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FORAGING ECOLOGY OF THE GREAT GREBE *PODICEPHORUS MAJOR* IN MAR CHIQUITA LAGOON (BUENOS AIRES, ARGENTINA)

ECOLOGÍA DE FORRAJEO DEL MACÁ GRANDE *PODICEPHORUS MAJOR* EN LA LAGUNA MAR CHIQUITA (BUENOS AIRES, ARGENTINA)

María Laura JOSENS* [1], María Susana BÓ**
and Marco FAVERO***

SUMMARY.—*Foraging ecology of the great grebe* Podicephorus major *in Mar Chiquita Lagoon (Buenos Aires, Argentina).*

We studied the foraging ecology of the great grebe *Podicephorus major* through diet, prey energy return and foraging behaviour across three increasingly marine sites in the coastal lagoon of Mar Chiquita, Argentina. Grebes were followed by focal observations; we recorded dive duration, number of apparent successful and unsuccessful dives, size and type of captured prey and handling time above water. We analysed foraging effort as capture rate (i.e. number of prey eaten per minute) and capture success (i.e. number of successful dives per total dives made); and foraging efficiency as the number of captured prey per foraging time, the total biomass consumed and the energy intake obtained per time. We expected a piscivorous diet, but the most frequent prey were crabs, represented by *Cyrtograpsus angulatus* and *Neohelice granulate*, followed by diverse fish species. Diving time for different prey types and foraging sites did not differ. Handling time was higher for crabs. Foraging effort and foraging efficiency were higher for grebes that preyed on crabs, but in terms of biomass and energy return no differences were found, not even between sites. This suggests an opportunistic foraging behaviour for the great grebe in response to the possible higher availability of crabs in this and possibly other estuaries.

Key words: Argentine, diet, energy intake, foraging behaviour, great grebe, *Podicephorus major.*

* Laboratorio de Limnología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. Funes 3250, (7600), Mar del Plata; and Comisión Nacional de Investigaciones Científicas y Tecnológicas (CONICET), Avenida Rivadavia 1917, (C10333AAJ), Buenos Aires, Argentina.

** Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata.

*** Laboratorio de Vertebrados, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata; and Comisión Nacional de Investigaciones Científicas y Tecnológicas (CONICET).

[1] Corresponding author: laurajosens@yahoo.com

RESUMEN.—*Ecología de forrajeo del macá grande* Podicephorus major *en la laguna Mar Chiquita (Buenos Aires, Argentina).*

Se estudió la ecología de forrajeo del macá grande *Podicephorus major* a través de la dieta, el rendimiento calórico de las presas y el esfuerzo y eficiencia de forrajeo en una laguna costera del sudeste de Argentina. El comportamiento de forrajeo fue cuantificado utilizando observaciones focales, donde se registró la duración del buceo, número de buceos aparentemente exitosos y no exitosos, tamaño y tipo de presa capturada, y tiempo de manipulación sobre el agua. Se analizó el esfuerzo de forrajeo medido como tasa de captura (número de presas ingeridas por minuto); éxito de captura (número de buceos exitosos sobre el número de buceos totales); eficiencia de forrajeo como el número de presas capturadas por tiempo de forrajeo, la biomasa total consumida y por el retorno energético (tiempo de forrajeo por unidad temporal). Se esperaba una dieta piscívora, pero las presas más frecuentes fueron los cangrejos, representados por *Cyrtograpsus angulatus* y *Neohelice granulata*, seguido por diversas especies de peces. El tiempo de buceo para diferentes tipos de presa y los diferentes lugares de forrajeo no varió. El tiempo de manipulación fue mayor para los cangrejos. El esfuerzo y la eficiencia de forrajeo fue mayor para los individuos que se alimentaron de cangrejos, pero en términos de biomasa consumida y retorno energético no hubo diferencias, tampoco para las áreas de forrajeo. Esto sugiere un comportamiento trófico oportunista para el macá grande en respuesta a la posible alta disponibilidad de cangrejos en el área de estudio y posiblemente en otros estuarios.

*Palabras clav*e: Argentina, comportamiento de forrajeo, consumo energético, dieta, macá grande, *Podicephorus major.*

INTRODUCTION

The great grebe *Podicephorus major* is a diving bird and the largest South American grebe. This species inhabits mainly open waters like lakes, shores and estuarine marshes. They apparently forage on fish, including some species from open waters and others linked to aquatic vegetation, and also on insects, crustaceans and molluscs (Llimona and del Hoyo, 1992). The great grebe is similar in appearance to the western grebe *Aechmophorus occidentalis* from North America and to the great crested grebe *Podiceps cristatus* from Europe. Other studies have revealed that different grebe species live mainly on a piscivorous diet, and secondly on crustaceans or insects (Gwiazda, 1997; Kloskowski, 2004; Ulenaers and van Vessem, 1994; Wagner and Hansson 1998; Gagliardi *et al*., 2007). The information about the foraging ecology of the great grebe is anecdotic, though some observations indicated that crabs are important food items (Fjeldså, 2004).

In the southeast of Buenos Aires province, Argentine, the great grebe lives isolated or in pairs in coastal areas, but in Mar Chiquita lagoon it forms small groups during the entire year (Martínez, 2001). This lagoon supports a large number of waterbirds and is an important site for migratory shorebirds. Many waterbird species use the beach for feeding and roosting, where they concentrate in large flocks (e.g., Blanco *et al.,* 1995; Palomo *et al*., 1999; Martínez, 2001). Moreover, this estuary is also an important nursery and feeding area for fish (Díaz de Astarloa *et al*., 1999; Cousseau *et al*., 2001). Large quantities of crabs also inhabit its intertidal zone (e.g., Spivak *et al.,* 1994; Iribarne *et al.,* 1997; Martinetto *et al*., 2005).

The purpose of this study was to investigate the foraging ecology of the great grebe in Mar Chiquita lagoon, analyzing dive duration, dive success, prey type, handling time, and the energy return from preys. We expected that the great grebe would forage foremost on fish, based on records of similar grebe species and

anecdotic observation of the study species. Moreover, when crabs were consumed, we hypothesised that they would be the most profitable species in terms of biomass and energy content (i.e. *Neohelice granulata*, Spivak *et al.,* 1994). For dive duration and handling time above water, we hypothesised that grebes would spend more time preying on fish than on crabs because fish are more dispersed and faster. Furthermore, when fish are caught, they have to be placed in the correct position to be swallowed (Ulenaers *et al.,* 1992).

METHODS

Study area

The study was conducted in Mar Chiquita lagoon (Argentina 37º 32' S, 57º 19' W), a Provincial Reserve and UNESCO MAB Reserve. This body of brackish water (≈ 46 km^2) has low amplitude tides (≤ 1m) and is characterised by mudflats surrounded by a large marsh of mainly *Spartina densiflora* grassland. It is also inhabited by a large number of intertidal crabs (Fasano *et al*., 1982; Bortolus and Iribarne, 1999). Two dominant burrowing semi-terrestrial crabs, *Neohelice granulata* and *Uca uruguayensis*, are dominant in the upper littoral zone, while a third species, *Cyrtograpsus angulatus*, mostly inhabits the lower littoral zone and rocky shores (Spivak *et al.,* 1994). Fish distribution and abundance show particular characteristics explained by habitat heterogeneity. The main orders represented are Clupeiformes (eg., *Brevoortia aurea*), Mugiliformes (eg., *Mugil lisa*), Atheriniformes (eg., *Odonthestes argentinensis* and *Sorgentinia incisa*), Perciformes (eg., *Micropogonias furnieri*), Pleuronectiformes (eg., *Parallichthys orbignyanus*) and Siluriformes (eg., *Pimelodella gracilis* and *Corydoras* sp) (Cousseau *et al.,* 2001).

The study area was divided into three sites in the vicinity of the estuary mouth, according to differences in microhabitat features, referred to as: inner site (site A), characterised by broad beaches and more influence of freshwater streams; intermediate site (site B), where a breakwater forms small beaches with low depth and areas with little running water; and the outer site (site C), strongly influenced by seawater and adjacent to the coastal area (fig. 1).

Foraging behaviour and prey

The foraging behaviour of the great grebe was quantified by observation of non-marked randomly selected individuals (Martin and Bateson, 1993). The observations were con-

Foraging ecology of great grebe.
[Ecología de forrajeo del macá grande.]

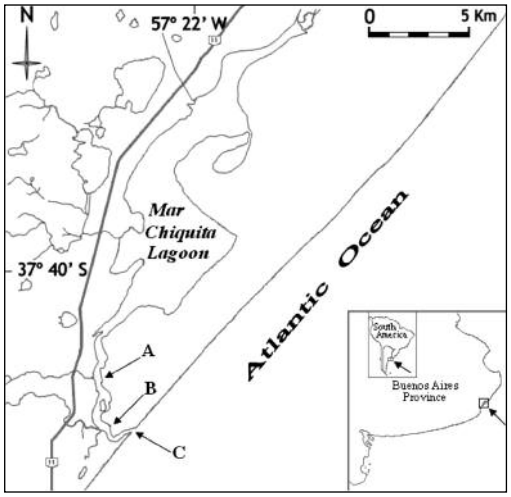

FIG. 1.—Mar Chiquita Lagoon, Buenos Aires Province, Argentina. Study area and sampling sites. A: inner site, B: intermediate site and C: outer site.
[Laguna de Mar Chiquita, Provincia de Buenos Aires, Argentina. Área de estudio y localidades de muestreo. A: área interna, B: área media, C: área externa.]

ducted once a week from October 2003 to September 2004, from the shore, at a distance of 10 to 150 m from the bird, using a 20 x 60 telescope and tape recorder. The observation was initiated when a grebe had begun to dive, or when the bird was already diving, and stopped when the grebe had finished foraging or when the individual could not be observed any longer (i.e. if the bird had moved far away or if confusion with another individual was possible). Since most birds reproduce from November onwards, only a few observations were made during the austral summer. The mean observation duration was 15 minutes, and observations lasted a maximum of 60 minutes, with samples shorter than 5 minutes being excluded.

We recorded dive duration as searching time under water, the number of apparent successful and unsuccessful dives, size and type of captured prey and handling time above water. Possible cases of grebes consuming prey under water may lead to underestimation of foraging success, due to the fact that grebes may eat small prey under water (e.g., Ulenaers *et al*., 1992; Gwiazda, 1997). We analysed the foraging ecology of the great grebe using the following variables: foraging effort as capture rate (i.e. number of prey eaten per minute), and capture success (i.e. number of dives in which a prey was caught divided by the total number of dives made), foraging efficiency as (i) the number of captured prey per foraging time (diving time plus handling time), (ii) the total biomass consumed (digestible fresh weight in grams) per foraging time (diving time plus handling time), and (iii) the energy intake as the total energy obtained per unit time $\left(\text{in Kj min}^{-1}\right)$.

The consumed prey species were identified according to their diagnostic shapes and colours, and their size through carapace width (CW) for crabs, and body length (FL) for fish. The total size of prey was estimated in relation to the adult average bill length (approximately x = 70, 9 ± 8, 0 mm, N = 38). Prey were divided into three size-classes: for crabs 'small' (15 mm ≤ CW≤ 25 mm), 'medium' (25 mm ≤ CW≤ 35 mm) and 'large' (CW > 35 mm); and for fish 'small' (FL < 80 mm), 'medium' (80 mm ≤ FL ≤ 100 mm), and 'large' (FL > 100 mm). The biomass consumed was estimated as the total wet weight for each type of prey registered during the focal sampling. The biomass of fish species was estimated using regressions between total length and mass (Favero *et al*., 2001), and that for crabs was estimated by the analysis of fresh prey in the laboratory (N = 60). We determined the caloric content (Kj / animal) and concentration $\left(\text{Kj g}^{-1}\right)$ for both prey types through bomb calorimetry (Series 1230; Moline, IL) (table 1).

Statistical analysis

The data were tested for normality and homogeneity of variances prior to any statistical analyses; nonparametric tests were used when assumptions could not be met. The proportion of consumed prey in the great grebe diet was analyzed using χ^2 tests. Diving times for different prey were compared using the Student's t-test, and for different sites with ANOVA. Comparisons in handling prey time above water for fish *vs*. crabs and for different crab species and sizes were performed with the Mann Whitney U Test (U). Size comparisons between both crab species were performed with Kruskal-Wallis One Way Analysis (H) and Dunn's Method. Foraging effort and foraging efficiency were compared with the Student's t-test. For the three study sites, foraging effort, foraging efficiency and energy intake were compared with an analysis of variance (ANOVA) and Tukey *post-hoc* comparisons (Zar, 1999).

TABLE 1

Prey types, biomass and energy content per prey in the diet of the great grebe at Mar Chiquita Lagoon, Buenos Aires, Argentina. (a) Fish biomass and crab biomass without skeletons. Prey categories: S (small), M (medium) and L (large). Sites: A: inner site, B: intermediate site and C: outer site. *[Tipo de presas, biomasa y contenido energético por presa en la dieta del macá grande en la laguna de Mar Chiquita, Buenos Aires, Argentina. (a) Biomasa de peces y cangrejos sin esqueletos. Presas: S (pequeña), M (mediana) y L (grande). Áreas: A: área interna, B: área media, C: área externa.]*

	Species	Biomass (g) per prey [(a)]	Energy content (Kj g^{-1})	Prey frequency by site (%)		
				A (N = 95)	B (N = 64)	C (N = 57)
Fish	*Micropogonias furnieri*	S = 1.58 ± 1.2, M = 6.78 ± 3.5, L = 41.53 ± 0.9	27.9 ± 1.4	–	–	91 %
	Sorgentinia incisa	S = 1.54 ± 2.3, M = 3.63 ± 2.2, L = 5.76 ± ND	23.6 ± 4.7	–	–	9 %
	Corydoras spp.	S = 1.2 ± 0.5, M = 3.32 ± 2.3	19.5 ± 6.1	5 %	–	–
	Odonthestes argentinensis	S = 2.12 ± 0.9, M = 4.27 ± 2.1, L = 8.7 ± 3.5	22.8 ± 0.3	–	26.5 %	–
	Brevortia aurea	S = 2.66 ± 1.1, M = 7.78 ± 2.3, L = 32.97 ± 12.3	15.7 ± 2.5	–	5 %	–
	Mugil lisa	S = 1.02 ± 0.5, M = 8.03 ± 0.7	24.1 ± 1.4	–	3 %	–
	Paralichthys sp.	S = 2.41 ± 0.3, M = 3.27 ± 1.5, L = 4.34 ± 1.2	15.4 ± 0.8	–	3 %	–
Crabs	*Cyrtograpsus angulatus*	S = 2.9 ± 0.32 , M = 5.0 ± 1.4 L = 8.8 ± 2.6	20.6 ± 9.6	76 %	26.5 %	–
	Neohelice granulata	S = 4.3 ± 1.5 , M = 6.6 ± 0.55, L = 9.5 ± 2.3	25.8 ± 4.2	19 %	36 %	–

RESULTS

Foraging time budget

For 122 observations homogeneously distributed across sites (≈ 12 hours per site) we observed a total of 246 grebes. For each foraging area, we observed 2.1 ± 2.1 individuals at A, 2.1 ± 2.7 at B and 1.8 ± 1.2 at C. Grebes spent 45 % of the time swimming (45.4 ± 12.9 s), 44 % diving (45.6 ± 15.8 s) (either searching or pursuing prey), 8 % handling a prey (7.8 ± 10.3 s.) and 2 % in interactions (1.4 ± 1.9 s.), that mainly consisted of intra and interspecific kleptoparasitic attempts performed generally by two species of gull, brown-hooded gull *Larus maculipennis* and Olrog's gull *L. atlanticus*.

Diet

We observed a total of 217 prey consumed by the great grebe, with crabs being the most frequent, represented by *Cyrtograpsus angulatus* (41 %) and *Neohelice granulata* (19 %). Crabs were followed by fish, represented by the white croaker *Micropogonias furnieri* (24 %), silversides *Odonthestes argentinensis* and *Sorgentinia incisa* (10 %), catfish *Corydoras* sp. (2 %), Brazilian menhaden *Brevoortia aurea* (1 %), flounder *Paralichthys* sp. (1 %) and striped mullet *Mugil platanus* (1 %).

The proportion of consumed prey differed significantly between foraging sites ($\chi^2_2 = 98.1$, $P < 0.001$ for fish, and $\chi^2_2 = 88.8$, $P < 0.001$ for crabs) (table 1). Most of the consumed crabs were small and medium-sized (52.2

TABLE 2

Parameters estimated for prey types (mean ± SE). Prey categories: (S): small, (M): medium and (L): large. (*) Biomass consumed per unit time searching, handling or foraging (g min^{-1}). (1) Include *C. angulatus* and *N. granulata*. (2) All fish species in table 1 pooled (N = 83).
[Parámetros estimados para los tipos de presas (media ± SE). Presas: S (pequeña), M (mediana) y L (grande). (*) Biomasa consumida por unidad de tiempo de búsqueda, manipulación o forrajeo (g min^{-1}). (1) Incluye C. angulatus *y* N. granulata*. (2) Incluye todos los peces de la tabla 1 (N = 83).]*

	Crabs (1)	**Fish** (2)
Return biomass	3.6 g (S) 5.82 g (M) 9.16 g (L)	1.95 g (S) 6.28 g (M) 22.24 g (L)
Energy content	22 Kj g^{-1}	18.3 Kj g^{-1}
Diving time	18.7 ± 6.9 s	22.8 ± 9.2 s
Capture rate	0.12 ± 0.9	0.09 ± 0.06
Capture success	0.22 ± 0.11	0.18 ± 0.13
Handling time	25.1 s (S) 50.7 s (M) 75.9 s (L)	29.7 s (S) 70.1 s (M) 60.5 s (L)
Searching efficiency (*)	0.05 ± 0.06	0.04 ± 0.04
Handling efficiency	0.22 ± 0.34	0.55 ± 0.55
Foraging efficiency	0.03 ± 0.02	0.03 ± 0.03
Intake (grams) min^{-1}	1.89 ± 1.97	2.04 ± 2.18

and 41.8 %, respectively), while only 6% of them were large-sized (N = 134). Regarding fish, 39.7 % were large, 38.6 % medium and 21.7 % were small-sized (N = 83).

Foraging behaviour

Diving time for feeding on fish or crabs did not differ significantly ($t_{217} = 0.81$, $P = 0.42$). Neither did diving time differ between sampling sites (ANOVA: $F_{2, 122} = 1.81$, $P = 0.17$). Handling time was significantly shorter when grebes preyed on fish than on crabs (Mann Whitney U Test: $U_{217} = 3.21$, $P = 0.001$). Handling time did not differ either for the different crab species ($U_{138} = 3{,}128.5$, $P = 0.19$) or for the different crab sizes ($U_{56} = 601.5$, $P = 0.46$ for small crabs, $U_{70} = -1.039$, $P = 0.30$ for medium-sized crabs, and $U_{16} = 65$, $P = 0.14$). However, handling time differed for both species across different sizes ($H_{2, 138} = 34.4$, $P = 0.001$), the comparison between large-small, and small-medium sizes being significant ($P < 0.05$) (table 2).

Foraging effort as capture rate and capture success for the individuals that preyed on crabs was higher than for those that preyed on fish ($t_{65} = 3.26$, $P = 0.002$; $t_{65} = 2.75$, $P = 0.007$ respectively). Foraging efficiency was higher for grebes preying on crabs ($t_{80} = 3.559$, $P = 0.001$), but in terms of biomass, no differences were found ($t_{80} = 0.54$, $P = 0.593$) (fig. 2). With respect to sites, neither foraging effort (ANOVA: $F_{2, 84} = 1.55$, $P = 0.22$) nor foraging efficiency analyzed in terms of prey or biomass consumed (ANOVA: $F_{2, 83} = 0.61$; $P = 0.543$; $F_{2, 83} = 0.76$, $P = 0.47$ respectively) varied significantly. The same result was observed for energy intake according to foraging sites (ANOVA: $F_{2,55} = 2.77$, $P = 0.07$).

Foraging behaviour of great grebe.
[Ecología trófica del macá grande.]

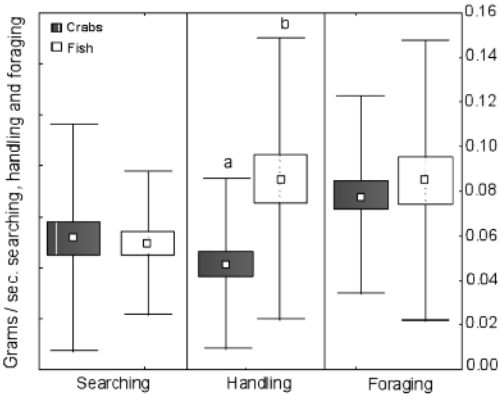

FIG. 2.—Searching, handling and foraging efficiency in terms of fish or crab biomass consumed by grebes. Mean values (points) are given together with standard errors (boxes) and standard deviations (whiskers). Letters (a, b) indicate significant differences.
[Eficiencia de búsqueda, manipulación y forrajeo del macá grande en términos de biomasa consumida de peces o cangrejos. Valores medios (puntos) junto a su error (cajas) y desviación estándar (líneas). Letras (a, b) indican diferencias significativas.]

DISCUSSION

The diet composition of the great grebe *Podicephorus major* was dominated in number by two grapsid crabs, *Cyrtograpsus angulatus* and *Neohelice granulata*, which are dominant species in the study area (Spivak *et al*., 1994). Our results differed from those obtained in the estuary of Río de la Plata and Paraná River (Argentine), where fish were reported as the main type of prey (Llimona and del Hoyo, 1992). Neither did they agree with those of other research studies (Gagliardi *et al.,* 2007; Kloskowski, 2004; Wagner and Hansson, 1998; Ulenaers and van Vessem, 1994) where fish were also described as the main prey category. Therefore, the hypothesis concerning grebes preying foremost on fish was not supported. This could be attribu-

ted, at least partially, to the absence of differences in energy content between fish and crabs for our laboratory analysis data. Although we do not know the availability of prey, in Mar Chiquita lagoon a large proportion of the intertidal area is occupied by high densities of crabs (Botto and Iribarne 1999, Martinetto *et al.,* 2005).

Due to the fact that *N. granulata* have a mass-size ratio higher than *C. angulatus* (Spivak *et. al*, 1994), we originally supposed that consumption of the first species would be more profitable in terms of biomass acquired. However, the great grebe consumed more *C. angulatus*, which contradicts the latter hypothesis. Unfortunately, our observations were not accurate enough to determine the causes of grebe prey preferences.

Foraging effort in terms of diving time across sites was similar, both for the consumption of crabs and fish. Similar searching times across sites could be due to the slight variation in depth in Mar Chiquita Lagoon (Fasano *et al*., 1982). A study of red-necked grebes *Podiceps grisegena* showed that searching time was similar for fish and invertebrates, while handling time above water was higher for fish (Kloskowski, 2004). We originally suggested that the handling time of grebes preying on fish would be longer than that of grebes foraging on crabs; however, we observed otherwise. After catching a crab, the great grebe usually removed its limbs before consuming it*;* such particular behaviour implies additional time. Furthermore, the fish that were consumed most frequently were small or medium-sized; it is known that handling time above and under water increases with fish size (Ulenaers *et al*., 1992).

The capture success and capture rates of the grebes showed a decrease from the inner (A) to the outer site (C). This is attributed to more frequent captures of crabs, probably due to a higher occurrence of these prey in areas better protected inside the estuary, such as the inner site (Spivak *et al*., 1994). The lack of differences in grebe foraging behaviour across sites in terms of foraging effort, efficiency and energy intake, suggests a response to the higher availability of crabs in this estuary. This resource apparently plays an essential role in the great grebe's diet, apart from fish. Further studies are needed to explore the potential spread of this foraging behaviour across seasons and to other estuaries and to research the availability of different prey in order to elucidate the importance of Mar Chiquita for grebes.

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