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# Effect of age on the foraging behaviour of Grey Heron *Ardea cinerea* L., 1758 at a submontane dam reservoir in the post-breeding season

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## ABSTRACT

The components of foraging behaviour and success of adult and juvenile Grey Heron *Ardea cinerea* were studied at the Dobczyce Reservoir (southern Poland) in July and September 2015. Juvenile and adult birds moved at similar rates during both months. Fish capture attempt rate was significantly higher for juvenile birds than for adults in July but not in September. Capture rate and foraging success probability (number of captures over all attempts) was significantly lower in juveniles in July but not in September. The foraging success probability of juveniles increased from July to September. Adult and juvenile birds caught mostly small fish, with no differences in size. However, handling time in juvenile birds was much longer than in adults in July but not in September, after controlling for differences in prey size. Thus, juvenile Grey Heron increased their efficiency of catching fish from July to September by reducing the number of mistakes, probably as a result of experience.

**Keywords**: heron, behaviour, foraging success, fish size, bird age

## 1. INTRODUCTION

Studies on differences in foraging behaviour of birds belonging to different age classes enable an understanding of how life strategies change with age. According to optimal foraging theory, foragers search for prey that will provide the highest energetic benefit (Stephens and Krebs, 1986). However, individuals differ in their behavioural choices, especially juvenile birds with a lack of relevant experience and abilities and are usually less effective in finding food due to selection of less favourable areas, times for feeding and making mistakes (Draulans and Hannon, 1988; Voisin, 1991; Watson and Hatch, 1999; Kushlan and Hancock, 2005; Skórka *et al.*, 2016). However, since many studies compare foraging success of different age classes at the same time (*e.g.* Bertellotti and Yorio, 2000; Skórka and Wójcik, 2008), there is poor, direct evidence that the same young birds increase their foraging efficiency in one area during a short period.

The Grey Heron *Ardea cinerea* L. is an excellent model to study age-related feeding efficiency because of marked differences between young and adult birds (large body size and specific characteristics of the foraging behaviour) that are easy to note in the field. Grey Heron feeding behaviour has been studied in several habitats during the breeding season (Owen, 1995; Lekuona, 1999; Gwiazda and Amirowicz, 2006; Choi and Yoo, 2011), post-breeding season (Cook, 1978) and winter period (Regos, 2011). Heron may adopt different tactics and achieve variable foraging efficiencies in response to habitat conditions and prey characteristics (Dimalexis *et al.*, 1997; Regos, 2011). The important elements of Grey Heron foraging strategy seems to be prey selection among those available at a foraging site (Jakubas and Manikowska, 2011). Fish size can play an important role in the choice of prey, and heron generally show a preference for larger prey (Britton and Moser, 1982; Feunteun and Marion, 1994; Gwiazda and Amirowicz, 2006). Various authors have suggested that juvenile heron are less successful at feeding and spend more time perfecting feeding skills than adults (Carss, 1993; Lekuona, 2002; Papakostas *et al.*, 2005). Juvenile birds must learn to catch and handle prey in aquatic habitats (Voisin, 1991; Kushlan and Hancock, 2005). Changes in the effectiveness of hunting over time, since fledging, has not yet been studied in juvenile Grey Heron.

The objectives of the study were to compare: (1) the components of foraging behaviour (steps, attacks and captures rates, foraging success, prey size and handling time) of adult and juvenile Grey Heron in the same habitat; and (2) the changes of foraging success of juvenile Grey Heron in the first three months of life in one habitat.

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## 2. METHODS

### 2.1 Study area

The study was carried out at the Dobczyce Reservoir (49°52′N, 20°02′E) located on the Raba River in southern Poland about 30 km south of Cracow (Figure 1). The reservoir was established in 1986. It is a submontane, eutrophic reservoir with an area of 985 ha, a mean depth of 11.0 m and a shoreline of approximately 42 km (Amirowicz, 1998). The main function of the Dobczyce Reservoir is the storage of water for municipal purposes. The littoral zone is narrow because of the relatively steep slopes of the inundated river valley. The aquatic macrophytes are restricted to the shallow bay and some other small areas. More abundant are *Phragmites australis* (Cav.) Trin. ex Steud. and *Polygonum amphibium* L.

Five cyprinid and percid species dominate the fish community (Roach, *Rutilus rutilus* L.; Bream, *Abramis brama* L.; Bleak, *Alburnus alburnus* L.; Perch, *Perca fluviatlis* L.; and Pikeperch, *Sander lucioperca* L.). The fish biomass in the littoral zone, as estimated by shore seining, reached 233 kg ha$^{-1}$ (method captures only individuals $>20$ cm of total length (TL); Starzecka *et al.*, 1999). Relative fish density in the limnetic zone, as estimated in acoustic surveys, was 3390–5625 ind. ha$^{-1}$ (Godlewska and Świerzowski, 2003). The avifauna is dominated by Great Crested Grebe, *Podiceps cristatus* L.; Mallard, *Anas platyrhynchos* L.; and Black-headed Gull, *Chroicocephalus ridibundus* L. (Gwiazda, 1996). Grey Heron have been present since the reservoir was created in 1986 (Gwiazda, 1989), but breeding had not been recorded until 1999. Breeding colonies of heron in the small forest on the shore of the reservoir (area about 8 ha) numbered 60–70 nests in 2013, 45–50 nests in 2014 and 30 nests in 2015. Grey Heron foraged mostly in the flat and shallow backwater of the reservoir (Gwiazda, 2005), and the most abundant prey was Roach (Gwiazda and Amirowicz, 2006).

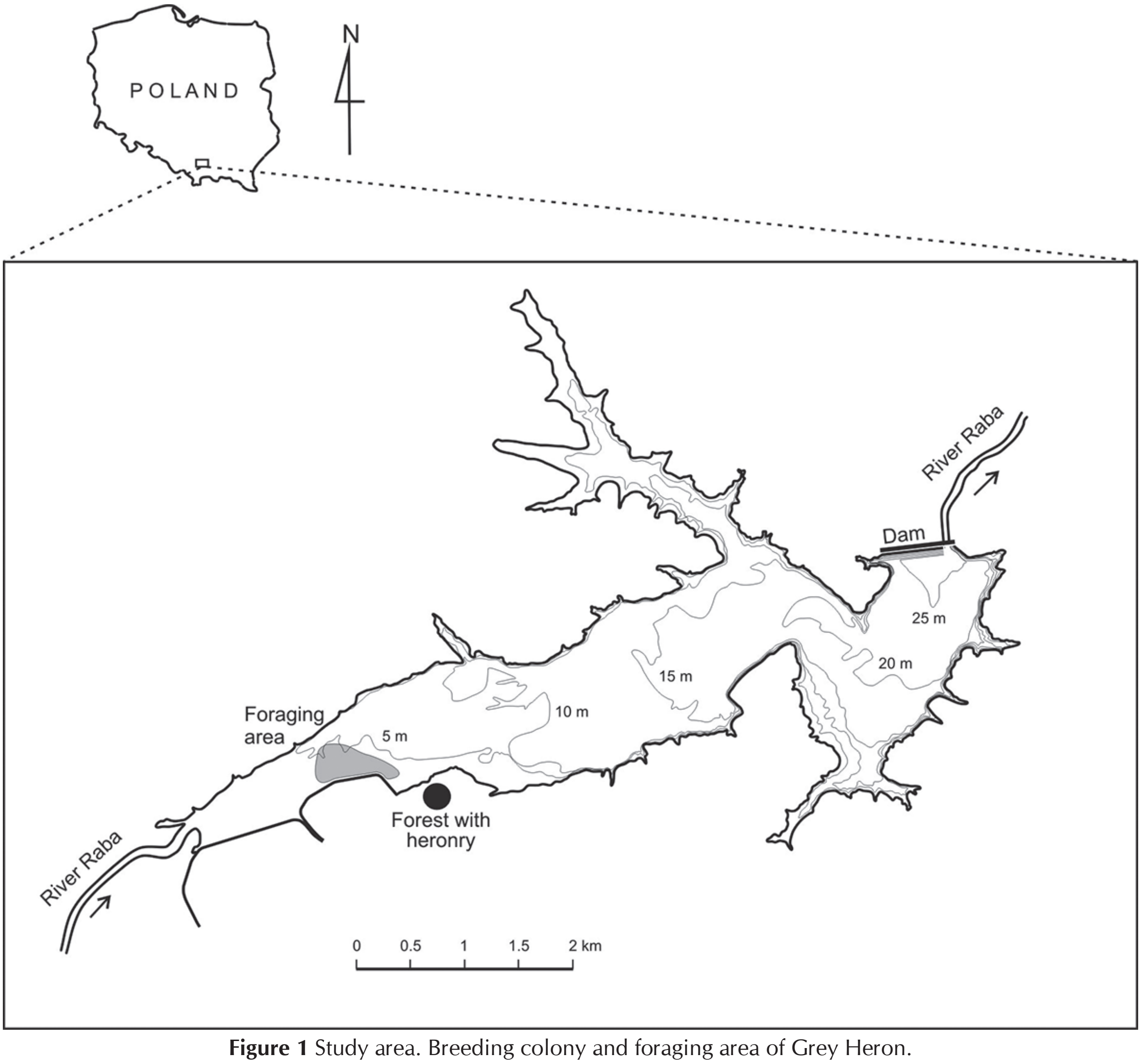

**Figure 1** Study area. Breeding colony and foraging area of Grey Heron.

### 2.2 Materials and statistical analysis

The foraging behaviour of Grey Heron was observed in the backwater areas of the reservoir. During observations and data collection the foraging birds were not disturbed. Birds were chosen opportunistically and followed for 10 min sessions according to the methodology proposed by Altmann (1974). Individual feeding birds were recorded from shore from distances of 100–500 m, using 20–60 × 60 and 38 × 82 telescopes. Because the birds were not individually marked in the study area, during each day of fieldwork only a few adult and juvenile individuals were observed within sessions to be sure that at each time a different bird was observed in the same day. Observations of birds which were feeding for less than the time of a standard session were rejected. Only standard 10 min feeding sessions were taken forward to be analysed.

The plumage characteristics of juvenile (first year) birds allow them to be readily distinguished from older ones. Adults and juveniles were observed in July 2015 and September 2015. We also counted Grey Heron in the backwaters of the reservoir during every survey: 34–57 individuals in July and 46–72 in September. Observations were carried out mostly in the morning (05.00–10.00) because the foraging activity of birds was lower at noon. Time of day was divided in four groups in both periods: $<2$ hours after sunrise; 2–5 hours after sunrise; 2–4 hours before sunset; and $<2$ hours before sunset. In July, the observations were made for 10 days; in August and September, observations were made for seven days each month. All observations were conducted under stable weather conditions, with small or moderate cloud cover, without strong wind and rain.

The number of steps taken during foraging, number of attacks, and number of captures were counted in each 10 min observation period. Movement rate was measured as the number of steps per minute in accordance with the methodology suggested by Rodgers (1983). Feeding behaviour was divided into three categories: standing (stand in one place without any steps); walking slowly (fewer than 60 steps per minute); and walking quickly (faster than 60 steps per minute). Walking, attack and capture rates were calculated per minute. Fish size (TL, cm) was estimated relative to bill length (culmen length *ca* 2 cm) and divided into three classes, $<0.5\times$, $0.5–1\times$ and $1–1.5\times$ bill length. We assumed that prey in the first class was $<6$ cm, prey in the second class was 6–12 cm, and prey in the third class was $>12$ cm TL. Based on field data, foraging success was calculated as the ratio between the number of successful attacks to total attacks. Handling time of caught prey was measured using a chronometer. Prey biomass taken by birds in a unit of time was calculated based on the capture rate and mean fish biomass. Mean fish biomass was estimated for Roach, which was the most abundant species in the diet of Grey Heron at the Dobczyce Reservoir (Gwiazda and Amirowicz, 2006). The biomass of this species was calculated using regression formulas to estimate fish mass based on the mean total length of Roach at age 0+ (Dirksen *et al.*, 1995).

All statistical analyses were performed using SPSS IMAGO 25 software (IBM, Armonk, NY). We examined the relationships between occurrence of foraging behaviours and bird age using a chi-squared test. The rate of walking (number of steps per minute), attacks, captures and prey handling times were compared between adult and juvenile birds using a general linear mixed model. Rates were square-root transformed (except handling time that was ln-transformed) to homogenise variances between groups. To analyse success of foraging (number of successful attacks over failed) we used a generalised linear mixed model with binomial error distribution and logit-link function. We used a multinomial (ordinal) generalised linear mixed model with logit link function to compare the probability of fish from different size categories (small, medium and large) being caught by adult and juvenile birds in different months. In each general and generalised linear model, the explanatory fixed variables were age class (juvenile *vs* adults), month (July *vs* September) and interaction between age class and month. If the interaction term (age × month) was statistically significant in GLMMs, we used paired contrasts to test which means were statistically different. Specifically we compared if there were differences between ages in two months and if there is a change in behaviour of juvenile and adult birds across two months. Moreover, we included number of steps in the model for rates of attacks and successful attacks as a covariate to control for possible changes in behaviour with foraging duration. In a model for the handling time, we also included prey size as a categorical explanatory variable. The birds were not individually marked on the study area but we attempted not to observe the same bird during the same session and day. However, we cannot be sure that we observed different individuals in different days. To resolve this problem in each GLMM we included individual identity nested in a session (part of the day) and the latter nested in a day as a random effect. Session was nested in a day because days differed in longevity. Day was a third random factor. If the probability of type I error was $\geq 0.05$, results were considered to be statistically significant.

## 3. RESULTS

A total of 70 sessions for adults and 70 sessions for juvenile birds were recorded (Table 1). Both adult and juvenile birds foraged by standing and walking slowly, but both adults and juveniles preferred to hunt by walking slowly in July and September (91.3%, $n = 80$ and 88.3%, $n = 60$ for all sessions) compared to standing (8.7%, $n = 80$ and 11.7%, $n = 60$ for all sessions). We found differences in the manner adult and juvenile birds foraged in July and September ($\chi^2 = 7.67$, df = 1, $P < 0.01$, $n = 80$;

**Table 1** The mean (±SD) number of steps during foraging, attacks and captures performed by juvenile and adult Grey Heron during the post-breeding period in July and September at the study site

| | Steps $\min^{-1}$ | Attacks $\min^{-1}$ | Captures $\min^{-1}$ |
|---|---|---|---|
| July juvenile ($n=40$) | 7.51±4.98 | 1.52±1.34 | 0.02±0.06 |
| July adult ($n=40$) | 8.82±7.53 | 0.61±0.66 | 0.37±0.51 |
| September juvenile ($n=30$) | 4.70±4.03 | 0.28±0.34 | 0.08±0.14 |
| September adult ($n=30$) | 5.69±3.11 | 0.28±0.39 | 0.06±0.10 |

$\chi^2=7.92$, df=1, $P<0.01$, $n=60$, respectively). Juveniles foraged more by walking slowly in July and by standing in September.

There was no statistically significant effect of age class and month or the interaction between these two factors on the number of steps performed by birds during foraging (Table 2, Figure 2a). We found statistically significant differences in the attack rates between age classes and months (Table 2). However, there was also significant interaction between age and month (Table 2, Figure 2b). Juveniles had significantly higher rates of attack than adults in July (contrast estimate ±SE=0.476±0.100, $t_{108}=4.756$, $P<0.001$) but not in September (contrast estimate ±SE=0.023±0.116, $t_{116}=0.212$, $P=0.833$; Figure 2b). Moreover, the attack rate in juveniles was higher in July than in September (contrast estimate ±SE=0.694±0.125, $t_{49}=5.563$, $P<0.001$; Figure 2b). The rate of fish capture differed between age classes but not between months, however, there was a statistically significant interaction between these two factors (Table 2, Figure 2c). Fish capture rate in adults was higher than in juveniles in July (contrast estimate ±SE=0.377±0.060, $t_{116}=6.272$, $P<0.001$) but not in September (contrast estimate ±SE=0.059±0.057, $t_{85}=1.03$, $P=0.302$; Figure 2c). However, the difference in capture rates between months was non-significant in juveniles (contrast estimate ±SE=–0.090±0.095, $t_8=-0.953$, $P=0.127$). Finally, success probability depended on age but not month, and there was significant interaction between the age class and month (Table 2, Figure 2d). Adult birds had higher foraging success probability than juvenile birds in July (contrast estimate ±SE=0.527±0.144, $t_{11}=3.662$, $P=0.004$), but not in September (contrast estimate ±SE=0.151±0.157, $t_{74}$ =0.962, $P=0.339$). Moreover, foraging success probability in juveniles significantly increased between July and September (contrast estimate ±SE=0.170±0.078, $t_{26}=2.179$, $P=0.038$; Figure 2d). Foraging success probability did not differ statistically between the two months (contrast estimate ±SE=–0.207±0.211, $t_{14}=0.981$, $P=0.343$, Figure 2d).

Adult and juvenile heron both usually caught small fish. Prey >12 cm accounted for only 2.4% ($n=167$) of the total fish consumed by adults, and no such fish consumed by

**Table 2** Summary of general(ised) linear mixed models describing components of foraging behaviour of juvenile and adult Grey Heron in July and September. Estimates of variance associated with random effects are also shown (nested effects are given within brackets)

| Variables | *F* | $df_1$, $df_2$ | *P* |
|---|---|---|---|
| Rate of steps[a] ($n=140$) | | | |
| Age | 1.134 | 1, 19 | 0.300 |
| Month | 3.054 | 1, 13 | 0.104 |
| Age × Month | 0.046 | 1, 19 | 0.832 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 10.744 | 2.043 | 0.041 |
| Session (day) | 3.383 | 1.278 | 0.201 |
| Day | 4.185 | 1.339 | 0.181 |
| Attack rate[a] ($n=140$) | *F* | $df_1$, $df_2$ | |
| Age | 9.406 | 1, 135 | 0.003 |
| Month | 29.581 | 1, 101 | <0.001 |
| Age × Month | 11.482 | 1, 135 | 0.001 |
| Steps | 5.896 | 1, 133 | 0.017 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 0.045 | 1.299 | 0.194 |
| Session (day) | 0 | – | – |
| Day | 0.009 | 0.707 | 0.479 |
| Capture rate[a] ($n=140$) | *F* | $df_1$, $df_2$ | |
| Age | 27.78 | 1, 132 | <0.001 |
| Month | 3.299 | 1, 115 | 0.072 |
| Age × Month | 14.888 | 1, 132 | <0.001 |
| Steps | 10.107 | 1, 133 | 0.002 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 0.043 | 4.580 | <0.001 |
| Session (day) | 0 | – | – |
| Day | 0 | – | – |
| Success of attacks[a] ($n=118$) | *F* | $df_1$, $df_2$ | |
| Age | 19.345 | 1, 23 | <0.001 |
| Month | 1.784 | 1, 14 | 0.203 |
| Age × Month | 9.883 | 1, 23 | 0.005 |
| Steps | 0.007 | 1, 73 | 0.935 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 0.637 | 1.393 | 0.164 |
| Session (day) | 0.267 | 0.719 | 0.472 |
| Day | 1.308 | 1.518 | 0.129 |
| Prey size[a] ($n=197$) | *F* | $df_1$, $df_2$ | |
| Age | 0.891 | 1, 189 | 0.346 |
| Month | 0.001 | 1, 189 | 0.995 |
| Age × Month | 0.419 | 1, 189 | 0.518 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 0 | – | – |
| Session (day) | 0 | – | – |
| Day | 7.440 | 1.478 | 0.139 |
| Handling time[a] ($n=197$) | *F* | $df_1$, $df_2$ | |
| Age | 1.089 | 1, 15 | 0.313 |
| Month | 2.003 | 1, 10 | 0.188 |
| Age × Month | 4.969 | 1, 15 | 0.039 |
| Prey size | 98.61 | 2, 55 | <0.001 |
| Random effects | Estimate | *Z* | |
| Bird identity (session [day]) | 0.009 | 0.407 | 0.684 |
| Session (day) | 0.077 | 1.286 | 0.198 |
| Day | 0.078 | 0.962 | 0.601 |

[a] Response variable.

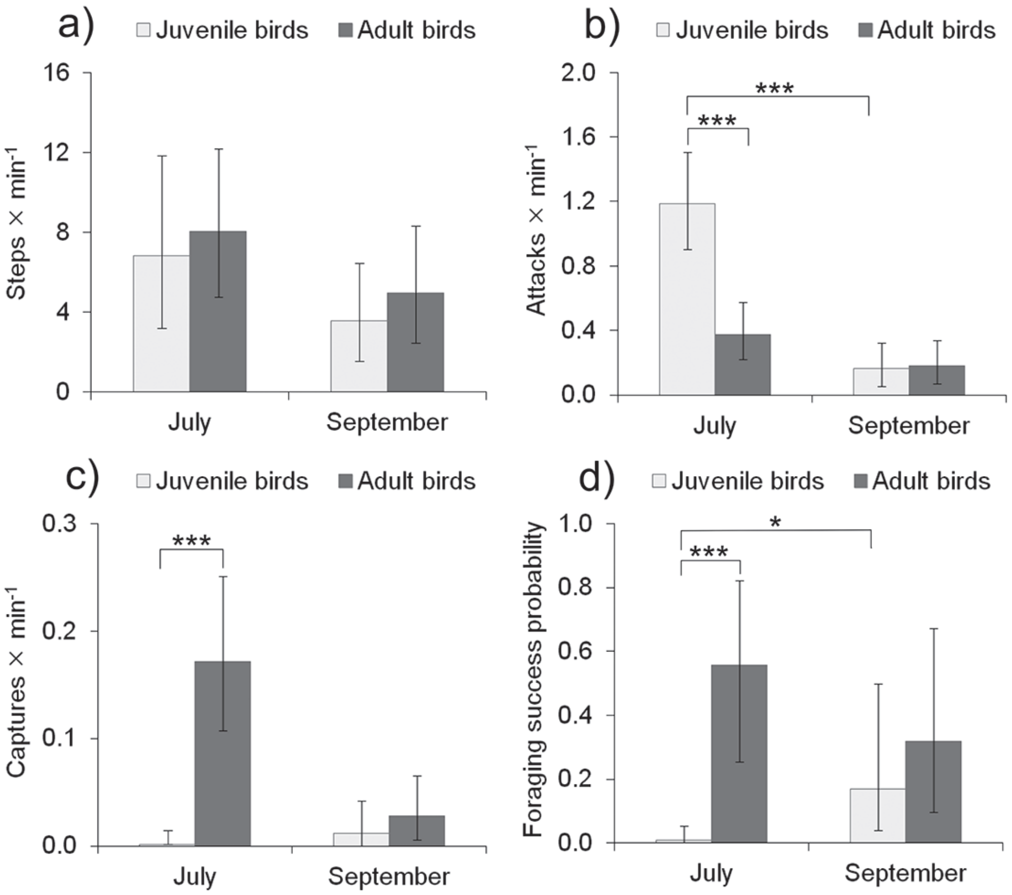

**Figure 2** The effect of age and month on (a) the rate of steps, (b) rate of attacks, (c) rate of fish captures and (d) foraging success probability. Means and 95% confidence intervals estimated from general(ised) linear mixed models are presented. Statistical differences between factor levels were estimated by paired contrasts. *, *P*<0.05; **, *P*<0.01; ***, *P*<0.001.

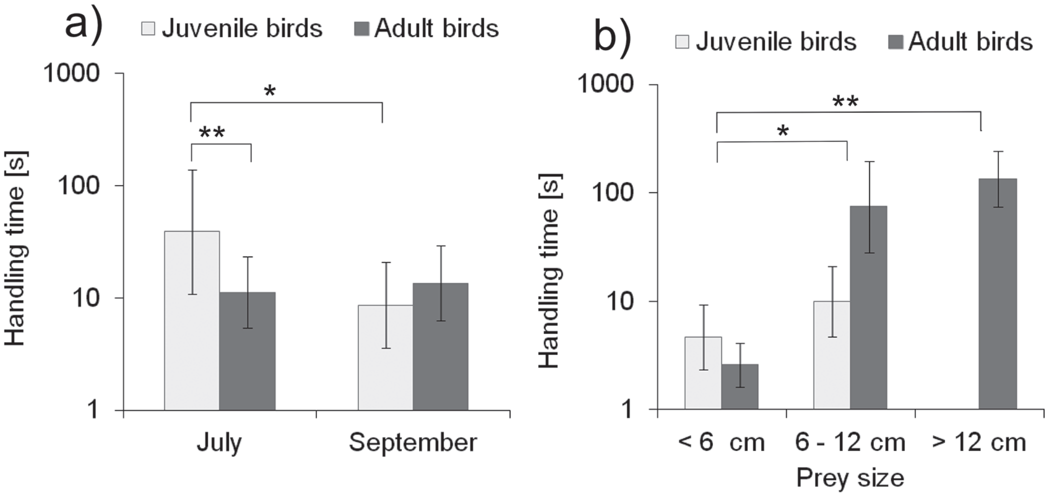

**Figure 3** Factors affecting handling time of fish by Grey Heron: (a) the effect of age and month; and (b) the effect of prey size. Means and 95% confidence intervals estimated from general linear mixed models are presented. Statistical differences between factor levels were estimated by paired contrasts. *, *P*<0.05; **, *P*<0.01; ***, *P*<0.001. Note the y-axis is in logarithmic scale.

juveniles at all in the study period. A generalised linear mixed model showed that there was no statistically significant effects of age class, month and interaction between the two factors on the probability of capturing fish of different size category (Table 2). We did not find significant differences between age classes and between the two months in handling time (Table 2). However, there was a significant effect of interaction between these factors on the handling time (Table 2, Figure 3a). The fish handling time in juveniles was higher than adults in

July (contrast estimate $\pm$SE$=1.244\pm0.532$, $t_9=2.338$, $P=0.045$; Figure 3a) but not in September (contrast estimate $\pm$SE $=-0.462\pm0.355$, $t_{27}=-1.302$, $P=0.204$, Figure 3a). Moreover, handling time in juveniles was higher in July than in September (contrast estimate $\pm$SE$=1.503\pm0.652$, $t_{11}=2.305$, $P=0.042$, Figure 3a). Larger fish had a longer handling time (Table 2, Figure 3b). Moreover, juvenile birds, but not adults, attacked inanimate objects (sticks, feathers, *etc.*) at least once in 60% ($n=40$) of sessions in July and in 16.7% ($n=30$) of sessions in September. Prey biomass taken by juveniles per unit of time was only 0.05 g min$^{-1}$ (15 times lower than adults) in July and 0.17 g min$^{-1}$ (slightly higher than adults) in September.

## 4. DISCUSSION

Foraging methods of adult and juvenile Grey Heron at the Dobczyce Reservoir were different. Young birds made many mistakes *e.g.* often picked unpalatable objects. However, the difference between age classes disappeared with time. Juvenile birds improved their foraging efficiency mostly by the decrease in number of unsuccessful attacks and by reducing handling time of large fish prey.

Similarly to Choi and Yoo (2011), who carried out a study at a reservoir in Bongiae in Asan City (South Korea), we showed that the movement rates of adult and juvenile Grey Heron were similar. Cook (1978) showed that significantly more fish were caught by stalking than by standing Grey Heron in the Ythan Estuary (Aberdeenshire, Scotland). Juvenile birds spent significantly more of their time stalking in the water in this habitat than did adults. Juveniles with little experience spend more time exploring feeding areas and searching for food than adult birds with local experience (van Vessem and Draulans, 1987, Kushlan and Hancock, 2005). At these times, juvenile heron learn how to catch prey and very often seize all kinds of floating objects, such as bits of wood, feathers and plants (Voisin, 1991).

Juvenile birds made more frequent attacks (three times more) than adults on the Dobczyce Reservoir but with lower hunting success. Similar results were obtained by Choi and Yoo (2011). Generally, if the cost of foraging is low (*e.g.* involves only walking) then young birds often make mistakes because achieving certain levels of food intake requires only improving the speed of foraging. However, when the cost increases (*e.g.* when foraging includes energetically costly flying, hovering or capturing mobile prey) then birds try to improve their foraging success by making less mistakes (Skórka and Wójcik, 2008).

The foraging experience of juvenile Grey Heron increases with age (Kushlan and Hancock, 2005). Therefore foraging success of older juveniles is higher. Snow (1974) showed that the fishing abilities of juvenile Galapagos Heron *Butorides sundevalli* (Reichenow) are equal to those of adult birds when they reach 81 days old.

Juvenile birds were less efficient in hunting in July due to their lack of experience in catching and manipulating prey at the Dobczyce Reservoir. Observations of feeding Grey Heron on the Ythan Estuary indicate that inexperienced first-year birds are less efficient (29% successful attempts) than adults (50% successful attempts) at foraging for food (Cook, 1978). Immature Great White Egrets, *Ardea alba* L., in Florida are even less efficient than adult birds, averaging a 9% success rate (Rodgers, 1983). Recher and Recher (1969) also found differences in foraging efficiency between immature and adult Little Blue Heron, *Egretta caerulea* L., in terms of the success rate and food obtained per minute. In contrast, no statistically significant differences were found between juvenile and adult Grey Heron with respect to foraging efficiency at O Bao Inlet (Spain) (Regos, 2011).

Adult and juvenile birds caught primarily small fish (6–12 cm) in the Dobczyce Reservoir. Regos (2011) showed that small (6–12 cm) and very small (<6 cm) prey were the captured sizes selected by Grey Heron at the wetland studied in Spain. This could be because this prey size was the most abundant and the most profitable in this area in terms of biomass per time unit (Lekuona, 1999; Campos and Lekuona, 2000). Small fish were also the most profitable for adult Purple Heron *Ardea purpurea* L. in rivers of northern Spain (Campos and Leukona, 2000). However, Gwiazda and Amirowicz (2006) showed that sites with larger fish were preferred by Grey Heron. It is also possible, that a preference for small fish results from the fact that they often gather in flocks in shallow shore water where heron are able to hunt while older fish usually avoid shallow water.

We showed a marked increase in handling speed in juvenile birds from July to September. Contrary to this, handling time in adults was similar between the two months. Adult Grey Heron usually spend less time handling prey than juvenile birds. Handling time increased significantly with prey length among Grey Heron (Moser, 1985; Campos and Lekuona, 2000; Regos, 2011) and we confirmed this finding. However, we found a statistically siginficant interaction between age, month and prey size. Namely, bird age was related to handling time and fish size but not in birds that manipulated small fish in the Dobczyce Reservoir. Similar behaviour has been shown in other heron species, such as the Yellow-crowned Night Heron *Nyctanassa violacea* L. and the Great Blue Heron *Ardea herodias* L., among which the handling time of small prey was the same for juveniles and adults, but juveniles swallowed medium size or bigger prey over much longer periods than adults (Quinney and Smith, 1980; Laubhan *et al.*, 1991).

Marchetti and Price (1989) showed that juvenile-adult differences in foraging can result from: (1) morphological constraints; (2) learning constraints; (3) nutritional differences; and (4) social interaction. In the Grey Heron, skeleto-muscular and neurological system or nutritional requirements are similar in juvenile and adult birds, so the most important factor seems to be hunting skills. The results suggest that juvenile Grey Heron compensate for a lack of experience by more frequent attacks in order to obtain a suitable amount of food. Biomass taken by juveniles was very small in comparison to biomass taken by adults in July. At the beginning of the fledgling period, the young birds are able to start hunting independently of adults, but they still return to the nest for supplementary feeding by their parents (Voisin, 1991). Adult Grey Heron captured prey more successfully than juveniles but the ability to do so improved with age. Juvenile Grey Heron greatly increased their efficiency at catching fish from July to September, probably as a result of experience.

## 5. ACKNOWLEDGMENTS

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