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Pied Kingfishers: ecological causes and reproductive consequences of cooperative breeding

H.-U. REYER*

Studies on the adaptive significance of behavioral strategies are most promising when there is high variability, both in the behavioral trait and the ecological conditions under which it occurs. This allows comparison of the costs and benefits of pursuing different strategies under the same conditions and of pursuing the same strategies under different conditions. The Pied Kingfisher (*Ceryle rudis*) shows such variability in its helper system. I have studied this species over eight breeding seasons (1976–83) at Lake Naivasha and Lake Victoria in Kenya. The following account of the results consists of four sections: (1) a description of the life history and the helper structure; (2) a functional interpretation of the cooperative breeding from the helpers' and from the breeders' points of view; (3) an analysis of the causal mechanisms which allow the birds to choose the strategy which maximizes their fitness under the prevailing ecological conditions; and (4) some speculations as to the origin of this helper system.

Life history and helper structure *General biology*

Pied Kingfishers range, in three subspecies, from eastern Asia through Asia Minor to South Africa. They occur along many rivers, but are particularly frequent in the marginal regions of big freshwater lakes. They feed almost exclusively on fish. To catch their prey, they either dive from papyrus stems, dead trees or other perches along the shore, or – more often – fly over the water searching, sometimes hovering above the surface, and plunging swiftly when they see a fish. Although individual birds have preferential perches and hunting areas, there are no defended territories. A

* Present address: Zoologisches Institut der Universität Zürich, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland.

suitable perch may be used by as many as 10–15 birds simultaneously. The foraging areas not only overlap considerably but also shift during the day with changing conditions such as velocity and direction of wind.

Outside the breeding season, Pied Kingfishers can be seen singly, in pairs or in small groups along the whole shore area. In the breeding season (April–August), the beginning of which coincides with the rains, they concentrate at rivers, canals, road embankments, and other places having sandy or clay banks, not too far from the lake (Fig. 17.1). Here, several birds excavate and defend nesting-holes, which can be as close as half a meter to each other. In this way breeding colonies are formed. Both males and females of the breeding pair, who can be distinguished by plumage differences, take turns digging the nest hole and incubating the four to six eggs. After 18 days the young hatch, naked and blind. From the first day they are fed with fish brought from the lake, mainly by the male and possible helpers; later, when brooding declines, the female joins

> Fig. 17.1. Section of the river where the Lake Victoria Pied Kingfishers breed during the rainy season. A positive effect of the rain is that the banks become soft enough for digging nest holes; a negative effect is that the river may become a torrent and make parts of the banks collapse. For the birds this often results in loss of a nesthole and clutch, while the native Luo people welcome the sand and clay as building material.



increasingly in feeding the young. Nestlings are fully fledged after about 26 days and can fish for themselves roughly two weeks later, but stay with their parents away from the breeding site for several months.

Demographic data

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Using only clutches in which all young could be sexed, the male: female ratio among nestlings was 0.9:1 (n = 38) at Lake Victoria and 1.1:1 (n = 104) at Lake Naivasha. Neither is significantly different from each other ($\chi^2 = 0.3$, d.f. = 1, not significant (n.s.)) or from a 1:1 ratio (both z < 0.5, n.s., Binomial test, two-tailed). However, out of 36 marked juveniles returning as yearlings only one was a female while 35 were males. This 3%:97% ratio differs significantly from expectation based on the even sex ratio among the nestlings (z = 5.5, P < 0.001). Thus, young females disperse before the end of their first year, while males return (e.g. male 298, born in 1980, and males 594 and 9245, born 1982; Fig. 17.2).

After the first year, there seems to be no dispersal of either sex – unless breeding conditions become unfavorable. This is exemplified by a comparison of the two lakes. At Lake Naivasha, fluctuations in the lake level and fortification of banks by men made some previously occupied breeding sites unavailable (colonies A and B in Fig. 17.3), while digging of ditches opened new possibilities (colony C in Fig. 17.3). Thus, birds were forced (and able) to move, which precluded any reliable calculation of return and mortality rates.

At Lake Victoria, conditions were more stable (Fig. 17.3). Here, in 1979 and 1982, a total of 351 adult Pied Kingfishers were checked in three neighboring colonies lying 2, 4 and 9.5 km away from the main study area where in the previous years (1978 and 1981) 110 marked adults had been present. Only one of these marked adults, a female, was found in the nearest separate colony. This limited extent of colony change (0.9%) allows the use of return rates as a measure of survival. The resulting figures are 64.9% (n = 185) for males and 56.5% (n = 106) for females (breeding and nonbreeding birds combined). In addition, the year-to-year stability in colony size, plus the fact that reproduction is seasonal, allows the calculation of the mean adult survival of males from the number of breeding adults surviving into the next year, divided by the number of surviving male yearlings plus adults (see e.g. Vehrencamp 1978). The resulting figure is 53.8% (n = 52), similar to the fractions of male breeders returning the year after ringing, which is 57.1% (n = 49). Thus, under stable conditions, male mortality seems to be compensated for by juvenile males from the same colony.

For females the latter method of calculating survival could not be used,

as juvenile females do not return to their natal area. Consequently, mortality of females must be completely compensated for by females immigrating from other areas. As these immigrating females were not ringed and could not be aged by plumage characteristics, their precise age is

> Fig. 17.2. Life histories of some Pied Kingfishers at Lake Victoria from 1980 to 1983. White boxes at the top of the broken lines denote breeding groups, gray boxes below broken lines show the young produced by the respective groups. Members of the breeding groups are separated into male breeders (\mathcal{J}), female breeders (\mathcal{P}), primary helpers (p) and secondary helpers (s). For further explanations, see the text.



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unknown. But with almost no dispersal of adults, they can be assumed to be yearlings. These females bred in the year of their arrival and hand-reared birds of both sexes bred in captivity at the age of 11 months. Thus, sexual maturity and breeding *can* be reached within the first year and probably *is* in all females. Males, however, rarely breed in their first year (see p. 542), but act as helpers for one to two years. In some of these helpers, even sexual maturity appears to be delayed until the age of two or three years (see p. 543).

Two types of helper

During all early stages of the breeding season (i.e. before hatching) several pairs in both colonies were accompanied by one or two additional adults. These extra birds do not participate in tunneling, incubating and brooding, nor do they copulate. But they feed the male of the breeding pair, support it in feeding the female, and assist the pair in chasing off rivals and nest predators such as the monitor lizard (*Varanus niloticus*), cobras (*Naja* spp.), and the ichneumon (*Herpestes* spp.). Finally, after the young have

Fig. 17.3. Population sizes from 1977 to 1983 for one colony of Pied Kingfishers at Lake Victoria (filled symbols) and three colonies (A–C) at Lake Naivasha (open symbols). —, Colony A; …, colony B; -----, colony C; \bullet and \bigcirc , total mated birds; \blacktriangle and \triangle , total population size.



hatched, they help the parents to feed the nestlings. Such birds which accompany pairs from the very beginning of the breeding season I call 'primary helpers'.

About one week after the young hatch, the number of breeding pairs with helpers and the number of helpers per pair increases. These additional helpers, although present in the colony from the beginning of the breeding season, are firmly associated with pairs only after hatching and are called 'secondary helpers'. Secondary helpers join breeders with, and breeders without, primary helpers about equally often (Table 17.1, rows 5 and 6) and there can be as many as one primary plus three secondary helpers per pair. The proportion of pairs with primary helpers was similar at the two lakes, both before and after hatching (Table 17.1, rows 2 and 4). Pairs with secondary helpers, however, were relatively more frequent at Lake Victoria than at Lake Naivasha, where a higher proportion of breeding pairs remained unassisted ($\chi^2 = 17.4$, d.f. = 3, P = 0.0006; χ^2 -test, applied to rows 3–6 of Table 17.1). This makes the average breeding group size at Lake Victoria higher than at Lake Naivasha (Fig. 17.4; z = 2.635, P < 0.01, Mann–Whitney U-test, two-tailed).

Table 17.1. Percentage of mated pairs of Pied Kingfishers at Lake Victoria and Lake Naivasha with no helpers, with primary helpers only, with secondary helpers only and with primary plus secondary helpers

Mated pairs with	Percentage at:		
	Lake Victoria	Lake Naivasha	
(a) Before hatching (1) No helpers	67.6	74.3	
(2) Primary helpers	32.4	25.7	
Sample size	142	74	
(b) After hatching			
(3) No helpers	34.9	61.5	
(4) Primary helpers	20.6	28.8	
(5) Secondary helpers	19.0	5.8	
(6) Primary plus secondary helpers	25.4	3.8	
Sample size	63	52	

By definition, pairs with secondary helpers can occur only after the young have hatched. Sample sizes after hatching (b) are lower than those before (a), because not all mated pairs produced young, not all breeding groups were completely marked, and not all groups were left undisturbed (see pp. 549–51).

Among the 71 primary and the 53 secondary helpers that I have recorded all were males. Eight of the secondary helpers were mated males who did not breed in the year in which they helped (e.g. s 195 in 1981, Fig. 17.2), the remaining 93.5% of all helpers were unmated. The high number of unmated males results from a highly biased sex ratio. At Lake Victoria, adult males outnumbered adult females by 1.58:1 (s.D. = 0.44, n = 8 years), and at Lake Naivasha by 1.57:1 (s.D. = 0.36, n = 7 years). The reason for, and the significance of, this bias will be discussed on pp. 551–5.

The date at which helpers associate with breeders is one characteristic in which primary and secondary helpers differ. The way in which they associate with breeders is a second characteristic (Fig. 17.5). From the very beginning of the season, primary helpers restrict their activities to one mated pair only, e.g. helper A to pair 1, helper B to pair 2. Color-banding over eight years has revealed that most primary helpers are the sons of at least one mate of that pair. This means that they usually assist in raising younger siblings. Of all cases, 38% were full siblings (e.g. p. 594 in 1983, Fig. 17.2), 54% were half-siblings (e.g. p. 298 in 1981), and for only 8% were primary helpers not related to the young (n = 24). The resulting average coefficient of genetic relationship between primary helpers and nestlings is r = 0.32.

Secondary helpers, on the other hand, do not appear to be closely related

Fig. 17.4. Relative frequency of breeding group sizes of Pied Kingfishers at Lake Victoria (open blocks; n = 63 groups) and Lake Naivasha (filled blocks; n = 52 groups). Group sizes were measured after the young hatched but include adults only.



to the young that they raise. They were certainly not the young of the breeding pairs that they joined; and color-banding showed no evidence for any other close genetic relatedness down to the level of 1/8. As inbreeding seems to be low (no incestuous matings were observed and young females disperse before breeding), the average coefficient of relatedness between a secondary helper and the random young he helps to rear can be calculated to be $r \leq 0.05$. This is more than six times lower than with primary helpers. The 'random choice' of secondary helpers is also supported by the way they join the breeders (Fig. 17.5). Unlike the primary helper, a potential secondary helper, such as C, initially approaches various pairs, e.g. 3, 6 and 7; and one pair, such as 6, may be visited by different potential helpers, e.g. by C, E and F. But by and by the secondary helpers focus on one particular pair e.g. helper C on pair 7, helper E on pair 6. If that pair is not successful, secondary helpers may switch again (e.g. s 309 in 1981, Fig. 17.2). But normally they finally restrict their activities to this pair and help in warding off predators and feeding young in the same way as the primary helpers do.

Quantitatively, however, there are large differences between the two helper categories (Fig. 17.6). Primary helpers invest as much as male and female breeders do, no matter whether we consider nest-guarding against predators or food contributions to young in terms of numbers of fish/day,

Fig. 17.5. Schematic representation of associations between primary helpers (A-B), secondary helpers (C-?) and breeding pairs (1-7) at the beginning of the Pied Kingfisher breeding season. ?, Unmarked bird. Secondary helpers C and D are bracketed to indicate that they are brothers joining different pairs.



Fig. 17.6. Investment of Pied Kingfisher breeders (\mathcal{J}, \mathcal{Q}), primary helpers (ph) and secondary helpers (sh) in nest-guarding (a), and in feeding, with respect to number of fish per day (b), energy content per fish (c) and total energy per day (d) (1 cal = 4.184 J). Shaded bars and thin vertical lines, pairs with ≤ 2 helpers; filled bars and thick lines, pairs with >2 helpers. Bars represent means, vertical lines 95% confidence limits. Bars are connected by horizontal lines if the difference between them is significant (continuous line $P \leq 0.01$; dashed line $P \leq 0.05$), or tends to be so (dotted line $P \leq 0.10$; Mann-Whitney U-test). Numbers under the graphs are sample sizes for pairs with ≤ 2 helpers and those with >2 helpers (in parentheses).



average size of fish and total energy/day. Secondary helpers, on the other hand, take it much more easy: they spend less time nest-guarding (Fig. 17.6(*a*)), feed both fewer fish (Fig. 17.6(*b*)) and smaller ones (Fig. 17.6(*c*)). In total they provide the young with only about a quarter of the energy which the other birds provide (Fig. 17.6(*d*)). Thus, the investment in nestlings is a third characteristic in which primary and secondary helpers differ.

Treatment of helpers by breeders

The differences between primary and secondary helpers in time and mode of joining breeders do not only result from the behavior of the helpers themselves, but also from the way they are treated by male breeders. At both lakes, primary helpers were tolerated from the very beginning, whereas potential secondary helpers were constantly repelled from the vicinity of the nest, at least until the young had hatched. In the Naivasha colony, expulsion usually continued even after hatching, whether or not the potential secondary helper carried a fish when approaching the male breeder. Consequently, there were many potential, but hardly any accepted, secondary helpers at this lake. In the Victoria colony, however, expulsion only continued towards birds that approached without prey. Attacks on those carrying a fish ceased within the first week after hatching, and secondary helpers remained where they were first tolerated. This differential treatment results in the different proportions of breeders with secondary helpers and in different average group sizes at the two lakes (Table 17.1 and Fig. 17.4).

Reproductive success

The reasons for the differential treatment of helpers probably stem from the reproductive success at the two lakes shown in Fig. 17.7. Average clutch sizes and hatching rates were the same for Lake Victoria and Lake Naivasha. And yet, the breeding success of individual pairs, expressed as the number of fledglings per group, differs significantly between the two lakes. On average, groups of two (i.e. parents without helpers) at Lake Naivasha could rear as many as 4.0 (i.e. 83% of the number that hatch), but only 1.9 young (or 45%) at Lake Victoria; the others starve to death. And while Lake Naivasha groups of three and four (i.e. pairs with one or two helpers) are not more successful than pairs without helpers, at Lake Victoria helpers do improve the reproductive success: groups of three to five or more produced significantly more young than groups of two (all P < 0.001, *t*-test, two-tailed) and groups of five or more were also more

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successful than groups of three (P < 0.02). If Lake Victoria pairs are split into those having only primary and those having only secondary helpers, it turns out that the number of additionally surviving nestlings per primary helper is 45% higher than that per secondary helper (Fig. 17.7). This very likely results from the higher feeding contribution of primary helpers (Fig. 17.6).

Ecological reasons

There are two main ecological reasons for the differences in reproductive success between the two lakes: (1) the type of prey and (2) its availability.

(1) At Lake Victoria, the main prey item is the cyprinid fish Engraulicypris argenteus. At Lake Naivasha the birds feed mainly on cichlid species. Because of its slender body shape, an Engraulicypris of about 5 cm length yields less energy than a bulky cichlid of the same length. Moreover, Engraulicypris does not grow

Fig. 17.7. Clutch size, number of hatched, and number of fledged young for different group sizes of Pied Kingfisher. Bars give average values for Lake Victoria (open blocks) and Lake Naivasha (filled blocks), vertical lines represent one standard deviation. For Lake Victoria the numbers of additionally surviving young per primary (stippled) and per secondary (hatched) helper are also shown.



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as big as cichlids. To compensate for that, Lake Victoria parents have to catch more fish for their young than do Lake Naivasha parents.

(2) To catch and feed one fish demands more time in hovering and flying from a Lake Victoria bird than from a Lake Naivasha bird. This is because the distance between the fishing grounds and the colony at Lake Victoria is about twice that at Lake Naivasha (c. 600 m versus 300 m). It is also because of differences in water conditions. At Lake Victoria, one of the largest freshwater lakes in the world, there is always a strong wind sweeping from across the lake, roughening the surface and forming breakers along the shore. Under these conditions, the Pied Kingfishers have to fly out far and only 24% of their dives are successful (n = 107). In contrast, at the much smaller Lake Naivasha the wind comes from the land and there is a coastal zone of calm, relatively clear water, protected by a high papyrus belt. Here 79% of all dives are successful (n = 52), a highly significant difference ($\chi^2 = 42.704$, P < 0.001).

These two environmental conditions taken together have the effect that Lake Victoria parents must invest more time and energy than Lake Naivasha parents to feed their young – apparently so much more that they cannot do it alone, but need helpers to prevent their young from starving. This energy aspect will be dealt with in more detail on pp. 546–9). For the moment it suffices to conclude that: (1) helpers are more valuable for Lake Victoria parents than for Lake Naivasha parents, and (2) primary helpers with their high feeding contribution are more valuable than the 'lazy' secondary helpers.

The adaptive significance of cooperative breeding

Fitness calculations

The foregoing description of the Pied Kingfishers' cooperative breeding system poses three questions:

- (1) Why do helpers help at all rather than breed on their own?
- (2) Why do some of them become primary helpers and help their relatives, while others become secondary helpers and help non-relatives?
- (3) Why do breeders accept primary helpers from the very beginning and in both colonies, but secondary helpers only at Lake Victoria and only after the young have hatched?

All three questions concern the costs and benefits accruing from the observed behavior. In order to analyze these costs and benefits, I calculated

the genetic fitness of birds following different behavioral strategies (e.g. helper versus breeder, primary versus secondary helper, rejecting helpers versus accepting them) which is basically the product of the following three factors:

- (1) The probability P, that a bird will obtain a certain status (e.g. become a breeder or a helper).
- (2) The number of young which are produced as a consequence of the bird's contribution. If he is breeder, this is simply the number of his own young. If he is a helper, it is the difference between the number of young surviving with his contribution (N⁺) and the number of young which would have survived without his contribution (N⁻), divided by the total number of helpers at this nest (H).
- (3) The coefficient of genetic relationship between the bird and the young, estimated as r = 0.50 for breeders, r = 0.32 for primary and $r \le 0.05$ for secondary helpers (pp. 535–6).

Figure 17.8 shows the result of such calculations for young Lake Victoria

Fig. 17.8. Sequence of choices a young male Pied Kingfisher has to make between four different strategies (dendrogram) and inclusive fitness after two years if he starts as a breeder, a primary helper, a secondary helper or a delayer (stippled bars). The highest inclusive fitness value from Table 17.2, that of breeders, has been set to 1, values of the three other categories have expressed relative to it.



0.65.

males starting as breeders, primary helpers, secondary helpers or 'delayers'. Delayers are birds, which – when not mated in their first year – do not help, but wait for a breeding opportunity to occur the next year. I have restricted the calculations to the first two years of life, partly because this is the period in which males differ in their behavioral strategies, partly because it is the period for which reasonably large sample sizes are available. Details about the calculation and the data on which it is based have been given by Reyer (1984b). Where results differ from those in previous publications (Reyer 1984b, 1986) new data have been added.

Costs and benefits for helpers

According to the histograms in Fig. 17.8, helping is superior to delaying, but inferior to breeding. Why then do not all young males breed? The answer is simple: they cannot. For their own reproduction they need females, and with sex ratios of 1.6:1 females are a limited resource at both lakes. Under these conditions of high competition for females, it is mainly the young, unexperienced males who do not get a mate. Only three of 64 males of known age (4.7%) obtained a female in their first year. Hence, helping becomes the second best strategy (Fig. 17.8) and will be favored by selection over delaying. This answers the first functional question, why helpers help rather than breed on their own: they choose the best *available* strategy. If breeding becomes possible (e.g. by the occasional appearance of unmated females after the breeding season has started), then surplus males will immediately give up their helper status and become breeders. Such switching to the better strategy was observed three times, e.g. in 1982 by the primary helper 298 after the mate of female 296 had died (Fig. 17.2).

In Fig. 17.8 the inclusive fitness of primary and secondary helpers after two years is similar. Its composition, however, is different. This is shown in Table 17.2, where the inclusive fitness values from Fig. 17.8 have been split into two components: the direct fitness resulting from the rearing of their own young, and the indirect fitness resulting from the rearing of relatives other than their own young, e.g. siblings (Brown and Brown 1981).

During their first year, neither primary nor secondary helpers gain in direct fitness; they both have no young of their own. But primary helpers in their first year improve their indirect fitness by 0.45. The reason is that more young survive with the contribution of the primary helper than without it (Fig. 17.7) and, with r = 0.32, the relatedness between the helper and these additional young is fairly high. There is an additional indirect fitness gain in the second year, partly because some birds do serve as primary helpers for more than one year, partly because their help during the first year has a

long-term effect on their parents' survival and future reproduction of siblings. In total, the primary helpers' indirect fitness gain after two years is

For secondary helpers it is only 0.05, primarily because of the low relatedness between secondary helpers and the young they help to rear ($r \le 0.05$). Because of this low probability that secondary helpers and young will share genes identical by descent, it would not pay the secondary helpers to invest as much as primary helpers and parents do. This probably explains why they guard less and feed fewer and smaller fish (Fig. 17.6).

But being a secondary helper offers other advantages: it markedly improves the chances of breeding in the following season, hence boosting the direct fitness component. When a male breeder dies, it is usually his former secondary helper who takes over the female (e.g. s 309 in 1982, Fig. 17.2). There even occur prolonged fights between male breeders and their secondary helpers with a 9% probability that the helper will displace the breeder. Overall, 91% of the surviving marked secondary helpers were mated in the next season (n = 23), 47.6% of them to the female they had helped the year before (for details see Table 3 of Reyer 1986). This, and a high survival rate of 74%, results in a high breeding probability. From these

Table 17.2. Direct, indirect and inclusive fitness values for primary and secondary helpers of Pied Kingfishers during their first two years of life

Status	Year	Gain in fitness		
		Direct	Indirect	Inclusive
First-year breeder		0.96 0.80	0 0	0.96 0.80
Total		1.76	0	1.76
Primary helper	1 2	0 0.42	0.45 0.20	0.45 0.62
Total		0.42	0.65	1.09
Secondary helper	1 2	0 0.87	0.04 0.01	0.04 0.87
Total		0.87	0.05	0.92
Delayer	1 2	0 0.30	0 0	0 0.30
Total		0.30	0	0.30

Bold figures are the overall sums.

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data it follows that in his second year a secondary helper can expect 0.87 in direct fitness (Table 17.2). This is more than for all other male categories.

Delayers, who have an equally high survival rate (70%), gain only 0.30 because they have much lower mating chances (33%). Breeders, with high chances to be mated again (98%), gain 0.80 due to lower survival rates (57%), while primary helpers gain only 0.42 because of their low survival rates (54%) and medium probability of obtaining a mate (60%). The lower survival of primary helpers and breeders probably results from their higher feeding effort (Fig. 17.6). The poorer mating chances of primary helpers are due to the fact that, even if they do survive, they rarely take over the female that they have helped the year before. In many cases this would lead to a son mating with his mother, which may be prevented by incest avoidance.

Thus, in terms of direct fitness, being a primary helper is worse than being a secondary helper, whereas in terms of indirect fitness it is the other way round. Adding both components together results in similar inclusive fitness values for the two strategies (1.09 versus 0.92; Table 17.2 and Fig. 17.8). Why then do some surplus males become primary helpers to their parents, while others become secondary helpers to strangers?

The answer to this question is in the probability that a young male will attain a particular status. Remember that breeding is the best strategy but is only achieved by 4.7% of yearling males. Potential secondary helpers face a similar problem: not always can they become secondary helpers. Under certain ecological conditions, such as those prevailing at Lake Naivasha, helpers will not be tolerated by breeding males. Then, they may be forced into the inferior delayer strategy. For primary helpers, who experience much greater tolerance, the likelihood of being forced to become a delayer is much lower. It is therefore not surprising that unmated males prefer the primary over the secondary helper status. If at least one of his parents is still breeding, an unmated male will usually remain as a primary helper rather than become a secondary helper elsewhere. Thus, surplus birds choose the best available strategy, which - depending on conditions - for some is the primary, for others the secondary, helper strategy. There were only two exceptions to this rule. Both concerned breeding pairs which arrived in the colony with two primary helpers each. Only one helper of each pair remained, while the others left and became secondary helpers before their siblings hatched.

The above benefits accrue only to males. Females, as the dispersing sex, find themselves among unrelated birds so that raising young of others does not improve their indirect fitness. It would not increase their direct fitness either, because, being the limiting sex, females can always be sure to get a mate. With breeding being highly superior to helping, it is therefore not surprising that we have never witnessed a helping female.

Costs and benefits for breeders

With the above information in mind, we can also answer the third question as to why the two types of male helpers are treated differently, both within and between colonies. One only has to assume that potential helpers are accepted when the benefits they contribute to the breeders' fitness override the fitness costs, but are rejected when the reverse is true. Benefits derive from improved survival of present young through additional feeding; costs result from lowered chances of having young in the future as the helper may displace the breeder in the next season.

Because of the male surplus, these costs accrue only to male breeders. Therefore it is not surprising that female breeders are much more tolerant towards potential secondary helpers. With equal sex ratios at both lakes (1.6:1), the likelihood that a mated male will be displaced is probably similar at the two lakes. We can thus focus on differences in benefits in order to understand the cost/benefit ratios and the resulting behavior of male breeders.

At Lake Victoria, with its poor feeding conditions, the reproductive benefits of having helpers are high (Fig. 17.7). Therefore, both primary and secondary helpers are accepted. At Lake Naivasha, however, with its good feeding conditions, having helpers is not crucial for high reproductive success. Under such conditions, a male breeder should reject those helpers which feed little and threaten his status. These are the secondary helpers. Primary helpers, on the other hand, pose no such threat and can be tolerated even when the benefits they offer are low as at Lake Naivasha.

The same argument holds for the time at which helpers are accepted by breeders. Before the young hatch, helpers are of little value at either lake, because no feeding is required. Therefore, they should be rejected when the probability for competition is high (as in secondary helpers), but can be accepted when this probability is low (as in primary helpers). On a proximate level, these differential probabilities are reflected by differences in blood plasma levels of testosterone (Reyer *et al.* 1986). While average titers of potential secondary helpers (0.58 ng/ml) were found to be similar to those of mated males (0.51 ng/ml), those of primary helpers (0.17 ng/ml) were significantly lower (P < 0.01; Mann–Whitney U-test, two-tailed). As low titers were paralleled by small gonad sizes and no sperm production, primary helpers, in contrast to potential secondary helpers, may not be able to fertilize eggs and therefore do not threaten the mated male's paternity.

Thus, primary helpers are tolerated from the beginning of the breeding season because of the lower competitive threat that they pose to breeding males, while secondary helpers are only accepted when the need for help is high, as it is late in the season at Lake Victoria.

Proximate mechanisms of decision-making

Thus, Pied Kingfishers seem to choose the strategy which, under the prevailing ecological and demographic conditions, yields the highest inclusive fitness. But what are the proximate mechanisms for this decisionmaking? A bird cannot calculate inclusive fitness values – and even if he could, the information would be available to him only at the end of his life, and then it is too late to choose a better strategy. Therefore, we must look for proximate mechanisms which are (a) constantly available and (b) good predictors of inclusive fitness.

Decision mechanisms for young males

For young males, these mechanisms follow immediately from the foregoing discussion about the availability and profitability of the various strategies (Fig. 17.8). The first thing a male has to do at the beginning of a breeding season is to check whether or not unmated females are present. If yes, he should join her and breed, if not, he should try to become a helper. In the latter case the next question is whether or not his parent(s) are still alive. If yes, he should join them as a primary helper, if not, he should approach various other pairs as a potential secondary helper. The final decision is not one of the young male, but one of the breeders with whom he wants to associate. If they tolerate him, the potential helper turns into an actual helper, if not, he will be forced into the delayer strategy. In our study, this happened only to potential secondary helpers, but there may be conditions where primary helpers are not tolerated either. Then the rejected bird perhaps would try to become a secondary helper (? in Fig. 17.8). A behavioral program which tells the young male to follow this hierarchy of decisions and to react according to the actual situation will automatically lead to the best available strategy. This program is effective regardless of the ecological conditions at the colony.

Decision mechanisms for breeders

For breeders, the marked differences between Lakes Victoria and Naivasha in food availability and reproductive success suggested that their decision whether or not to accept secondary helpers could be based on need, i.e. on the food requirements of the young and the feeding capacities of the parents. To test this hypothesis, we first measured the daily energy expenditure (DEE) of feeding adult Pied Kingfishers with the doublylabeled water technique (Reyer and Westerterp 1985). We then related the DEE of parents to their reproductive success, their behavior towards potential secondary helpers and the food requirements of their young. Finally, we manipulated clutch size in order to change these food requirements and hence the energetic stress of parents (Reyer and Westerterp 1985).

Energy expenditure of parents

As the daily energy expenditure of adults increases, the amount of food delivered to nestlings rises in a linear fashion at both lakes, but with significantly different slopes (Fig. 17.9). Thus, a Lake Victoria bird will achieve a lower feeding contribution than one from Lake Naivasha for the same amount of energy expended (see e.g. dashed line at 210 kJ day^{-1} in Fig. 17.9). The ecological reasons for this have been mentioned before: (1) less profitable fish and (2) poorer hunting conditions at Lake Victoria than at Lake Naivasha. The line at 210 kJ was not chosen arbitrarily. Pied Kingfishers expending less than 210 kJ day⁻¹, on average maintained or even increased their body weight, those expending more than $210 \text{ kJ} \text{ dav}^{-1}$ lost an average of 3 g day^{-1} , which is 3.8% of the mean body weight of 78 g. Thus, 210 kJ seems to represent a physiologically determined energy threshold. Although a bird may exceed this threshold for a day or two, it apparently cannot maintain such a high performance for prolonged periods without a decline in body condition that is large enough to threaten survival. The threshold, 210 kJ, is about $4 \times BMR$ (basic metabolic rate), an upper limit which seems to hold for many more bird species. By combining this threshold with the regression lines of Fig. 17.9, one can predict the average feeding capacities for the two lakes: at Lake Victoria a parent Pied Kingfisher can bring a maximum of 102 kJ day⁻¹, at Lake Naivasha he can deliver as much as 267 kJ, or 2.6 times more.

Growth and survival of young

The effect of these feeding capacities on nestling development can be deduced from Fig. 17.10, which plots the daily weight change per young against the amount of food he receives. The resulting solid regression line intersects the line of constant weight at about 90 kJ. Provided with that much energy, a nestling will neither gain nor lose weight. At Lake Victoria with a maximum food contribution of 102 kJ through one parent and with an average clutch size of 4.6 at hatching, each nestling will receive an

average of 44 kJ day⁻¹ (= $2 \times 102/4.6$; black arrow on x-axes) if parents try to raise their offspring without helpers. This is insufficient and would lead to an average daily body mass loss of 5.6 g (black arrow on y-axes) if it were not for competition between nestlings; some will get enough and survive at the expense of others. At Lake Naivasha, with a maximum food contribution of 267 kJ per parent, each nestling will receive an average of 111 kJ day⁻¹, which is sufficient for all of them to add weight (white arrows), even if their parents have no helpers. These energy calculations support the data on reproductive success in Fig. 17.7.

The information for the parents on whether or not their young have enough food very likely comes from the begging of the nestlings, which has a clear influence on the adults' feeding patterns. Parents resting in the

Fig. 17.9. Amount of food delivered to Pied Kingfisher nestlings (kJ $adult^{-1} day^{-1}$) in relation to daily energy expenditure of feeding adults (kJ day^{-1}). \bigcirc , Lake Victoria; \bigcirc , Lake Naivasha;, upper limit of energy expenditure and resulting feeding capacities, respectively.



colony were regularly observed approaching the nest entrance and either resuming rest when the begging response was soft or immediately flying to the lake when it was intense. Also, begging duration increases with

the lake when it was intense. Also, begging duration increases with decreasing food supply (Fig. 17.10). Consequently, nestlings at Lake Victoria can be expected to beg more than nestlings at Lake Naivasha.

Manipulation experiments

According to these results, the different demands of the nestlings (as communicated in their begging) plus the different energetic stress on parents (Fig. 17.9) could indeed provide the proximate mechanisms responsible for the different treatment of secondary helpers at Lake Victoria and Lake Naivasha. In order to test this hypothesis further, energetic stress and begging duration in the two colonies were reversed through manipulation of clutch size and by comparing the treatment of helpers under normal and manipulated conditions (Reyer and Westerterp 1985). Under normal conditions, with a clutch size of four to six nestlings,

Fig. 17.10. Body mass change of Pied Kingfisher nestlings (--) and begging duration (+---+) in relation to the amount of food received. Arrows show the average amount of food per day and the average daily change in body mass for a nestling at Lake Victoria (filled arrows) and Lake Naivasha (open arrows).



each parent in a pair without helpers has to care for two to three young. Under these conditions, the vast majority of the breeders rejected potential secondary helpers at Lake Naivasha, whereas at Lake Victoria all accepted them (Fig. 17.11; $\chi^2 = 48.398$, P < 0.001). Some clutches at Lake Naivasha were then experimentally increased to eight to ten young, or four to five young per parent. According to the energy measurements, this put the parents into a position similar to that of Lake Victoria birds: they could no longer provide enough food. And indeed, in 10 such experiments eight pairs accepted secondary helpers (Fig. 17.11). This differs significantly from normal conditions at this lake (P < 0.001; Fisher's Exact probability test, one-tailed). The reverse experiment was equally conclusive. When at Lake Victoria clutch size was reduced to one to two nestlings, so that each parent had to care for no more than one, potential secondary helpers were not

> Fig. 17.11. Treatment of potential Pied Kingfisher secondary helpers by breeders under normal conditions (four to six young) and when clutch size was increased to eight to ten young or reduced to one to two young. Lake Naivasha left, Lake Victoria right. The 2×2 contingency tables in the center of the graph give the number of pairs which rejected (-) or accepted (+) secondary helpers. The histograms show the proportion of encounters in which male breeders either attacked (stippled) or greeted (open) potential secondary helpers when meeting them near the nest. Histograms above the tables are for normal conditions; histograms below are for manipulated clutch sizes.

L. VICTORIA L. NAIVASHA 1.0 attacks areetina 0.5 ф + 31 2 4-6 23 no. young 7 1 2 8-10 1-2 8 1.0 0.5 - $\overline{}$ 0 -

allowed in all but one case; again significantly different from normal conditions (P < 0.001).

It could be argued that this result is not very surprising, because breeders spending more time in getting food for more young, of course, have less time to chase away potential secondary helpers, which then may sneak in undetected. Such an explanation is ruled out by looking at the actual encounters between male breeders and potential secondary helpers shown in Fig. 17.11. When clutch size was normal, attacks prevailed at Lake Naivasha, and greeting prevailed at Lake Victoria. When clutch size was increased, Naivasha birds switched from attacking helpers to greeting them, whereas Victoria birds switched from greeting to attacking when clutch size was reduced. Thus, the tolerance towards helpers is, indeed, determined by the demands of young and the parents' energetic abilities, which in turn depend on the ecological conditions, particularly the type of food and its availability.

The basis for the cooperative breeding system

From the foregoing scenario, two features emerge as the most crucial components for the Pied Kingfishers' cooperative breeding system.

- (1) Under *severe ecological conditions* breeders alone cannot successfully raise all their young.
- (2) A *strongly biased sex ratio* among adults leads to a surplus of unmated males.

Condition (1) creates the need for helpers, while condition (2) creates a supply of potential helpers. Breeding in colonies allows the potential helpers to choose among various breeding pairs, and allows the needy breeders to choose among various helpers, including related (= primary) and unrelated (= secondary) ones. What, however, is the origin of the parents' limitation and the reason for the biased sex ratio?

(1) The feeding capacities of parents seem to be limited by physiological mechanisms constraining the maximum daily energy expenditure to about $4 \times BMR$, a threshold which has also been found in other birds (Drent and Daan 1980). Recruiting helpers when food conditions are poor is one way to guarantee sufficient feeding rates despite such parental limitation. Apparently, this is true not only for Pied Kingfishers. Using published data on 15 species of other cooperative breeders, I found a significant positive correlation between hourly feeding rates of unassisted pairs and the percentage increase in feeding rates when helpers are present (r = 0.820, P < 0.001). In other words, in species with low parental feeding rates (i.e.

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 $< 10 \text{ trips h}^{-1}$) helpers did not increase the overall food contribution to the young; they only reduced the parents' contribution. But in species with high $(> 20 \text{ trips h}^{-1})$ and in some species with medium $(10-20 \text{ trips h}^{-1})$ parental feeding rates the overall contribution went up and parents did not reduce their effort when helpers were present. This suggests that in harder working species parental feeding capacities are limited and helpers are needed (recruited?) for better food supply (Reyer, unpublished results).

An alternative answer to parental feeding limitations would be to select better areas, where one can have a higher reproductive success without risking competition from helpers. So, why do Lake Victoria Pied Kingfishers not move to places such as Lake Naivasha? The main limiting resource seems to be suitable nesting sites (=sandy banks) close to the fishing grounds. This is indicated by the changing availability of breeding sites at Lake Naivasha and by the birds' readiness to accept man-made features (p. 530), which is also known from other areas (Douthwaite 1970). Even where suitable nesting sites appear to be superabundant, they may not be, due to the properties of the soil. If the soil is too loose, burrows may collapse; if it is too hard digging may become difficult or even impossible, as in 1980 when at Lake Victoria the rains failed. Out of 27 pairs which congregated in the colony in that year, only three found places soft enough for excavating nesting-holes. Also, the tunnel and the nest chamber must be constructed and oriented in such a way that the young are buffered against stressful temperature fluctuations and are protected from a harmful buildup of CO₂ and NH₃ and a diminution of O₂ caused by the metabolism of the birds and of microorganisms living on the accumulating feces and pellets (White et al. 1978).

There are probably few places which fulfil all these breeding site requirements and, in addition, offer good feeding conditions. Because of such resource limitations, Pied Kingfishers will not only be forced to breed colonially – sometimes even in unsafe areas where high predation pressure and human disturbances lead to a very poor reproductive success (Douthwaite 1978). Many of them will also be driven to places such as Lake Victoria, where obtaining food is time and energy consuming and reproductive success is low, unless helpers are recruited.

(2) A biased sex ratio among adults with a surplus of unmated males exists in most cooperative breeders and has often been invoked as an important component for the evolution of cooperative breeding (Brown 1978; Emlen 1984). Alternatively, some authors have argued that the biased sex ratio may be a result rather than a source of cooperative breeding (Koenig and Pitelka 1981). Basically, the first hypothesis assumes that the bias is produced by the parents and, therefore, already present at the end of parental care, while the second assumes that the bias occurs after parental care has terminated and is caused by differential dispersal and mortality resulting from the differing breeding options for males and females.

The first idea is exemplified by the 'repayment model' proposed by Emlen et al. (1986) and extended by Lessels and Avery (1987). If grown offspring of one sex remain with their parents and help them to rear successive young, they 'repay' part of the costs of their production. Consequently, they become the 'cheaper' sex. With parents investing equally in the production of sons and daughters (Fisher 1930), the evolutionarily stable sex ratio will deviate from 1:1, because selection will favor females who produce more offspring of the helping than of the non-helping sex.

For testing this hypothesis, it is essential to know the sex ratio among offspring at the termination of parental care (TPC), which in Pied Kingfishers is three to four weeks after fledging. Unfortunately, the young follow their parents to the lake within a few days after leaving the nest and I am thus unable to compile these data. Yet, there are two reasons why the repayment model is unlikely to apply to Pied Kingfishers.

(a) Any 'intended' shift from a 1:1 sex ratio among nestlings to an excess of males could only be produced by selectively starving females as the more expensive sex. (More expensive because they do not repay through helping and not because they require more food; there is no sex difference in fledgling size.) The benefits of such selective starvation should increase with increasing stress on parents. Consequently, the bias in sex ratios should occur before the parents engage in maximum effort (Clutton-Brock *et al.* 1985), which is around the end of the second week after hatching. My data, however, give absolutely no evidence to support these predictions. The 1:1 ratio is still present in nestlings of three weeks and older.

(b) Although the 1:1 ratio among nestlings may shift *slightly* toward a surplus of males until the end of parental care, it is unlikely that a few weeks will produce a *marked* bias toward males. Thus, assuming that the TPC and nestling sex ratios are the same, I fitted my data into equations (12) and (16) of Lessels and Avery (1987). The resulting predictions for the evolutionary stable male:female ratios were very different for the two lakes, namely 1.44:1 for Lake Victoria and 0.97:1 for Lake Naivasha. Yet, neither the nestling nor the adult sex ratio differed significantly between the two colonies.

Therefore, the surplus of males in adult Pied Kingfishers cannot be satisfactorily explained through an overproduction of a cheaper and more valuable sex. Differential mortality after the termination of parental care

seems to offer a better explanation for the shift from a 1:1 ratio among nestlings to the 1.6:1 ratio among adults. In Pied Kingfishers there are two sources for higher female than male mortality.

- (1) Juvenile females disperse while juvenile males remain near and return to their natal colony (p. 531). Although quantitative data are lacking because of the difficulty of finding dispersing birds, it seems likely that juvenile females on their way into unknown areas suffer higher mortality than juvenile males remaining at home.
- (2) Female breeders take a bigger share in incubating the eggs and brooding the young than do male breeders; consequently females are more endangered by nest predators or when nesting-holes cave in or are flooded. This results in different male and female mortality rates among adults (p. 531).

The notion that higher female than male mortality creates a surplus of males, who are potential helpers, does not automatically mean that cooperative breeding originates from differential mortality. It also could be the other way round: if cooperative breeding (or any other behavioral trait) makes it worthwhile for females to disperse and take the greater share in reproduction, then differential mortality would be a result rather than a cause of helping (Koenig and Pitelka 1981). In both cases, however, the question arises: why do young females take the greater risk?

The reasons for dispersal in general and sexual differences in particular are still poorly understood. According to Greenwood (1980) the following link between dispersal patterns and mating systems exists: if males invest little in the offspring, and if the acquisition of females as the limiting resource, mainly depends on the distribution of the females themselves, then males can enhance their reproductive success by moving around in search of mates. This is the typical pattern in mammals, in which males usually disperse more than females. If, however, the acquisition of females requires the defense of limited resources such as feeding territories or breeding sites, and if such defense is facilitated through familiarity with the locality, then philopatry of males should result. This is the typical pattern in birds, including Pied Kingfishers. At the beginning of the breeding season, malebiased groups of three to nine Pied Kingfishers perform noisy aerial chases and ground displays which seem to attract females to a suitable breeding site where pair formation takes place (Douthwaite 1970). Suitable breeding sites, however, are limited at least in some areas (see above). Those males who have found one stick to it very closely year after year. At Lake Victoria, 83% of the helpers nested within a few meters of the place where they had Pied Kingfishers

helped the year before (n = 30) although the colony stretched over more than 500 m. In eight cases concerning breeders, the male and female of a newly formed pair had bred the previous year more than 50 m apart. In seven of these cases the female joined the male in his previous site and in one case the reverse was true. This differs from an equal probability of site change (P = 0.035, binomial test, one-tailed). Thus, for males but not for females, there seems to exist a 'home advantage' effect, which favours philopatry of male Pied Kingfishers.

This, however, does not explain why females disperse in Pied Kingfishers and most other bird species. Greenwood (1980) suggests that dispersal has evolved as a mechanism against inbreeding depressions. We do not know whether or not such depressions would occur in Pied Kingfishers, but inbreeding is definitely avoided. Even when their fathers die, primary helpers do not mate with their widowed mothers (Reyer 1986). The costs of such possible fitness depressions, which have to be weighed against the costs of dispersal, would affect both sexes equally. The costs of dispersal, however, would be higher for males, who would lose the benefits they derive from philopatry. Consequently, 'which sex disperses may be the outcome of a conflict between the sexes, where the relative costs and benefits of dispersal and philopatry to the sexes determine the outcome' (Greenwood 1980, p. 1155).

Similarly, the answer to the question 'who takes the bigger share and risk in reproductive effort' will also depend on the relative costs and benefits to the sexes. Although reproduction, through its effects on mortality, imposes higher costs on female than on male Pied Kingfishers, these may be offset by higher benefits for females. Females breed from their first year on, whereas young males usually have to go through the less profitable helper and delayer strategies before they can reproduce. Overall, the fitness gain for the two sexes may turn out to be the same, despite the marked differences in dispersal and reproductive patterns. This, however, cannot be proved verbally, but requires some modelling.

Although such models can test whether or not the observed sex ratios are adaptive under the present system, they will not enable us to say that the entire system is more adaptive than others. The pattern of female-biased dispersal, incubation and mortality and of male-biased sex ratios is so widespread among birds that it will be very difficult to circumvent the 'phylogenetic inertia' argument, i.e. that the pattern, the function of which we do not yet know, may have nothing to do with cooperative breeding but be merely something intrinsic to birds. I am grateful to the many helpers in this project, all of them unrelated and yet of 'primary' importance. My particular thanks go: to W. Wickler for giving me the opportunity to work in Kenya and for his continued interest in and support of the study; to D. Schmidl for his untiring and competent help during many years in the field and the Institute; to K. Westerterp, J. Dittami and M. Hall, who cooperated with me on energy expenditure and hormone titers; and – last but not least – to my wife, H. Reyer, for encouraging my work and patiently tolerating my repeated absence from home. The research was financed by the Max Planck-Gesellschaft with additional funds from the DFG (Re 553/1-1). E. K. Ruchiami (Office of the President) and M. L. Modha (Wildlife Conservation and Management Department) issued and extended my research permit (OP. 13/001/C1891/14). Permission to live and work on their properties was kindly given by C. Clause, J. Geoffrey, M. and S. Higgins, E. Sketch and J. Ndolo. Finally, I am grateful to my colleagues in Seewiesen for discussing with me various stages of the study and to W. Koenig and P. Stacey for their helpful comments on an earlier version of this article.

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