

Modelling the feeding behavior of Grey Heron (*Ardea cinerea*) in a coastal wetland of NW Iberian peninsula during the wintering season

A. Regos

Regos, A., 2011. Modelling the feeding behavior of Grey Heron (*Ardea cinerea*) in a coastal wetland of NW Iberian peninsula during the wintering season. *Animal Biodiversity and Conservation*, 34.2: 249–256.

Abstract

Modelling the Feeding Behavior of Grey Heron (Ardea cinerea) in a Coastal Wetland of NW Iberian Peninsula during the Wintering Season.— For a better understanding of the foraging behavior of Grey Heron in an intertidal area we developed predictive models of number of attempts/10' using Poisson regression. The models were obtained considering the following four variables: age of bird, tidal hours, bi-monthly period, and substrate type, obtaining a total of 15 models. The most parsimonious model obtained using the Akaike Information Criteria included tidal hour, age of bird and substrate type as predictive variables. The mean number of attempts/10' was highest in the four hours around low tide and in water and muddy substrates, while foraging activity was scarcely recorded in sandy substrates. No differences of effectiveness were found between adult and juvenile birds. Grey Heron showed preference for very small and small prey, increasing handling time with prey length.

Key words: *Ardea cinerea*, Feeding behavior, GLMM, Tidal cycle, Substrate type, Age of birds.

Resumen

Modelado del comportamiento trófico de la garza real (Ardea cinerea) en un humedal costero del NO ibérico durante el periodo invernal.— Para mejorar el conocimiento de la estrategia de forrajeo de la garza real en una zona intermareal se obtuvieron modelos predictivos del número de intentos/10' empleando la regresión de Poisson. Los modelos candidatos resultaron de la consideración de cuatro variables: edad, hora mareal, periodo bimensual y tipo de sustrato. El modelo más parsimonioso obtenido de acuerdo con el Criterio de Información de Akaike incluyó la edad, la hora mareal y el tipo de sustrato como variables predictivas. El promedio de intentos/10' fue mayor en las cuatro horas más próximas a la bajamar, y en sustratos con agua o fango que en medios arenosos. No se encontraron diferencias significativas en la efectividad entre adultos y juveniles. La garza real mostró preferencia por presas pequeñas o muy pequeñas, aumentando el tiempo de manejo con el tamaño de la presa.

Palabras clave: *Ardea cinerea*, Comportamiento trófico, GLMM, Ciclo mareal, Tipo de sustrato, Edad.

(Received: 14 VI 10; Conditional acceptance: 3 X 10; Final acceptance: 14 IV 11)

Adrián Regos, Dept. of Zoology and Physical Anthropology, Univ. of Santiago de Compostela, Campus Sur s/n., 15782 Galicia, España (Spain).

Corresponding author: adrianregos@hotmail.com

Introduction

In recent years, the population of Grey Heron (*Ardea cinerea* L., 1758) in Spain has increased considerably both in number and in geographic range and it can now be found in several areas where it was previously scarce or absent (Prieta & Campos, 2003). This population growth could be due to factors such as the protection of wetlands, the creation of new artificial wetlands (ponds and dam reservoirs) and fish farms, the introduction of exotic fishes or eutrophication of water bodies (Prieta & Campos, 2003).

Grey Heron feeding behavior has been studied in several habitats, mainly during the breeding season (Owen, 1995; Campos & Lekuona, 1997; Lekuona, 1999). According to Cramps & Simons (1977) Grey Heron feed by day in some places, especially in the morning and evening, while in other areas they feed mainly around dusk and at night. Besides differences concerning feeding hours, the foraging behavior of herons is also affected by factors such as: tidal cycles (Dimalexis & Pyrovetsi, 1997; Lekuona, 1999; Matsunaga, 2000), age of birds (Lekuona, 2002a), substrate type and habitat characteristics (Hampl et al., 2005; Papakostas et al., 2005; Gwiazda & Amirowicz, 2006). In a tidal flat the availability of foraging sites varies according to tidal cycles. Previous studies have demonstrated that the daily cycle of high and low tides affected the foraging strategies of herons (Lekuona, 1999; Matsunaga, 2000). Few studies, however, have examined the effect of tidal cycles on feeding behavior in relation to substrate type and age of birds, especially in the wintering season. Regarding the age of birds, various authors have suggested that juveniles are less successful at feeding and spend longer feeding than adults (Carss, 1993; Lekuona, 2002a, 2002b; Papakostas et al., 2005). However, it is not clear whether there are differences between juvenile and adult birds regarding the effectiveness of foraging. Moreover, feeding behavior in herons changes during the breeding season because of the energy requirements of chicks during this period (Campos & Lekuona, 1997; Lekuona, 1999). Studies on the feeding ecology during the winter period, however, are scant.

In this study we examined the effect of tidal cycle, age of birds and substrate type on foraging activity. We compared the effectiveness of adult and juvenile birds and analyzed this as another possible factor affecting foraging activity. We also investigated associations between foraging activity rates, prey size and success so as to improve knowledge of Grey Heron behavior in an intertidal area in the wintering period.

Material and methods

The study was carried out in O Bao inlet, situated in the Umia-O Grove intertidal complex of 2.561 hectares of extension, located in the northwestern Iberian peninsula (42° 28' N, 8° 51' W) (fig. 1). This wetland is characterized by its great ornithological relevance, being one of the most important wintering and mi-

grating sites of water birds in northwestern Spain. It has been declared a Site of Community Importance (SCI), Special Protection Area (SPA) and Wetland of International Importance (RAMSAR site).

The area consists of a bay that is separated from the open sea by a large sandy beach-dune system. It has extensive muddy intertidal flats covered by *Zostera* sp., with small areas of bulrushes and sandbanks, influenced by tidal dynamics.

During our study, 193 Grey Herons wintered in the area, in a mixed-species colony, together with Little Egret (*Egretta garzeta*), Spoonbill (*Platalea leucorodia*) and Great Cormorant (*Phalacrocorax carbo*) (Xunta de Galicia, unpublished data). Data were collected from six observation sites located at strategic locations in the inner part of the bay (fig. 1). Surveys were carried out from November 2005 to February 2006, coinciding with the wintering period of Grey Heron. Two telescopes were used (20–60x and 20–70x) for observations and 13 field visits were carried out: seven in November–December and six in January–February. The surveys were planned according to tidal cycles, so that only days allowing surveys from three hours before to three hours after diurnal low tide were selected.

To avoid pseudoreplication of data, simultaneous surveys were carried out in two other sites of the wetland, during a period of observation not exceeding two hours.

Birds were chosen arbitrarily and followed for 10' according to the methodology proposed by Altmann (1974) and Martin & Bateson (1986). During the monitoring we recorded the following variables: (I) age of birds, considering two categories: adults and juveniles (birds were categorized on their plumage characteristics according to Cramp & Simmons, 1997); (II) tidal hour; (III) substrate type: sand, mud, water to tibia–tarsus and water to tarsus–metatarsus; (IV) bi-monthly period, considering two periods: November–December and January–February; and (V) day: survey date.

To measure the foraging effort of each bird we recorded feeding attempts and their results (successful and unsuccessful). Foraging times were recorded for each prey, using a chronometer. Prey size was calculated in relation to the size of Grey Heron's beak: 12 cm (Cramp & Simmons, 1997). In this way, four classes of prey size were established: very small (< 6 cm), small (6–12 cm), medium (12–18 cm) and large (> 18 cm).

During the survey four further behavioral variables were recorded: interspecific and intraspecific presence, number of kleptoparasitic attempts made by Grey Heron and number of attempts made by other species. In addition, four meteorological variables were measured: isolation, rainfall, temperature and wind. The number of kleptoparasitic attempts recorded was very low and was therefore not considered in the final model. Meteorological variables were also categorized. Most of the values recorded were concentrated in one or two categories of the initially defined list so none of these variables were finally taken into account in the analysis.

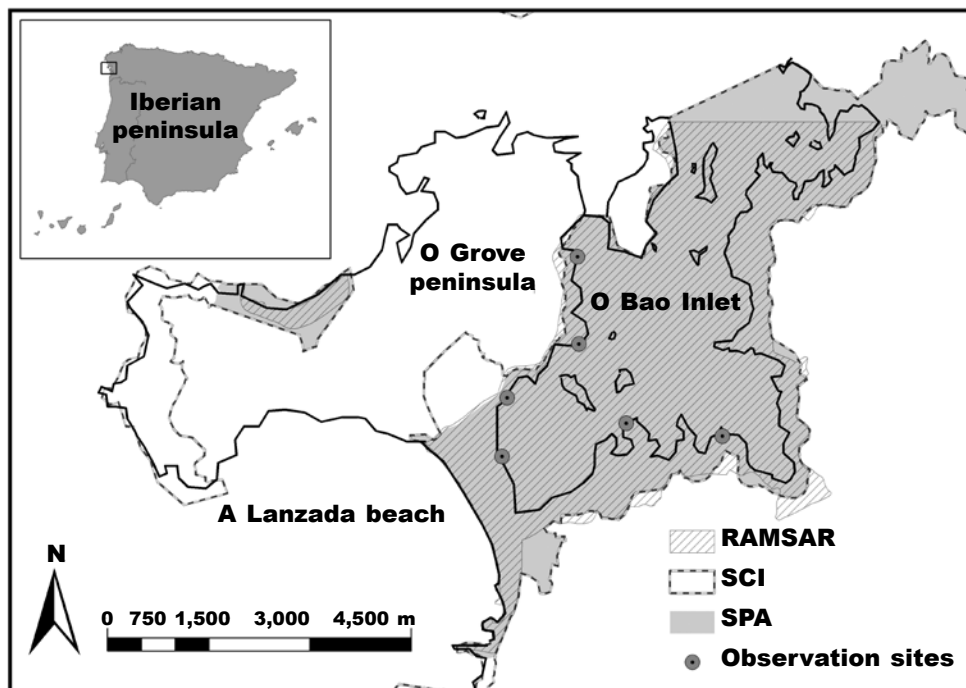


Fig. 1. Study area, located in the north–west Iberian peninsula.

Fig. 1. Área de estudio, localizada en el noroeste de la península ibérica.

Based on field data, a new variable was calculated: Effectiveness (Ef). This variable was calculated from the ratio between number of successful attempts (Pr) and total attempts (successful and unsuccessful) (At). Calculated effectiveness values ranged between 0 (minimum effectiveness) and 1 (maximum effectiveness).

$$Ef = Pr / At$$

This concept explains the capacity of each bird to capture prey, whereas the term 'trophic efficiency' is used on continuation to refer to the capacity of each bird to obtain a biomass intake.

Generalized Linear Mixed Models (GLMMs) were derived to model the foraging effort of birds, estimated by number of attempts/10'. As the response variable (feeding attempts/10') is count data, we used a Poisson model with a log link. The mean number of attempt/10' within different groups of variables was less than 5, so Laplace approximation was used. This analysis was conducted using a PROC GLIMMIX in SAS (Bolker et al., 2009; Dean & Nielsen, 2007).

The candidate models were obtained by using four variables (age of birds, tidal hour, bi-monthly period and substrate type) as fixed effects and the variable 'day' as random effect, obtaining a total of 15 candidate models. For each model i , the values of AIC (Akaike information criteria) and Δ_i were obtained, where

$$\Delta_i = AIC_i - AIC_{\text{minimum model}}$$

The Akaike weight for each model was calculated as W_i :

$$W_i = \frac{\exp(-1/2 \Delta_i)}{\sum_{r=1}^R \exp(-1/2 \Delta_r)} \quad (\text{Anderson et al., 2000})$$

The sum of all weights equals the unit, and the value of each W_i indicates that model i is the best overall model (Anderson et al., 2000). This model is chosen from 15 well-defined candidate models using Akaike Information Criteria (Anderson et al., 2000; Seoane & Bustamante, 2001). The importance of each variable was obtained by adding the Akaike weights to the model in which that variable was present (Burnham & Anderson, 1998). The addition of the weights of each variable was considered consequential when $\sum W_i > 0.5$ (Taylor & Knight, 2003).

To compare the foraging effectiveness of adults and juveniles, and to test the differences in foraging efforts in four types of substrate, we used non-parametric statistics (Mann–Whitney test & Kruskal–Wallis test respectively) after verifying the assumptions of normality and homogeneity of variance. We also analysed the foraging effort during 6 tidal hours (Kruskal–Wallis test). One way ANOVA was used to test differences in the handling time of four classes of prey size since data were adjusted to a normal distribution. The *post hoc* comparison was done using a Student–Newman–Keuls test (Quinn & Keough, 2002).

All data were analyzed using SAS System v.9.1.3.

Results

A total of 319 birds were studied, 124 juveniles and 195 adults. No statistically significant differences were found between juveniles and adult regarding foraging effectiveness ($Z = -1.642$; $N = 132$; $P > 0.05$).

Foraging effort was highest in the four hours around low tide for juveniles ($\chi^2 = 43.219$; d.f. = 5; $P < 0.05$) and in the 2 hours around low tide for adults ($\chi^2 = 36.074$; d.f. = 5; $P < 0.05$) (fig. 2).

The highest foraging effort was recorded in water with birds wading up to the level of the tarsus–metatarsus or tibia–tarsus ($\chi^2 = 69.091$; d.f. = 3; $P < 0.05$). This was followed by foraging in muddy substrate, whereas foraging activity was scarcely recorded in sandy substrate (fig. 3). Of the total consumed prey, 69.2% were smaller than 6 cm; of these, 56.6% were consumed by younger birds and 43.3% by adults. Prey larger than 18 cm accounted for only 6.8% of the total, all of which were exclusively consumed by adults (fig. 4). All prey larger than 18 cm were eels (*Anguilla anguilla*). Handling time increased significantly with prey length ($F_{3,132} = 89.49$; $P < 0.001$) (fig. 5). A *post hoc* comparison (Student–Newman–Keuls) showed

that the average handling time differed significantly between the four classes of prey size, except for between small and medium prey.

Regarding the effects of the fixed factors (age of birds, tidal hour, bi-monthly period and substrate type) on the foraging effort, once all these factors were included in the model, three of them were found to have a significant effect: age of birds ($\sum W_{age} = 0.97$), tidal hour ($\sum W_{tidal\ hour} = 1$) and substrate type ($\sum W_{substrate\ type} = 1$). However, there was no evidence of any effect of bi-monthly period ($\sum W_{bi-monthly\ period} = 0.26$) because this variable could not be considered consequential, since its $\sum W_i$ was below 0.5. The final model chosen, that which included age of birds, tidal hour and substrate type as predictive variables (table 1), was the only one of the 15 models initially analyzed that was considered competent ($\Delta_i < 2$).

Discussion

Previous studies have emphasized the role of tidal cycle, age of birds and substrate type as decisive factors in feeding behavior in several heron species (Matsunaga, 2000; Lekuona, 2002a; Hampl et al., 2005; Papakostas et al., 2005; Gwiazda & Amirowicz, 2006). In the present study, these factors were all

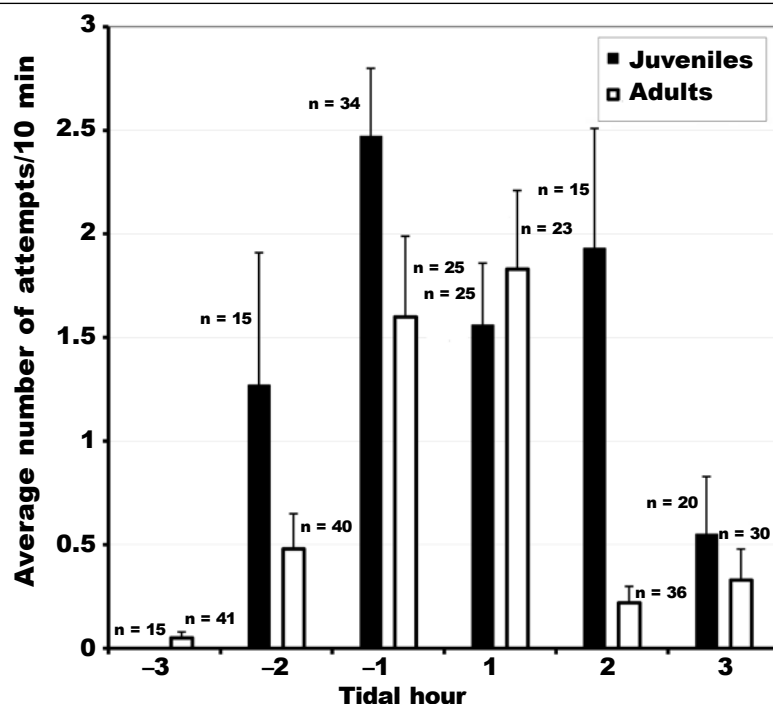


Fig. 2. Average number of attempts/10 min of adult and juvenile birds for each tidal hour during the wintering season 2005–2006.

Fig. 2. Promedio de intentos/10 min de adultos y juveniles por hora mareal durante el periodo invernal 2005–2006.

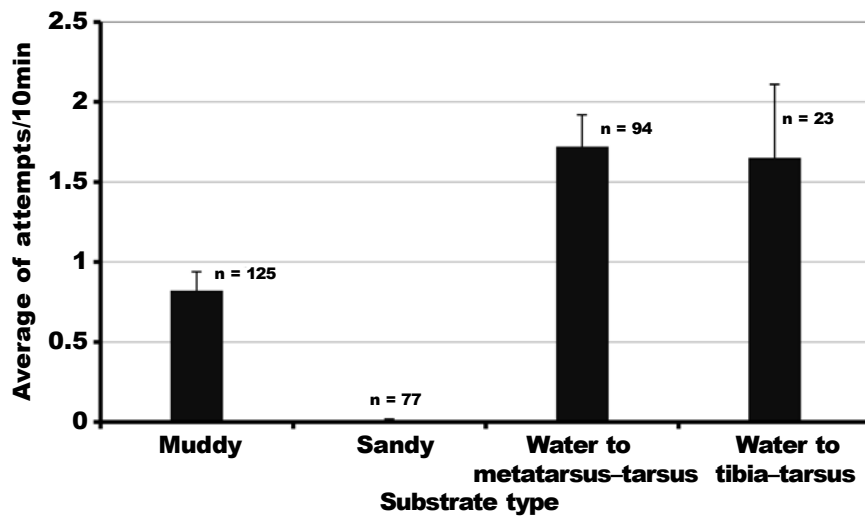


Fig. 3. Average number of attempts/10' of Grey Heron for each substrate type.

Fig. 3. Promedio de intentos/10' de la garza real para cada tipo de sustrato.

found to have a significant effect on the foraging effort of Grey Heron. Our results confirm that these variables are critical factors and should be taken into account for a better understanding of the feeding behavior of Grey Heron in an intertidal area. More specifically, they help us to understand which environmental factors most directly affect their feeding strategy and how herons

respond to these factors in terms of trophic effort. To analyze the effect of these factors in the study area, we discuss each one separately.

Several authors have studied the effect of water level and tidal cycle on the foraging activity of wading birds (Voslamber, 1996; Dimalexis & Pyrovetsi, 1997; Matsunaga, 2000). Lekuona (1999) demonstrated

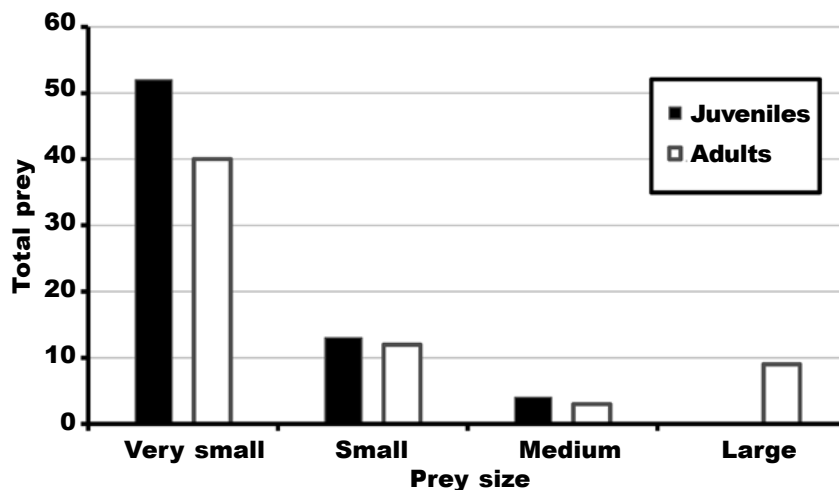


Fig. 4. Total prey captured by adult and juvenile birds for each prey size in O Bao inlet during the wintering season 2005–2006.

Fig. 4. Presas totales capturadas por adultos y juveniles de garza real según el tamaño de cada presa durante el periodo invernal 2005–2006 en la ensenada de O Bao.

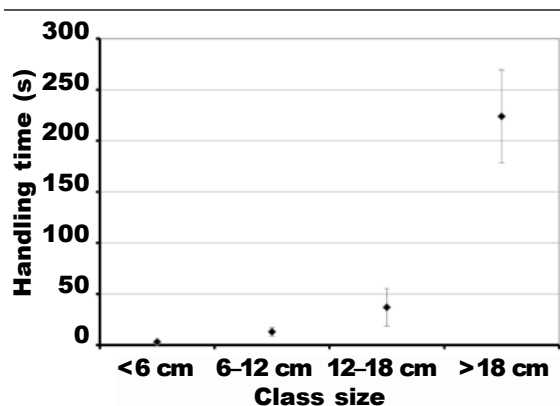


Fig. 5. Average (\pm SE) of Grey Heron handling time in seconds (s) for each prey size.

Fig. 5. Valor medio (\pm EE) del tiempo de manejo en segundos (s) de las presas para cada clase de tamaño.

that most waders feed in the two hours before and the two hours after low tide, and our results support this finding.

Regarding the age of birds, various authors have suggested that juveniles are less successful at feeding and spend more time feeding than adults (Carss, 1993; Lekuona, 2002a, 2002b; Papakostas et al., 2005). Our findings concerning more time spent feeding coincide with these authors. We found that foraging effort was higher in the four hours around low tide for juveniles and in the two hours around low tide for adults, indicating that juveniles spend more time in foraging areas than adults. Moreover, the age of birds was a consequential variable in the model obtained to explain the foraging effort. However, and contrary to the expected results, we did not find any differences between juvenile and adult birds regarding the effectiveness of foraging. The differences in trophic effort between adults and juveniles was not due to greater effectiveness in the adults but to the fact that the adults had the ability to capture more energetically profitable prey, making them more efficient but not more effective.

Hérons may adopt different tactics and may achieve

variable foraging efficiencies in response to particular habitat conditions and prey characteristics (Dimalexis et al., 1997; Wong et al., 2000; Gwiazda & Amirowicz, 2006). Carss & Elston (2003) found that Grey Herons show preference for particular substrate types, and may even select areas dominated by specific algae species. Our results support this finding that substrate type is a decisive factor in the foraging strategy. In our study, the foraging effort was highest in water substrate. It was lower in muddy substrate and scarce in sandy substrate.

Grey Heron usually capture fishes of 10–25 cm long, although fish up to 40 cm (Del Hoyo et al., 1992) and eels up to 60 cm may be also taken (Owen, 1995; Cramp & Simmons, 1977). According to other published works, size can play an important role in the choice of prey and herons generally show preference for larger prey (Britton & Moser, 1982; Feunteun & Marion, 1994). Gwiazda & Amirowicz (2006) concluded that larger prey were more profitable for Grey Heron to forage. However, our data show that small (6–12 cm) and very small (< 6 cm) prey were the preferred sizes selected by Grey Heron in the studied wetland. This could be because this prey size was the most abundant or the most profitable in the study area in terms of biomass per time unit, an aspect previously suggested in other studies (Lekuona, 1999; Campos & Lekuona, 2000). Campos & Lekuona (2000) suggested two possible hypotheses to explain why adults captured larger prey during the breeding season if smaller prey were really more profitable: I) larger prey would provide the energy need to compensate for the energetic cost of frequent trips to and from the breeding colonies and the feeding areas. This hypothesis can be ruled out in our case because the data were recorded in the non-breeding season; II) when small prey are scarce the herons may be forced to capture larger prey for their own food. However, small prey were the most abundant in our study area. Taking this into account we suggest that: I) older birds have greater trophic efficiency –but not effectiveness– due to their greater ability to capture large and slippery prey, like eels. This could explain why all large prey were only consumed by adults; II) adults spend less time than juvenile birds do in foraging areas because the largest prey provide the quantity of biomass they require.

Handling time of prey increased with prey length. Comparing values obtained for Purple Heron in the Ebro River valley (Campos & Lekuona, 2000) and our data, we can conclude that, for similar prey size,

Table 1. Models obtained for the foraging effort showing Akaike information criteria values.

Tabla 1. Modelos obtenidos para el esfuerzo de forrajeo mostrando los valores del criterio de información de Akaike.

Model	AIC	Δ_i	W_i
Age + tidal hour + substrate type	762.51	0	0.721

Grey Heron spend more handling time than Purple Heron. This can be related to the type of available prey or size differences between these two species of herons. In both species, results show that the trophic effort per time unit depends directly on the prey type and size, determining a specific feeding strategy. The feeding strategy for large and more difficult to manage prey is more time-consuming and occurs in the two hours around low tide. In contrast, for smaller prey, which require less handling time, activity continues for a further two hours.

Previous studies have also shown that feeding behavior in herons changes during the breeding season (Campos & Lekuona, 1997; Lekuona, 1999). However, in the present study, the bimonthly period did not affect the trophic activity of the birds. This allowed us to conclude that their foraging effort does not vary during the wintering season and remains constant throughout this period.

Acknowledgements

I wish to thank Cristina González Álvarez, Ibama Pineda Josseulin and Virginia Mena Ramos for their collaboration in the field work, and especially Dr. Jesús Domínguez Conde (Department of Zoology and Physical Anthropology, USC) and Dr. Raquel Díez Arenas for their advice throughout the study. I also thank Esther Miguéns Alonso, Douglas Naismith and Giuseppe di Pinto for linguistic revision and the contribution of Oliver Valero for his advice with the statistical methods (www.uab.es/s-estadistica). The comments and constructive remarks of the journal editor and two anonymous referees are also gratefully acknowledged.

References

- Altmann J., 1974. Observational Study of Behavior: sampling methods. *Behavior*, 49: 227–267.
- Anderson, D. R., Burnham, K. P. & Thompson, W. L., 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildlife Manage*, 64: 912–923.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens M. H. H. & White, J. S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24(3): 127–135.
- Burnham, K. P. & Anderson, D. R., 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Britton, R. H. & Moser, M. E., 1982. Size specific predation by Herons and its effect on the sex ratio of natural populations of the mosquito fish *Gambusia affinis* Baird and Girard. *Oecologia*, 53: 146–151.
- Campos, F. & Lekuona, J. M., 1997. Temporal variations in the feeding habits of the Purple Heron *Ardea purpurea* during the breeding season. *Ibis*, 139(3): 447–451.
- 2000. Fish profitability for breeding purple herons. *Ardeola*, 47(1): 105–107.
- Carss, D. N., 1993. Grey heron, *Ardea cinerea* L., predation at cage fish farms in Argyll, western Scotland. *Aquaculture and Fisheries Management*, 24(1): 29–45.
- Carss, D. N. & Elston, D. A., 2003. Patterns of association between algae, fishes and grey herons *Ardea cinerea* in the rocky littoral zone of a Scottish sea loch. *Estuarine Coastal and Shelf Science*, 58(2): 265–277.
- Cramps, S. & Simmons, K. E. L., 1977. *The bird of Western Palearctic*, Vol. 1. Oxford University Press, Oxford.
- Dean, C. B. & Nielsen, J. D., 2007. Generalized linear mixed models: a review and some extensions. *Lifetime Data Anal*, 13: 497–512.
- Del Hoyo, J., Elliott, A. & Sargata, J., 1992. *Handbook of de Birds of the World*, Vol. 1. Lynx Edicions, Barcelona.
- Dimalaxis, A. & Pyrovetsi, M., 1997. Effect of water level fluctuations on wading bird foraging habitat use at an irrigation reservoir, Lake Kerkini, Greece. *Colonial Waterbirds*, 20(2): 244–252.
- Dimalaxis, A., Pyrovetsi, M. & Sgardelis, S., 1997. Foraging ecology of the grey heron (*Ardea cinerea*), great egret (*Ardea alba*) and little egret (*Egretta garzetta*) in response to habitat, at 2 Greek wetlands. *Colonial Waterbirds*, 20(2): 261–272.
- Feunteun, E. & Marion, L., 1994. Assessment of Grey Heron predation of fish communities: the case of the largest European colony. *Hydrobiologia*, 279/280(0): 327–344.
- Gwiazda, R. & Amirowicz, A., 2006. Selective foraging of Grey Heron (*Ardea cinerea*) in relation to density and composition of the littoral fish community in a submontane dam reservoir. *Waterbirds*, 29(2): 226–232.
- HAMPL, R., Bures, S., Balaz, P., Bobek, M. & Pojer, F., 2005. Food provisioning and nestling diet of the black stork in the Czech Republic. *Waterbirds*, 28(1): 35–40.
- Lekuona, J. M., 1999. Food and foraging activity of grey herons, *Ardea cinerea*, in a coastal area during the breeding season. *Folia Zoologica*, 48(2): 123–130.
- 2002a. 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 Zoologica*, 51(1): 23–34.
- 2002b. Kleptoparasitism in wintering grey heron *Ardea cinerea*. *Folia Zoologica*, 51(3): 215–220.
- Martin, P. & Bateson, P., 1986. *Measuring Behaviour: an introductory guide*. Cambridge, Cambridge University Press.
- Matsunaga, K., 2000. Effects of tidal cycle on the feeding activity and behavior of Grey Herons in a tidal flat in Notsuke Bay, northern Japan. *Waterbirds*, 23(2): 226–235.
- Owen, D. F., 1995. The food of the Heron (*Ardea cinerea*) in the breeding season. *Ibis*, 97: 276–295.
- Papakostas, G., Kazantzidis, S., Goutner, V. & Charalambidou, I., 2005. Factors affecting the foraging

- behavior of the Squacco Heron. *Waterbirds*, 28(1): 28–34.
- Prieta, J. & Campos, F. 2003. Garza real, *Ardea cinerea*. In: *Atlas de las Aves Reproductoras de España*: 116–117 (R. Martí & J. C. del Moral, Eds.). Dirección General de Conservación de la Naturaleza–Sociedad Española de Ornitología, Madrid.
- Quinn, G. P. & Keough, M. J., 2002. *Experimental design and data analysis for biologist*. Cambridge University Press, Cambridge
- Seoane, J. & Bustamante, J., 2001. Modelos predictivos de la distribución de especies: una revisión de sus limitaciones. *Ecología*, 15: 9–21.
- Taylor, A. R. & Knight, R. L., 2003. Wildlife responses to recreation and associated visitor receptions. *Ecol. Appl.*, 13(4): 951–963.
- Voslamber, B., 1996. Effects of eater level management and grazing on fish eating birds. *Levende Natuur*, 97(1): 4–10.
- Wong, L. C., Corlett, R. T., Young, L. & Lee, J. S.Y., 2000. Comparative feeding ecology of Little Egrets on intertidal mudflats in Hong Kong, South China. *Waterbirds*, 23(2): 214–225.
-