Age-specific Diving and Foraging Behavior of the Great Grebe *(Podicephorus major)*

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Abstract.—The foraging and diving behavior of the Great Grebe (*Podicephorus major*) was studied in southern Brazil, from June to October 2005. A total of 547 dives performed by adult birds and 578 dives of juveniles were recorded. There was no age-related difference in dive duration (adults = 19.43 s; juveniles = 20.00 s) but the time elapsed between two successive dives (pause or recovery time) differed among age-classes (adults = 16.1 s; juveniles = 15.0 s). Duration of dive and pause times were weakly correlated in adults and not correlated in juveniles. Both age classes had feeding bouts of similar durations. Adults were more efficient in capturing prey (0.2 prey/min) in comparison with juveniles (0.1 prey/min) and took significantly larger prey. The main food item was the White Croaker (*Micropogonias furnieri*), an abundant demersal fish in the area. Juveniles had higher prey handling time in comparison with adults (78.2 s *vs.* 20.1 s), making them more prone than adults to being cleptoparasitized by other seabirds. Diving duration varied during daytime hours, with juveniles diving longer during early morning and late afternoon, while adults avoided foraging during midday hours. Feeding throughout the day could be a mechanism used by juvenile grebes to compensate for low foraging efficiency. *Received 3 April 2007, accepted 11 September 2008.*

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In terms of survival, vertebrate juveniles perform more poorly than adults (i.e. fish: Eckert 1987; mammals: Gillis 1998; birds: Weimerskirch 2002). In birds, a common reason for age-related performance is foraging efficiency (Brandt 1984; Marchetti and Price 1989; Wunderle 1991; Forslund and Pärt 1995), which can be due to: a) morphological limitations such as incomplete skeletal, bill, muscle or neurological maturity; b) as yet undeveloped learning which can be developed by observation, previous experience and the need for a prey searching image; c) different nutritional requirements (adults allocate energy and nutrients for moulting and juveniles allocate protein for growth); d) social interactions such as hierarchic access to feeding areas, cleptoparasitism, and predation risk (Orians 1969; Verbeek 1977; Morrison *et al.* 1978; Burger 1980; MacLean 1986; Marchetti and Price 1989 and review in Wunderle 1991). These differences between juveniles and adults appear to be responsible for the delayed breeding in birds in general and seabirds in particular, whose breeding frequently occurs after three-four years and sometimes after ten years (Ashmole 1963; Lack 1966; Weimerskirch 2002). In addition, inefficient foraging in juveniles contributes to elevated mortality during this stage (Lack 1954; Ashmole 1963), and has important implications for the low breeding performance in new breeders (Forslund and Pärt 1995).

For birds in general, mechanisms to compensate for reduced foraging efficiency include more time searching for and handling prey (Groves 1978; Burger 1980), use of different areas and foraging methods (Brandt 1984; Edwards 1989) or juveniles relying on different prey species or different prey sizes (Wunderle 1991; Papakostas *et al.* 2005). However, regardless of the mechanism used by juveniles to obtain sufficient amounts of food, their increased efforts imply increasing energy expenditure (Buckley and Buckley 1974; Morrison *et al.* 1978). Here, we compare the two main variables of the diving behavior (dive duration and time at surface) and investigate differences in foraging efficiency between adult and juvenile Great Grebes (*Podicephorus major* [Boddaert 1783], synonym *Podiceps major*). We also studied circadian changes in foraging behavior and diving and speculated on the possible compensatory mechanisms used by juveniles to obtain sufficient amounts of food.

The Great Grebe is a poorly known aquatic bird with a wide distribution in South America, from southeastern Brazil to southern Argentina, Uruguay, Paraguay and Peru (Storer 1963; Sick 1997; Narosky and Yzurieta 2003). The species breeds throughout the year according to region (Escalante 1980; Greenquist 1982), is predominantly piscivorous, with insects, crabs, amphibians and small chicks as secondary items in the diet (Storer 1963; Escalante 1980; Beltzer 1983; Daciuk *et al.* 1985). There is no external sexual dimorphism, but juveniles and adults differ in plumage (Harrison 1985). Age at first breeding is unknown, but is probably two years old as in other similar sized European grebes (Cramp and Simmons 1977).

METHODS

Observations of Great Grebe diving behavior were carried out between June and October 2005, in the oceanic beach adjacent to the west jetty in the entrance of the Patos Lagoon channel, Rio Grande do Sul state, Brazil (32°10'S; 52°10'W). The west jetty stretches for 3 km from the beach, making the area between the jetty and Cassino Beach a calm area protected from the prevailing northeastern winds (Braga and Krusche 2000). Bugoni and Vooren (2005) presented a detailed description and map of the area. In spite of being oceanic, the area is strongly influenced by highly productive freshwaters from the Patos Lagoon (Castello 1986). This estuarine-marine system is a very important nursery and feeding ground for commercially significant fish species, such as White Croaker (*Micropogonias furnieri*), Catfish *Netuma* spp. and Mullets (*Mugil* spp.) (Vieira *et al.* 1998). Few species have adapted to the physiological stress caused by fluctuations in salinity in the estuarine region; however, compensation is provided by abundant food and shelter in the shallow waters. The few fish species able to handle the salinity stress are abundant (Castello 1986; Vieira *et al.* 1998).

In the area, Great Grebes occur from May to November with mean peak numbers of 211 individuals in August (censuses in 2001, 2002 and 2004; L. Bugoni, unpubl. data). During the non-breeding period, corresponding to the period above, Great Grebes which occur predominantly in freshwaters may be found in marine waters close to the coast (Sick 1997), similar to other Northern Hemisphere grebe species which use marine areas for wintering (Cramp and Simmons 1977; Paszkowski *et al.* 2004).

For age identification of Great Grebes we followed Escalante (1980): adults—dorsum darker and shinier than juveniles, light grey and shiny on the sides of the head, ferruginous throat with white ventral parts; juveniles or immatures—general plumage shaded, white sides of the head and throat, slightly tinged with red. According to this classification, a juvenile refers to a fledged bird with size similar to an adult, but of unknown age, probably less than two years old. Circadian differences in diving and feeding behavior were tested by comparing data divided into five two-hour blocks, from 08.00 to 18.00 h. A total of ten hours were devoted to each block, with a total sampling effort of 50 h in 12 different days. Data were collected by two people, one performing the observations with 10 × 40 mm binoculars while the other took notes and checked the chronometer. One active grebe was chosen randomly and observed continuously along the entire feeding bout through the focal animal sampling method (Altmann 1974). Data recorded were number of dives, immersion duration, pause time between two consecutive dives, outcome of the dive, prey handling duration, total duration of the feeding bout, prey size in comparison with the bill size, and prey species. Only bouts with at least ten consecutive dives were used (Morrison *et al.* 1978). The end of a feeding bout was defined visually as the focal grebe remaining on the surface for at least two minutes, thus ending a clear series of consecutive dives. Infrequently the observer was unable to track the bird after a dive because it moved away from the visual field or due to confusion with other grebes foraging nearby. Pause times are characteristically short (15-16 s, see Results) and pauses longer than 50 s were not analyzed because they could indicate the bird stopped foraging. Dive efficiency, defined as the dive/pause (d/p) ratio, was calculated using the mean dive and pause values.

Prey sizes were approximates obtained by comparing them with the focal individual's culmen length (8 cm on average, N = 3 birds measured at CA-FURG Coleção de Aves da Fundação Universidade Federal do Rio Grande and CRAM-FURG Centro de Recuperação de Animais Marinhos). Categories of the fish length were: I - half bill length or about 4 cm. II - bill length or about 8 cm; III - 1.5 times the bill length or 12 cm; IV - twice the bill length or 16 cm; and V - 2.5 times the bill length or 20 cm. Successful capture was recorded when the grebe was seen handling and swallowing the prey, and not when the prey was lost during handling. The 22 grebe species living today have a wide range of body size and bill size, characteristics accounting for their different foraging and prey capture methods. They rely on many prey species from small insects, leeches and snails to large fish, frogs and bird chicks (Fjeldså 1983, 2004). Generally, small grebe species feeding among vegetation rely on either small invertebrates or small fish, frequently swallowing prey underwater, while large grebes with large bills and foraging in open waters rely mostly on large fish (Fjeldså 1983; Doornbos 1984). This last group, which includes the Great Grebe, rarely swallows prey underwater. Mayr (1988 in Ulenaers *et al.* 1992) showed that only 5% of prey of the Great Crested Grebe (*Podiceps cristatus*) is swallowed underwater and Enstipp *et al.* (2007) observed underwater swallowing of small fish by Double-crested Cormorants (*Phalacrocorax auritus*) in only 3.3% of the cases. In addition, we found Great Grebes handling prey for long periods on the surface (see Results), which also could suggest that none or a few prey are swallowed underwater. Thus, in this study we assumed that all prey were handled at the surface before being swallowed.

By sampling grebes not individually identified or measuring consecutive dives from the same birds, we could risk pseudoreplication. However, the use of non-independent observations is valid if the replicates are pooled to estimate a mean value (Hurlbert 1984). In addition, from one to three birds were sampled every session, with minimal possibility that the same individual was sampled during the same day. This procedure assured that we sampled a significant number of individuals rather than a few. The chi-square test was used to compare age-related differences in capture efficiency and prey size preferences. Both dive and pause duration times of juveniles and adults were normally distributed and homoscedastic, according to Levene and Kolmogorov-Smirnov tests, respectively, and were compared by the t-test (Zar 1999). Correlation analysis was used to analyze the relationship between dive and subsequent pause, in both adults and juveniles. Handling time and duration of feeding bouts did not meet the requirements of parametric tests and were tested using non-parametric Mann-Whitney test. Similarly, circadian variation in prey capture efficiency was analyzed using non-parametric Kruskal-Wallis test (Zar 1999). One-way ANOVA and post hoc Tukey tests were used to compare circadian variation in diving time (Zar 1999).

RESULTS

Diving Proficiency

A total of 547 dives performed by adult Great Grebes (1.6 dives/min, Total = 344.3 min) and 578 dives of juveniles (1.6 dives/min, Total = 374.7.) were recorded (Table 1). Dive duration of adults was 19.4 ± 7.6 s (mean ± sd), with minimum of one and maximum of 49 s and was similar to the juvenile dive duration of 20.00 ± 7.56 s (range = 3 - 55 s) (t_{1123} = 1, 14, n.s.; Table 1; Fig. 1). However, adults had longer pause duration on the surface (16.1 ± 8.95 s, N = 480), than juveniles (15.0 ± 7.9 s, N = 518) ($t_{996} = 1.9$; $P < 0.05$, Table 1).

Correlation between dive time duration and subsequent pause duration was weak but significant for adults ($r_{480} = 0.11$; $P < 0.05$), but these were not correlated in juveniles ($r_{518} = 0.03$; n.s.). Mean diving efficiency (mean dive duration time/mean pause time) was 1.2 for adults and 1.3 for juveniles (Table 1). Duration of feeding bouts was similar in adults and juveniles (adults = 12.2 ± 6.8 min, range = 5.1 - 35.5 min, N = 24; juveniles = 10.5 ± 4.8 min, range = 4.6 - 20.8 min, N = 27; U = 280.0; n.s.) (Table 1).

Foraging Efficiency

Adult Great Grebes were more efficient than juveniles in capturing prey (N = 65 and 36, respectively), considering number of prey captured per dive ($\chi^2_1 = 10.02$; $P < 0.01$) and number of prey captured per minute diving (adults = 0.2 prey/min; juveniles = 0.1 prey/min) (Table 1).

Fish length was recorded for an unknown number of individual grebes, with adult and juveniles grebes capturing, respectively, 49 and 33 prey. Juveniles captured predominantly prey of size classes I (N = 10 prey) and II (N = 13) ($\chi^2_4 = 20.18$; $P < 0.001$). On the other hand, adults preyed preferentially upon prey of classes II (N = 21 prey) and III (N = 15 prey) ($\chi^2_4 = 27.22$; $P < 0.001$). Adults were identified as preying significantly upon larger fish than juveniles ($\chi^2_4 = 9.8$; $P = 0.05$).

Table 1. Diving and foraging parameters of juvenile and adult Great Grebes (*Podicephorus major*), in southern Brazil.

	Adults	Juveniles
Number of Dives (N)	547	578
Mean Diving Duration (s)	19.5	20.0^{ns}
Mean Pause Duration (s)	16.1	15.0^{*}
Diving Efficiency (mean diving duration/mean pause duration)	1.2	1.3
Diving Rate (Number of dives/min)	1.6	1.6
Absolute Number of Successful Dives (%)	65 (11.9)	36 $(6.2)^{**}$
Capture Rate (prey/min)	0.2	0.1
Handling Prey Time (s)	20.1	78.3^{***}
Duration of Feeding Bouts (min)	12.2	10.5^{ns}

^{ns}= Not significant.
*= $P < 0.05$.
**= $P < 0.01$.
***= $P < 0.001$.

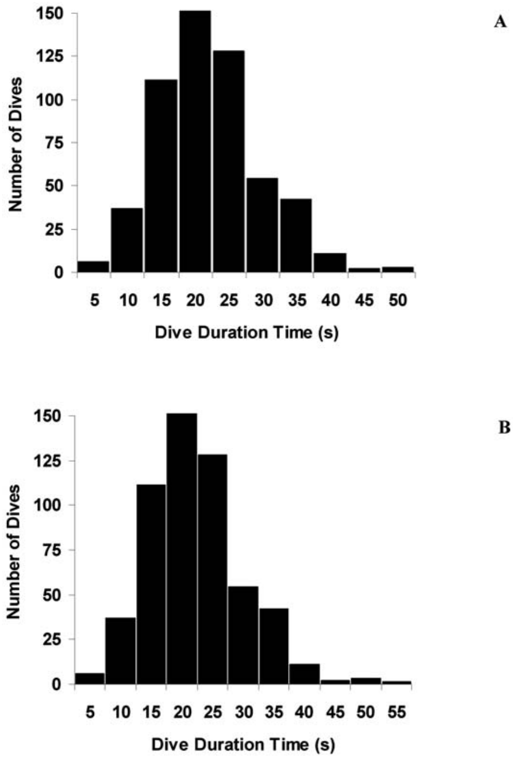

Figure 1. Dive duration time of great grebe, *Podicephorus major*, (A) adults (N = 547 dives) and (B) juveniles (N = 578) in a near shore environment in southern Brazil.

Thirty-eight prey were identified as the White Croaker (27 preyed by adults and 11 by juveniles), while all other prey were also fish but species could not be identified from distance.

Juveniles spent 3.9 times longer than adults handling prey, between returning to the surface and swallowing the prey (juveniles = 78.3 ± 94.7 s, adults = 20.1 ± 17.1 s; U = 152.5; $P < 0.001$, Table 1). In addition, juveniles lost the fish prey five times during handling, an event not recorded in adults, in spite of more prey being captured by the later group. Cleptoparasitic behavior (*sensu* Schnell *et al.* 1983) of Brown-hooded Gull (*Chroicocephalus maculipennis*), Neotropic Cormorant (*Phalacrocorax brasilianus*) and Amazon Tern (*Sternula superciliaris*) was recorded six times in juveniles, but never in adult grebes, despite adults and juveniles foraging in the same area. Only once was an adult grebe recorded chasing a juvenile, which could suggest that the bird was defending a territory. Both class ages use the same foraging areas.

Circadian Variations in Diving and Foraging Behavior

Dive duration time of both age classes, analyzed separately, varied along daylight hours ($F_1 = 6.4$; $P < 0.05$). In addition, circadian variation was different between age-classes ($F_4 = 7.44$; $P < 0.001$), with juveniles diving longer during early morning and late afternoon (Tukey test $P < 0.001$ and $P < 0.05$ respectively).

Regarding circadian diving frequency (dives/min), no clear pattern was identified, in spite of adults diving more frequently from 8.00-10.00 h and 12.00-14.00 h periods (both 1.8 dives/min). In juveniles, diving frequency was higher from 10.00-12.00 h and 14.00-16.00 h, with 2.0 and 1.6 dives/min, respectively (Table 2).

Adults and juveniles had similar circadian variation in prey capture efficiency (Kruskal-Wallis H = 4.00; n.s.). Overall, adults had higher capture rates during the whole day, except in the late afternoon (16.00-18.00 h), when juveniles were slightly more efficient. During this sampling block, juveniles had longer dives and longer feeding bouts (Table 2).

Feeding bouts of adults were longer during early morning (08.00-10.00 h) and afternoon (14.00-16.00 h). On the other hand, juveniles had longer feeding bouts between 10.00 and 12.00 h, and between 16.00 and 18.00 h (Fig. 2).

DISCUSSION

Diving Proficiency

There was no difference in diving duration time between adult and juvenile Great Grebes in southern Brazil; a result also found in Neotropic Cormorants and Brown Pelicans *Pelecanus occidentalis* elsewhere (Morrison *et al.* 1978; Coblentz 1986). In spite of juvenile grebes spending significantly less time on the surface between successive

Table 2. Circadian variation in diving and foraging parameters of adult and juvenile Great Grebes, in southern Brazil.

Day Hours	Number of Dives		Diving Frequency (dives/min)		Dive Duration (s)		Absolute Foraging Success (No. of prey)		Prey Capture Rate (prey/min)	
	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles	Adult	Juveniles
08-10 h	145	98	1.8	1.4	16.5	20.8***	13	7	0.16	0.10ns
10-12 h	79	121	1.1	2.0	19.7	17.8ns	13	4	0.19	0.06ns
12-14 h	105	111	1.8	1.3	17.4	17.4ns	12	10	0.21	0.12ns
14-16 h	142	199	1.5	1.6	21.5	21.1ns	18	9	0.18	0.07ns
16-18 h	77	49	1.4	1.4	21.6	25.6*	9	6	0.16	0.18ns

ns= Not significant.
*= P < 0.05.
***= P < 0.001.

dives in comparison with adults, the difference was only 1.1 s, and this could be an artefact of the large sample size with limited biological meaning. The significant but weak correlation between dive duration and subsequent pause time (d/p) in adults could also be related to the large number of dives measured. The absence of correlation in juveniles was probably due to shorter times on the surface, even after long dives, again a behavior that could cause physical exhaustion. The d/p is commonly used as an indication of physiological capacity in birds (Dow 1964), and indicates that juvenile and adult Great Grebes had similar diving capacity. Similarly, Neotropic Cormorants studied in Argentina and in the United States did not show age-related differences in diving capacity (Morrison *et al.* 1978). Stonehouse (1967) argued that the d/p is a common feature of species among a given bird family. The time spent on the surface is a period that the animal uses to recover from the previous dive and prepares for the next one, but anaerobic dives make the interpretation of this parameter quite difficult (Frere *et al.* 2002; Wilson and Quintana 2004). Therefore, we opt to call this *pause duration time* instead of the more commonly used *recovery time*, because the time on the surface could occur after a sequence of anaerobic dives. In addition, because juveniles are less efficient in capturing prey they need to intensify foraging effort to gather a sufficient amount of food. In adults, this additional effort is unnecessary and they forage below their physiological constraints to avoid exhaustion (Stonehouse 1967). Due to these characteristics, if there are differences in foraging efficiency, the d/p is not a good parameter for comparison between ages.

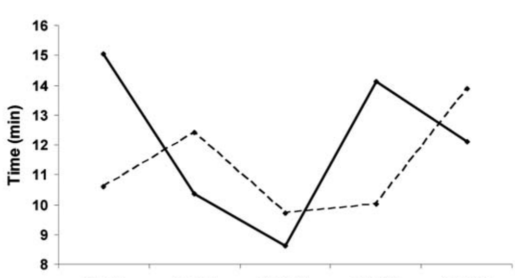

Figure 2. Circadian variation in the duration of the feeding bouts of adults (——) and juveniles (- - - -) of the Great Grebe, *Podicephorus major*, in southern Brazil.

Feeding bouts had similar duration in adults and juveniles, a result also reported in other species (Dunn 1972; Groves 1978), but diverging results were found by Buckley and Buckley (1974), Morrison *et al.* (1978), Burger (1980), Coblentz (1986) and MacLean (1986). Morrison *et al.* (1978) argue that juveniles spent more time feeding to compensate for their lower proficiency in capturing prey. Apparently, this is not a compensatory mechanism used by juvenile Great Grebes.

Foraging Efficiency

We have shown that adult Great Grebes forage more efficiently than juveniles, an age-related feature common in other birds

(Orians 1969; Morrison *et al.* 1978; Searcy 1978; Burger 1980; Schnell *et al.* 1983; Brandt 1984; MacLean 1986; Carl 1987; Arnqvist 1992; Papakostas *et al.* 2005). Foraging efficiency is supposed to increase with age and experience (Buckley and Buckley 1974; Morrison *et al.* 1978; Schnell *et al.* 1983; Brandt 1984), and foraging inefficiency of juveniles has been suggested as contributing to their higher early age mortality (Lack 1954; Ashmole 1963; Weimerskirch 2002). Foraging efficiency could therefore be expected to be under strong selection pressure, which means that individuals able to learn fast have high survival rates (Morrison *et al.* 1978). Food delivery by adults to juveniles during their first wintering period, as reported in Sandwich Terns (*Thalasseus sandvicensis*) and in Royal Terns (*Thalasseus maximus*) (Ashmole and Tovar 1968; Shealer and Burger 1995) appears to be a way of increasing offspring survival during critical periods, while chicks develop their abilities to search, capture and handle prey. In the current study, adults and juveniles were not observed to segregate in particular areas and were seen to feed mostly on White Croaker. Nevertheless, juveniles preyed upon smaller fish prey (fish classes I and II by juveniles and fish classes II and III by adults). This difference is probably related to the inability of juveniles to catch larger fish with larger energetic content, but which could sustain higher escape speed and be more able to avoid predators. Edwards (1989) showed that juvenile Ospreys (*Pandion haliaetus*) progressively capture larger fish prey with age. Small prey captured by juveniles is a widespread feature in birds feeding upon different prey types and demonstrates the inefficiency of juveniles in capture and handling prey (Dunn 1972; Brandt 1984; Coblentz 1986; Wunderle 1991; Papakostas *et al.* 2005). An alternative hypothesis is that juveniles opt to capture prey of sizes with high availability while experienced adults are able to select prey of larger size. For instance, immature Bald Eagles (*Haliaetus leucocephalus*) have foraging strategies that need lower skill, gradually using more elaborate feeding tactics (Bennetts and McClelland 1997). In summary, adult Great Grebes used more efficient strategies than juveniles, selected prey of larger energy content and were probably more able to evaluate the trade-off between longer dives or longer feeding sequences.

In addition, the inability of juveniles to handle prey resulted in prey being lost frequently, which contributed to reduced foraging success. However, even considering prey lost by handling inability as effectively captured, the capture rate of juveniles (0.1 prey/min) was only half that of adults (0.2 prey/min). Thus, lower foraging success refers to both inability to locate and capture prey, as well as inability to handle and avoid cleptoparasitism. In Ruddy Turnstones (*Arenaria interpres*) it was demonstrated that the lack of experience of juveniles in locating and handling prey was a primary factor in determining their reduced foraging efficiency (Groves 1978). The general pattern of juveniles handling prey for longer periods and losing prey more frequently was also demonstrated in several birds feeding on different food items (MacLean 1986; Wunderle 1991). Juveniles are more vulnerable to cleptoparasitism, probably due to longer handling time on the surface, which attracts more parasites (Schnell *et al.* 1983; Dunn 1972), or because parasites identified juvenile grebes as better targets with higher probability of successful attack.

The subadult White Croaker, preyed on by grebes in southern Brazil, is common to shallow waters in the study area (Castello 1986; Vieira *et al.* 1998) and an important fish resource in south and southeastern Brazil, being targeted both in estuarine and oceanic areas (Haimovici *et al.* 1996). Also, the species is an important prey of other seabirds such as Common Tern (*Sterna hirundo*) and the Neotropic Cormorant (Bugoni and Vooren 2004; Barquete *et al.* 2008). The Great Grebe in Chile preys mainly upon Atherinidae Silversides (Storer 1963) and in Uruguay large proportions of crabs and small fish were reported in the diet (Escalante 1980). In freshwater systems, 71% of prey were fish (sizes between 20 and 50 mm), with minor proportion of molluscs, crustaceans and insects (Beltzer and Oliveros 1982).

Circadian Variations in Diving and Foraging Behavior

Adult Great Grebes concentrated their foraging effort during particular periods of the day (i.e. more frequent dives), while juveniles maintained high activity levels throughout the day. In addition, adults seem to have longer feeding bouts during early morning and late afternoon, while the pattern for juveniles is not clear. Preferential foraging in early morning is common in other coastal seabirds such as adult Common Terns (Bugoni and Vooren 2005) due to long overnight fasting. The observed constancy of foraging throughout the day by juveniles could be one of the mechanisms used by juvenile Great Grebes to compensate for their reduced foraging efficiency, as suggested by Buckley and Buckley (1974), Morrison *et al.* (1978), Burger (1980) and MacLean (1986). Alternatively, these periods could correspond to higher prey availability and better foraging opportunities. Juveniles could also prefer to forage in periods with reduced predation pressure over fish schools (10.00-14.00 h and 16.00-18.00 h), when adults were not active, or had not developed their ability to identify best foraging periods, as indicated by low foraging efficiency of juveniles in comparison with adults.

In summary, we have shown similar diving parameters between juvenile and adult Great Grebes, but lower foraging success, reduced capture rate and smaller prey size in juveniles compared with adults feeding on similar area and prey species. In addition, there are age-related differences in daytime periods spent in foraging activity, with juveniles apparently spending more time in foraging activity. Taking into account the capture rate of juveniles, they need to perform 92% more dives than adults to obtain the same number of prey. Their relative foraging inefficiency is exacerbated by the smaller prey sizes compared with that of adults. Therefore, it is possible that the juveniles struggle to meet their energy requirements despite their energetic requirements being lower than those of adults due to the lack of moult during their first winter (Paszkowski *et al.* 2004). This result is consistent with frequent mortality of juveniles by emaciation in several bird species (Wunderle 1991).

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