Factors Affecting the Foraging Behavior of the Squacco Heron

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Abstract.—The foraging behavior of adult and recently fledged juvenile Squacco Herons (*Ardeola ralloides*) was studied during the breeding season at the Axios Delta, northern Greece. Adults were more efficient foragers than young birds and they had a 37% higher success per peck rate. The majority of adults captured some large prey items, while most juveniles caught only small prey. A comparison between the two age classes, as well as seasonal trends in adult data, indicated a negative association between prey size and foraging rates. Adult and juvenile foraging behavior did not vary significantly between morning and evening. Herons that moved faster also had higher pecking and capture rates, but a lower success ratio. Moving rate did not appear to be correlated with prey size. Herons moved at a slower rate along the edge of dense reed beds, probably in response to this habitat's physical structure. Adults caught a greater proportion large prey items in open-water areas than in areas with more vegetation. *Received 15 May 2004, accepted 19 September 2004.*

Key words.—Squacco Heron, *Ardeola ralloides*, foraging behavior, foraging success, peck rate, Greece.

Foraging activity is an essential aspect of the life of birds, being necessary for their survival and reproduction. The feeding behavior of herons and their relatives has been the subject of many field studies, because of their large size and conspicuous activities, which facilitate observations. Some studies have addressed issues of foraging distribution and time budgets (van Vessem and Draulans 1987; Marion 1989), resource use and partitioning in communities (Kent 1986a, b; Fasola 1994), the optimality of alternative strategies and decisions (Erwin 1985; Richner 1986) and the consequences of feeding success for reproduction (Hafner *et al.* 1993). Other studies have examined the effects on foraging behavior of herons: of the bird's age (Quinney and Smith 1980; Cezilly and Boy 1988), prey availability (Draulans 1987; Wong *et al.* 2000), time of the year (Campos and Lekuona 1997) and day (Kersten *et al.* 1991), weather conditions (Quinney and Smith 1980), and habitat characteristics (Hafner *et al.* 1982; Dimalexis *et al.* 1997), including the hydrological regime (Strong *et al.* 1997; Matsunaga 2000) and pollution level (Maccarone and Brzorad 2000) of wetlands.

The Squacco Heron (*Ardeola ralloides*) is a small ardeid with a limited distribution in the western Palearctic (Cramp and Simmons 1977) and less conspicuous foraging habits than sympatric relatives (Voisin 1978, 1991). Probably due to this, relatively little information is available about its foraging ecology. Fasola (1986, 1994) has examined its preference for different habitat and prey types in comparison with those of other ardeids in southern Europe, while Hafner *et al.* (1982) have compared its feeding behavior and food intake with those of the Little Egret (*Egretta garzetta*) in two habitats in the Camargue, southern France. In this study, we compare the foraging behavior of adult and recently fledged (referred to as juvenile) Squacco Herons. We also examine foraging behavior over the later part of the breeding season, between morning and evening and in three microhabitats. The associations of foraging activity rates, success and prey size were also investigated.

STUDY AREA AND METHODS

The study was conducted at the Axios Delta, northern Greece (40°30'N, 22°53'E). The delta is part of a wetland complex of international importance, which

stretches along the west coast of Thermaikos Gulf, near the city of Thessaloniki. This area comprises a variety of habitats, including saltwater and freshwater marshes, lagoons, tidal mudflats, open sea, coastal islets, sandy shores, riparian forest and tamarisk bushland. Rice fields, irrigation channels and drainage canals also attract waterbirds, including foraging ardeids (Kazantzidis and Goutner 1996), and especially the Squacco Heron, which feeds exclusively in freshwater habitats (Voisin 1991). During our study, 150-200 pairs of Squacco Heron nested in the area, in a mixed-species colony, together with Little Egret, Black-crowned Night Heron (*Nycticorax nycticorax*), Spoonbill (*Platalea leucorodia*) and Great Cormorant (*Phalacrocorax carbo*).

We studied the behavior of Squacco Herons foraging in a vegetated drainage canal, in the west part of the Axios Delta, between 26 June and 3 August 1995. Observations were made from a car on an elevated road running parallel to the canal. Within our study, such canals were the main foraging sites of the Squacco Heron. Data were collected from adult herons throughout the study (52 h of observations). Data collection on juveniles (10 h) started on 10 July, when they first appeared at the study site. Observations were made in the morning (08.00-11.00 h) and in the evening (17.00-20.00 h), under favorable weather conditions (no strong wind or rain), with a 20-60× telescope. Information was audio-recorded for later transcription, while activities were timed with a stopwatch. Each observation started with a strike at a prey item and also ended with a strike. Only observations that lasted ≥4 min were included in analyses, totaling 246 observations on adults and 45 on juveniles.

The following information was recorded for each observed bird: age class, date, time of day, microhabitat type, foraging method, duration of observations, size of prey items, and the number of pecks, captures and steps made. Each of the last three variables was divided by the duration of observations to calculate, respectively, each bird's pecking rate (pecks/min), capture rate (captures/min) and moving rate (steps/min). Each bird's success ratio was calculated as captures/strikes. We used the three activity rates, the success ratio and prey size to describe the herons' foraging behavior and success. Squacco Herons captured fish, frogs and tadpoles, aquatic invertebrates, and Mole Crickets (*Gryllotalpa gryllotalpa*). By comparison with the birds' bill (mean bill length of 63 mm in both sexes; Cramp and Simmons 1977), prey items were estimated as 1-7 cm long. We categorized prey items as small (<1/3 of bill), medium (1/3-2/3 of bill) and large (>2/3 of bill), but we did not always record the number of captured items in each size class. Therefore, for the purposes of data analysis, observations were divided in two groups: a) those where birds caught only small prey items and b) those where birds caught at least some larger items (20-100% of each individual's prey items were medium or large). Hereafter, we will refer to both medium and large prey items as "large", to contrast them with the original "small".

Five variables represent factors whose potential effects on heron foraging were examined. "Age class" had two levels (adult and juvenile), and "time of day" also two (morning and evening). "Calendar period" had three levels, which were based on the date of observations: 26 June-9 July, 10-20 July, and 21 July-3 August. Since we did not observe any foraging juveniles in the first period, we excluded adult data from this period when we examined the effects of age on the dependent variables, in order to avoid potential biases. Three

microhabitat types were distinguished in our study site: a) open water, where herons often stood and walked on submerged aquatic vegetation; b) edge of dense vegetation, mainly *Phragmites* sp. reed beds, where birds used reed stalks for support; c) canal bank, with sparse and low vegetation, where birds stood and walked on land or in shallow water. A total of 36 adult and six juvenile observations were excluded from the analysis of microhabitat effects, where birds used more than one microhabitat and thus their foraging behavior could not be associated solely with any particular habitat type.

Most of the herons used two foraging methods, *stand-and-wait* and *walking slowly* (as in Kushlan 1976, 1978). Birds waiting for prey were often perched on the edge of dense reed beds, up to 30 cm above water level, but also on wooden canal markers, about one m above the water. The former mostly struck at prey with a rapid extension of the neck, while the latter had to dive into the water, after which they flew back to their perch. Herons stalked prey by walking slowly in the canal, on submerged aquatic vegetation, or along its banks. Before striking, they either froze, sometimes slowly extending their necks, or they took some rapid steps. A few adult herons, mostly birds in the canal and standing on submerged vegetation, used a third, active foraging method, which had not been described before in this species. They took numerous rapid steps, sinking in the water as the supporting plants subsided under their weight, extending and flapping their wings to keep their balance and reduce sinking, and pecking repeatedly at the water surface, in various directions. This chasing behavior could be classified as *disturb-and-chase* feeding (Kushlan 1976, 1978), because the strike pattern seems to indicate that birds were not pursuing a focal prey item, but pecked at any prey that became visible in the dense, submerged vegetation. When such birds caught a prey item, they flew to a nearby perch to swallow it and then returned to the same general area to repeat the procedure. During the observation period, some birds (10% of adults and 5% of juveniles) exclusively waited for prey and took no steps at all, but all others employed a combination of the above methods, mostly waiting and walking slowly (chasing was used only by a few adults). For the purposes of data analyses, observations were grouped into a) those with a moving rate ≤ the sample median (2.53 steps/min for juveniles and 3.44 steps/min for adults) and b) those with a higher moving rate, and we compared the foraging behavior of slow- and fast-moving birds.

Statistical analyses were performed on SYSTAT 8.0, following the guidelines of Zar (1996). Prey size is a categorical variable and trends were analyzed with contingency tables. In all 2×2 tables, Yates' correction was used in the calculation of χ^2. With the exception of the comparison between age classes, we used only adult data in prey-size analyses, because only two juveniles caught large prey items. The other four dependent variables are continuous, but their distributions deviate significantly from normality. The distributions of pecking and capture rate data were normalized with a logarithmic transformation, while the square root transformation normalized the distribution of moving rate. The transformed data were analyzed with t-tests and ANOVAs, depending on the number of factor levels; multiple pairwise comparisons after a statistically significant ANOVA were made with Tukey's tests. Sample means of these three variables and their upper and lower 95% confidence limits are presented in tables and figures in

their original units, after reverse transformation. The success ratio data could not be normalized by either of the above methods, or by the angular transformation, because large percentages of individuals, especially in adult samples (e.g., 61% of slow-moving adults), had a success ratio of 1.0 (every peck led to prey capture). Therefore, we analyzed the raw success ratio data with non-parametric Mann-Whitney U and Kruskal-Wallis tests, and present sample medians with their 95% confidence intervals.

RESULTS

Data on adult and juvenile foraging are shown in Table 1. Moving rate did not vary significantly between the two age classes (t_{246} = 1.24, n.s.). Juveniles attempted to and succeeded in capturing more prey items per unit time than adults: their mean pecking rate was three times as high as that of adults (t_{246} = 10.8, P < 0.001), and their mean capture rate was 2.4 times as higher than adults (t_{246} = 7.74, P < 0.001). Adults, however, had a 37% higher median success per attempt ratio than juveniles (U_1 = 2816, P < 0.001). Moreover, most adults (137 out of 199, or 69%) caught some large prey, while the vast majority of juveniles (43 out of 45, or 96%) caught only small items (χ^2_1 = 59.5, P < 0.001). Juveniles thus appeared to be less proficient foragers than adults and may have exhibited higher pecking and capture rates because they pursued smaller prey (see Discussion).

There was no significant seasonal variation in the juvenile data. Adult pecking rate varied significantly among the three observation periods ($F_{2, 243}$ = 12.7, P < 0.001), and, as can be seen in Figure 1, its mean was higher by 55% in the first period than in the second (Tukey's P < 0.001) and by 85% in the third period (Tukey's P < 0.001). Figure 1 shows that the same trend occurred for the adult capture rate ($F_{2,243}$ = 21.7, P < 0.001): its mean in the first period was almost twice as high as in the second (Tukey's P < 0.001) and

more than twice as high as in the third (Tukey's P < 0.001). The percentage of adults that caught only small prey varied significantly among the three successive periods (χ^2_2 = 23.4, P < 0.001) and was, respectively, 67% (29 out of 43), 25% (26 out of 104) and 38% (36 out of 95). Pairwise comparisons showed that it was significantly greater in the first period than in the second (χ^2_1 = 21.6, P < 0.001) and third periods (χ^2_1 = 9.22, P < 0.01). The adult pecking and capture rates were higher in the first period, when a greater proportion of adults caught only small prey.

The time of day had no significant effect on either adult or juvenile foraging behavior. Foraging method (high *vs* low moving rate) affected all adult foraging rates (Table 2): fast-moving individuals (mean = 7.30 steps/min) had a 62% higher mean pecking rate (t_{244} = 5.16, P < 0.001) and a 46% higher mean capture rate (t_{244} = 3.80, P < 0.001), but slow movers (mean = 1.16 steps/min) achieved a 20% greater median success ratio (U_1 = 9477, P < 0.001). The same trends were also observed between fast-moving (mean = 5.33 steps/min) and slow-moving (mean = 1.19 steps/min) juveniles (Table 2): the former had more than twice the mean pecking rate of the latter (t_{43} = 3.45, P < 0.001) and a 75% higher mean capture rate (t_{43} = 2.20, P < 0.05), but the latter enjoyed a 36% greater median success ratio (U_1 = 348, P < 0.05). Foraging method did not significantly affect the proportion of adults who caught large prey (60% of 122 slow movers and 65% of 120 fast movers; χ^2_1 = 0.48, n.s.).

There was no significant variation in juvenile foraging behavior among the three microhabitats. However in adults, there was significant microhabitat effects in moving rate ($F_{2,192}$ = 19.3, P < 0.001), pecking rate ($F_{2,192}$ = 3.36, P < 0.05) and in the propor-

Table 1. Adult and juvenile Squacco Heron mean pecking, capture and moving rates, and median success ratio; 95% confidence intervals are shown in parentheses.

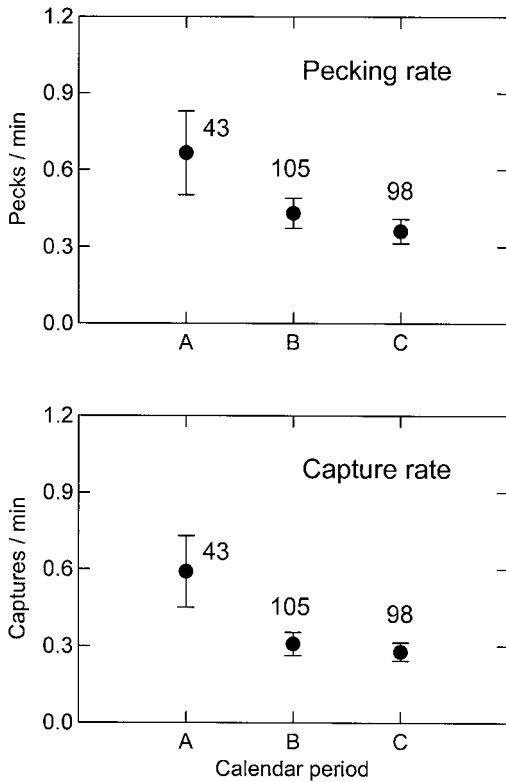| Age class	Mean pecking rate (pecks/min)	Mean capture rate (captures/min)	Mean moving rate (steps/min)	Median success ratio (captures/pecks)
Adult (N = 203)	0.40 (0.36, 0.43)	0.29 (0.27, 0.32)	3.61 (3.09, 4.16)	0.86 (0.80, 1.00)
Juvenile (N = 45)	1.20 (0.93, 1.51)	0.70 (0.52, 0.89)	2.89 (2.18, 3.70)	0.63 (0.52, 0.71)

Figure 1. Adult Squacco Heron pecking and capture rates (means ± 95% confidence limits) by calendar period (A: 26 June-9 July; B: 10-20 July; C: 21 July-3 August). Sample sizes are indicated above or next to their respective sample means.

tions of birds which caught prey of different sizes ($\chi^2_2 = 15.3$, P < 0.001). As can be seen from Figure 2, the mean adult moving rate on the edge of vegetation (microhabitat B) was only a third of the mean in open water areas (microhabitat A; Tukey's P < 0.001) and less than a quarter of the mean along canal banks (microhabitat C; Tukey's P <
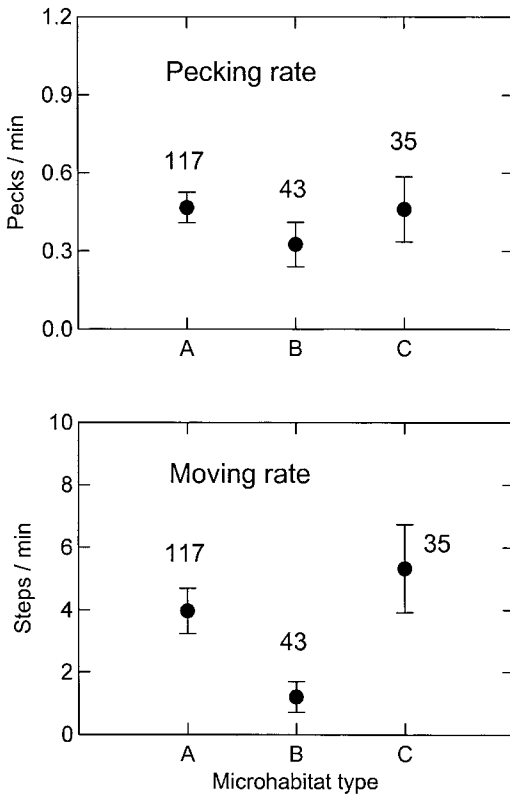
0.001). The mean adult pecking rate on the vegetation edge (Fig. 2) was 30% lower than in open water areas (Tukey's P < 0.05), but was not significantly lower than along canal banks. The proportion of adults that captured some large prey items was greater in open-water areas (90 out of 116, or 78%) than on the edge of dense vegetation (22 out of 42, or 52%; $\chi^2_1 = 8.31$, P < 0.01) or along canal banks (17 out of 35, or 49%; $\chi^2_1 = 9.60$, P < 0.01).

DISCUSSION

Adult Squacco Herons had a significantly higher success per peck ratio than juveniles (86% vs 63%, Table 1). The same relationship has been found in many ardeids (Recher and Recher 1969; Quinney and Smith 1980; Lo and Fordham 1986; Burger and Gochfeld 1989), though juveniles may attain as high a success ratio as adults in flocks (Cezilly and Boy 1988) or at high prey density sites (Draulans 1987). The lower foraging success of young herons may stem from a lack of sensorimotor maturity (Cezilly and Boy 1988) and/or experience (Burger and Gochfeld 1989). The latter may involve the location of high-yield sites at profitable times (Draulans and van Vessem 1985), the formation of a search image for prey items and the coordination of foraging with other activities, such as vigilance (Cezilly and Boy 1988). Juvenile herons also tend to capture smaller prey items than adults (Siegfried 1972; Quinney and Smith 1980; Draulans 1987) and thus achieve a lower food intake rate (Recher and Recher 1969; Draulans and van Vessem 1985). In our study, 96% of juveniles

Table 2. Adult and juvenile Squacco Heron mean pecking and capture rates, and median success ratio, by foraging method; 95% confidence intervals are shown in parentheses.

Foraging method	Mean pecking rate (pecks/min)	Mean capture rate (captures/min)	Median success ratio (captures/pecks)
Adult			
Slow-moving (N = 124)	0.34 (0.29, 0.39)	0.28 (0.23, 0.32)	1.00 (1.00, 1.00)
Fast-moving (N = 122)	0.55 (0.49, 0.61)	0.41 (0.36, 0.46)	0.83 (0.73, 0.88)
Juvenile			
Slow-moving (N = 23)	0.81 (0.55, 1.10)	0.52 (0.36, 0.69)	0.71 (0.60, 0.81)
Fast-moving (N = 22)	1.71 (1.23, 2.29)	0.91 (0.58, 1.31)	0.52 (0.40, 0.69)

Figure 2. Adult Squacco Heron pecking and moving rates (means ± 95% confidence limits) by microhabitat type (A: open water; B: vegetation edge; C: canal bank). Sample sizes are indicated above or next to their respective sample means.

ture) rates are probably related to the fact that they caught smaller prey items than adults. A similar association was found in adults, over the three observation periods: foraging rates were significantly higher in the first period (Fig. 1), when a significantly greater proportion of birds caught only small prey. Food intake rate depends both on capture rate and on prey size (Dimalexis *et al.* 1997; Campos and Lekuona 2001). Herons which capture small prey may need to intensify their foraging rates, in order to meet dietary demands. At the same time, the foraging rates of individuals which capture large prey may be constrained, because the pursuit and capture of such prey is often more time-consuming (Dimalexis *et al.* 1997; Wong *et al.* 2000).

A smaller proportion of adults caught large prey in the first observation period, and this may be because such prey were less available at that time. Seasonal variation in heron food type and size often reflects changes in prey availability (Matsunaga 2000; Richardson *et al.* 2001). Another possibility is that in the first period, a greater proportion of adults selected small prey, because they were feeding small nestlings that could not swallow large items (Moser 1986; Campos and Lekuona 1997). We found no significant seasonal variation in juvenile data. The foraging skills of juvenile herons often improve with increasing age and experience (Rodgers 1983), even over weekly intervals (Quinney and Smith 1980). One reason why we did not observe any such trend over 25 days of observation may have been because the feeding skills of juvenile Squacco Herons develop slowly, although it was evident that newly fledged, inexperienced birds were continually added to the foraging juvenile group, thus keeping the average feeding performance at a low level.

The foraging behavior of adult and juvenile Squacco Herons varied little and non-significantly between morning and evening. The feeding activity of herons in estuaries is usually affected by the tidal cycle, and is often independent of time *per se* (Richner 1986; Matsunaga 2000). In non-tidal habitats, ardeids may vary their foraging methods

caught exclusively small prey, while 69% of adults also captured large items in substantial proportions. This difference in prey size between the two age classes, as well as the higher success ratio of adults, indicate greater foraging efficiency in the older birds.

Adult and juvenile pecking rates are often similar in ardeids, while adults commonly attain a greater capture rate (Quinney and Smith 1980; Draulans and van Vessem 1985; Lo and Fordham 1986). In some cases, however, juveniles strike at prey items at a higher rate than adults, presumably to compensate for their lower success ratio (Rodgers 1983). In our study, the pecking rate of juveniles was three times that of adults (Table 1), so that, while having a lower success ratio, juveniles still captured 2.4 times as many prey items per minute as adults (Table 1). The juveniles' greater foraging (pecking and cap-

and intensity between morning and evening hours (Erwin *et al.* 1985; Lo and Fordham 1986), but changes often occur at times outside our observation periods (Fasola 1984; Kersten *et al.* 1991). The foraging activity of Little Egrets in Camargue marshes closely followed changes in prey availability (Kersten *et al.* 1991). Therefore, we may infer that the availability of prey did not differ significantly between the morning and evening.

Adult and juvenile Squacco Herons that moved at a faster average rate had greater pecking and capture rates (Table 2). Similar trends have been found in this species in Camargue (Hafner *et al.* 1982), as well as in other ardeids (Forbes 1987; Dimalexis *et al.* 1997). The underlying reason is probably that, by moving, birds encounter, and thus get opportunities to strike at and catch, more prey items, at least when the latter are not highly mobile (Fasola 1984). Fast-moving herons of both age classes had a significantly lower success ratio (Table 2), which has also been found in some North American ardeids (Rodgers 1983; Kent 1987). Birds moved fast mostly when they pursued escaping prey, which should be more elusive than the sedentary or undisturbed prey that is usually caught by walking or standing (Kent 1987). A negative association between heron moving rate and prey size and/or mobility has been found in many species (Kent 1986a; Forbes 1987; Dimalexis *et al.* 1997; Wong *et al.* 2000), including the Squacco Heron (Hafner *et al.* 1982). Therefore, we would expect large prey to be captured more often by slow-moving birds, assuming that large prey items are more elusive than small ones (<2 cm in length). However, we found that moving rate was not associated with the proportion of adults that caught large prey. This may merely result from the fact that most birds varied their moving rate during the period they were observed.

The foraging behavior and success of many ardeids, including the Squacco Heron (Hafner *et al.* 1982), can be affected by the habitat (Hafner *et al.* 1986; Maccarone and Brzorad 2002), or even by the microhabitat (Kersten *et al.* 1991) where they feed. This may be due to differences in habitat struc-ture (Dimalexis *et al.* 1997) and/or prey availability (Richner 1986; Maccarone and Parsons 1994; Campos and Lekuona 2001). We found that the moving rate of adult Squacco Herons was significantly lower on the edge of dense vegetation (reed beds) than in open-water areas or along canal banks (Fig. 2), probably in response to the physical characteristics of the different microhabitats. Reeds grew out of deep water and submerged plants were not abundant next to their patches. Thus, in order to move, herons would have to scramble from one reed stalk to the next, while they could walk or wade more freely along banks, in shallow water or on thick submerged vegetation in deep open-water areas. In agreement with the positive association between moving and foraging rates discussed in the previous paragraph, we found that the adult pecking rate was also lower on the edge of reed beds (Fig. 2). A significantly higher proportion of adults caught large prey in open-water areas than in the other two microhabitats, possibly because such prey was more highly available there (Campos and Lekuona 2001; Richardson *et al.* 2001).

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