a), a secondary helper (b) or a breeder (c) the following year, whereas secondary helpers are most likely to become breeders. In any one year the sum of the expected fitness gains from the respective strategies gives the total expected gain. (Strategies which do not occur, e.g. a first-year secondary helper becoming a second-year primary helper, or yield genetic equivalents of less than 0.01 on average, e.g. a first-year breeder becoming a second-year secondary helper, have been omitted from Table VII.)

A further increase in the helper's future indirect fitness can arise from a long term improvement in the breeders' reproductive success by (a) 'supplying' them with more primary helpers for the next year and (b) enhancing their survival. With regard to (a), a primary helper increases the number of fledglings by 62% (4.05 versus 2.51, Table VII). With an even sex ratio among the nestlings (Reyer 1980) this leads to 31% more yearling males, 65% of which become primary helpers ($n = 34$). The resulting 20% increase in primary helpers raises the proportion of pairs with primary plus secondary helpers from 19.6 to 29.9% and that of pairs with only primary helpers from 21.6% to 32.0% — if the 20% increase is divided between these two groups according to their relative frequencies in Table VI. Correspondingly, the proportion of pairs with no helpers decreases from 37.3% to 24.3% and that of pairs with only secondary helpers from 21.6% to 14.1%. From the proportion of parents in each of the four categories in Table VIa and from the average reproductive success in these categories (Table VIb) the number of young fledging the year following helping

(N'_2) and non-helping (N'_1) can be calculated (equation (2) extended to include all categories).

With regard to (b), it follows from Table III that one helper improves the survival of a male breeder by an average of 3.4% ($= (64.3 - 58.6)/(2.21 - 0.55)$), and that of a female breeder by 24.6% ($= (85.7 - 44.8)/(2.21 - 0.55)$). Thus, by helping his parents or any other breeding pair a helper increases the probability that the same mates will breed again and consequently he increases the coefficient of relatedness between himself and future young of that pair (r'_2) over that of a non-helper (r'_1). In Table VII r'_2 and r'_1 (in parentheses) are listed under code d. The general formula for calculating r' is:

$$r' = l_m \cdot l_f \cdot r + (l_m \cdot d_f + d_m \cdot l_f) \cdot r/2 \qquad (4)$$

Here l_m and l_f are the proportions of male and female breeders, respectively, surviving to a particular year, d_m and d_f ($= 1 - l$) are the proportions of birds dying, and r is the coefficient of relatedness between the helper and the offspring during the year of help. Resulting from that help the helper gains an additional future indirect fitness i which can be mathematically expressed as:

$$i = N'_2 \cdot r'_2 - N'_1 \cdot r'_1 \qquad (5)$$

The i values are listed in Table VII under code d. Together with the immediate gain in indirect fitness (I) and the direct fitness gain (D) they give the inclusive fitness W.

Also given in Table VII are the figures for birds that, during their first year, neither breed nor help ('delayer'). In this category, mating chances of non-helping primary helpers (Table Vb) have been used to calculate q for both primary and secondary helpers, as this probably reflects the chances of yearlings better than the figure for non-helping potential secondary helpers (Table Vb) which are usually older.

The differences in direct fitness (ΔD) and indirect fitness ($\Delta(I + i)$) between a helper and a delayer can be used to express the relative importance of indirect fitness in the decision of a bird to adopt the helping strategy (Vehrencamp 1979 Brown, in press):

$$I_k = \frac{\Delta(I + i)}{\Delta(I + i) + \Delta D} \qquad (6$$

For secondary helpers this results in $I_k = 0.1$ which means that 87% of the inclusive fitness after 2 years arises from personal advantage gained through helping as opposed to 13% from

investment in kin other than own offspring. For primary helpers, however, an index of $I_k = 1.13$ was found. As indices greater than one can only occur if ΔD is negative (as in Table VII: $0.20 - 0.29 = -0.09$), the result suggests that primary helpers sacrifice their personal reproduction for the benefit of relatives. The reliability of the above figures will be discussed later (see Discussion).

First-year Breeders and Best Reproductive Strategy

In Table VII I have also attempted to calculate the inclusive fitness of males that mate and breed in their first year. As first-year breeders are rare ($n = 3$), and no data about their reproductive success are available, this calculation can be only a very rough estimate based on the following assumptions:

(1) A yearling breeder can have no primary helpers; thus theoretically his reproductive success could be 2.51 (Table VII). But as an inexperienced bird will probably raise fewer young, this figure was reduced by 25% to 1.88 (see Woolfenden 1974; Rowley 1981).

(2) Survival into the next year is the same as for a yearling primary helper (Table II).

(3) The probability that a surviving mated yearling will have a mate in the following year is the same as for other mated males (Table IV).

(4) Allowing for the above-mentioned 25% lower reproductive success during the first year, the number of young fledging in the second year can be calculated as outlined in the previous section.

According to Table VII, delaying helping or breeding for 1 year is inferior to all other strategies. The best strategy for a yearling male is to breed. And indeed, in all cases where an unmated female appeared in the colony after the beginning of the breeding season, she was immediately joined by a surplus male who had previously helped or tried to help.

Second to breeding, being a primary helper seems to yield the highest inclusive fitness. Although the difference from secondary helpers is small, this result is also in line with behavioural observations. If at least one parent is around, an unmated male will remain as its primary helper instead of becoming a secondary helper elsewhere.

There seem to be only two situations in which a bird will leave its parents to join other pairs. One is when the parents fail to breed and the other is when, at the beginning of the breeding season, another primary helper is also present.

Three breeding pairs which arrived with two primary helpers each were assisted by both birds only during the first stages of the reproductive period. When one pair failed to breed, both primary helpers left. In the other two pairs, one helper of each left to become a secondary helper, although the parents had a clutch of eggs, while the brother remained as a primary helper. These observations are consistent with expectation. The second primary helper can increase the number of surviving siblings only with regard to the number that hatches ($N_2 = 4.6$). But even without his help, an average of $N_1 = 4.05$ will fledge and the survival of his parents will be improved due to the contributions of his brother and of secondary helpers, joining his parents with a certain probability (calculated from equation (2) and Table VI). According to formula 3b this reduces his benefit from indirect fitness to $\Delta I = 0.20$ and his inclusive fitness after 2 years to 0.44. As this value is much lower than that for the first primary helper and that for a secondary helper, switching pays. In the above calculations, differences in mating chances (as a preliminary measure of reproductive success) are the main reason for differences in inclusive fitness. Results could change if the reproductive output of mated birds differed with age, either directly or indirectly through the number of helpers assisting. My data are not sufficient to test such a possible influence thoroughly, but if it is there, it does not seem to be very pronounced. The average number of young raised to fledging (irrespective of number of helpers) is 3.3 ($SD = 1.4$, $n = 7$) for 2-year-old males and 3.5 ($SD = 0.8$, $n = 12$) for males of 3 years and older.

Discussion

The foregoing cost/benefit analysis has shown that helping in the pied kingfisher cannot be considered a uniform phenomenon. For secondary helpers it appears to be a possible way to improve their own future reproductive success (=direct fitness). But a distinction must be made between the personal advantages (and disadvantages) of associating with a breeder (e.g. in his territory) that have been shown to exist in several species, and the effects of helping per se that have never been demonstrated (Taborsky 1984; Brown, in press). Although the result of Table Vb is not conclusive either, it at least suggests that in secondary helpers the act of helping may raise their direct fitness over that of non-helping birds.

This possible augmentation probably arises from the secondary helper's chances of developing a bond with a female (by feeding her) and of becoming accepted by neighbours through its association with an established pair. Generalizing Gaston's (1978b) hypothesis that in group-territorial species helpers 'pay' for consuming resources, here the act of helping may be considered the 'payment' for being tolerated by the resident male.

Where for ecological reasons a breeder's fitness cannot be markedly improved by helpers, the potential disadvantage of being dislodged by a secondary helper may prevail. The 'payment' is no longer accepted and the secondary helper driven away. This happens at Lake Naivasha and clearly illustrates the existence of a breeder–secondary helper conflict (Emlen 1978, 1982b; Reyer 1980).

In primary helpers the situation is different. Compared with secondary helpers they seem to sacrifice their personal reproduction for the benefit of relatives. This has never been shown for a cooperatively breeding vertebrate. Are primary helpers really altruists sensu Hamilton (1964)?

Besides some simplifying assumptions about dispersal and survival, and in calculating coefficients of inbreeding and relatedness (Markl 1980) a weakness of this study is the small sample size for some of the variables. This also forced me to analyse 2 years only instead of whole lifetimes, and to use some crude measures of fitness such as number of fledglings, or even probability of getting a mate, instead of the number of young surviving to reproductive age. How do such simplifications affect the results?

Although there is good evidence that for adult pied kingfishers more than 1 year old in general, movement is extremely conservative (see above), dispersal could be differential, mainly involving primary helpers with few chances at home. If, for example, we assume that by moving to another colony a primary helper has a 50% higher probability of obtaining a mate than stated in Table IV, a relative importance of indirect fitness, $I_k = 0.57$ instead of 1.13 will result. But for two reasons I feel that breeding in other colonies is no more probable (and successful) for primary helpers than for other males. (a) In all colonies recorded so far there is a high surplus of males, probably resulting in strong competition for females (Douthwaite 1978; Reyer 1980). It seems unlikely that a bird who fails to get a mate in his familiar area will be more successful by dispersing to an unfamiliar one. Breeders returning to the same colony nested almost without exception within a few metres of their previous site, although the colony stretched over more than 500 m. And 88% of secondary helpers nested where they had helped the year before (see above). Thus there seems to be a strong 'home advantage' effect. Also, breeding in colonies makes it easy to associate with several birds, and thus allows choice among alternative possibilities without moving to other areas, as birds with all-purpose territories have to do. (b) The assumption that the low return rate of primary helpers indeed reflects low survival is supported by the significant correlation between energy expenditure and return rate if other males are included (Table III). Preliminary results from a doubly-labelled water technique (Lifson & McClintock 1966) indicate that the total feeding contributions shown in Fig. 2d result in an average daily metabolic rate (ADMR) of 4.0 × BMR (basic metabolic rate) for secondary helpers and of 4.9–5.2 × BMR for breeders and primary helpers (Reyer & Westerterp, in preparation). Studies on other birds have suggested that 4 × BMR may represent some sort of energetic threshold not to be exceeded for long periods without a decline in body condition that may finally reduce survival (Drent & Daan 1980). This apparently holds for pied kingfishers also and for primary helpers in particular, which seem to exceed the threshold by about 25%.

I consider differences in energy expenditure between primary and secondary helpers to be more important than differences in nest-guarding risks (Fig. 2). Although birds in the nest can fall victim to predators (probably one reason why mortality of females is higher than that of males), this will not affect helpers as they neither incubate eggs nor brood young. And outside the nest, adult pied kingfishers are unlikely to be caught by terrestrial predators as they fly fast and skilfully.

Another reduction in the relative importance of indirect fitness could arise if personal benefits from being a primary helper became obvious only after the 2 years considered here. Such benefits might include increased experience and improved energy budgets, finally resulting in more surviving offspring per clutch and/or more clutches per lifetime. Although there is evidence from other studies that experience can be important for reproductive success, its effect on males is usually smaller than on females and decreases sharply with the number of broods

(Woolfenden 1974; Rowley 1981). Previous helping may therefore have some costs and benefits for a bird's first breeding season, but thereafter it is unlikely to remain significant. This is supported with respect to mating chances by the result that once a male pied kingfisher gets a mate he is likely to remain mated (Table IV). Expressed in terms of equation (6), ΔD and $\Delta(I+i)$ (the differences in fitness between a helper and a nonhelper) quickly approach zero and I_k does not change any more, irrespective of the bird's future reproduction.

If the amount of experience depends on the amount of helping, then secondary helpers will start breeding with less experience than primary ones, unless they have been primary helpers before or part of the shortcoming is compensated for by age. Thus the number of fledglings a secondary helper raises in his first breeding season may not be 2.51 (Table VII) but rather the 1.88 of an inexperienced first-year breeder. This would reduce his inclusive fitness after 2 years from 0.90 to 0.69 which is 30% lower than that of primary helpers.

It is interesting to note that, with the immediate effects of helping considered alone, the primary helper strategy would have appeared less advantageous than the secondary helper strategy. It is mainly the helper's long-term effect on its parents survival and reproductive success and on its own future indirect fitness that makes its strategy superior. This bears out findings on other birds that lightening the load of breeders is of major importance (Brown et al. 1978). A further but smaller benefit in indirect fitness arises from the fact that a bird remaining unmated can serve as a primary helper for more than one year (see Gaston 1978a; Stallcup & Woolfenden 1978; Brown & Brown 1981; Rowley 1981).

The importance of indirect fitness for primary helpers is further supported by the observation that when two primary helpers per pair are present, one leaves to become a secondary helper. Although an additional bird would increase the overall reproductive success, it would lower the indirect fitness gain on a per capita basis (see equation (3b)). Such a negative correlation between group size and per capita success exists in almost all cooperative breeders (Koenig & Pitelka 1981), but I know of no corresponding observation in any other species. However, most cooperative breeders live in all-purpose territories (Brown 1978) which probably offer so many advantages for the helper's own survival

and/or reproduction that staying pays, even if the indirect fitness component approaches zero (Brown 1978, in press; Emlen 1978, 1982a; Woolfenden & Fitzpatrick 1978; Koenig & Pitelka 1981; Ligon 1983; Taborsky, 1984). But in colonial species with common hunting grounds, such as the pied kingfisher, benefits from remaining with the parents must be greatly reduced. This will make the effects of indirect fitness more obvious.

The most important reason for the high gain in indirect fitness for primary helpers lies in the time- and energy-consuming hunting method of pied kingfishers. This impairs the survival of parents and drastically limits their possible feeding rate, leading to a low nestling survival. Through their assistance, primary helpers markedly improve survival of both their parents and their siblings.

Some authors have warned that a positive correlation between group size and nestling survival does not prove a cause–effect relationship, as both could result from differences in habitat quality and/or parents' age (Brown & Balda 1977; Brown et al. 1978; Lewis 1981). Habitat differences are unlikely in colonial pied kingfishers as birds defend only the area immediately surrounding the nest and all colony members hunt in the same area. Age differences seem to be small. More important are number and types of helper (Table VI). The improvement in survival per secondary helper is lower than that per primary helper (1.30 versus 1.75) which is consistent with the differential feeding contribution of the two helper categories (Fig. 2).

Further data are needed to show whether the calculated values for the relative importance of indirect fitness are good estimates or whether they are too high or too low. Although any $I_k < 1$ would preclude use of the term altruism, it would probably not change the finding that the relative benefit from indirect fitness for primary helpers is much higher than for secondary ones, and also than for any other cooperatively-breeding vertebrate for which similar indices have so far been calculated (Vehrencamp 1979; Rowley 1981).

Some authors have cautioned that a high proportion of indirect fitness is no proof of the operation of kin selection, even if the helper's direct fitness is reduced. They maintain that there are alternative explanations (Vehrencamp 1979; Emlen 1981; Koenig & Pitelka 1981; Ligon 1983) such as group selection, parental manipulation and reciprocity. But group selection

works only when demes are no bigger than 10–20 individuals, have a foundation and extinction rate of about 50% per generation and less than 5% gene flow per generation (Wilson 1975; Maynard-Smith 1976). These conditions definitely do not apply to the pied kingfisher and thus the relative importance of group selection must be low.

Parental manipulation is difficult to imagine as a breeder will hardly be able to force his son to stay as a primary helper. But there may be subtle forms of manipulation such as tolerating sexual interactions with the female, which could result in shared paternity (Stacey 1979; Emlen 1982b). Helpers have been observed copulating in a variety of birds and mammals. I have no corresponding observations for pied kingfishers although their early association with breeders gives primary helpers the chance to copulate. Yet, even if they did, they might not be able to fertilize eggs, as their average androgen titre is even lower than that of mated non-breeding males (Douthwaite et al., in press; Reyer & Dittami, in preparation). This could reflect some sort of psychological castration of primary helpers by dominant males (see Brown, in press), as yearlings not associated with older birds are quite able to breed successfully (Reyer 1980).

Reciprocity as a mechanism of selection for helping requires small stable groups with long-lived members, recognizing each other individually and frequently encountering the same participants with which they change roles as donors and recipients of help (Trivers 1971; Axelrod & Hamilton 1981). Cases of reciprocity in cooperative breeders involve helpers recruiting the young they helped to rear and interactions between adult birds (Brown 1978; Ligon & Ligon 1978; Emlen 1982b; Ligon 1983). But the relatively high mortality of pied kingfishers, combined with seasonal breeding, reduces the probability of role reversal between adults. This is particularly true for yearling primary helpers, which may not attain breeding status until the recipient of his help has died. The low probability of breeding the year following helping (Table IV) also makes it unlikely that a primary helper will recruit a helper from the young he helped to rear. In fact, both cases in which such a recruitment occurred involved a secondary helper. As secondary helpers also recruited females and took over nest-sites, reciprocity seems a more likely explanation for their assistance than for that of primary helpers (see Ligon 1983). Moreover, reciprocity requires low costs of helping

(Trivers 1971; Axelrod & Hamilton 1981), which may apply to secondary helpers, but definitely not to primary ones.

From these arguments I feel that indirect fitness gain is still the most likely explanation for the behaviour of primary helpers. This is not saying that helping is superior to breeding. Table VII and the birds' behaviour when a breeding opportunity occurs show that the reverse is true; this also holds for most other cooperative breeders (Brown 1974; Koenig & Pitelka 1981; Emlen 1982a). But if for ecological and/or demographic reasons the chance of successful reproduction is sufficiently restricted to make helping a better alternative than merely waiting, relatedness is the most important factor determining the investment of pied kingfisher helpers. The different coefficients of relatedness that lower the threshhold for helping differentially must be the main explanation why surplus males prefer the primary helper strategy, with a high cost/benefit ratio to their own reproduction, over the secondary helper strategy with a low ratio.

REFERENCES

Armitage, K. B. & Johns, D. W. 1982. Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. *Behav. Ecol. Sociobiol.*, **11**, 55–63.

Axelrod, R. & Hamilton, W. D. 1981. The evolution of cooperation. *Science, N.Y.*, **211**, 1390–1396.

Balda, R. P. & Balda, J. H. 1978. The care of young pinon jays, (*Gymnorhinus cyanocephalus*) and their integration into the flock. *J. Ornithol.*, **119**, 146–171.

Barrowclough, G. F. 1980. Gene flow, effective population sizes, and genetic variance components in birds. *Evolution*, **34**, 789–798.

Boucher, D. H. 1977. On wasting parental investment. *Am. Nat.*, **111**, 786–788.

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

Brown, J. L. 1975. *The Evolution of Behavior*. New York: W. W. Norton.

Brown, J. L. 1978. Avian communal breeding systems. *Ann. Rev. Ecol. Syst.*, **9**, 123–155.

Brown, J. L. In press. The evolution of helping behavior — an ontogenetic and comparative perspective. In: *The Evolution of Adaptive Skills: Comparative and Ontogenetic Approaches* (Ed. by E. S. Gollin). New York: Academic Press.

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

Brown, J. L. & Brown, E. R. 1981. Kin selection and individual selection in babblers. In: *Natural Selection and Social Behavior: Recent Results and New Theory* (Ed. by R. D. Alexander & D. Tinkle), pp. 244–256. New York: Chiron Press.

Brown, J. L., Dow, D. D., Brown, E. R. & Brown, S. D. 1978. Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behav. Ecol. Sociobiol.*, **4**, 43–59.

Curio, E. 1980. An unknown sex determinant of sex-specific altruism. *Z. Tierpsychol.*, **53**, 139–152.

Dawkins, R. & Carlisle, T. R. 1976. Parental investment, mate desertion and a fallacy. *Nature, Lond.*, **262**, 131–132.

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

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

Douthwaite, R. J., Reyer, H.-U. & Dunn, E. K. In press. The pied kingfisher, *Ceryle rudis*. In: *Handbook of the Birds of Europe, the Middle East and North Africa* (Ed. by S. Cramp & K. E. L. Simmons). Oxford: Oxford University Press.

Dow, D. D. 1977. Reproductive behaviour of the noisy miner, a communally breeding honeyeater. *Living Bird*, **16**, 163–185.

Drent, R. H. & Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.

Emlen, S. T. 1978. The evolution of cooperative breeding in birds. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 245–281. Oxford: Blackwell.

Emlen, S. T. 1981. Altruism, kinship, and reciprocity in the white-fronted bee-eater. In: *Natural Selection and Social Behavior: Recent Results and New Theory* (Ed. by R. D. Alexander & D. Tinkle), pp. 217–230. New York: Chiron Press.

Emlen, S. T. 1982a. The evolution of helping. I. An ecological constraints model. *Am. Nat.*, **119**, 29–39.

Emlen, S. T. 1982b. The evolution of helping. II. The role of behavioral conflict. *Am. Nat.*, **119**, 40–53.

Fryer, G. & Iles, T. D. 1972. *The Cichlid Fishes of the Great Lakes of Africa*. Edinburgh: Oliver & Boyd.

Gaston, A. J. 1978a. Demography of the jungle babbler, *Turdoides striatus*. *J. Anim. Ecol.*, **47**, 845–870.

Gaston, A. J. 1978b. The evolution of group territorial behavior and cooperative breeding. *Am. Nat.*, **112**, 1091–1100.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I, II. *J. theor. Biol.*, **7**, 1–51.

Harvey, P. H., Baker, M. C., Bateson, P., Bischof, N., Emlen, S. T., Holldöbler, B., Kramer, B., Linsenmair, K. E., Markl, H., Marler, P., Wenzel, E. W., Jr, Michener, C. D., Milinski, M. & Trillmich, F. 1980. Mechanisms of kin-correlated behavior. In: *Evolution of Social Behavior: Hypotheses and Empirical Tests* (Ed. by H. Markl), pp. 183–202. Weinheim: Verlag Chemie.

Joste, N. E., Koenig, W. D., Mumme, R. L. & Pitelka, F. A. 1982. Intragroup dynamics of a cooperative breeder: an analysis of reproductive roles in the acorn woodpecker. *Behav. Ecol. Sociobiol.*, **11**, 195–201.

Koenig, W. D. & Pitelka, F. A. 1981. Ecological factors and kin selection in the evolution of cooperative breeding birds. In: *Natural Selection and Social Behavior: Recent Research and New Theory* (Ed. by R. D. Alexander & D. Tinkle), pp. 261–280. New York: Chiron Press.

Lewis, D. M. 1981. Determinants of reproductive success in the white-browed sparrow weaver, *Plocepasser mahali*. *Behav. Ecol. Sociobiol.*, **9**, 83–93.

Lifson, N. & McClintock, R. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *J. theor. Biol.*, **12**, 46–74.

Ligon, J. D. 1981. Demographic patterns and communal breeding in the green woodhoopoe, *Phoeniculus purpureus*. In: *Natural Selection and Social Behavior: Recent Research and New Theory* (Ed. by R. D. Alexander & D. Tinkle), pp. 231–243. New York: Chiron Press.

Ligon, J. D. 1983. Cooperation and reciprocity in avian social systems. *Am. Nat.*, **121**, 366–384.

Ligon, J. D. & Ligon, S. H. 1978. Communal breeding in green woodhoopoes as a case for reciprocity. *Nature, Lond.*, **276**, 496–498.

Markl, H. 1980. *Evolution of Social Behavior: Hypotheses and Empirical Tests*. Weinheim: Verlag Chemie.

Maynard-Smith, J. 1976. Group selection. *Q. Rev. Biol.*, **51**, 277–283.

Maynard-Smith, J. 1977. Parental investment: a prospective analysis. *Anim. Behav.*, **25**, 1–9.

Milinski, M. 1978. Kin selection and reproductive value. *Z. Tierpsychol.*, **47**, 328–329.

Power, H. W. 1981. Searching for altruism in birds. *Auk*, 98, 422–425.

Reyer, H.-U. 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher (*Ceryle rudis rudis* L.). *Behav. Ecol. Sociobiol.*, 6, 219–227.

Reyer, H.-U. 1982a. Soziale Strategien und ihre Evolution. *Naturw. Rundschau*, 35, 6–17.

Reyer, H.-U. 1982b. Nutzen und Kosten bei brütenden und helfenden Graufischern. *Naturw. Rundschau*, 35, 31–32.

Riedman, M. L. 1982. The evolution of alloparental care and adoption in mammals and birds. *Q. Rev. Biol.*, 57, 405–435.

Robertson, R. J. & Bierman, G. C. 1979. Parental investment strategies determined by expected benefits. *Z. Tierpsychol.*, 50, 124–128.

Rood, J. P. 1978. Dwarf mongoose helpers at the den. *Z. Tierpsychol.*, 48, 277–287.

Rowley, I. 1978. Communal activities among white-winged choughs, *Corcorax melanorhamphus*. *Ibis*, 120, 178–197.

Rowley, I. 1981. The communal way of life in the splendid wren, *Malurus splendens*. *Z. Tierpsychol.*, 55, 228–267.

Royama, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *Ibis*, 108, 313–347.

Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science, N. Y.*, 197, 1246–1253.

Sherman, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. *Behav. Ecol. Sociobiol.*, 8, 251–259.

Stacey, P. B. 1979. Kinship, promiscuity, and communal breeding in the acorn woodpecker. *Behav. Ecol. Sociobiol.*, 6, 53–66.

Stallcup, J. A. & Woolfenden, G. E. 1978. Family status and contributions to breeding by Florida scrub jays. *Anim. Behav.*, 26, 1144–1156.

Taborsky, M. 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Anim. Behav.* 32, 1236–1252.

Taborsky, M. & Limberger, D. 1981. Helpers in fish. *Behav. Ecol. Sociobiol.*, 8, 143–145.

Tallamy, D. W. 1982. Age specific maternal defence in *Gargaphia solani* (Hemiptera: Trigidae). *Behav. Ecol. Sociobiol.*, 11, 7–11.

Tinbergen, J. M. 1981. Foraging decisions in starlings. *Ardea*, 69, 1–67.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.*, 46, 35–57.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.

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

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

Vehrencamp, S. L. 1979. The roles of individual, kin and group selection in the evolution of sociality. In: *Handbook of Behavioural Neurobiology, Social Behavior and Communication* (Ed. by P. Marler & J. G. Vandenberg), pp. 351–394. New York: Plenum Press.

Weatherhead, P. J. 1979. Do savannah sparrows commit the Concorde fallacy? *Behav. Ecol. Sociobiol.*, 5, 373–381.

Weigel, R. M. 1981. The distribution of altruism among kin: a mathematical model. *Am. Nat.*, 118, 191–201.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge, Mass.: Belknap Press.

Woolfenden, G. E. 1974. Nesting and survival in a population of Florida scrub jays. *Living Bird*, 12, 25–49.

Woolfenden, G. E. 1981. Selfish behavior by Florida scrub jay helpers. In: *Natural Selection and Social Behavior: Recent Research and New Theory* (Ed. by R. D. Alexander & D. Tinkle), pp. 257–260. New York: Chiron Press.

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

Yamada, M. 1963. A study of blood-relationship in the natural society of the Japanese macaque. *Primates*, 4, 43–65.

Zahavi, A. 1981. Some comments on sociobiology. *Auk*, 98, 412–415.