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Sex-specific foraging behaviour of the Whiskered Tern (*Chlidonias hybrida*) during the breeding season

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Sexual size dimorphism is common in many bird species. It can lead to sex-specific differences in foraging ability. The Whiskered Tern (*Chlidonias hybrida*) exhibits sexual size dimorphism. Sex-specific differences in the foraging behaviour of Whiskered Terns were investigated in carp ponds during the breeding season. Foraging behaviour was different between the sexes. Males foraged mainly by shallow plunge diving into the water, while females foraged mainly by picking prey from plants and the water surface. We attributed these differences to sexual size dimorphism, as males are significantly larger than females. The foraging success of vertebrate prey capture by Whiskered Terns was high (male average = 61%, female average = 65%), and not significantly different between sexes. Males had more aggressive encounters than females. Generally, we did not find correlations between the rate of main foraging techniques of male and female Whiskered Terns and weather conditions (cloud cover and wind speed). This was probably due to the high prey availability in carp ponds.

1. Introduction

More than 90% of bird species have biparental care, where females and males both participate in chick feeding (Trivers 1972, Clutton-Brock 1991). The contribution of both sexes to feeding of the offspring is often necessary to guarantee reproductive success. Differences in the foraging and provisioning behaviours of male and female parents have been documented in a several number of birds and they can differ in foraging area, foraging behaviour and size and type of prey, among others (Wendeln 1997, Lewis *et al.* 2002, Anderson *et al.* 2004, Weimerskirch *et al.* 2006, Mariano-Jelicich *et al.* 2007, Bluso-Demers *et al.* 2008). These differences have usually been attributed to sexual size dimorphism, which leads to differences in flight efficiency (Shaffer *et al.* 2001) and consequently to sex-specific differences in foraging techniques. The smaller-sex usually has better flight efficiencies, and as such be able to travel further or be able to forage in a different type of location than the larger-sex (González-Solis *et al.* 2000, Lewis *et al.* 2005). Meanwhile, the larger-sex may dominate intra-specific interactions close to the colony, forcing the smaller-sex to travel further away for food (González-Solis *et al.* 2000).

Recent studies in monomorphic seabirds, however, indicate that sex-specific foraging patterns can occur independently of sexual size dimorphism (Lewis *et al.* 2002, Peck & Congdon 2006, Welcker *et al.* 2009). Foraging differences between sexes in monomorphic species reduce intrapair and inter-sexual food competition, and decrease diet overlap, thus separating male and female feeding niches. This phenomenon could be important for successful chick rearing during food shortages (Shaffer *et al*. 2001, Peck & Congdon 2006, Lewis *et al*. 2005). The Whiskered Tern (*Chlidonias hybrida*) is a medium-sized, long-lived, socially monogamous, colonial tern, with both sexes participating in incubating, feeding, and rearing the chicks (Cramp and Simmons 1985, Ledwoń 2010). Generally, parents deliver two types of food to chicks: vertebrates (fish, tadpoles, and frogs) and invertebrates (mainly small dragonflies) (Betleja 2003, Ledwoń 2010). These two types of prey are captured via two distinctive foraging techniques: by shallow plunge diving into the water from a few metres high; or by hovering above the water with periodic dipping to take prey (apparently from the water surface or plants). When successful, parents always bring a single item of prey in their bills to the chicks. Whiskered Tern displays greater sexual size dimorphism in almost all measurements compared with other terns – males are significantly larger than females in all morphological characters, particularly in head length (7% larger than females), bill measurements (10% larger than females), and body mass (6% larger than females) (Ledwoń 2011).

Little is known about foraging behaviours in terns. The majority of published studies described the frequency, size, and type of food brought to the chicks (Wagner & Safina 1989, Wiggins & Morris 1987, Quinn 1990, Uttley 1992, Burness *et al*. 1994, Fasola & Saino 1995, Wendeln 1997, Sorokaitė 2005) but accurate information describing the foraging behaviour and feeding strategies of males and females is very scarce.

We hypothesized that, due to sexual size dimorphism, male and female Whiskered Terns would develop different foraging behaviours. Males, being larger, should forage mainly on larger preys such vertebrates, which are captured by shallow plunge diving. Females, due to their smaller body mass, have higher flight efficiencies than males and therefore should be more predisposed to capture smaller prey such as invertebrates by picking. Additionally, we investigated whether certain weather conditions (e.g., cloud cover and wind speed) influenced foraging behaviour or modified foraging techniques. The effect of wind speed on foraging efficiency has been studied in some species of terns, but these studies did not focus on differences between the sexes (Reed & Ha 1983, Taylor 1983, Stienen *et al*. 2000).

2. Material and methods

2.1. Study area

The study was carried out in the Upper Vistula River Valley (southern Poland), at three carp pond complexes: Spytkowice (50°01'N, 19°29'E; 480 ha); Bugaj (49°59'N, 19°26'E, 180 ha); and Rudze (49°58'N, 19°26'E; 120 ha) (Fig. 1). Each complex contains dozens of ponds whose areas vary from 1 to 45 ha, mainly approximately 10 ha. The mean water depth at all sites was 1.0–1.5 m. The emergent vegetation formed 3–6 m wide belts of reeds, and some ponds were covered with yellow floating heart (*Nymphoides peltata*) plants. In addition, there were islands of various sizes on some ponds, on which bushes or trees grew. All sites were surrounded by agricultural lands or human settlements. Carp (*Cyprinus carpio*) was the main fish species reared in the ponds. Similar production rates and fish densities were recorded at the studied sites according to data of fish farm owners. The ponds in this study area are of great importance to waterfowl (Bukacińska *et al*. 1995), including Whiskered Terns during the breeding season (Ledwoń *et al*. 2014).

2.2. Field observations

Whiskered Terns were studied during the breeding season (May–August) of 2007 in two breeding colonies (Rudze and Spytkowice) and in 2008 in other two colonies (Bugaj and Spytkowice). Breeding colonies contained approximately 20–50 nests, which were located mainly on *N. peltata* leaves. Adult birds were caught at the nest with a roof trap during the incubation period or when brooding downy chicks (until 3–4 days old) (Ledwoń 2011, Ledwoń *et al*. 2013). All individuals were ringed, measured, weighed, and marked individually by painting some parts of their feathers with hair dye. Blood samples of approximately

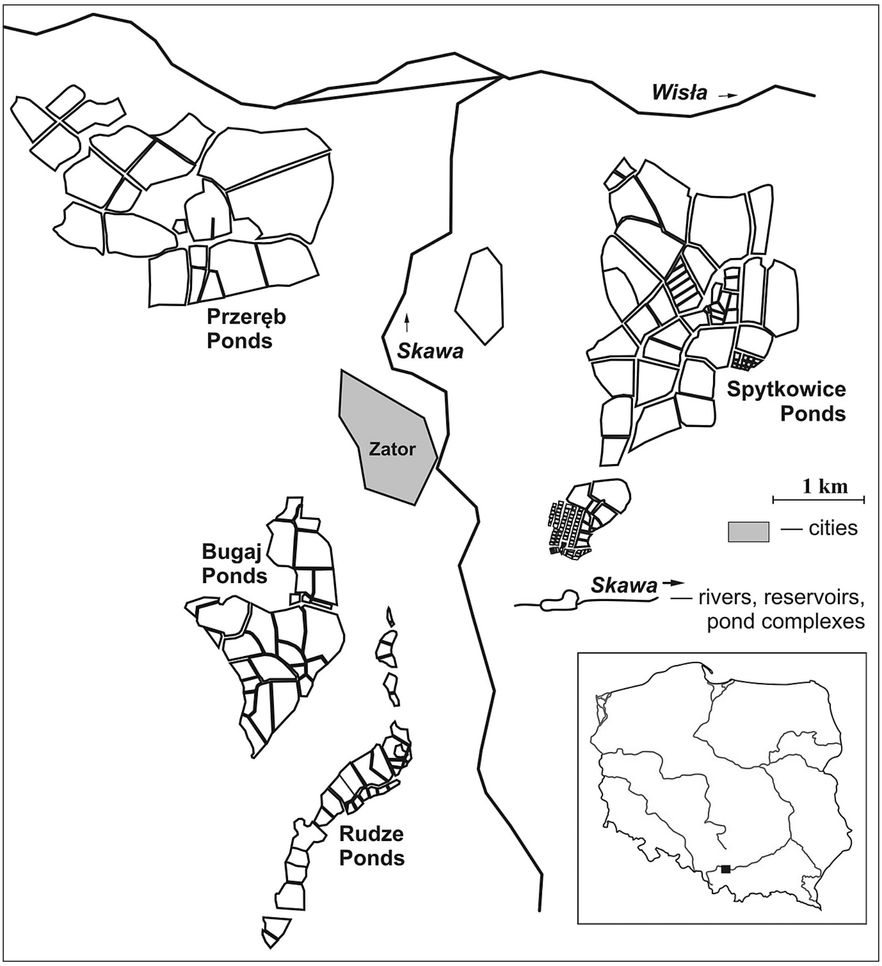

Fig. 1. Carp pond complexes in the Upper Vistula River Valley where the Whiskered Tern was studied. Inset, position of the study area within Poland.

0.2 ml were taken from the tarsus vein for molecular sex analysis. The sex of Whiskered Terns was determined from the CHD gene (chromodomain helicase DNA binding protein gene) on sex-specific chromosomes (for molecular methods, see Ledwoń 2011).

Adult birds were observed mainly during the chick-rearing period. Hatching dates were calculated by flotation of eggs, assuming a 21-day incubation period (Betleja 2003). Birds foraged mainly at the complex on which they bred; however, several birds breeding at the Bugaj pond foraged also at the Rudze complex, 2 km from the breeding colony. Every 3–7 days, the observers visited the pond complexes with the studied breeding birds and, moving along the dike of each pond, used binoculars and a spotting scope to look for marked foraging terns. Sessions (observations) of foraging birds started when the observer saw a marked bird and were stopped when the tern flew out of the observation area. In 651 sessions, 56 individually marked terns (15 females and 14 males in 2007, 13 females and 14 males in 2008) were observed for a total of 38 h 9 min.

During observations, the following variables were recorded: foraging techniques (shallow plunge diving into the water from a height of a few metres, picking prey from the water surface or plants, and catching flying invertebrates); number of feeding events; number of captures; and number of aggressive encounters.

The captured food items were visually identified. Cloud cover (0–25, 25–50, 50–75, or 75–100%) was determined during the observations. Wind speeds during observations were measured using a Kaindl wind gauge at the study area. The measurements were taken over 60 s, and mean wind speed was determined. Average wind speeds varied between 0 and 25 km h^{-1}.

2.3. Data and statistical analysis

During data analysis, the number of incidences of each foraging technique was calculated for each session in the chick-rearing period. The results were standardised as the number of observations per minute. To avoid a bias due to differences in observation duration, only observations lasting more than 30 s were included in the analysis. We did not separate data from 2007 and 2008 because rates of particular techniques (N min^{-1}) in males and in females did not differ between years (plunge diving rate, males t = 2.05, df = 26, $P >$ 0.05; females t = 1.42, df = 26, P = 0.17; picking rate from water surface, males t = 0.71, df = 26, P = 0.48; females t = 0.67, df = 26, P = 0.51; picking rate from plants, males t = 1.72, df = 26, P = 0.10; females t = 0.11, df = 24, P = 0.91; catching in air, males t = 0.46, df = 26, P = 0.65; females t = 0.85, df = 26, P = 0.41).

Capture success was calculated as number of successful dives as a percentage of the number of diving attempts in each session. Generalized Linear Mixed Model (Poisson-model) was used to examine differences in rates of foraging technique and in rates of aggression between sexes. Generalized Linear Mixed Model (logistic model) was used to determine if the capture success differed between sexes. The explanatory variable was sex (factor with fixed effect) including individual (factor with random effect). Response variables were: rate of foraging technique, capture success, aggression rate.

Chi-squared tests with Yates' correction were used to study differences in the proportion number of aggressive individuals between males and females. Spearman correlation coefficients (r) were used to examine the relationships between diving rates and capture rates in males and females. Correlation coefficients were also used to study: (1) the relationships between diving rates, captures rates, capture success and wind speed in both sexes; (2) the relationships between diving rates, capture rates, capture success and cloud cover in both sexes; and (3) the relationships between picking rates from water and wind speed and between picking rates from water and cloud cover in both sexes.

The scale of variables was: continuous (foraging techniques rate, capture rate, capture success, aggression rate, wind speed), ordinal (cloud cover) and nominal (sex). The number of attempts was the response variable and wind speed or cloud cover were explanatory variables. Statistical analyses were performed using STATISTICA 10 software (StatSoft, Inc. 2011).

3. Results

3.1. Foraging behaviour

Whiskered Terns captured fish, frogs (adults and tadpoles), and insects. Birds foraged by diving, catching prey on plants or from the water surface, catching aerial prey, and by food stealing. Foraging techniques were distinctly different between the sexes (plunge diving: $W_{1,518}$ = 24.02, $P <$ 0.001; picking from the water surface: $W_{1,518}$ = 68.80, $P <$ 0.001; picking from plants: $W_{1,518}$ = 67.82, $P <$ 0.001; catching in air: $W_{1,518}$ = 13.72, $P <$ 0.001). Plunge diving was the most common foraging technique seen in males (mean = 0.64 attempts min^{-1}, standard error [SE] = 0.17, N = 280). Picking prey from the water surface (mean = 0.55 attempts min^{-1}, SE = 0.13, N = 238) and picking prey from plants (mean = 0.63 attempts min^{-1}, SE = 0.09, N = 238) were the most used techniques in females (Fig. 2). The differences observed in the foraging techniques used by male and female Whiskered Terns gave rise to differences in the type of prey captured between sexes. We identified four individuals (7.1%, N = 56; only males) kleptoparasiting Whiskered Tern, Common Tern (*Sterna hirundo*), and Little Grebe (*Tachybaptus ruficollis*) individuals.

The proportion of successful vertebrate captures was similarly high for both sexes (mean = 61%, SE = 2.47, N = 214 for males; and mean = 65%, SE = 4.28, N = 98 for females; $W_{1,312}$ = 0.79, P = 0.37). Capture rates were correlated with diving rates in both females (r = 0.56, df = 98, $P <$ 0.001) and males (r = 0.76, df = 214, $P <$ 0.001). The proportion of successful invertebrate captures was significantly higher for females than males (mean

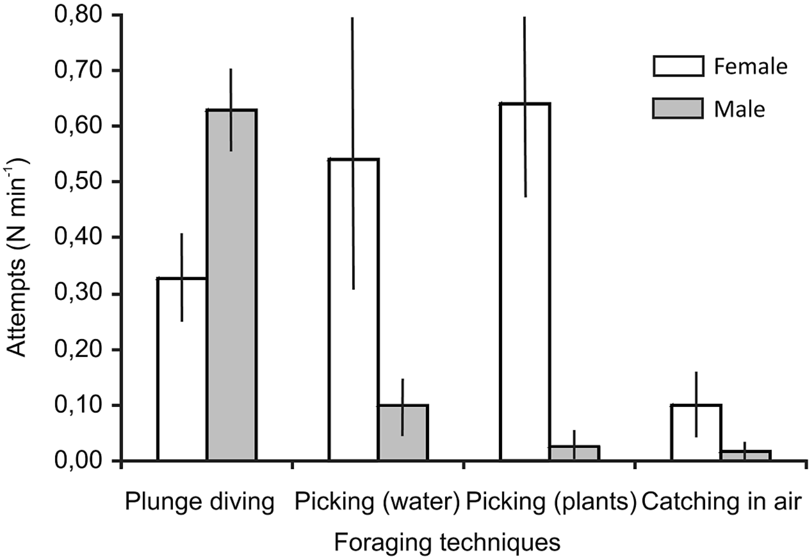

Fig. 2. Mean rates of foraging techniques of female and male Whiskered Terns (*Chlidonias hybrida*) in fish ponds. Vertical lines show 95% confidence intervals.

= 81%, SE = 6.06, $N = 33$ for males; and mean = 97%, SE = 1.40, $N = 47$ for females; $W_{1,80} = 8.19$, $P = 0.004$).

We found aggressive behaviour in 6 females ($N = 28$) and 17 males ($N = 28$) in small ponds where terns aggregated. The proportion of aggressive males was higher than that of aggressive females (Chi-squared: $\chi^2 = 7.38$, df = 1, $P < 0.01$). The aggression rates were significantly higher in males than females (males, mean = 0.22 aggressive attempts min^{-1}, SE = 0.03, $N = 316$; females, mean = 0.03 aggressive attempts min^{-1}, SE = 0.01, $N = 264$; $W_{1,580} = 27.91$, $P < 0.001$).

3.2. Impact of weather conditions

There was no clear relationship between foraging techniques and wind speed or clouds cover in males and females. We found only a weak relationships in females between picking from water and wind speed ($r = -0.366$, df = 146, $P < 0.001$) and between capture success and cloud cover ($r = 0.266$, df = 82, $P = 0.02$). We did not find relationships between rates of plunge diving and wind speed in both sexes (males: $r = 0.060$, df = 186, $P = 0.42$; females: $r = 0.105$, df = 146, $P = 0.21$). Furthermore, no relationship was found between the capture rates and wind speed in either sex (males: $r = 0.039$, df = 186, $P = 0.60$; females: $r = 0.096$, df = 146, $P = 0.25$).

4. Discussion

Male and female Whiskered Terns used different foraging techniques – males mainly foraged by shallow plunge diving, while females mainly foraged by picking invertebrates from the water surface. We showed that both males and females of breeding Whiskered Terns foraged on both vertebrates and invertebrates. Because vertebrates are captured mainly by plunge diving (nearly 100%, unpubl. data) and invertebrates by picking from water or plants and by catching in air (nearly 100%, unpubl. data), each sex specialized in foraging on different types of prey; males foraged mainly on vertebrates, while females mainly caught invertebrates. Similar sex-specific diets in Whiskered Terns were shown in non-breeding birds in Australia (Crawford 1977, Dostine & Morton 1989).

The different foraging patterns of females and males could be a result of the morphological differences between sexes, as males are significantly larger in size than females (Ledwoń 2011). The differences in foraging behaviour between males and females may be explained by quite different costs of capture for particular prey (veretebrates and invertebrates). Males dived more frequently than females as they are heavier than females and, for dipper diving, this is advantageous (Norberg 1995). On the other hand, it is more profitable to be lighter, as females are, when catching invertebrates from the water surface or in the air. If sexual segregation in feeding resources is favoured by a difference in size between sexes, natural selection may act to exaggerate sexual size dimorphism (González-Solis 2004). However, sex-specific differences in foraging behaviour have also been observed in a monomorphic seabird (Lewis *et al.* 2002; Peck and Congdon 2006; Welcker *et al.* 2009, Navarro *et al.* 2011). Differences in the prey species selected reduce inter-sexual and/or intra-pair competition for food (Shaffer *et al.* 2001, Peck & Congdon 2006, Lewis *et al.* 2005). Different niche utilisation by male and female Whiskered Terns may be important in successful chick rearing (Gosler 1987, González-Solis 2004, Gilbert & Servello 2005).

In our study, aggressive behaviour in the Whiskered Terns was recorded only when individuals foraged in very small ponds, with a high density of carp fingerlings, and thus where birds aggregated (RG and ML unpublished data). No aggressive behaviour was recorded when birds were feeding on large ponds, where prey (especially invertebrates) was more dispersed and probably more abundant. We found that males were more aggressive than females during foraging. This could be a consequence of sexual size dimorphism – the larger sex might be dominant over the smaller sex (González-Solis *et al.* 2000, González-Solis 2004). Therefore, female Whiskered Terns, being smaller than the males, are more vulnerable to dominance by males, and thus are forced to use a different niche.

Kleptoparasitism is a well-known foraging strategy used opportunistically by many seabirds and waterbirds (Furness 1987), but has not been described anywhere outside the studied ponds in the Whiskered Tern (Cramp & Simmons 1985, Gwiazda 2008). The low level of kleptoparasitism found in our study (observed only in males) could be a consequence of a high prey density, so that birds preferred to capture food directly rather than resort to kleptoparasitism. For example, intra-specific kleptoparasitism in the Black Tern (*Chlidonias niger*) was triggered by problems in finding food (Beintema 1997). Kleptoparasitism among Roseate Terns (*Sterna dougallii*) at Falkner Island (USA) was also shown to be a specialised behaviour practised regularly by only 3–4% of the birds (Shealer & Spendelow 2002).

We found a relationship between the frequencies of plunge dives and capture rates in the Whiskered Terns, which were lower that those seen for individual Roseate Terns in Puerto Rico (Greater Antilles) ($r^2 = 0.954$) (Shealer & Burger 1993). Feeding rates may reflect food availability. The rate of diving of Whiskered Terns in ponds was lower than that seen in Common and Forster's Terns on Wallops Island (Virginia, USA) and Roseate and Sandwich Terns in the Tropical Atlantic (Puerto Rico) (1.3–1.6 attempts min^{-1}) (Reed *et al.* 1982, Shealer 1996). However, the foraging success of Roseate and Sandwich Terns in the inshore shallows of south-western Puerto Rico was only 26% and 42%, respectively (Shealer 1996). Similarly low foraging efficiencies were also recorded in Common and Forster's Terns (32% and 46%, respectively), in the bay of Wallops Island (Virginia, USA) (Reed *et al.* 1982). Therefore, although the mean diving rate of Whiskered Terns in our study was lower, the foraging success of diving or capture rate was higher. This may be a reflection of the great availability of fish in the carp ponds.

Weather conditions have been described as factors influencing the foraging ability of terns (Dunn 1973). Strong cloud cover may affect visibility of prey by foraging terns, but this variable had no significant effect on foraging success (Monticelli *et al.* 2006). Increasing wind speed negatively affected the diving rates in Roseate, Common, Sandwich, and Forster's Terns (Reed & Ha 1983, Taylor 1983, Monticelli *et al.* 2006). Capture success of these species was not influenced by wind speed, which suggests that the wind did not directly inconvenience the birds (Taylor 1983, Monticelli *et al.* 2006). Here, no or weak relationships between plunge diving, picking from water, capture rates, capture success and wind speed or cloud cover were found. These results might be a result of the high prey availability in the ponds. Moreover, during strong wind birds could forage in sheltered places, but it was not examined in our study.

To summarise, our results show that male and female Whiskered Terns develop different foraging behaviours. Males foraged mainly on larger prey such as vertebrates, which were captured by shallow plunge diving. Females captured mainly smaller prey such as invertebrates, by picking. We attribute these differences to sexual size dimorphism of the Whiskered Tern, where males are larger than females (González-Solis *et al*. 2000, Ledwoń 2011).

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Sukupuolikohtainen ruokailukäyttäytyminen valkoposkitiiralla pesimäkauden aikana

Monilla linnuilla koiras ja naaras ovat erikokoisia. Tällainen sukupuolten välinen kokodimorfia voi johtaa sukupuolten erilaistumiseen ravinnonhankinnassa. Valkoposkitiiralla (*Chlidonias hybrida*) koiraat ovat selvästi naarasta suurempia. Me tutkimme sukupuolten välisiä eroja ruokailukäyttäytymisessä pesimäkauden aikana. Havaitsimme, että sukupuolet käyttävät erilaisia ruokailutekniikoita. Koiraat pääasiassa hankkivat ravintonsa sukeltamalla, kun taas naarat saalistivat kasvien ja veden pinnalta. Saalistustehokkuus oli korkea sekä koirailla (keskimäärin 61 %) että naarailla (65 %), eikä se eronnut sukupuolten välillä. Koirailla oli enemmän yhteenottoja kuin naarailla. Säätila (pilvisyys ja tuulen nopeus) ei ollut yhteydessä lintujen käyttämiin ruokailutekniikoihin kummallakaan sukupuolella.

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