CrossMark

An experimental evaluation of the influence of water depth and bottom color on the Common kingfisher's foraging performance

Antonio Vilches [a,b,*], Juan Arizaga [b], Ixai Salvo [a], Rafael Miranda [a]

[a] Department of Zoology and Ecology, University of Navarra, Irunlarrea 1, E-31080 Pamplona, Spain
[b] Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, E-20014 San Sebastián, Spain

ABSTRACT

To investigate how depth and bottom color affect prey selectivity in Common kingfisher (*Alcedo atthis*), we developed several experimental procedures using captive birds. We used 20 young kingfishers to test depth (25 or 50 cm) and color (natural gravel or white) effects on foraging behavior. Live freshwater fish were used as target prey. To assess differences resulting from the natural behavior of different fish, we chose bottom-dwelling [Ebro barbel (*Barbus graellsii*)] and open-water benthopelagic species [Ebro nase (*Parachondrostoma miegii*) and Pyrenean minnow (*Phoxinus bigerri*)]. The number of attempts and captures, as well as the effects of hunger and experience, were assessed relative to feeding behavior. The effect of fish behavior, as observed in grouped vs. isolated fish, on the kingfisher's performance was also tested. The results showed a significant effect of depth, with more attacks and greater success in shallow waters. No significant differences in catch success between natural- and white-colored bottoms were observed. Hunger had no effect on fishing success, but experience had a positive effect in shallow waters and on white bottoms. Both bottom- and open-water species were consumed equally. Kingfishers preyed more often upon grouped prey than upon isolated prey, although capture success did not vary between the two cases. Our results suggest that kingfishers prey upon the most accessible types of prey.

© 2013 Published by Elsevier B.V.

1. Introduction

Foraging strategy constitutes a fundamental chapter in the biology and ecology of species because it allows us to determine the ecological niche precisely and may often have direct conservation implications (Galarza and Tellería, 2003; Terraube et al., 2011). Given these considerations, it is highly relevant to know whether a particular species is a generalized forager or has evolved a particular foraging strategy (Bertellotti and Yorio, 2000; Grémillet et al., 1998; Sherry, 1990; Warburton and Thomson, 2006).

The Common kingfisher (*Alcedo atthis*) is a fish-eating predator that preys primarily on small fish using a plunge-and-dive technique. The diet of the species has been analyzed in a descriptive manner. Several studies have suggested that prey selection occurs (Campos et al., 2000; Hallet, 1982), whereas others have not addressed this question explicitly (Iribarren and Nevado, 1982; Isotti and Consiglio, 2002; Raven, 1986; Reynolds and Hinge, 1996). The evidence used to support the hypothesis of prey selection has been that the prey types consumed differed from the prey that were found in the river or water body where the species was present.

Previous field studies have shown that Common kingfishers typically tend to prey on more accessible fish species, i.e., on benthopelagic fish rather than on other species that swim near or close to the river bed (Vilches et al., 2012a). These results suggest the hypothesis that Common kingfishers are opportunistic and therefore do not fish for bottom-living prey because these species are much less accessible than benthopelagic fish. In this case, the depth of the water column is expected to be the principal factor affecting the type of prey consumed. In particular, it can be predicted that, under equal conditions, Common kingfishers would prey equally upon upper- or middle-water column and benthic fish, as has been found in other kingfisher species (Kelly, 1996; Laudelout and Libois, 2003; Remsen, 1990; Reyer, 1984; Reyer et al., 1988).

Another factor potentially affecting the apparent prey catchability is the ability of the fish prey to remain undetected by a predator. Prey detection may be affected by the ability to differentiate the prey from its background. In this case, the probability of detection would be proportional to the difference between the prey color and the color of the background (Endler, 1988). Thus, certain dorsal color designs might allow fish to be less detectable by predators such as kingfishers.

Prey densities have also been reported to be a factor affecting foraging behavior in other fish-eating birds (Draulans, 1987

* Corresponding author at: Department of Zoology and Ecology, University of Navarra, Irunlarrea 1, E-31080 Pamplona, Spain. Tel.: +34 948 425600.
E-mail addresses: antvilches@gmail.com (A. Vilches),
jarizaga@aranzadi-zientziak.org (J. Arizaga), ixaigaler@gmail.com (I. Salvo),
rmiranda@unav.es (R. Miranda).

Table 1
Characteristics (mean; range) of the fish prey used in the study. Body weight estimation (fresh weight, g) according to Miranda et al. (2006).

Species	Body length (mm)	Body weight (g)
Ebro barbel	60.2 (40–70)	2.5 (0.6–3.4)
Pyrenean minnow	55.1 (40–70)	2.5 (0.6–3.5)
Ebro nase	57.3 (50–70)	2.1 (0.9–2.7)

Fig. 1. Design of the aviary and experimental area. This diagram indicates the three resting rooms above and the experimental room below. Barred square: perching zone with vegetation. Open square: tank with food (live fish) ad libitum. Circle: tank with water for bathing and drinking. Transversal lines over tanks: perches. Four additional tanks outside the aviary were used to hold a stock of live fish.

in herons; Stewart et al., 2005 in cormorants). Grouping behavior in potential prey could make them more attractive to young, less competent predators (Lekuona, 2002). The degree of aggregation of prey could have an effect in the Common kingfisher, as in other kingfisher species (Reyer et al., 1988).

We conducted several experiments using captive birds to avoid possible confounding factors that occur under natural conditions. In this way, we assessed the influence of water depth and river bed characteristics (bottom color) on the Common kingfisher's foraging performance. The purpose of this study is to investigate how these characteristics of the river environment (depth and bottom color) determine or affect prey selection by the kingfisher. To our knowledge, this is the first study of this type involving captive Common kingfishers because of the difficulty of obtaining and maintaining specimens.

2. Materials and methods

2.1. Sampling area and capture protocol

Kingfishers were captured with mist nets at Jaizubia (municipality of Hondarribia, Gipuzkoa, Northern Iberia; 43°21′N, 01°49′W; 2 m above sea level), a stream surrounded by mudflats colonized by reed beds (*Phragmites* spp.) and lower-marsh associated vegetation in a tidal marsh close to the mouth of the Bidasoa River. Jaizubia is used as a stopover site by non-breeding Common kingfishers in the summer and autumn (Arizaga et al., 2010). Sampling was carried out from 10 July to 5 September 2009. In all, 204 linear meters of mist nets were placed across the marsh. The nets were opened for 4 h beginning at dawn.

Overall, we captured 20 juvenile kingfishers (i.e., birds hatched in 2009). After capture, the birds were placed in individual cotton bags for transport and released in an aviary 6 km from the capture site.

The fish preys used in this study were obtained by electrofishing (for methodological details see Beaumont, 2011) in nearby rivers in Gipuzkoa (Leitzaran, Oiartzun, Oria). After capture, the fish were kept in a tank containing freshwater and anesthetic (2-phenoxyethanol, 0.2 mg l^{-1}). From the fish caught [species: Pyrenean minnow (*Phoxinus bigerri*), Ebro nase (*Parachondrostoma miegii*), or Ebro barbel (*Barbus graellsi*)], we selected those of adequate size for consumption by Common kingfishers (40–70 mm body length; Cramp, 1985; Vilches et al., 2012a) (Table 1). The remaining fish were released. The selected individuals were introduced into a tank supplied with freshwater and an air pump and then transported to the aviary. These captured fish were used both as daily food and as prey in the experimental settings.

2.2. Housing conditions

The aviary consisted of a fenced room subdivided into (1) three individual resting rooms (3 m × 2 m × 2 m, length × width × height) and (2) an experimental room of 3 m × 6 m × 2 m (Fig. 1). Both the experimental room and the individual resting rooms were covered with an opaque synthetic fabric that prevented the birds from observing either each other or the surrounding area.
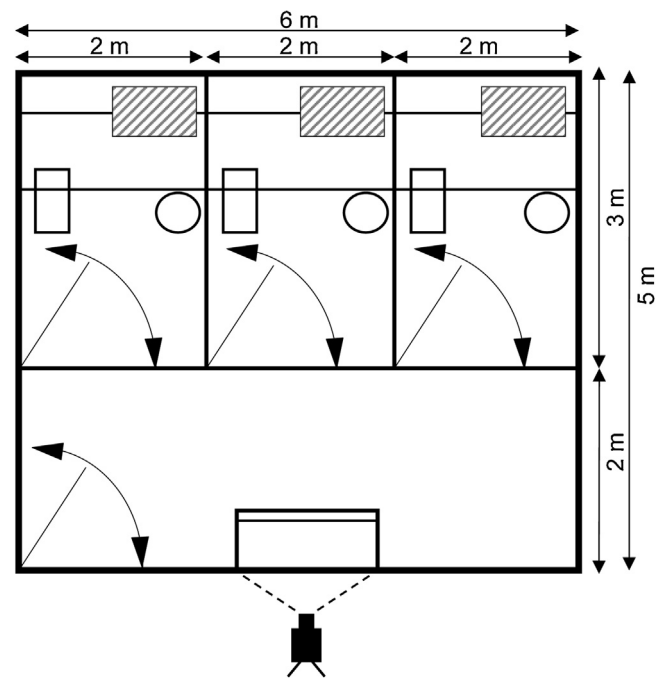
In each resting room, a bird was kept separately and provided with food ad libitum. Live food (Pyrenean minnow, Ebro nase, or Ebro barbel) of 40–70 mm body length was offered inside a 40 l glass tank. According to Tjomlid (1973), the Pied Kingfisher (*Ceryle rudis*) has a daily food intake rate equivalent to ca. 25% of its body mass. Assuming this rule, with a mean body mass of 35 g, Common kingfishers would need approximately 9 g of food per day. The kingfishers were fed with a mixture of the same fish prey provided in the experimental settings. The mean body mass of our fish prey was 2.4 g (Table 1). Accordingly, we needed a minimum of 4 fish per bird per day.

Applying the exponential relation between energy metabolism and body weight described in Lasiewski and Dawson (1967), 6.93 kcal/day would meet the energetic needs of a kingfisher. Assuming average energetic values of 1.35, 1.36, and 1.14 kcal (for Ebro barbel, Pyrenean minnow, and Ebro nase, respectively; Vilches et al., unpublished data), 5.5 daily prey would be enough to meet energetic needs. More current studies propose an energy intake of up to 16.45 kcal/day for 35 g non-passerine birds (Nagy, 1987). According to that calculation, 13 daily preys would be sufficient to meet the energy demands of the kingfisher.

To ensure food ad libitum during a period of seven days, we provided each bird with 20 fish prey. The amount of fish prey in the tank was reviewed daily to ensure that sufficient food was always available.

The water in the tanks was kept in good condition using an oxygen pump and periodic water changes. Each room was also equipped with two perches, one placed over the tank containing the fish prey and another located in a zone that contained vegetation (branches with abundant leaves) to offer the kingfishers a hidden roosting site. Birds were provided with an additional 10 l tank for drinking and bathing. The kingfishers were kept isolated in these resting rooms for one complete day before the experiments started and also during the remainder of the next six days, apart from the

time they spent in the experimental room. Thus, the experiment was performed twice with each specimen for each setting.

After the adaptation day, food access in the non-experimental room was prevented from dusk until the time when the kingfishers began the experiment the next morning. This was to motivate the kingfishers to feed in the experimental room. Water access was allowed at all times.

The three resting rooms were connected with the experimental room with a door that could be opened and closed from the outside using a pulley system. The experimental room was equipped with a 300 l glass tank (size: 1 m × 0.5 m × 0.6 m). A perch was sited 50 cm above the water surface to ensure that the kingfishers had no difficulties in accessing the fish prey. This tank was equipped with a mobile bottom tray so that the water column depth could be modified. A video camera (Panasonic SDR-H40) was installed behind the experimental tank to record both fish and bird behavior during the experimental periods. The filming axis of the camera was perpendicular to the front glass of the experimental tank, with its field of view including only the tank section that contained the fish. The observer was located in a hide behind the experimental room. A small window allowed confirmation of the successful attempts and observation of the condition of the bird.

2.3. Experimental design

We utilized three different experimental settings to test foraging efficiency and prey selection according to (1) water column depth and (2) bottom color. All experiments were carried out between 09:00 and 14:00 h.

In setting 1, kingfishers were allowed to fish during a 1 h period in a tank with a water column depth of 50 cm and a bottom tray containing natural gravel to imitate the river bed. Overall, we introduced 20 fish into the tank: 10 bottom fish (Ebro barbel) and 10 open-water species (Pyrenean minnow or Ebro nase).

Setting 2 was similar to setting 1 but had a water column depth of 25 cm. Settings 1 and 2 were used to test the effect of water column depth on foraging rate and efficiency and the potential selectivity between different prey species. The proportion of open-water fish intake was expected to increase with increasing water column depth because in this situation, fish typically found on the river bed would be expected to become less accessible to the birds.

Setting 3 was similar to setting 2, but in this case the tray on the bottom of the tank was covered with white PVC foil. Settings 2 and 3 were used to test the effect of the bottom color (and thus prey detectability) on the foraging rate and the potential selectivity between fish species with different color patterns. The Ebro barbel (note that we used juvenile fish) had dark mottling across the dorsal part of its body. In contrast, the Pyrenean minnow and the Ebro nase both had uniform dorsal color patterns. Based on this information, we considered that the Ebro barbel was better camouflaged than the other two species if observed against a gravel bottom (Cox et al., 2009; Kottelat and Freyhof, 2007).

Overall, we used 20 kingfishers. A total of 18 birds were used to compare settings 1 and 2, and 18 birds were used to compare settings 2 and 3. Sixteen of the birds were used in both of these comparisons, and the remaining two birds were different in each case.

In all the settings, we noted a total of six variables: the number of attempts to fish, number of fish captured, depth at which the attack was produced (depth reached by the bill tip with 1 cm accuracy), depth at which the attacked prey was situated, number of captures of each fish prey species, and number of captures of fish prey that were swimming solitarily or grouped in a shoal. Except for the number of captures of each fish prey species (which was determined by counting the number of each that remained after the experiment), all the variables were recorded during the

experiment using a video camera. Additionally, the capture success was calculated as the ratio between the number of captures and the number of attempts. Fish that showed an erratic swimming pattern or any other atypical behavior were removed before testing.

2.4. Statistical analyses

To test for the effect of water column depth on foraging behavior, we compared the number of attempts, prey captured, and capture success between settings 1 and 2 and between settings 2 and 3. These variables obeyed a normal distribution but were highly overdispersed (SD/mean > 0.93). Therefore, they were all log-transformed. We then conducted an ANOVA for each log-transformed variable with water column depth (25 cm vs. 50 cm, settings 1 and 2) or river bed color (settings 2 and 3) as a factor.

When comparing both settings 1–2 and 2–3, we also controlled for two additional covariates: experience and hunger. As reported in earlier studies (e.g., Gendron, 1986), experience could have a positive effect on foraging behavior. To control for this effect, we assigned each experiment a number (from 1 to 6 according to the chronological order of the experimental presentation). Not all birds were used in the experiments at the same time in the morning. For this reason, and because all birds were prevented from accessing food before the experiments, the birds used in an experiment later in the morning were expected to be hungrier and therefore potentially more highly motivated to use the experimental tank. Accordingly, hunger was also controlled in the statistical models by adding the time elapsed since dawn as a covariate.

Additionally, we also calculated the effect size (Arizaga and Barba, 2009) as $d = (\text{mean}_a - \text{mean}_b)/\text{SD}_{\text{pooled}}$ and the $\text{SD}_{\text{pooled}} = [[(n_a - 1)\ \text{SD}^2_a + (n_b - 1)\ \text{SD}^2_b]/(n_a + n_b)]^{0.5}$, where a and b are the two groups compared and n is the sample size. An effect size > 0.5 (difference between means explains > 50% of the pooled SD) was considered to indicate a significant difference between samples (Cohen, 1969).

To test whether the kingfishers preyed more often on isolated prey or groups, we conducted a contingency test on the type of prey (swimming isolated or within a shoal) by the number of prey caught.

The assumptions of normality of distributions and homogeneity of variances were verified with a Shapiro–Wilk and a Levene's test, respectively. All statistical analyses were performed with SPSS v. 17 (SPSS Inc., Chicago, IL, USA). The significance level was set at $\alpha = 0.05$.

2.5. Ethical note

We received authorizations (from the Gipuzkoa and Navarra Administration) to both catch and keep Common kingfishers in captivity, as well as to collect fish as food for them. No bird suffered any noticeable damage during the time they were housed. Releases were performed at the same site where the birds were caught. Bird and fish captures were performed by trained personnel (professional bander number A0145) who had already conducted animal collections in the same study area in previous studies (e.g., Vilches et al., 2012a,b). Thus, the wildlife experienced no adverse effects. All fish recovered fully from the anesthetic. Moreover, all field, transportation, and housing procedures complied with the animal use and care regulations of Europe and Spain.

3. Results

Eighteen kingfishers were used in each experiment (comparison of settings 1 and 2 and comparison of settings 2 and 3); 16 of the birds were used in both experiments, whereas four individuals were used only in one experiment (two in the first experiment

Table 2
ANOVAs used to test the effect of water depth and river bed color (settings 1 and 2, and 2 and 3, respectively) on capture attempts (attacks/h), number of fish prey captured (captures/h) and capture success (captures/attack). Experience and time since dawn are covariates. We show the F and P-associated values as well as the standardized (Sd.) B-parameters of each factor/covariate.

Experimental design	Tested variable	Factor/covariates	F	P	Sd. B-parameters
Setting 1 vs. 2	Attacks/h	Water depth	19.88	0.000	−0.42
		Time since dawn	4.18	0.049	−0.15
		Experience	0.76	0.394	−0.02
	Captures/h	Water depth	79.14	0.000	−0.34
		Time since dawn	2.43	0.129	−0.05
		Experience	5.93	0.024	+0.03
	Captures/attack	Water depth	83.03	0.000	−1.11
		Time since dawn	0.98	0.335	−0.10
		Experience	13.24	0.002	+0.15
Setting 2 vs. 3	Attacks/h	Color	1.13	0.295	−0.09
		Time since dawn	0.04	0.833	−0.01
		Experience	0.88	0.354	−0.02
	Captures/h	Color	3.60	0.067	−0.12
		Time since dawn	0.65	0.425	−0.03
		Experience	4.07	0.052	+0.03
	Captures/attack	Color	1.08	0.306	−0.16
		Time since dawn	2.36	0.134	−0.13
		Experience	12.22	0.001	+0.15

and two in the second). In total, 134 h of experimentation were recorded, and 825 attacks on fish prey were detected and analyzed (Table 3).

3.1. Effect of water column depth (settings 1–2)

The number of capture attempts, fish prey capture rate and capture success were significantly higher at the lower water depth (Fig. 2). In addition, the time since dawn was observed to have a marginal and positive effect on the number of capture attempts (Table 2), but not on the fish prey capture rate and capture success. Experience, however, did have a positive effect on both the fish capture rate and capture success (Table 2).

Fish prey tended to swim near the tank base (i.e., all of them behaved as if they were bottom-living fish). For this reason, their swimming depth differed when we used a 25- and 50-cm tank depth ($t = 5.65$, $P < 0.001$; Fig. 3). When we used the deeper tank, however, the kingfishers were unable to fish at a depth below ca. 25 cm ($t = 1.69$, $P = 0.104$; Fig. 3). The kingfishers preyed upon both bottom fish and open-water fish independently of the depth ($\chi^2 = 0.000$, $P = 1.000$).

3.2. Effect of bottom color (settings 2–3)

The number of capture attempts and capture success did not differ significantly between the white-colored bottom and the bed of gravel used to imitate the natural color of a river bed (Table 2 and Fig. 2). Only experience had a significant effect on capture success, which was higher over the white-colored bottom than over the

Table 3
Differences in capture success between isolated and grouped fish at different depths (setting 1: 50 cm, setting 2: 25 cm) and against differently colored bottoms (setting 2: natural gravel, setting 3: white foil).

Prey state	Failed attempts	Successful attempts	χ^2	P
Setting 1				
Isolated	33	3	6.76	0.009
Group	79	0		
Setting 2				
Isolated	117	38	1.93	0.164
Group	228	53		
Setting 3				
Isolated	76	34	0.26	0.610
Group	118	46		

natural-colored one (Table 2). The kingfishers preyed upon both bottom and open-water fish independently of the bottom color ($\chi^2 = 0.565$, $P = 0.588$).

3.3. Additional analyses: shoaling vs isolated

Overall, kingfishers preyed more often upon shoals than upon isolated prey. However, the capture success did not vary between these prey types (Table 3). Only in setting 1 (where we used a water column depth of 50 cm) did we observe that the capture success was significantly higher for isolated prey than for shoals, but this result must be considered with caution because of the small sample sizes (very few fish were captured in this setting).

4. Discussion

4.1. Effect of water column depth

We observed that the water column depth had a remarkable effect on the foraging behavior of the kingfishers. In particular, the kingfishers showed a higher number of capture attempts and greater capture success when they were exposed to shallow water, where their prey was much more accessible.

As all prey tended to swim near the bottom, the open-water fish (Pyrenean minnow and Ebro nase) did not behave as expected. In contrast, they behaved normally in a previous study conducted with exactly the same fish species. In this previous study, they occupied their natural position within the water column shortly after their release into the tank. The reason for the behavior of the open-water fish in the current study may be that the kingfishers were highly visible when they perched over the tank. Under natural conditions, kingfishers' fishing activities originate from perches in zones with good vegetation cover (Boag, 1986; Cramp, 1985). It is probable that in these conditions, their outline does not contrast with the sky. As a result, few perched kingfishers are visible, and the fish occupy a position in the water column corresponding to their ecological niche. Both bottom- and open-water fish moved toward the bottom as a defense response and were equally accessible to the kingfishers. This outcome did not prevent us from testing our hypothesis that kingfishers are opportunistic and prey on the most accessible fish. We observed that the kingfishers did not show a particular preference for any prey species (bottom- vs. open-water fish). These observations indicated that the kingfishers behaved opportunistically if fish were equally accessible.
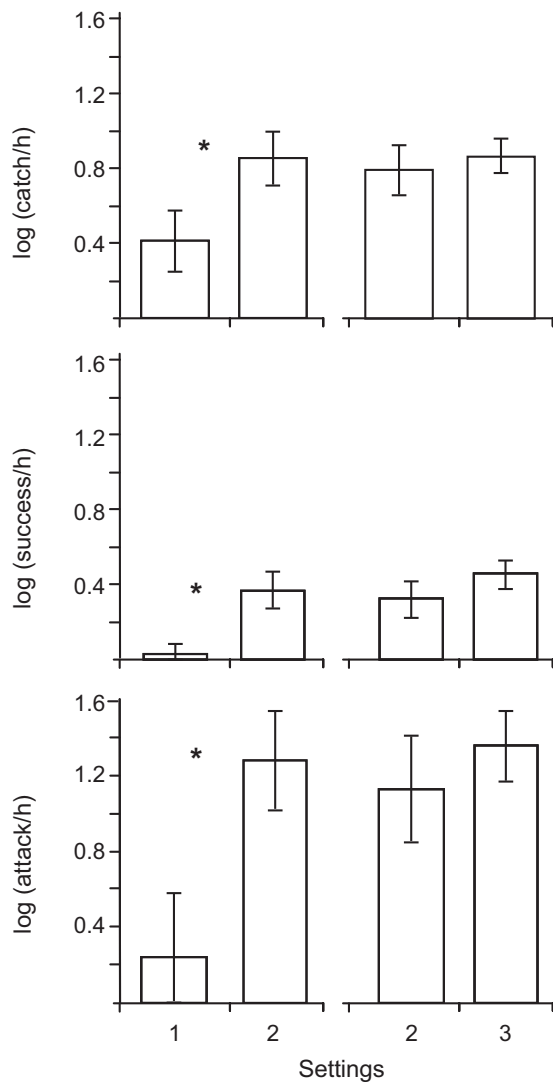
Fig. 2. Comparison of foraging behavior of kingfishers for settings 1 (depth of 50 cm, natural gravel) vs. 2 (depth of 25 cm, white foil) and 2 vs. 3 (depth of 25 cm, natural gravel). The results are log-transformed mean values ± 95% CI. Asterisks indicate significant differences between settings according to the ANOVAs shown in Table 2 (P < 0.05). We used a total of 18 birds in both cases. However, we did not use exactly the same birds in the comparison of setting 2 with setting 1 and in the comparison of setting 2 with setting 3.

Fig. 3. Depths (mean values ± 95% CI) of fish and depths of attack reached by diving kingfishers in settings 1 and 2 (i.e., when the depth of the water in the tank was 50 cm and 25 cm, respectively). The asterisk shows significant differences according to a t-test (P < 0.05). Values were calculated from a sample of 18 attacks in setting 1 and 27 attacks in setting 2.

We found that capture success was lower if the kingfishers were forced to fish in deep water. However, several factors not investigated in the study could have affected our results. Light refraction could affect capture success because the difference between the perceived position and the real position is greater if prey are located deeper in the water column (Reyer et al., 1988). Antipredator escape behaviors, such as the initiation of movements when predators contact the water or immediately before that moment (Reyer et al., 1988), could also benefit fish swimming in deeper water, where they could be more likely to escape from predators that catch their prey using a plunge-diving strategy. The perch height from which kingfishers begin their attack could also have a significant effect on fishing depth (Borah, 2011; Reyer et al., 1988).

Interestingly, we observed that kingfishers avoided fishing in deep water, most likely because their capture rates were low under such conditions. This observation shows that the kingfishers can evaluate whether the effort of fishing is energetically justified. The negative effect of deep water on foraging rate and success may be the ultimate reason for the preference of kingfishers to fish in
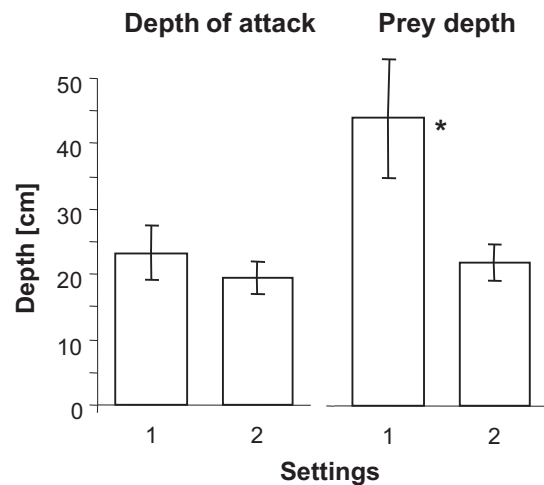
shallow water (Labinger et al., 1991; Reyer et al., 1988; Wanink and Kees, 1994).

Our results show a tendency for the kingfishers to fish preferentially in shallow water. The number of attacks and capture success were both greater at a depth of approximately 25 cm, the usual depth limit in nature (Cramp, 1985; Chandler and Llewellyn, 2010). The kingfishers do not perform hovering attacks, although this tactic might allow them to feed at greater depths. Therefore, it appears that the depths achieved in diving plunges are determined by the height of the perches used.

4.2. Effect of bottom color

Because kingfishers base their fishing strategy on visual perception (Cramp, 1985; Gendron, 1986; Moroney and Pettigrew, 1986) prey visibility is a fundamental aspect of the fishing process. We observed that kingfishers tended to take more fish (we did not obtain significant differences, but we found an effect size >0.5) when fishing over a white bottom rather than a natural gravel bed. We can conclude that clear or sandy river beds offer the best conditions for fishing; hence, kingfishers can fish more successfully over relatively homogeneous beds. This result is consistent with the findings of other studies on similar kingfisher species (Kelly, 1996).

4.3. Grouped or isolated fish prey

Although isolated prey have been reported to be more vulnerable to capture than those forming shoals (Rountree and Sedberry, 2009), we observed that the kingfishers focused their attacks more often on shoals than on isolated fish, although the capture success did not differ between these two types of prey. This tendency to attack groups of fish was common to all experiments and is consistent with previous studies in which the prey density was an important determinant of fishing site selection in kingfishers (Reyer et al., 1988).

4.4. Capture success

The fishing success rate, 24.9%, differed greatly from the success rates found with other kingfishers reared in captivity (100%, Labinger et al., 1991; Reyer et al., 1988). In these previous studies, however, the birds used in the experiments had much longer

accommodation periods (hand-reared birds). Nevertheless, our results more closely resembled those obtained for other fish-eating birds (Greig et al., 1983; Lotem et al., 1991) and also agree with studies where lower capture rates were reported in young herons than in adult birds (Draulans, 1987; Quinney and Smith, 1980; Recher and Recher, 1969).

5. Conclusions

Although the number of attacks and captures were higher over the gravel bottom, the size effect test showed that the fishing skills of the kingfishers improved over light (white) backgrounds. The lack of significant differences in our findings could be explained if the gravel bottom used in the experiments was not sufficiently natural. Our results agree with the findings of previous studies carried out with similar kingfishers, where better foraging success appears to be related to clearer river beds (Kelly, 1996).

Our investigations of foraging strategy show that the Common kingfisher behaved as an opportunistic predator, preying upon the most accessible types of fish, and that the depth of the river bed and the bottom color were two factors that affected the success of captures.

References

Arizaga, J., Mendiburu, A., Alonso, D., Cuadrado, J.F., Jáuregui, J.I., Sánchez, J.M., 2010. Common Kingfisher *Alcedo atthis* along the coast of northern Iberia during the autumn migration period. Ardea 98, 161–167.

Arizaga, J., Barba, E., 2009. Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps *Sylvia atricapilla*. Ardea 97, 297–304.

Beaumont, W.R.C., 2011. Electric fishing: a complete guide to theory and practice. Game and Wildlife Conservation Trust.

Bertellotti, M., Yorio, P., 2000. Age-Related feeding behaviour and foraging efficiency in Kelp gull *Larus dominicanus* attending coastal trawlers in Argentina. Ardea 88, 207–214.

Boag, D., 1986. The Kingfisher. Shire Natural History. Blandford Press, Pool, Dorset.

Borah, J., 2011. Occupancy pattern and food-niche partitioning among sympatric kingfishers in Bhitarkanika mangroves, Orissa. Masters' degree dissertation Saurashtra University, Rajkot.

Campos, F., Fernández, A., Gutiérrez-Corchero, F., Martin-Santos, F., Santos, P., 2000. Diet of the Eurasian kingfisher (*Alcedo atthis*) in northern Spain. Folia Zool. 49, 115–121.

Chandler, D., Llewellyn, I., 2010. Kingfisher. New Holland Publishers, London.

Cohen, J., 1969. Statistical Power Analysis for the Behavioural Sciences. Academic press, New York.

Cox, S., Chandler, S., Barron, C., 2009. Benthic fish exhibit more plastic crypsis than non-benthic species in a freshwater spring. J. Ethol. 27, 497–505.

Cramp, S., 1985. Handbook of the Birds of Europe the Middle East and North Africa. Oxford University Press, Oxford.

Draulans, D., 1987. The effect of prey density on foraging behaviour and success of adult and first-year grey herons (*Ardea cinerea*). J. Anim. Ecol. 56, 479–493.

Endler, J.A., 1988. Frequency-dependent predation, crypsis and aposematic coloration. Phil. Trans. R. Soc. London 319, 505–523.

Galarza, A., Tellería, J.L., 2003. Linking processes: effects of migratory routes on the distribution of abundances of wintering passerines. Anim. Biodivers. Conserv. 26, 19–27.

Gendron, R.P., 1986. Searching for cryptic prey: evidence for optimal search rates and the formation of search images in quail. Anim. Behav. 34, 898–912.

Greig, S.A., Coulson, J.C., Monaghan, P., 1983. Age-related differences in foraging success in the herring gull (*Larus argentatus*). Anim. Behav. 31, 1237–1243.

Grémillet, D., Argentin, G., Schulte, B., Culik, B.M., 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? Ibis 140, 113–119.

Hallet, C., 1982. Étude du comportement de predation du Martin-Pêcheur *Alcedo atthis* (L.): taille prefentialle de capture du Chabot Cottus gobio L. et de la truitte *Salmo trutta* L. Rev. Ecol. (Terre Vie) 36, 211–222.

Iribarren, I.B., Nevado, L.D., 1982. Contribution a l'étude du régime alimentaire du Martin-Pêcheur (*Alcedo atthis* L. 1758). Alauda 50, 81–91.

Isotti, R., Consiglio, C., 2002. Dieta del Martin pescatore '*Alcedo atthis*' in alcune aree a carattere Mediterraneo. Riv. Itali. Orn. 71, 157–162.

Kelly, J.F., 1996. Effects of substrate on prey use by belted kingfisher (*Ceryle alcyon*): a test of the prey abundance-availability assumption. Can. J. Zool. 74, 693–697.

Kottelat, M., Freyhof, J., 2007. Handbook of European Freshwater Fishes. Steven Simpson Books, Switzerland.

Labinger, Z., Katzir, G., Benjamini, Y., 1991. Prey size choice by captive pied kingfishers *Ceryle rudis* L. Anim. Behav. 42, 969–975.

Lasiewski, R.C., Dawson, W.R., 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69, 13–23.

Laudelout, A., Libois, R., 2003. On the feeding ecology of the Pied Kingfisher, Ceryle rudis at Lake Nokoué, Bennin. Is there competition with fishermen? In: Cowx, I.G. (Ed.), Interactions Between Fish and Birds: Implications for Management. Blackwell Science, Oxford, pp. 165–177.

Lekuona, J.M., 2002. Food intake, feeding behaviour and stock losses of cormorants *Phalacrocorax carbo*, and grey herons, *Ardea cinerea*, at a fish farm in Arcachon Bay (Southwest France) during breeding and non-breeding season. Folia Zool. 51, 23–34.

Lotem, A., Schechtman, E., Katzir, G., 1991. Capture of submerged prey by little egrets *Egretta garcetta* garcetta: strike depth, strike angle and the problem of light refraction. Anim. Behav. 42, 341–346.

Miranda, R., Oscoz, J., Leunda, P.M., Escala, M.C., 2006. Weight–length relationships of cyprinid fishes of the Iberian Peninsula. J. Appl. Ichthyol. 22, 297–298.

Moroney, M.K., Pettigrew, J.D., 1986. Some observations on the visual optic of kingfishers (Aves, Coraciformes Alcedinidae). J. Comp. Physiol. A 160, 137–149.

Nagy, K.A., 1987. Field metabolic rate and food requirements scaling in mammals and birds. Ecol. Monogr. 57, 111–128.

Quinney, T.E., Smith, P.C., 1980. Comparative foraging behaviour and efficiency of adult and juvenile blue herons. Can. J. Zool. 58, 1168–1173.

Raven, P., 1986. The size of minnow prey in the diet of young Kingfishers *Alcedo atthis*. Bird Study 33, 6–11.

Recher, H.F., Recher, J.A., 1969. Comparative foraging efficiency of adult and immature little blue herons (*Florida caerulea*). Anim. Behav. 17, 320–322.

Reyer, H.-U., 1984. Invested and relatedness: a cost/benefit analysis of breeding and helping in the Pied kingfisher (*Ceryle rudis*). Anim. Behav. 32, 1163–1178.

Reyer, H.-U., Migongo-Bake, W., Schimdt, L., 1988. Filed studies and experiments on distribution and foraging of Pied and Malachite kingfishers at Lake Nakuru (Kenya). Anim. Behav. 57, 595–610.

Reynolds, S.J., Hinge, M.D.C., 1996. Foods brought to the nest by breeding Kingfishers *Alcedo atthis* in the New Forest of southern England. Bird Study 43, 96–102.

Remsen, J.V., 1990. Community Ecology of Neotropical Kingfishers. University of California Publications in Zoology, California.

Rountree, R.A., Sedberry, G.R., 2009. A theoretical model of shoaling behaviour based on a consideration of patterns of overlap among the visual fields of individual members. Acta Ethol. 12, 61–70.

Sherry, T.W., 1990. When are birds dietarily specialized? Stud. Avian Biol. 13, 337–352.

Stewart, D.C., Middlemas, S.J., Gardiner, W.R., Mackay, S., Armstrong, J.D., 2005. Diet and prey selection of cormorants (*Phalacrocorax carbo*) at Loch Leven, a major stocked trout fishery. J. Zool. 267, 191–201.

Terraube, J., Arroyo, B., Madders, M., Mougeot, F., 2011. Diet specialization and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. Oikos 120, 234–244.

Tjomlid, S.A., 1973. Food preferences and feeding habits of the Pied Kingfisher *Ceryle rudis*. Ornis Scand. 4, 145–151.

Vilches, A., Miranda, R., Arizaga, J., 2012a. Fish prey selection by the Common Kingfisher *Alcedo atthis* in Northern Iberia. Acta Ornithol. 47, 167–175.

Vilches, A., Miranda, R., Arizaga, J., Galicia, D., 2012b. Habitat selection by breeding Common Kingfishers (*Alcedo atthis* L.) in rivers from Northern Iberia. Ann. Limnol.: Int. J. Lim. 48, 289–294.

Wanink, J.H., Kees, P.C.G., 1994. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria East Africa, on the diet of Pied Kingfishers (*Ceryle rudis*). Hydrobiologia 279/280, 367–376.

Warburton, K., Thomson, C., 2006. Cost of learning: the dynamics of mixed-prey exploitation by silver perch *Bidyanus bidyanus*. Anim. Behav. 71, 361–370.