

Foraging and diving patterns of the Great Crested Grebe *Podiceps cristatus* in a fishpond

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Abstract

Diving and foraging patterns of the Great Crested Grebe *Podiceps cristatus* were studied on Vrbje fishpond in Central Slovenia. Three pairs and their 10 young were studied. The duration of 348 dives of the six adults before hatching, 295 dives of the three pairs of adults with young, and 185 dives of the immature birds were recorded during the breeding season in 1998 (from June through October). Mean dive duration was 31 sec for adults before hatching, 41 sec for adults with young, and 25 sec for immatures.

Diving success varied significantly between groups, the most successful were grebes with young. Adult grebes without young caught a higher proportion of large fish than the other groups did. Fish size was negatively correlated with duration of dives in adult grebes without young and in adults with young but not in immatures.

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Introduction

Considerable interest has been shown in the diving and foraging patterns of diving birds (see e.g. Cooper 1986, Trivelpiece et al. 1986, Burger & Wilson 1988, Croxall et al. 1988, Wanless et al. 1991). However, most of these studies have focused on marine birds, e.g. penguins and cormorants while data from freshwater birds, e.g. grebes are more scarce.

The Great Crested Grebe *Podiceps cristatus* is a predator that occurs in most freshwaters in Europe. The behaviour and ecology of the Great Crested Grebe have been studied extensively in several countries (e.g. Cramp & Simmons 1977, Glutz von Blotzheim et al. 1987 and references therein), but the feeding habits and foraging patterns were poorly known at the onset of this study (but see Gwiazda 1997 and references therein).

In this paper, I report on the foraging pattern of adult and immature Great Crested Grebes during the breeding season. I show that swallowing the prey under the water by Great Crested Grebe depends on the experience and breeding status.

Study area

Vrbje pond is situated in the Lower Savinja Valley near the town Žalec (approximately 46°14' 15°09').

The pond area is 13.5 ha and the average depth is about 1.2 m (0.5–2 m). Immersed (*Typha latifolia*, *T. angustifolia*) and floating (*Potamogeton crispus*, *P. natans*, *P. spicatum*, *Myriophyllum spicatum*, *Elodea canadensis*) vegetation covers between 40% and 60% of the surface of the pond (Vogrin 1999). The pond is managed for fish rearing and it is usually discharged once a year (autumn/spring) for about 1 to 5 months. Culturing of carp has always been carried out there and has been done with supplementary feeding. During the whole study period the conditions of the pond (e.g. vegetation, fish stock) were the same; however, we should take into account that fish also grow up during the study period as well as vegetation. For more information about the study area see Vogrin (1996, 1997). Because of the empty pond during early spring, waterfowl start to breed in June.

Methods

All observations were made from a car on the banks with most observations being made with naked eye, since during a dive the birds frequently moved out of the field of view of the binoculars. However, binoculars and telescope were used to estimate the size of prey.

In 1998, three pairs of Great Crested Grebe bred. No other birds than these six adults and their young were present in the pond. All three pairs produced young which survived to fledging. The number of young and immatures that were involved in the study was 3, 3, 4 young per pair respectively; no young died. Since the adult birds were the same throughout the study, I could compare “foraging success” before and after hatching of the young.

“Foraging success” was measured by recording the number of dives when the birds appeared at the surface with and without a fish. Continuous observations, for as long as possible, of individual birds were arbitrarily selected to cover different hours of the early part of the day and with the days distributed over the whole season from June through October and watched for 5 to 23 min. When two birds of the same age started to feed close to each other the watch was abandoned. Data were collected only for birds which did not show any obvious signs of disturbance or courtship behaviour. All timing was done with a stopwatch and the observations were mainly dictated to a tape recorder. The observations were made between June (at the start of breeding season) and October (when the young were independent) in 1998. Up to ten observation days in the morning (ranging from 4 to 10 hours) per month were made. During these observations the number of dives, the number of prey, and the duration of the dives were recorded.

The size of the prey was estimated in relation to the size of the Great Crested Grebe beak (around 5 cm;

Cramp & Simmons 1977, Glutz von Blotzheim et al. 1987). In this way, three size classes of fish were established: small (< 5 cm), medium (5–15 cm) and large (>15 cm). Altogether the length of 232 prey was estimated (73 for adults without young, 112 for adults with young and 47 for immatures).

Data for adults (only before hatching), adults with young, and immatures that were feeding independently were collected separately. For all groups I collected more than 180 dives (295 for adults before hatching, 348 for adults with young and 185 for immatures).

Diving success was normalized for parametric analyses by $\sqrt{\text{arc-sine}}$ transformation. Fish size and duration of dives were log transformed. Tests (one-way ANOVA, Kruskal-Wallis test) were performed with SPSS 8.0 statistical packages. Since the data come from only three pairs and their young, the sample is small. We should be aware that I pool data from the same individuals. This means that the data are not strictly independent, and the statistical tests may not be fully valid.

Results

Both immatures and adults without young (before hatching) dived less often than did grebes associated with young (Table 1). The difference remains significant when immature birds were excluded ($F = 4.7, P < 0.01$).

The mean dive time differed significantly between groups. Grebes without young dived for less time

Table 1. Frequencies, duration of dives, fish brought to the surface (fish per min) and diving success (measured as the proportion of occasions when grebes brought fish to the surface) by adults without young, adults with young and immature Great Crested Grebes *Podiceps cristatus* during June–October 1998 on Vrbje fishpond.

Frekvenser, dyktider, fiskar per minut som togs till ytan och dykframtåg (mätt som andel dykningar med fångst) för adulta med ungar, adulta utan ungar och ungfåglar av skäggdopping under juni–oktober i Vrbje fiskdamm.

	Adults without young <i>Gamla utan ungar</i>			Adults with young <i>Gamla med ungar</i>			Immatures <i>Ungfåglar</i>		n	F	P <
	mean	SD	N	mean	SD	N	mean	SD			
Dives per min <i>Dykningar per min.</i>	0.71	0.31	348	0.95	0.43	295	0.30	0.60	185	20.3	0.001
Duration of dives (s) <i>Dyktid (sekunder)</i>	31	6.3	253	41	9.8	190	25	11.1	105	13.4	0.005
Fish per min <i>Fiskar per min.</i>	0.09	2.8	348	0.21	1.3	295	0.11	3.1	185	15.9	0.01
Diving success (%) <i>Dykframtåg (%)</i>	21	5.4	348	38	4.1	295	25	7.8	185	7.39	0.01

Table 2. Number (n) and percentage of fishes in relation to their size taken by Great Crested Grebe *Podiceps cristatus* according to groups.

Antal (n) och procent fiskar i förhållande till storleken som togs av skäggdoppingarna, fördelade på de tre grupperna.

Fish size Fiskstorlek	Adults without young Gamla utan ungar		Adults with youngs Gamla med ungar		Immatures Ungfåglar	
	n	%	n	%	n	%
< 5 cm	18	25	39	35	21	45
5–15 cm	19	26	42	38	16	34
> 15 cm	36	49	31	27	10	21
Total	73	100	112	100	47	100

than did adults with young ($F = 20.2$, $P < 0.01$). Significant differences were also found between adults and immature grebes ($F = 12.4$, $P < 0.001$).

In 62–79% of 828 dives, grebes brought nothing to the surface, either no prey was caught, or the prey was swallowed under water. However, diving success (measured as proportion of occasions when grebes brought fish to the surface) varied significantly between groups, the most “successful” group being grebes with young (Table 1). Interestingly, the immature grebes brought prey to the surface more frequently than adults without young ($F = 3.15$, $P < 0.05$).

Both adults and immature grebes were feeding exclusively on fish (all 232 prey items were fish). The mean fish length captured by Great Crested Grebe, divided into three length categories, varied during the breeding season (Table 2). The total fish sizes varied between 3 cm and 22 cm. Average size

of fish caught by adults without young, adults with young and immatures measured 13, 10, and 8 cm, respectively. The differences between the groups were significant ($F = 2.15$, 4.07, and 2.80, respectively, in all cases: $P < 0.05$). The average fish caught by adults with young differed significantly between months (Kruskal-Wallis test, Chi-square = 18.3, $df = 2$, $P < 0.001$). The smallest fish were caught in July when the chicks were still very small (Figure 3).

The fish size was negatively correlated with duration of dives in adult grebes without young ($r = -0.48$, $P < 0.05$, $n = 23$; Figure 1) and in adults with young ($r = -0.35$, $P < 0.05$, $n = 38$, Figure 2). However, no significant relationship was found for immatures grebes ($r = -0.15$, n.s.). In the case of adults without young, the negative relationship seems to be particularly clear for longer dives (16–32 seconds), and the relationship may not be linear over

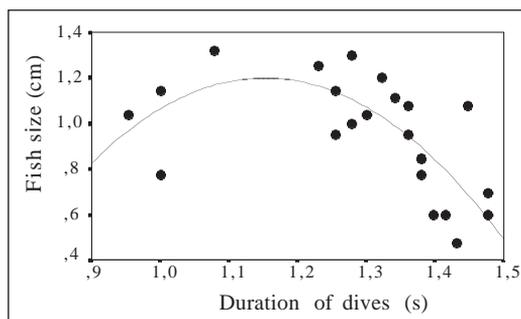


Figure 1. Relationships between duration of dives and fish size for adult great Crested Grebes *Podiceps cristatus* without young. Note that the axes show the logarithms of size and duration.

Förhållandet mellan dyktid och fiskstorlek för gamla skäggdoppingar utan ungar. Notera att axlarna visar logaritmerade värden för storlek och dyktid.

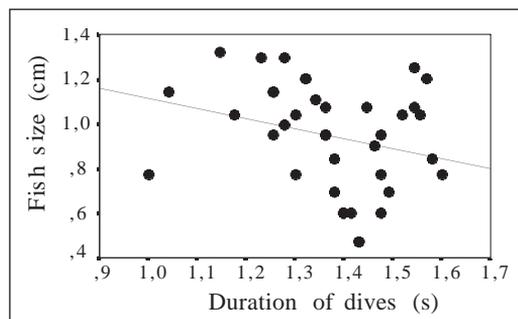
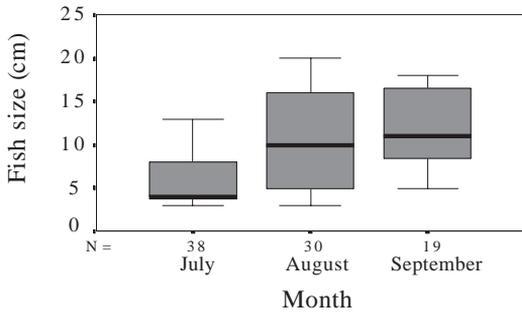


Figure 2. Relationships between duration of dives and fish size for adult great Crested Grebes *Podiceps cristatus* with young. Note that the axes show the logarithms of size and duration. Förhållandet mellan dyktid och fiskstorlek för adulta skäggdoppingar med ungar. Notera att axlarna visar logaritmerade värden för storlek och dyktid.



Figur 3. Size of fish captured by adult Great Crested Grebes *Podiceps cristatus* feeding young in different months. Mean values are shown as thick lines, boxes represent SD and the thin lines minimum and maximum values.

Storleken hos fiskar som fångades av adulta skäggdoppingar som matade ungar under olika månader. Medelvärdena visas med tjock linje, standardavvikelsen med en grå box och minsta och största värde med tunna linjer.

the whole range of dives (see the fitted line in Figure 1).

Discussion

This study showed that adult Great Crested Grebes had a markedly higher diving frequency than immatures and that prey "capture rate" was much lower in immature grebes. Moreover immature grebes in average dived for less time than adults.

Diving frequency was significantly higher in birds feeding their young, and the same holds true also for fish caught per minute. In comparisons with previous studies both measurements were much higher (see e.g. Winfield 1990, Ulenaers et al. 1992, Gwiazda 1997). As was already previously stressed by Gwiazda (1997), such high diving frequency and high capture rate are probably connected with small depth of the pond and high density of fish. However, in my study area this is only partly true, since the pond is really shallow (see also study area) but fish density was not so high (pers. obs.).

Since dive time increases with depth (e.g. Wilson & Wilson 1988, Hustler 1992, Lea et al. 1996), in a more shallow pond the diving frequency should be higher and the duration of dives should be shorter. However, in my study area in comparisons with other studies (e.g. Winfield 1990, Gwiazda 1997) both measurements were much higher but limited to only three pairs.

Cooper (1986) who studied diving patterns in cormorants Phalacrocoridae stressed that larger animals could dive for longer time. However,

according to our results, the body size could not be the only determinant of dive time (see also Lea et al. 1996 for cormorants). Experience and better condition in adults must also be involved.

Dive time was significantly longer in adults with young than in adults without young. It could be that adult grebes who are feeding young sometimes during diving time catch more than one fish, one for themselves (and swallow it under water) and one for their young (bring to the surface).

Observations of prey brought to the surface indicate that adults grebes with young took fish more often than did adults without young or immature grebes. The same result was obtained also by Gwiazda (1997) who explained that such differences between groups are observed because adults who are feeding young bring more prey to the surface to pass it over to their young. On the other hand immature grebes have higher diving success (bring a fish more often to the surface) than adults. Presumably adults grebes are more skilled than immatures and could eat more fish under water, particularly smaller ones (see also Lea et al. 1996, Gwiazda 1997 and references therein). In line with these observations, we must take into account that foraging context must be identified as provisioning and feeding. These are distinct foraging processes (Ydenberg et al. 1994). The difference is that feeders consume prey (in our example adult grebes and immatures), but provisioners deliver food to their young (in our example adults birds with young). Since provisioners must obtain the metabolic power for delivery by consuming some of the prey captured (Kacelnik 1984) or by searching for and consuming different foods (Waite & Ydenberg 1994), a process termed self feeding, we could reasonably assume that adult grebes with young eat some fish under the water (see also above).

Among birds, the time to learn foraging skills seems to be a common cause for differences in feeding between juveniles and adults (Marchetti & Price 1989). The same was probably true also for the duration of diving time. Nevertheless, diving success was much higher in all groups than those obtained by e.g. Lammi & Ulfvens (1988) on a lake in Finland Ulenaers et al. (1992) working on fishponds in the Netherlands, and Gwiazda (1997) on a reservoir in southern Poland.

Adult grebes with young captured smaller and medium sized fish than adults. In the area I studied, I found a seasonal variation in the size of prey items. The grebes captured more small prey items in July (when most of young were still small) and larger prey in September (when chicks became independent;

pers. obs.). This variation may well be due to small chicks being unable to swallow large prey items, whilst the older chicks were able to swallow prey of the same size as that adults (pers. obs.). The fact that in July they selected small fish would seem to confirm this. However, we should take into account that fishes also grow. But the difference between average fish size captured by adult grebes between July and August was too large (see Figure 3) for fish growth to have any major influence. Fish grow with the same rate during the season and the “jump” in fish size from July to August (but not from August to September) should not be so high. The reasonable explanation is that adults grebes prefer smaller fish in July due to the feeding of the young.

In comparison with data from Winfield (1990) and Gwiazda (1997), grebes in my study area captured bigger fish. However this is connected with the abundance of different prey size. In general the prey size caught by grebes observed in my study area was essentially the same as elsewhere in Europe (Madsen 1957, Cramp & Simmons 1977, Buttiker 1985, Renevey 1989, Winfield 1990, Gwiazda 1997). However the span of prey size was even greater than in previous studies.

It seems paradoxical that grebes could capture bigger fish in shorter time. A possible explanation of this is that smaller fishes move faster than bigger ones, especially between water vegetation. However the negative relationships between prey size and duration of dives did not exist in immature grebes. Some other parameters may also be involved here, such as a seasonal effect and growing vegetation.

The foraging habits of the Great Crested Grebe at the Vrbje pond differed markedly from those found elsewhere (Winfield 1990, Ulenaers et al. 1992, Gwiazda 1997). Diving times were longer, dive frequency and diving success were higher, and the fish caught were considerably longer. However, many data from the other sites were collected from birds diving in much deeper water than was the case in my study (see e.g. Winfield 1990, Gwiazda 1997). It could be that the apparent differences were caused by differences in feeding habitat. Nevertheless, the differences were still great if we compare data from similar habitats, i.e. fishponds (see Ulenaers et al. 1992).

In connection with this, hatching success appears also important, this being high in my study area (3.3 chicks/per pairs, pers. obs.). As Lack (1966) pointed out, the main factor regulating brood size is the mortality of chicks from starvation, which could be high in the Great Crested Grebe (Glutz von Blotzheim

1989). Therefore, to be successful in rearing large broods, the adults must bring sufficient food to the chicks to avoid their starvation and mortality. This can be achieved either by taking a large fish to the young and/or by taking a small fish to young more frequently. My data on the high diving frequency, diving success and number of fish caught seem to support this hypothesis. Moreover, high breeding success and low young mortality (Vogrin 2002) additionally confirm this hypothesis.

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Sammanfattning

Skäggdoppingens Podiceps cristatus fiske- och dykmönster i en fiskdamm.

Dykning och födosök har främst studerats hos marina fåglar, medan det finns mindre information för arter som lever i sötvatten. I denna uppsats rapporterar jag om dyktider och fiskelycka hos skäggdoppingen, som vid starten av min studie var relativt

okänd i dessa avseenden.

Undersökningen utfördes i en fiskdamm i nedre Savinjadalen nära staden Žalec i Slovenien. Dammen är 13,5 ha stor och mellan 0,5 och 2 meter djup. Både flytande och uppstickande vegetation täcker 40–60% av ytan. Dammen används för karpodling och töms vår och höst. Sedan dammen fyllts med vatten blir den tillgänglig för doppingarna att börja häcka i juni.

Undersökningen utfördes 1998 under hela säsongen från juni till oktober. Då häckade tre par, vilka fick fram 3, 3, resp. 4 ungar, vilka alla överlevde sommaren tills de blev självständiga. Det fanns inga andra skäggdoppingar i dammen än dessa tre par och deras tio ungar. Alla observationer gjordes från vallarna i bil. Observationerna gjordes under morgon och förmiddag, upp till tio dagar och under 4 till 10 timmar per månad. Enskilda individer följdes så länge som möjligt, vilket innebar mellan 5 och 23 minuter.

Dyktiderna mättes med ett stoppur och för varje dykning registrerades om doppingen kom upp med någon fisk eller ej. Fiskens storlek bedömdes i relation till näbbens längd (ungefär 5 cm). Längderna bedömdes i tre kategorier, mindre än 5 cm, 5–15 cm och större än 15 cm. Observationerna delades in i tre grupper som analyserades separat, nämligen för adulta fåglar före kläckningen (d.v.s. aduler utan ungar), adulta fåglar med ungar samt ungfåglar. Totalt registrerades 348 dykningar för adulta utan ungar, 295 för adulta med ungar och 185 för ungfåglar. Längden kunde uppskattas för 232 fångade fiskar, 73 för adulta utan ungar, 112 för adulta med ungar och 47 för ungfåglar.

Inga andra byten än fiskar noterades och resultaten blev följande (Tabell 1). Både gamla fåglar före kläckningen och ungfåglar dök mindre ofta än aduler med ungar. Dyktiden skilde sig också mellan grupperna. Aduler utan ungar gjorde kortare dykningar än aduler med ungar, och det var också skillnad mellan gamla och unga doppingar. I 62–79 % av dykningarna kom fåglarna upp utan att ha någon fisk med sig. Dykningsframgången varierade mellan grupperna och det var aduler med ungar som var mest framgångsrika. Däremot tog intressant nog ungfåglarna oftare fiskar till ytan.

Bytenas storlek varierade under säsongen (Tabell 2). Storleken av de fiskar som fångades av aduler med ungar var betydligt mindre i juni då ungarna var små (Figur 3). Fiskstorleken var negativt korrelerad med dyktidens längd för adulta, både utan och med ungar (Figur 1 och 2). Något sådant samband fanns däremot inte för ungfåglarna.

Hög dyk- och fångstfrekvens har tidigare påpekats bero på grunt vatten och tätt fiskbestånd. Detta kan dock bara delvis gälla min studie. Förvisso är dammen grund, men däremot är fiskbeståndet inte särskilt tätt. Att dyktiderna var längre för aduler med ungar kan bero på att de fångade en fisk åt sig själva, som de svalde under vatten, och ytterligare en fisk som togs till ytan och gavs till ungarna. Att ungfåglarna hade högre fiskeframgång än adulterna kan bero på att de förra är skickligare på att svälja sina byten under vattenytan och att alltså skillnaden bara är skenbar. Skicklighet i att fånga byten är generellt en orsak till sådana skillnader mellan unga och gamla bland fåglar. Den stora förändringen av bytenas storlek mellan juni och augusti (Figur 3)

skulle kunna bero på att fiskarna i dammen tillväxte i storlek. Förvisso skedde en sådan tillväxt, men fiskar växer kontinuerligt och inte så mycket i ett språng. Därför är orsaken till fångsten av små fiskar i juni troligen orsakad av att ungarna måste matas med små fiskar.

Jämfört med andra studier i liknande biotoper dök mina doppingar längre tider, dök oftare och fångade större fiskar. En förklaring, i varje fall i relation till vissa av de andra studierna, är att de senare utförts i djupare vatten. Under alla omständigheter visar min undersökning att det var en framgångsrik kombination av dykningar och fiskelycka som de tre paren i Vrbje-dammen uppvisade eftersom alla tio ungarna överlevde till flygg ålder.