

FIELD STUDIES AND EXPERIMENTS
ON DISTRIBUTION AND FORAGING OF PIED
AND MALACHITE KINGFISHERS AT
LAKE NAKURU (KENYA)

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SUMMARY

(1) In Lake Nakuru National Park (Kenya), fishing behaviour and distribution of pied (PK) and malachite kingfishers (MK) in time and space were studied in relation to two food conditions, five water conditions and six vegetation parameters. In addition, captive birds were given a choice between two ‘environments’ (fishing tanks) which differed in only one ecological parameter at a time.

(2) Fish density turned out to be the most important ecological parameter. In the field and in captivity, both species were equally attracted to high densities, but—reflecting their 2.6 times higher energy requirements—the bigger PKs took fish 2.4 times heavier than those of the MKs.

(3) With the exception of depth, water conditions had little or no influence on either species, except outside the range occurring naturally in the field.

(4) The role of vegetation was only analysed in the field and only for MKs. In parts of their territories, characterized by dense vegetation, MKs tended to spend less time and had less success than in more open and uniform areas.

(5) Possible costs and benefits of all preferences are discussed in relation to reproductive consequences. Differences between field and experimental results are analysed with respect to data distribution and methods.

INTRODUCTION

Knowing the precise relationship between an animal and its habitat is an essential precondition for many areas of biological research, including bio-geography, speciation and adaptive radiation, community structure, population dynamics, behavioural ecology and conservation. The basic question in all these areas is: ‘To which particular environmental conditions is the animal adapted?’ Analysis of these conditions is most often based on a comparative approach using variation within and between species. One problem in such comparisons, however, is determining which of the numerous ecological parameters in an environment are really relevant for the behaviour under study and which are only confounding variables.

One solution is application of multivariate statistical methods (see review of Clutton-Brock & Harvey 1984). Another is experimental manipulation of selected variables (e.g. cover or food) and observation of the behavioural consequences (e.g. in mating systems or

cooperative breeding; Fricke 1980; Pleszczyńska & Hansell 1980; Davies & Lundberg 1984; Reyer & Westerterp 1985).

The multivariate approach has the advantage of testing the interrelation between behavioural and ecological variables under natural conditions. There are, however, some restrictions in the nature of the data and some difficulties in interpreting the results (Wilkinson 1979; Sokal & Rohlf 1981; Clutton-Brock & Harvey 1984). The experimental approach with selected variables is then superior; but its disadvantage is that conditions are less natural. In this paper we use both methods to study the effects of various ecological variables on distribution and fishing behaviour of pied (*Ceryle rudis* L.) and malachite kingfishers (*Alcedo cristata* Pallas). The main aim of the investigation was to find ecological causes for the plasticity in kingfisher behaviour and social structure which has been reported elsewhere (Reyer 1980, 1984, 1986; Reyer & Westerterp 1985).

FIELD STUDY

Study area

The field study was performed between March 1976 and February 1977 along six fresh water inlets of Lake Nakuru, Kenya (Fig. 1): (A) Njoro river, (B) Makalia river, (C) Nderit river, (D) Tower streamlet, (E) Hide streamlet and (F) pond. All observation areas were mapped and the perches used by the kingfishers numbered.

Areas (A)–(E) stretched from the river mouths to about 150 m upstream. Along their mouths, all five rivers were fringed by mud flats, interspersed with patches of grass (Cyperaceae and Gramineae) in areas (C)–(E). While grassland (*Cyperus laevigatus* L.) continued to dominate the shores of area (C) even further up the river, the vegetation along the other streams graded into isolated pockets of sedge (*Typha domingensis* Pers.), mixed scrub and woodland (mainly *Acacia xanthophloea* Benth). Area (D) covered a small pond with a surface area of about 300 m². Its shoreline was partly bordered by grassland with a few *Acacia* trees and partly by dense sedge.

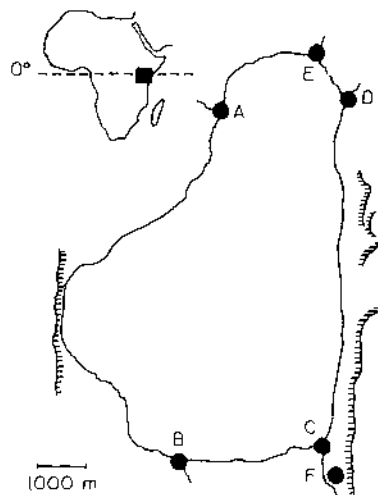


FIG. 1. Map of Lake Nakuru (Kenya) with location of observation areas (A)–(F).

Material and methods

Vegetation measurements

The type and distribution of the vegetation in areas (D) and (E) were examined by putting four parallel transects through each, two on either side of the streamlets (Fig. 2). Each transect was divided into eight subunits of *c.* 20 m length, numbered from 1 (near the mouth) to 8 (furthest upstream). Along each transect, vegetation measurements were taken every 6–7 m. This yielded 12 sampling points per subunit (4 transects \times 3 samples). A metal rod, subdivided into 10-cm sections, was placed vertically on each sampling point and the following information was recorded: (i) plant species within a 0.5 m radius around the rod; (ii) plant touching the rod 0–1 m, 1–3 m, 3–5 m and more than 5 m above the ground. The information was used to calculate six vegetation indices:

(1) *Vegetation density*. This is the percentage of rod subdivisions touched by vegetation in relation to the maximum possible. The 12 sampling points (representing horizontal density) and 4 height classes (representing vertical density) made a maximum score per subunit of 48.

(2)–(4) *Proportions of grasses (2), herbs (3) and shrubs and trees combined (4)*. The percentages of rods touched by each vegetation category was calculated. No height-classes were considered and so the maximum possible was equal to the number of sampling points, i.e. 12 per subunit.

(5) *Foliage height diversity (FHD)* = $-\sum p_i \ln p_i$ (MacArthur & MacArthur 1961). Here p_i is the proportion of the total number of rod divisions touched for each of the four height-classes (*i*).

(6) *Plant species diversity (PSD)* = $-\sum q_i \ln q_i$, where q_i is the proportion of plants belonging to species *i*. This proportion was the number of sampling points in which the species occurred at least once (maximum score per subunit = 12) over the total number of plant recordings for all *n* species and the 12 sampling points in that subunit.

Behavioural parameters

Data on PKs were collected in six locations: the five mouth regions of rivers (A)–(E) and around pond (F). Data on MKs were gathered in sixteen locations, namely in each of the eight subunits of areas (D) and (E). All observations were made from hides and lasted

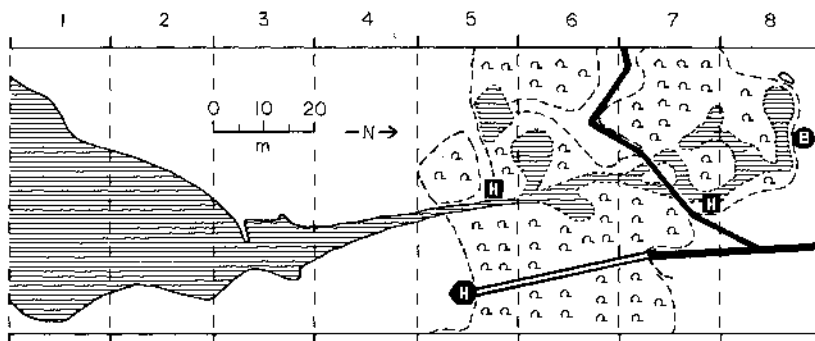


FIG. 2. Map of malachite kingfisher territory (E), showing the eight subunits (1–8), the course of the river (hatched), the location of the observation hides (H), the breeding site (B) and the boundaries of the dense tree vegetation (Q).

from 08.00 a.m. to 11.00 a.m. Three behavioural parameters were recorded: (i) time present; (ii) number of dives; and (iii) fishing success.

The time spent by each bird on a perch was recorded to the nearest minute and the number of successful and unsuccessful fishing dives from that perch counted. Data for all perches within the same observation area were totalled over the 3 h observation period and over all individually marked birds. It was then divided by the number of birds visiting the observation area during the 3 h. This gave the average time of sojourn per bird in a subunit, as well as the average number of total dives and the percentage of successful dives.

Environmental parameters

Immediately after the 3 h observation period, seven environmental parameters were measured in each of the observation areas. (i) Width and (ii) depth of water were recorded to the nearest cm. (iii) Water current (cm s^{-1}) was determined by measuring the time it took a small plastic bottle to float 2 m. (iv) Alkalinity (ppm) was calculated from the volume of 0.1*n* HCl necessary to neutralize a water sample mixed with an indicator. (v) Clearness of the water was determined with a lux-meter. The amount of light penetrating to 5 cm depth was expressed as a percentage of the amount of light on the surface. (vi) Fish density was determined by putting a net with a mesh size of 1.5 mm across the water. From a distance of 5 m upstream, the fish were chased downstream into the net by rapidly splashing the hands and feet. The fish were then emptied into a bucket, counted, measured and returned to the water. Density was expressed in fish m^{-2} after dividing the number caught by the area covered, which was the distance of the chase (5 m) multiplied by the width of the water at the sampling point. (vii) Fish length was measured as total length (to the nearest mm) and averaged over all fish caught.

Vegetation structure was only measured once (January 1976) and assumed to remain the same throughout the study period. All other measurements and the behavioural observations were carried out twice a month on consecutive days, and the two results were averaged to give one monthly value for each of the behavioural and ecological parameters at each of the sampling points. Water current, clearness and fish density, which were more variable than the other parameters, were measured 2–3 times per day in each sampling area. Thus, their monthly values represent the means of the daily means. Fish density was probably the variable with the biggest sampling error, because many fish escaped the net, especially when the water was deep and/or wide. Yet, it was the variable showing the most consistent results of all, not only for both species, but also when field and captivity data were compared. Thus, the potential error was probably small in relation to the importance of fish density.

Statistical analysis

For various reasons, several of the monthly data sets were incomplete or biased (e.g. technical failure of lux-meter; perturbation of distribution and fishing through reproductive activities; too few fishing dives to calculate reliable success rates). After eliminating them, the resulting Table for PKs comprised 22 rows (= number of cases) and 10 columns (3 behavioural, 5 water and 2 fish parameters). For the MKs the table comprised of 26 rows and 16 columns (3 behavioural, 5 water, 2 fish and 6 vegetation parameters), with all data from the non-breeding season.

This data reduction made the remaining data independent in the sense that the behaviour (e.g. the time spent) in one area or at one time could not be predicted from the behaviour in other areas or at other times. The problem that data were also dependent, because the same few individuals were observed throughout the study, was overcome by calculating averages for behaviours and thus considering only one 'average individual' per observation area.

The two tables, with variation in time and between sites, were subjected to stepwise multiple regression analysis, in order to find the set of ecological parameters (= independent variables) best predicting the behavioural parameters (= dependent variables). For compilation we used SYSTAT program MGLH, with $\alpha \leq 0.05$ as the criterion for entering an independent variable into the final model. For heuristic purposes we also experimented with $\alpha \leq 0.10$ (Sokal & Rohlf 1981).

Original data were used for the statistical analysis when parameters did not differ from a normal distribution ($P > 0.10$; Lillifors modification of the Kolmogorov-Smirnov one-sample test, Sachs 1978). For PKs this applied to fish size, width of water, current and clearness; for MKs it applied to fishing success, current, clearness and all six vegetation parameters. All other behavioural and ecological parameters were log-transformed to fit (or at least approximate) a normal distribution before entering the analysis (Frey & Pimentel 1978; Sokal & Rohlf 1981).

Results

General behaviour

During the study period, six adult PKs and five adult MKs, all individually marked with coloured plastic bands, were regularly seen around our study sites. Both species predominantly fed on *Tilapia grahami* the only fish species in Lake Nakuru and its inlets (Vareschi 1979). On a few occasions, the birds were seen to catch tadpoles, small frogs or unidentified prey, probably aquatic insect larvae.

PKs fished both from perches and from a hovering position over the water. Four of the six PKs were a breeding pair and its two grown-up offspring. The other two birds were single individuals with unknown histories. All PKs seemed to move between the study sites quite independently of each other; even the family would frequently split. All combinations of birds were possible and tolerance between family members and single birds seemed to be as high as tolerance among family members. During the 11-month study, PKs spent most of their time in area (F), followed in decreasing order by areas (E), (D), (A) and (B). They were never observed in area (C). By December 1976, all six had left Lake Nakuru.

MKs exclusively fished from perches, usually branches 20–50 cm above the water surface. Four of the five MKs belonged to two pairs, one each in areas (D) and (E). For some months, the pair in area (D) was accompanied by an adult offspring from a previous brood. In contrast to the PKs, which never bred during the study period, both MK pairs made several successful and unsuccessful breeding attempts. Young which fledged were not included in the observations because they did not fish during their first days of life and thereafter were much less skillful than adults. Also unlike PKs, the two MK groups were territorial throughout the study period. The birds rarely, and then only briefly, left these areas. Within these territories, the mates regularly moved up and down the streamlets, sometimes together, but usually separately.

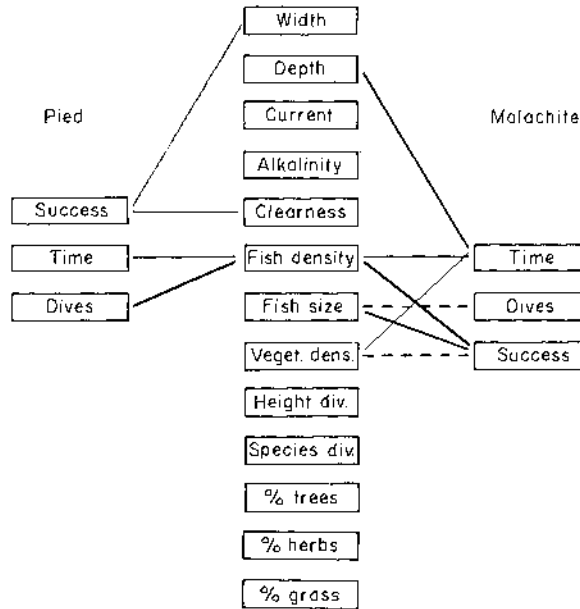


FIG. 3. Relationships between ecological parameters (centre) and behavioural variables (left for PKs, right for MKs), indicated by solid lines when positive, by broken lines when negative. Thick connecting lines represent the standardized partial regression coefficients (β) from the stepwise multiple regression models in Table 1. Thin lines show additional negative relationships emerging when statistical conditions are relaxed from $\alpha \leq 0.05$ to $\alpha \leq 0.10$. For further details see text.

Effects of food, water and vegetation conditions on distribution and foraging

When the effects of environmental conditions on distribution and fishing behaviour of PKs and MKs were analysed, only a few of the numerous ecological parameters remained in each of the various multiple regression models (Fig. 3, Table 1).

In the PK, fish density proved the only predictor variable for the time the birds spent in a particular area as well as for the number of dives they performed there (Fig. 3 left, Table 1a). The higher the density, the longer the birds visited the area and the more often they fished. Fishing success could not be explained by any of the recorded ecological parameters as long as α (the condition to enter an independent variable) was 0.05 or smaller. With less stringent conditions ($\alpha \leq 0.10$), clearness and width of water were found to decrease success rates (thin connecting lines in Fig. 3).

For MKs, the picture was more complicated (Fig. 3 right, Table 1b). This is partly due to the incorporation of six vegetation parameters as additional independent variables. The time which the birds spent in a particular area not only increased with fish density but also with the depth of the water. The two predictor variables together explained 33.5% of the variance, less than the single predictor variable in the PK (Table 1). Moreover, in MKs the variables predicting time differed from the one predicting the number of dives (fish size), while in PKs time and dives depended on the same variable (fish density). Also in contrast with PKs, fishing success of MKs could be predicted through three of the ecological parameters recorded: fish density and fish size increased the success, vegetation density decreased it.

TABLE 1. Stepwise multiple regression analysis of ecological parameters (= independent variables), affecting behavioural parameters (= dependent variables) in pied kingfishers (a) and malachite kingfishers (b). Standardized partial regression coefficients (β) and their significant levels (α) are shown together with squared multiple correlation coefficients (R^2), degrees of freedom (d.f.1, d.f.2) and significance levels (P) of the resulting regression model. P differs from α only when two or more predictor variables are included in the model. R^2 reflects the proportion of variance in the dependent variable that is explained by the respective combination of independent variables, e.g. in MK, fish density and depth of water together account for 33.5% of the variance in time spent. Only independent variables entered at $\alpha \leq 0.05$ are shown. For further explanations see text

Variables	β	α	R^2	d.f.1, d.f.2	P
(a) Pied kingfisher					
Time					
Fish density	0.713	0.001	0.508	1,20	0.001
Dives					
Fish density	0.550	0.008	0.302	1,20	0.008
(b) Malachite kingfisher					
Time					
Fish density	0.555	0.005	0.335	2,23	0.009
Depth of water	0.586	0.007			
Dives					
Fish size	-0.536	0.005	0.287	1,24	0.005
Success					
Fish density	0.434	0.040	0.382	3,22	0.013
Fish size	0.438	0.044			
Vegetation density	-0.445	0.044			

These results were obtained with α -values of 0.05 or lower. Relaxing the statistical conditions to $\alpha \leq 0.10$, did not change the dive and the fishing success models in MKs. For time, however, vegetation density emerged as an additional negative predictor variable. In those parts of their territories characterized by dense and diverse vegetation, the birds tended to spend less time than in areas with sparse vegetation (thin line in Fig. 3).

Role of competition

In addition to the ecological factors considered above, behavioural interactions might have influenced the distribution and fishing behaviour of the two species. We frequently observed that a MK left his perch when a PK landed close to him. Also, PKs were seen to attack MKs, particularly those emerging from the water with a fish. Yet, the times in an area, the number of dives and the success rates of the two species did not correlate negatively with each other (Spearman rank correlation). On the contrary, the times which PKs and MKs spent in the same area showed a positive correlation ($r_s = 0.536$, $n = 16$, $P < 0.05$). This indicates that competition as a possible deterring factor was much less important than those ecological factors which attracted the birds, in particular fish density.

Ecological conditions and breeding

For MKs, fish density was also the key variable for reproductive activities such as courtship, nest-digging, egg-laying, incubation and feeding young. Months with these activities differed from months without mainly in a 130% higher average fish density

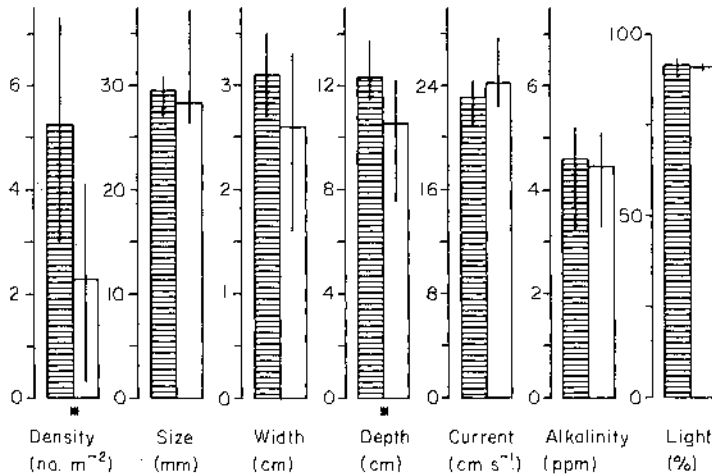


FIG. 4. Mean food and water conditions plus 95% confidence limits for 10 months with (■) and 11 months without (□) reproductive activities. Asterisks denote significant differences ($P < 0.05$, Mann-Whitney U -test). Data from areas (D) and (E) combined.

(Fig. 4). Differences in all other ecological parameters were less than 17% and most of them not significant.

During the reproductive phases, the MKs spent only 33.8% of their time in subunits 1-4 and 66.2% in subunits 5-8 where in all cases the nest was located. In the non-breeding seasons, on which the above multiple regression analyses are based, they spent 52% in subunits 1-4 and only 48% in subunits 5-8 ($P = 0.036$; Mann-Whitney U -test, one-tailed, applied to time differences between units 1-4 and 5-8 in the breeding and non-breeding season). Thus, the location of the nest exerted an additional influence on the distribution of the birds.

For PKs there are no comparable data, because they did not breed during the study period.

EXPERIMENTS IN CAPTIVITY

Methods

The experimental subjects were six adult PKs and five adult MKs, all hand-reared, tame animals. The PKs were kept in an aviary $13.1 \times 6.9 \times 2.9$ m (length \times width \times height), the MKs in another aviary $7.4 \times 5.0 \times 2.0$ m. They were observed from a hide adjacent to both aviaries. Each aviary was equipped with two fibreglass tanks $81 \times 62 \times 50$ cm in size and about 3 m apart. Ropes, 46 cm vertically apart, were stretched above the tanks, four for the PKs, two for the MKs. Together with the rims of the tanks, they were fishing perches which the birds could select according to the conditions in the tanks below them.

Both tanks were filled with water and stocked with fish (*T. grahami*) in such a way that during each of the five experimental series they differed only in one of the following five parameters: (i) fish density; (ii) fish size; (iii) depth of water; (iv) clearness; (v) alkalinity. The other ecological parameters measured in the field (width of water, current and vegetation) could not be manipulated in the aviaries. Each experimental series consisted

of 8–10 sessions, one per day. During each series conditions in one tank, the control tank, were kept constant, while conditions in the other, the experimental tank, were randomly varied between sessions, but kept constant within sessions. In order to keep fish density constant, each fish caught from the tanks was immediately replaced by washing a new one through PVC pipes running from the observation hide to each tank. Ranges of conditions in the experimental tanks and conditions in the control tanks (usually at one extreme of the respective range) can be deduced from Fig. 5. For further details see Migongo (1978).

A session lasted 2 hours. After 1 hour the locations of control and experimental tanks were swapped to control for site preferences of the birds perching above them. During each session the number of fish caught from each tank by all birds together was recorded and later converted into percentages of the total number caught (= choice index). In addition, the time spent on each perch height was measured during sessions in which the effect of water depth was tested. The dimensions of the tanks and the distance between them allowed all individuals to choose the same tank without interfering with each other. Fishing success was not recorded because pilot studies showed that success rate in captivity was almost invariably 100%. Conditions for the two species were the same unless stated otherwise.

Results

In the experiments, all five environmental parameters exerted a strong influence on the choice index of both the PKs and the MKs. Results are summarized in Fig. 5.

Depth of water. Both species preferred shallow to deep water. PKs, for which the control depth was 50 cm, increasingly fished in the experimental tank as its water depth increased from 5 to 20 cm. Thereafter the trend was reversed until at experimental depths of 45 and 50 cm, fishing rates in both tanks were equal. MKs preferred the experimental tank when it was shallower than the control tank (= 20 cm), but increasingly switched to the control tank as the experimental depth increased. Preference peaked at a depth of 8 cm; beyond 32 cm the experimental tank was avoided altogether.

With increasing depth of water, both species shifted their fishing from lower to higher perches (Fig. 6, left). PKs, fishing in 5–10 cm water, used the lowest perch (1) more often than all other perches, but did not use it at all when diving into 35–45 cm water. Conversely, the highest perch (5), never used at depths of 5 and 10 cm, was preferred at 35–45 cm. Fishing rates from intermediate perches 2–4 changed correspondingly. Similarly, MKs decreased their use of perch (1) from a maximum of 42% at depths 4–8 cm to a minimum of 0% at depths 32–40 cm, whereas the fishing rate from the higher perch (2) went up from 58% to 100% as the water became deeper. For unknown reasons, they never fished from the highest perch (3) (= 92 cm), although they did dive from higher perches in the field. As the depth which a diving bird can reach depends, among other things, on the height from which he dives (see Table 3 in Migongo 1978), this avoidance may partly explain why the MKs in captivity never dived into water deeper than 32 cm. It also forced us to use a lower control depth for MKs than for the PKs (20 vs. 50 cm).

The relationship between the time which birds perched at different heights over the experimental tank and the water depth from which they had to fish was less obvious (Fig. 6, right). Yet, for PKs, the proportion of time spent on the various perches correlates with the proportion of dives from these perches ($r_s = 0.721$, $n = 16$, $P = 0.002$; Spearman rank correlation), indicating that with increasing water depth, PKs spent more and more time on higher perches. For MKs, this correlation between the proportion of time on a perch

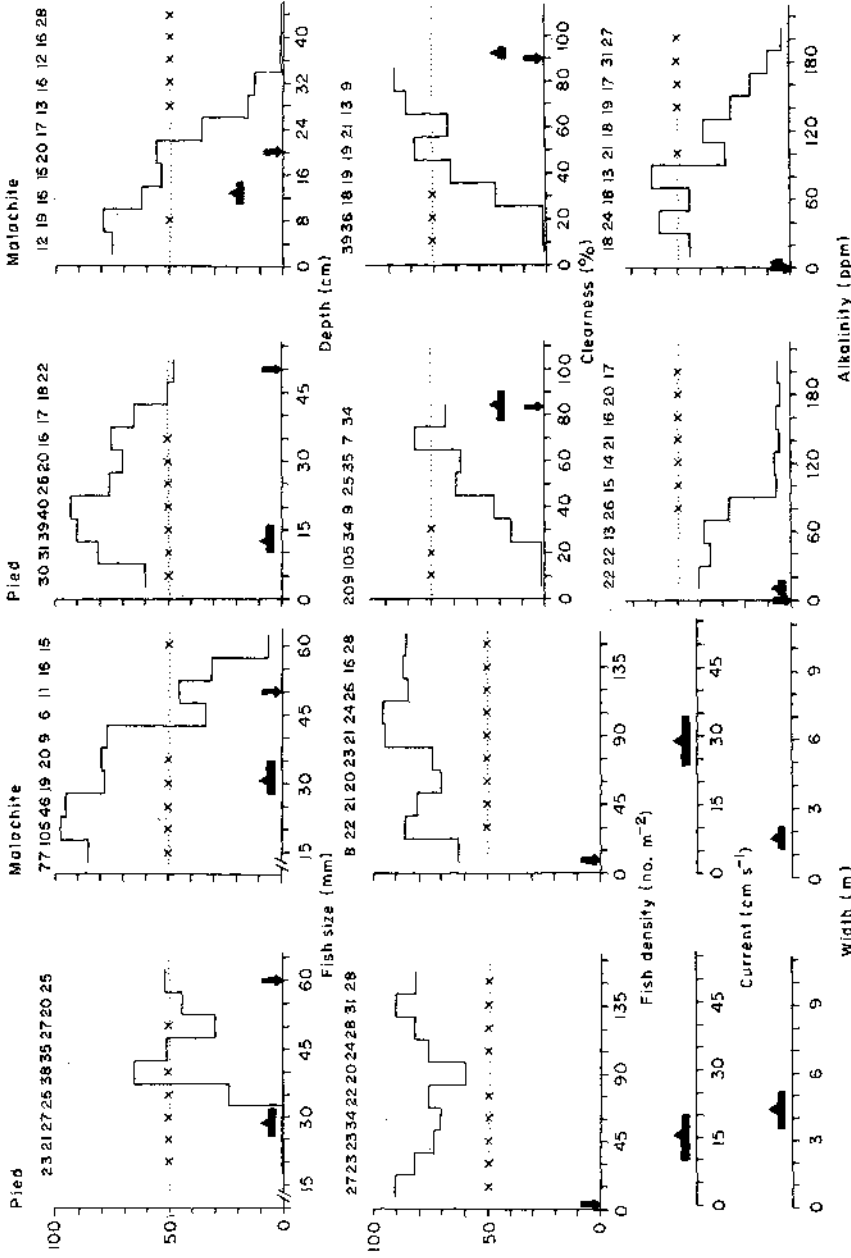


FIG. 5. Result of choice experiments on pied kingfishers (left) and malachite kingfishers (right) in captivity. The percentage of fishing dives into the experimental tanks is given in relation to two food conditions (fish density, fish size) and three water conditions (depth, clearness, alkalinity). Conditions in the respective control tanks are indicated by black arrows. X = significant deviation ($P < 0.05$) from an equal distribution between the two tanks (.....), tested with the binomial test and based on the number of dives given above each graph. For comparison, field conditions, including those not tested in captivity, are shown with means (▲) and 95% confidence limits (horizontal black bar).

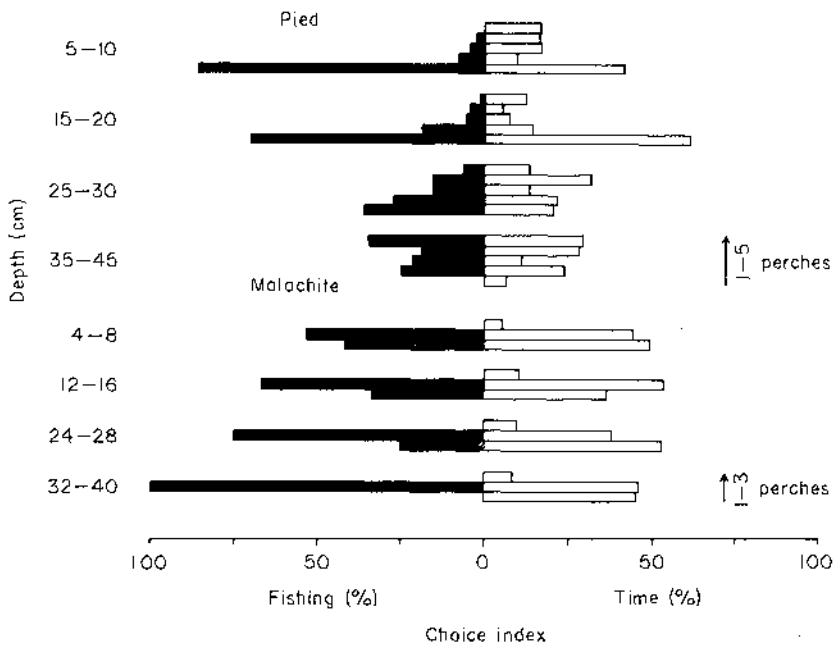


FIG. 6. Percentage fishing dives from and time spent on perches 1-5 (pied kingfisher, top) and perches 1-3 (malachite kingfisher, bottom) in relation to four water depths in the experimental tank. For both species, water depth increases from top to bottom of the figure, although in different steps. For each depth, perch height increases from the lowest horizontal bar (perch 1 = rim of the tank) to the highest bar in steps of 46 cm.

and the proportion of dives from it did not exist ($r_s = 0.000$, $n = 8$, N.S.). Thus, perching in MKs appears to be less determined by fishing than in PKs.

Clearness. When given the choice of clear water in the control tank (light penetration to the bottom 80-90%) and turbid water in the experimental tank, both species avoided the experimental tank only when light penetration there was very low (10-30%). For values of 40% and above there were no significant differences between fishing rates in the two tanks (Fig. 5).

Alkalinity. Both species fished less often in the alkaline experimental tank than in the freshwater control tank, but only when alkalinity was increased beyond 60 ppm for PK and beyond 70 ppm for MKs. At lower values no preference for freshwater could be detected.

Fish size. When confronted with big fish (= 60 mm) in the control tank and smaller ones in the experimental tank, PKs first increased their fishing rate in the experimental tank from 0 to c. 70% at fish sizes of 40 mm. Thereafter they decreased it again to about 30% at 50 mm. The subsequent rise is probably a result of the small difference between control and experimental sizes. The same argument holds for the finding that MK capture rates for 40 and 55 mm fish were not significantly different from those for the 50 mm controls. (For this species 50 mm had to be chosen because there were insufficient 60 mm fish for controls for all sessions.) When the experimental tank contained 15-35 mm fish, MK fishing rates were higher than in the control tank; when it contained 60 mm fish, the rate was lower. Thus, MKs preferred smaller fish than PKs, reflecting differences in their respective body sizes.

Fish density. Throughout all sessions, both species preferred the experimental tank with high fish densities over the control tank with low densities. The differences in fishing rates were significant in eighteen out of twenty sessions and did not vary with density in any consistent manner. The Spearman rank correlation coefficient between density and fishing rate in the experimental tank was $r_s = -0.027$ for PK and $r_s = 0.527$ for MK ($n = 10$ in both cases, N.S.). Thus, all other things being equal, a site A seems to be equally effective in attracting birds from site B whether it has 10 or 100 more fish. Field conditions for fish density are not given in Fig. 5 because of the difficulty in reliably calculating real densities from catch data (see Methods).

DISCUSSION

Comparison of field and experimental results

From Figs 3 and 5 it is obvious that in captivity more ecological parameters exerted an influence on distribution and foraging of PKs and MKs than in the field. This is only seemingly a discrepancy, because most effects in captivity occurred only in a range of conditions which in the field was rarely reached. Turbid water, for example, was avoided only when clearness dropped below 50% in PKs and below 40% in MKs. Both values are much lower than those usually found in our observation areas (see means and 95% confidence limits in Fig. 5). The same is true for alkalinity which had to be higher than 60 ppm (PK) or 80 ppm (MK) to be avoided by the birds. Moreover, for almost all ecological parameters, variance in the field was smaller than the difference between control and experimental tank had to be to detect a preference for, e.g. a certain fish size or for shallow over deep water. Where the preference for certain conditions was marked and consistent throughout the tested range, field and captivity results agreed. This is true for fish density.

In addition to these technical reasons, there may have been biological causes for the difference between field and captivity results and for the independence of some behavioural variables from ecological conditions. These include behavioural and/or ecological parameters other than those incorporated into the regression models; e.g. the need to sample changes in profitability between patches, which will inevitably take a bird to suboptimal areas (Charnov 1976; Krebs & McCleery 1984), or the necessity not only to maximize food intake, but also to minimize predation risk. Where such different demands cannot be met within the same area, they have to be balanced into an overall optimum which may deviate from the foraging optimum (e.g. Milinski & Heller 1978). This is more likely to occur in a large and heterogenous natural environment than under the uniform conditions of a small aviary.

Effect of ecological conditions on behaviour

Food conditions

For both species, fish density turned out to be the most important ecological determinant. In captivity, the birds consistently preferred high to low fish densities (Fig. 5), and in the field study fish density proved to be the best predictor of the time which the birds spent in the various areas (Fig. 3, Table 1). In addition, increasing fish density also increased the number of dives in PKs, but not in MKs (Fig. 3, Table 1). This difference probably resulted from differences in (a) fishing success and (b) food requirements.

(a) In MKs, increasing densities improved the success, thus decreasing the number of dives required for catching a certain amount of food. In PKs, where success was

independent of fish density, there was no counteracting effect and the positive association between time spent and number of dives could emerge. We cannot tell why fish density affected the success rate of MKs but not of PKs. However, as the observation areas for the two species overlapped only partially, differences in overall conditions and/or in unrecorded parameters may have played a role for these and other species differences found in Fig. 3.

(b) PKs are bigger and require about 2.6 times more energy input per day than do MKs (calculated from formula 8 in Walsberg 1983). In areas like ours, where both species encounter the same range of fish sizes (Fig. 5) these different requirements mean that the daily time budget of a PK is much more determined by fishing activities than is that of a MK. This may also explain why in captivity there was a significant correlation between time spent and number of dives for PKs, but not for MKs (Fig. 6).

The two species also selected different fish sizes, as did the two Asian species studied by Pring-Mill (1974) and the five South American species investigated by Remsen (1978). In the choice experiments with captive birds, the fish size preference of MKs peaked around 20–25 mm, that of PKs around 40 mm. These are only about half the size which the two species have been observed to catch and swallow in the field (Pring-Mill 1974; Junor 1969 cited in Whitfield & Blaber 1978; Douthwaite 1976; H.-U. Reyer, unpublished). As increasing fish size does not seem to decrease success rates (quite the contrary in MKs, Fig. 3b), the most likely explanation for the choice of smaller prey in captivity is the disproportionately long handling time which big prey requires in many predator species (e.g. Salt & Willard 1971; Davies 1977), including kingfishers (Douthwaite 1971). With increasing distance between perch and fishing grounds, travelling costs become relatively more important than handling costs and optimal food size should change towards the larger sizes observed in the field (see models of optimal foraging; e.g. Krebs & McCleery 1984).

Water conditions

Among water conditions, depth appeared to be most important. By and large, both species preferred shallow diving to deep diving as do other species preying upon aquatic organisms (e.g. terns: Safina & Burger 1985). This preference probably has several advantages, including (i) lower energy expenditure (due to less flapping under water), (ii) reduced risk of being preyed upon by big predatory fishes (cf. Remsen 1978) and (iii) higher success rates.

Although not obvious from the data analysis, the higher success rate is suggested by slow motion films we took of kingfishers diving under water. They show that the fish are usually startled only when the bird is already very close over the water or even as it hits the surface. Fish close to the surface have almost no time to escape. With increasing depth their chances improve, probably exponentially (Remsen 1978), because the water decelerates the approach of the diving bird. Also, the deeper the fish, the more distorted it appears, due to refraction.

Clearness and turbidity of the water also affect hunting success, but apparently not in a consistent way. As shown by the slight negative effect of clearness on PK success rates (Fig. 3), too clear and smooth water can be detrimental, probably because it allows the fish early recognition of the approaching aerial predator (cf. Dunn 1973). The longer it takes the PK to fly from his perch at the shore to his normal striking position over the middle of the water, the stronger this effect will be (cf. negative relation between width and success in Fig. 3). Too murky and rough water, however, can also be detrimental to

fishing success, probably because it impairs the predator's ability to aim at the prey. At Lake Victoria, which is choppy, fishing success of PKs was about three times lower than at Lake Naivasha with its relatively calm and clear water (Reyer 1980 and unpublished). Also, at Lake Naivasha, fishing success significantly decreased with increasing turbulence at the surface (H.-U. Reyser, unpublished). The PKs seem to avoid such rough conditions when possible. At the seashore, for example, they hover outside the breakers (Gill 1936) or fish in quiet creeks and lagoons (own observations at Mida and Kilifi Creeks, Kenya). Such detrimental turbidities are, however, much stronger than the ones caused in our study through current. Therefore, and because current could not be tested in captivity, no effect of turbidity was found.

Vegetation

The influence of vegetation on distribution and fishing behaviour was only investigated for MKs. The birds seemed to avoid the parts of their territories characterized by dense vegetation (Fig. 3). It is interesting that only the spatial structure of the vegetation (density) appeared to be relevant, but not its composition (species diversity and percentages of grasses, herbs and trees). The most likely explanation is that dense vegetation bordering and overgrowing a water course casts patterns of light and shadow on the surface. These may confuse the birds, especially when the plants are moving in the wind and, consequently, reduce fishing success (Fig. 3).

Reproduction in relation to environmental conditions

Ecological parameters which affect the foraging of animals will also influence their time and energy budgets. Consequently, they can be expected to play an important role in determining reproductive periods which usually form the bottleneck in these budgets.

For MKs this is supported by the observation that the birds tuned their breeding to periods of high fish density (Fig. 4), i.e. to the ecological parameter with the strongest influence on the time the birds spent in an area and the success they had there (Fig. 3). Increasing fish size also improved success; but parents also need smaller fish to feed their young. Therefore, adjusting breeding times to fish density makes more sense than adjusting them to fish size.

For PKs, the connection between environmental conditions and reproduction is more difficult to make. At L. Nakuru, where ecological parameters were measured, the birds did not breed, and for areas where they bred we have no detailed ecological data. A qualitative comparison, however, between Lakes Nakuru, Baringo, Victoria and Naivasha (all Kenya) suggests that the reproductive behaviour of this species is also determined by fish availability. When fish densities drop very low and fish sizes are smaller than those PKs prefer (Fig. 5) and what is economic (Douthwaite 1970), the birds may leave an area altogether. This happened at L. Nakuru during the last 3 months of the study. When fish availability is slightly better, birds may catch enough to stay, but not to breed. This situation probably prevailed at L. Nakuru during the first 8 months of our study and also at L. Baringo where extremely murky water appeared to be the main obstacle to an adequate food supply. Despite the fairly high population of PKs (average 80–100 birds), no breeding has been reported for L. Baringo. The marked fluctuations in numbers throughout the year suggest that the birds go elsewhere to reproduce (T. Stevenson, personal communication).

With still better food conditions, breeding may become possible but only with poor success. This holds for L. Victoria where parents lose more than half of their young

between hatching and fledging due to starvation, unless they are aided in feeding by helpers (Reyer 1980). Finally, at L. Naivasha, with high fish densities and excellent catching conditions, successful breeding is possible even without helpers. This difference in reproductive success and helper recruitment between L. Victoria and L. Naivasha is clearly related to differences in parental energy budgets (Reyer & Westerterp 1985).

Such gradients in ecological conditions and behavioural responses are likely to exist in many animal species. We feel that multivariate analysis of field data combined with experimental testing is a useful tool for analysing the causal relationship between a particular response and a particular set of conditions.

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