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ORIGINAL ARTICLE

Sex-specific growth of nestlings of the Whiskered Tern *Chlidonias hybrida*, a species with sexual size dimorphism and female brood desertion

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Abstract

The growth of a nestling during the first few weeks after hatching is crucial for its further life and is sensitive to the conditions experienced during this period. Among species exhibiting Sexual Size Dimorphism (SSD), one of the most important factors influencing growth parameters is the sex of the hatchlings. In this study, we tested whether sex and other factors (hatching date, egg volume, brood size and sex ratio in the brood) were related to sex on growth parameters in Whiskered Tern *(Chlidonias hybrida*) chicks. In this species, males are 3%–10% larger than females when adult. At hatching, only the total head length was greater in males than females, but values close to fledging were greater for most of the measured parameters (3%—tarsus, 4%—total head length, 13%—body mass). Moreover, the maximum body mass growth rate was higher in males but females entered the rapid growth phase somewhat earlier and achieved the final total head length sooner. Nestling growth was also significantly correlated with brood size and hatching date, though mostly negatively (e.g. lower tarsus and total head length asymptote, lower maximum growth rate and growth rate constant of total head length in bigger and later clutches). The occurrence of SSD during the nestling period and higher maximum growth rate of body mass in males indicates that the costs of raising sons may be higher than of raising daughters. However, we did not find evidence of either sex-biased nestling mortality or skewed sex ratio.

Keywords Chick growth · Sex-specific growth · Body mass · Body size · Sexual size dimorphism · Whiskered Tern · Sternidae

Zusammenfassung

Geschlechtsspezifisches Wachstum bei Nestlingen der Weißbart-Seeschwalbe *Chlidonias hybrida*, einer Art mit sexuellem Größendimorphismus, bei der die Weibchen die Brut verlassen.

Das Wachstum eines Nestlings in den ersten paar Wochen nach dem Schlupf ist für sein weiteres Leben entscheidend und hängt von den während dieser Zeit erfahrenen Bedingungen ab. Bei Arten mit sexuellem Größendimorphismus (SSD) ist das Geschlecht des Nestlings einer der wichtigsten Faktoren, die Wachstumsparameter beeinflussen. In dieser Studie haben wir getestet, ob das Geschlecht und andere Faktoren (Schlupfdatum, Eivolumen, Brutgröße und Geschlechterverhältnis der Nestlinge) bei Küken der Weißbart-Seeschwalbe (*Chlidonias hybrida*) zu Wachstumsparametern in Bezug standen. Bei dieser Art sind adulte Männchen 3–10% größer als adulte Weibchen. Beim Schlupf war lediglich die Kopflänge bei den Männchen größer als bei den Weibchen, während beim Ausfliegen die meisten der gemessenen Parameter bei den Männchen größer waren (3%—Tarsus, 4%—Kopflänge, 13%—Körpermasse). Zudem war die maximale Köpermassezunahmerate bei Männchen höher, doch bei den Weibchen begann die schnelle Wachstumsphase etwas früher, und sie erreichten ihre

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Endkopflänge eher als die Männchen. Das Nestlingswachstum korrelierte außerdem signifikant mit der Brutgröße und dem Schlupfdatum, jedoch überwiegend negativ (z.B. niedrigere Tarsus- und Kopflängenasymptote, geringere maximale Wachstumsrate und Wachstumsratenkonstante der Kopflänge in größeren und späteren Gelegen). Das Auftreten von SSD während der Nestlingsphase und die höhere maximale Körpermassezunahmerate der Männchen deuten darauf hin, dass die Aufzuchtskosten für Söhne höher sein könnten als für Töchter. Wir fanden allerdings keine Hinweise auf unterschiedliche Mortalität der beiden Geschlechter oder ein verschobenes Geschlechterverhältnis.

Introduction

The early development of an individual bird affects its subsequent life in several ways, including competition for territory and mate as well as its fitness and survival (Lindström 1999; Metcalfe and Monaghan 2001). This has long been of interest to ornithologists in view of the considerable variability in growth patterns among bird species (Ricklefs 1979; Richner 1991). We can also perceive significant differences within a species in respect of chick growth parameters, depending on the conditions experienced by individual birds during this crucial period. In this regard, it is extremely important to identify factors influencing growth.

The growth of hatchlings largely depends on the food resources available in an environment (Becker and Specht 1991; Owen and Pierce 2014) and supplied by parents (Klaassen et al. 1992), whose ability to appropriately feed their offspring is a function of their condition and experience (Velando 2002; Minias et al. 2012). Other related factors that influence chick growth include egg volume (Bogdanova and Nager 2008; Kalmbach et al. 2009; rev. Krist 2011; Diaz-Real et al. 2016), brood size (Müller et al. 2005; Bogdanova and Nager 2008; Gilliland et al. 2016), hatching date (Bogdanova and Nager 2008; Loonstra et al. 2018), laying and hatching order (Müller et al. 2005; Bosman et al. 2016; Diaz-Real et al. 2016), and sibling sex (Becker and Wink 2003; Müller et al. 2005).

One of the most important factors influencing growth parameters is the sex of hatchlings, particularly in species with sexual size dimorphism (SSD). A higher maximum growth rate and asymptotes of nestling mass and size (e.g. Velando 2002; Müller et al. 2007; Bogdanova and Nager 2008; Kalmbach 2009; Bosman et al. 2016; Požgayová et al. 2018) or a longer rapid growth phase (Velando et al. 2000) in the bigger sex are quite common. Differences in growth schemes between sexes, especially the asymptotes attained, can result in the larger sex being more costly to raise (Magrath et al. 2007) and sensitive to unfavourable growth conditions, like food shortages (Benito and González-Solís 2007; Loonstra et al. 2018).

SSD may become apparent during the prenatal phase as the embryonic growth rate of males and females may differ (Cordero et al. 2000). This could be due to inherited sexual differences or differences in maternal investment (hormones or nutrient deposition in eggs) in relation into sons and daughters (Petrie et al. 2001). Furthermore, SSD may begin to appear between the hatching and fledging periods, as a result of differences in growth rate or growth duration (Jordi and Arizaga 2016; Loonstra et al. 2018). SSD may also manifest itself more strongly during the fledging period (Magrath et al. 2007).

The majority of tern species Sterninae exhibit sexual differences in adult body size—males are larger than females (Ledwoń 2011; Lisnizer et al. 2014)—although these differences are usually slight and difficult for researchers to perceive visually. Nevertheless, growth parameters in terns in relation to hatchling sex are not well understood. Research addressing this problem has basically been limited to just three species. Common Tern (*Sterna hirundo*), a species with minimal SSD, exhibits a sex-dependent growth scheme in the case of body mass, a parameter only weakly differentiated in adults (Becker and Wink 2003). Some growth characteristics were investigated also in Gull-billed Tern (Villegas et al. 2013) and Roseate Tern (Nisbet and Szczys 2001; Szczys et al. 2005), but in those cases, the chicks were not individually monitored throughout the nestling period. To partly fill this knowledge gap, we investigated the sex-dependent growth of body mass and three other body size parameters of Whiskered Tern nestlings.

Whiskered Tern (*Chlidonias hybrida*) is a semi-precocial, colonial bird that nests on water bodies (Gochfeld et al. 2020). It exhibits the greatest SSD of any tern species (Ledwoń 2011). All the parameters investigated in this study, i.e. bill and head lengths, body mass, tarsus and wing lengths, are significantly larger (by 3–10%) in adult males than females. SSD in this species is particularly pronounced in the head and bill lengths and in the body mass. The degree of SSD in Whiskered Tern may be related to its strong, sex-specific utilization of foraging niches during both the breeding and non-breeding periods (Dostine and Morton 1989; Betleja 2003; Ledwoń 2010; Gwiazda and Ledwoń 2015, 2016; Gwiazda et al. 2017; Ledwoń and Neubauer 2017). In the population studied here, males bring more than 60% of all the heavier prey items (fish, frogs, tadpoles), whereas females deliver more than 90% of lighter prey (mainly small dragonflies) provided by both parents to the chicks. Overall, males supply ca 25% more food (kJ) than females. Catching a specific type of prey is related to different foraging techniques: males forage mainly by plunge diving, females mostly by plucking insects from the air, water surface or floating leaves. Hence,

it is profitable for males to be larger, as this predisposes them to catch larger prey. Among the Sterninae, Whiskered Tern has a unique system of parental care: females desert their offspring during the chick-rearing and post-fledging periods (Ledwoń and Neubauer 2017). After female desertion, males continue parental care for the next few weeks at least and intensify their deliveries of food to the chicks to compensate for the female's absence. These two aspects may select for heavier and larger males, which are then better able to deliver large and energy-rich prey items to their chicks. We can assume that SSD in Whiskered Tern should become apparent during the chick-rearing period or even during the prenatal phase, and that it should be especially pronounced in the body mass. In this study we (1) compare the growth parameters of male and female Whiskered Tern chicks, (2) compare SSD between hatchlings, older chicks and adults, (3) test the influence of hatching date, egg volume, sex ratio and number of siblings, as well as the interactions of these parameters with nestling sex on growth parameters and (4) test the influence of sex and hatching date, egg volume, sex ratio and number of siblings on chicks mortality.

Methods

Study site and field procedure

We carried out the fieldwork during two breeding seasons (2016–2017), between May and September to cover the whole breeding season of Whiskered Tern. It took place on three carp pond complexes (Spytkowice, Bugaj, Przeręb) in the northern part of the Upper Vistula Valley (50°00′ N 19°30′ E), southern Poland (for a detailed description of the study area, see Ledwoń et al. 2013, 2014; Gwiazda and Ledwoń 2015).

The nests in each colony were selected at random, and their monitoring usually started during the early stages of incubation. One week before hatching, on average, the nests were enclosed with plastic horticultural mesh to prevent the chicks from escaping from the nest site until they could fly. The inner side of the enclosure was covered with foil to prevent the chicks from pushing their bills through the mesh (for a detailed description of the enclosure, see Ledwoń et al. 2015). We enclosed 129 nests in four colonies (three in 2016 and one in 2017); the clutches/broods in 13 of them failed completely before fledging. The clutches in all the monitored nests were initiated between mid-May and late June. Incubation lasted 21 days (Betleja 2003) and 75% of the nestlings hatched between 17 June and 4 July (median 25 June). The length and breadth of eggs were measured manually with callipers to the nearest 0.1 mm (no differences were found between the three researchers). Egg volumes (v) were calculated from the formula: $v = k \times l \times b^2$, where k—volume coefficient ($k = 0.478$), l—length, b—breadth (Hoyt 1979; Betleja 2003). We visited the colonies every three to four days; each newly hatched chick was ringed with an individually numbered steel ring, and a small sample of blood was taken from tarsus vein for molecular sexing.

The exact hatching date was determined from the presence of wet feathers after emergence from the egg (first day of chick life); from the presence of a hatching star on the egg during the previous visit (day 0), indicating that the chick had started to hatch and would emerge from the egg within 24 h; on the basis of hatchling wing length (Paillisson et al. 2008; AB—unpublished data). Each alive nestling was measured every three or four days during subsequent visits to the nests. Measurements included total head length (from tip of bill to occiput, not measured in 2017) and tarsus length (both with callipers, to the nearest 0.1 mm); wing length (flattened and straightened, using a ruler with stopper, to the nearest 1 mm), and body mass (with a Pesola spring balance, to the nearest 1 g). The nestlings were measured by one person to exclude the inter-researcher effect. We defined the nestling period as the time elapsed between hatching and fledging (the latter takes place around the 21st day of a chick's life). In accordance with this definition, the fledging period started around the 22nd day of a chick's life.

Molecular sex determination

Nestling sex was determined from the CHD gene located on the sex chromosomes (Dubiec and Zagalska-Neubauer 2006). Blood samples were stored in 98% ethanol at − 20 °C. Prior to DNA extraction, ca 20 µl was dried at 43 °C and 80 µl of Tris added. DNA was extracted using a Blood Mini Kit (A&A Biotechnology).

PCR was conducted with two sets of primers—F2550 (5′-GTTACTGATTCGTCTACGAGA-3′) and R2718 (5′-ATTGAAATGATCCAGTGCTTG-3′) (Fridolfsson and Ellegren 1999), also used in previous studies of Whiskered Tern (Ledwoń 2011; Goławski et al. 2016), and P2 (5′-TCTGCATCGCTAAATCCTTT-3′), P8 (5′-CTCCCAAGGATGAGRAAYTG-3′) and P0 (5′-ATTGAGTTGGAACCAGAICA-3′) (Griffiths et al. 1998; Han et al. 2009). The methods were validated on samples from birds of known sex (adult sexed by biometrics and behaviour). Each of the 348 samples from the nestlings was tested at least twice. In 1.1% cases, the results were incompatible, so for these individuals, we repeated the test a further two times, taking the most common result to be the correct one.

Statistical analysis

We fitted a logistic function (Paillisson et al. 2008; Minias et al. 2012) of the form $y = A/(1 + B \times \exp(-k \times t))$ to the biometric data of every chick, where y was the total head

length, tarsus or wing length or body mass measured on day t, A—the asymptote (the expected final size, which could be much higher than the previous measurement if growth continued after fledging), B—the constant of integration (this places individuals on a common time scale and indicates the onset of rapid growth), k—the growth rate constant (day^{-1}, inversely proportional to the growth phase to the final size). In addition, the maximum growth rate (g_{max}), which occurs at the point of inflection, was calculated from the equation: $dy/dT = (k \times A/2)(1 - A/2A)$ reduced to $g_{max} = k \times A/4$ (Richner 1989, 1991).

We measured 353 individuals from hatch to fledge or to death. In the estimation of growth parameters and in models analysing the influence of factors (see below) on growth parameters we used 270 chicks. We included only birds classified as alive during the fledging period (20th–26th day of chick life, last measurement on the 16th–26th day of chick life). We excluded individuals that had been measured less than 4 times due to logistic problems (12 chicks, 3.4%), as an appropriate number of measurements of each parameter was needed to fit the logistic function, and individuals raised as one chick due to small sample size (5 chicks, 1.4%). Chicks that had died (50 chicks, 14.2%, carcasses were found) and disappeared (16 chicks, 4.5%—died and sank or were predated) before fledging were treated separately and only for illustrative purposes: we estimated one common growth curve based on all these chicks since individual growth curves were available for few of them. The individuals included in the analysis were measured on average 5.8 and 5.1 times in 2016 and 2017, respectively (range 4–8 times, between 1 and 26 days of age).

The influence of sex and the other factors on growth parameters were analysed using a Linear Mixed-Effect Model. The global model took the form: $Y = \text{sex} + \text{egg volume} + \text{hatching date} + \text{brood size} + \text{sex ratio} + \text{sex} \times \text{egg volume} + \text{sex} \times \text{hatching date} + \text{sex} \times \text{brood size} + \text{sex} \times \text{sex ratio} + \textit{nest(colony)}$, where sex and brood size were categorical fixed factors, egg volume, hatching date and sex ratio were continuous predictors, scaled prior to analysis. Nest ID and colony were categorical, random factors, nest was nested in colony (we did not consider 'year' as there was only one colony in 2017, so the year effect would be indistinguishable from the colony effect). Egg volume was the average volume of all the eggs in a clutch. Hatching date was the chick hatching date (measured in days numbered from 1st June each year; 1st June = day 1; this parameter was determined for each nestling individually). We did not take the hatching order into consideration because in most nests at least two chicks hatched simultaneously (almost 85% of nests—in most cases it would have been very hard to give the actual hatching order, as such a factor would have been highly unreliable). Brood size was the number of successfully hatched chicks (2 or 3) still alive on the 5th day of life (we excluded 5 nests with only one chick due to insufficient sample size for reliable analysis). Sex ratio was the percentage of male chicks in the brood alive on the 5th day of life. Chick mortality was the highest in the first 5 days and around the fledging time. Therefore, we decided to use brood size and sex ratio on the 5th day of life instead of the first day of chicks' life, since it is the former that has the most potential to affect growth. We did not add the brood reduction as additional factor to avoid overestimation. To test whether mortality until fledge was sex biased, we used a chi-square test. Furthermore, we divided broods into two groups—with and without chick mortality and we compared these groups used t test in terms of brood characteristics (e.g. brood size, see above). In this analysis we used hatching date of the oldest nestling in the brood and brood size and sex ratio on the 1st day of life as factors potentially influenced early mortality.

Prior to the next analysis, Likelihood Ratio Tests of Nested Models were used to determine whether the exclusion of colony improved the model fit (Zuur et al. 2009). Also, a few individuals with growth parameters having a Cook distance > 1 in a particular model were excluded for the analysis of that body measurement (see Supplementary Material Table S1). There was no problem with collinearity—the correlation coefficients between the covariates were < 0.3 in all cases. Model selection was performed using Akaike's Information Criterion with the correction for a small sample size (AICc) in the MuMIn library (Bartoń 2015, Supplementary Material Table S2). The coefficients of the models with $\Delta AICc < 2$ were averaged and used for final inference (Zuur et al. 2009).

In addition, we calculated SSD at different growth stages, expressed as the ratio of male and female dimensions or body mass (a result of > 1 meant that males were bigger or heavier than females). To calculate SSD at hatching and before fledging we used all the measurements from the 1st and 21st days of the nestlings' lives. To calculate SSD in the asymptote, we used the asymptote of all fledglings calculated from the logistic function. To compare our results with adult SSD, we took the body measurements of adult birds from Ledwoń (2011). T test were used to compare males' and females' dimensions and body mass. We used 0.05 value as the threshold of the statistical significance. All the analyses were conducted in R 3.6.1 and 3.6.3 (R Core Team 2019, 2020).

Results

Factors influencing growth

Sex significantly affected the asymptote for all body measurements except wing length—in all cases, males achieved

greater dimensions than females (Tables 1, 2; Fig. 1). Moreover, the maximum growth rate (g_{max}) in males was higher than in females, which means that males gain body mass faster than females (Tables 1, 2). In females, the constant of integration (B) of the total head length was lower and the growth rate constant (k) was higher than in males which indicate that in females, the rapid growth phase of the total head length began a little earlier and the final dimensions were reached earlier than in males. The mentioned above growth rate constant of the total head length was influenced by the interaction of the brood size and the sex of nestlings: females grew faster than males in two-chick broods, but there were no differences between the sexes in three-chick broods (Table 2).

Brood size influenced the maximum growth rate (g_{max}) and the growth rate constant (k) of the total head length, g_{max} of wing and the asymptote (A) of tarsus: in smaller broods, nestlings had a faster and shorter time period of the total head length growth, faster growth of wings, and achieved a longer tarsus dimension (Table 2). The maximum growth rate (g_{max}) and the growth rate constant (k) of the total head length negatively and the asymptote (A) positively correlated with the hatching date, which means that as the season progressed, nestlings had a slower growth of the total head length which took longer, but achieved a higher final size (Table 2). The last result was influenced by the interaction of the hatching date and the sex of nestlings: hatching date positively influenced the asymptote mainly in males, whereas this relationship was less pronounced in females (Table 2). Furthermore, the hatching date influenced also the tarsus asymptote (A) and the constant of integration (B) of the wing: as the season progressed, the tarsus achieved smaller dimensions and the wing began its rapid growth phase earlier. Again, the last result was influenced by the interaction of the hatching date and the sex of nestlings; in this case, the hatching date affected wing growth only in females (Table 2). Egg volume and sex ratio did not influence any growth parameters.

Sex ratio and mortality

Sex of hatchlings and fledglings did not deviate from parity (hatchlings: 178 females, 170 males, $\chi^2 = 0.14$, $p = 0.71$; fledglings: 141 females, 146 males, $\chi^2 = 0.06$, $p = 0.81$). Sex was also not biased among nestlings that died before fledging time (37 females, 26 males, $\chi^2 = 1.59$, $p = 0.21$). Sex ratio of hatchlings in brood and the hatching date did not differ between broods with and without chick mortality (sex ratio: $t = -0.89$, $p = 0.37$, hatching date: $t = -0.83$, $p = 0.41$). Broods with chick mortality were characterized by a greater number of hatchlings ($t = 2.38$, $p = 0.02$) and lower average egg volume ($t = -2.13$, $p = 0.03$). Chicks that have died achieved on average lower asymptotic values (A) than alive ones (i.e., that fledged successfully). Also, maximal growth rate (g_{max}) and growth rate constant (k) in most cases were lower for dead individuals (Fig. 2, Supplementary Material S3).

SSD in different stages

A statistically significant SSD on the 1st day of life was observed only with respect to total head length (Table 3). On the 21st day, males were significantly larger than females in all measurements except wing length. The SSD of total head length and wing length calculated for the asymptote was still lower than for adults. SSD was the highest in body mass when the birds were close to fledging: males on the 21st day were on average 13% heavier

Table 1 Averaged parameters (mean ± SD) of the logistic models (A—asymptote, B—constant of integration, k—growth rate constant), fitted to the biometrics of individual Whiskered Terns during the nestling period, for both sexes together (all) and separately for males (M) and females (F), g_{max}—the maximum growth rate calculated from the above parameters, N—number of measured individuals used to estimate parameters; only individuals surviving to fledging were used in the averaging

Body measurement	Sex	$A \pm$ SD	$B \pm$ SD	$k \pm$ SD	$g_{max} \pm$ SD	N
Total head length	All	58.95 ± 3.320	1.17 ± 0.133	0.150 ± 0.0192	2.19 ± 0.213	147
	M	60.45 ± 3.416	1.19 ± 0.129	0.147 ± 0.0203	2.20 ± 0.204	75
	F	57.38 ± 2.368	1.14 ± 0.132	0.152 ± 0.0199	2.17 ± 0.223	72
Tarsus	All	23.45 ± 0.973	0.93 ± 0.344	0.27 ± 0.0876	1.58 ± 0.498	262
	M	23.77 ± 0.995	0.94 ± 0.309	0.26 ± 0.0812	1.55 ± 0.464	133
	F	23.13 ± 0.836	0.92 ± 0.377	0.28 ± 0.0932	1.61 ± 0.531	129
Wing	All	167.4 ± 9.57	14.85 ± 3.069	0.229 ± 0.0175	9.56 ± 0.547	270
	M	168.6 ± 9.75	15.14 ± 3.216	0.229 ± 0.0172	9.63 ± 0.499	139
	F	166.1 ± 9.25	14.54 ± 2.886	0.229 ± 0.0179	9.49 ± 0.588	131
Body mass	All	89.73 ± 9.376	8.31 ± 2.798	0.301 ± 0.0493	6.69 ± 0.941	260
	M	93.63 ± 9.221	8.51 ± 2.708	0.298 ± 0.0517	6.89 ± 0.940	129
	F	85.77 ± 7.756	8.11 ± 2.883	0.305 ± 0.0466	6.49 ± 0.902	131

Table 2 Model-averaged coefficients from generalized linear mixed models used to explain the variation in the growth parameters of body measurements (models with ΔAICc < 2 after model selection were used for averaging)

Body measurement	Growth parameter	Fixed effects	Coefficient	SE	z	p
Total head length	A	Intercept	57.09	0.70	81.43	< 0.001***
		Sex: male	2.64	1.20	2.19	0.028*
		Brood size:3	0.21	0.64	0.33	0.740
		Egg volume	0.02	0.12	0.17	0.869
		Hatch date	0.93	0.41	2.22	0.026*
		Sex proportion	0.39	0.37	1.07	0.285
		Brood size:3 × Sex: male	− 0.88	1.24	0.71	0.481
		Hatch date × Sex: male	1.20	0.45	2.63	0.009**
	B	Intercept	1.17	0.04	26.75	< 0.001***
		Sex: male	0.05	0.02	2.38	0.017*
		Hatch date	0.03	0.02	1.27	0.205
		Brood size:3	− 0.06	0.04	1.28	0.200
		Egg volume	− 0.02	0.02	1.09	0.275
		Hatch date × Sex: male	0.02	0.02	0.95	0.342
		Egg volume × Sex: male	0.00	0.01	0.19	0.849
		Sex proportion	0.00	0.01	0.16	0.870
	k	Intercept	0.17	0.01	29.22	< 0.001***
		Sex: male	− 0.02	0.01	2.40	0.016*
		Hatch date	− 0.01	0.00	3.81	< 0.001***
		Brood size:3	− 0.02	0.01	2.67	0.007**
		Sex proportion	0.00	0.00	0.35	0.727
		Egg volume	0.00	0.00	0.18	0.859
		Brood size:3 × Sex: male	0.02	0.01	2.32	0.020*
		Hatch date × Sex: male	0.00	0.00	0.41	0.684
	g_{max}	Intercept	2.37	0.06	37.07	< 0.001***
		Sex: male	− 0.06	0.09	0.62	0.535
		Hatch date	− 0.10	0.03	3.29	< 0.001***
		Brood size:3	− 0.19	0.07	2.87	0.004**
		Egg volume	0.00	0.01	0.25	0.806
		Brood size:3 × Sex: male	0.13	0.09	1.42	0.156
		Hatch date × Sex: male	− 0.02	0.03	0.54	0.590
Wing	A	Intercept	167.17	2.53	65.86	< 0.001***
		Sex: male	0.83	1.04	0.80	0.425
		Date	− 1.55	1.21	1.27	0.203
		Sex proportion	0.08	0.30	0.25	0.803
		Hatch date × Sex	0.25	0.69	0.36	0.716
	B (log)	Intercept	1.17	0.02	50.59	< 0.001***
		Sex: male	0.01	0.01	1.05	0.295
		Hatch date	− 0.02	0.01	2.11	0.035*
		Brood size:3	− 0.02	0.02	1.04	0.298
		Egg volume	− 0.01	0.01	0.93	0.354
		Hatch date × Sex: male	0.02	0.01	2.13	0.034*
		Egg volume × Sex: male	0.00	0.01	0.65	0.518
		Brood size:3 × Sex: male	0.00	0.01	0.33	0.741

Table 2 (continued)

Body measurement	Growth parameter	Fixed effects	Coefficient	SE	z	p
	k	Intercept	0.23	0.00	50.55	< 0.001***
		Sex: male	0.00	0.00	0.13	0.897
		Brood size:3	0.00	0.00	1.34	0.180
		Hatch date	0.00	0.00	0.27	0.786
		Egg volume	0.00	0.00	0.36	0.719
		Sex proportion	0.00	0.00	0.36	0.720
	g_{max}	Intercept	9.68	0.14	69.02	< 0.001***
		Sex: male	0.05	0.07	0.81	0.420
		Brood size:3	− 0.24	0.10	2.39	0.017*
		Sex proportion	0.06	0.05	1.18	0.238
		Egg volume	0.02	0.03	0.51	0.614
		Hatch date	− 0.02	0.04	0.44	0.661
		Sex proportion × Sex: male	0.00	0.03	0.18	0.861
Tarsus	A	Intercept	23.79	0.19	127.08	< 0.001***
		Sex: male	0.66	0.15	4.31	< 0.001***
		Hatch date	− 0.17	0.07	2.26	0.024*
		Brood size:3	− 0.77	0.20	3.83	< 0.001***
		Egg volume	0.09	0.09	0.92	0.357
		Sex proportion	0.04	0.07	0.55	0.585
		Egg volume × Sex: male	− 0.02	0.06	0.34	0.736
		Brood size:3 × Sex: male	− 0.02	0.12	0.16	0.870
	B (log)	Intercept	− 0.03	0.04	0.74	0.462
		Sex: male	0.01	0.02	0.21	0.836
		Hatch date	− 0.01	0.01	0.76	0.446
		Brood size:3	− 0.03	0.03	1.07	0.285
		Sex proportion	0.02	0.01	1.56	0.118
		Egg volume	− 0.01	0.01	0.89	0.376
		Sex proportion × Sex: male	− 0.02	0.02	0.78	0.433
		Brood size:3 × Sex: male	0.01	0.03	0.38	0.705
		Egg volume × Sex: male	0.00	0.01	0.35	0.726
	k	Intercept	0.28	0.03	10.49	< 0.001***
		Sex: male	− 0.01	0.02	0.76	0.445
		Sex proportion	0.01	0.01	0.64	0.521
		Egg volume	0.00	0.00	0.08	0.935
		Brood size:3	0.00	0.01	0.07	0.948
		Brood size:3 × Sex: male	0.00	0.01	0.23	0.817
		Sex proportion × Sex: male	0.00	0.01	0.47	0.637
	g_{max}	Intercept	1.62	0.14	11.33	< 0.001***
		Sex: male	− 0.02	0.04	0.46	0.646
		Sex proportion	0.02	0.04	0.53	0.599
		Hatch date	0.00	0.02	0.11	0.911
		Egg volume	0.00	0.01	0.10	0.920
		Sex proportion × Sex: male	− 0.01	0.04	0.31	0.758

Table 2 (continued)

Body measurement	Growth parameter	Fixed effects	Coefficient	SE	z	p
Body mass	A	Intercept	85.92	1.37	62.22	< 0.001***
		Sex: male	7.03	1.09	6.42	< 0.001***
		Sex proportion	0.09	0.36	0.26	0.796
		Date	0.06	0.33	0.18	0.860
		Brood size:3	− 0.09	0.64	0.14	0.886
		Egg volume	− 0.03	0.40	0.06	0.950
		Egg volume × Sex: male	0.19	0.61	0.30	0.763
	B (log)	Intercept	0.91	0.04	25.80	< 0.001***
		Sex: male	0.02	0.02	1.53	0.125
		Hatch date	0.00	0.01	0.26	0.794
		Egg volume	− 0.02	0.01	1.92	0.056
		Brood size:3	− 0.04	0.03	1.31	0.191
		Egg volume × Sex: male	0.00	0.01	0.39	0.698
	k	Intercept	0.30	0.01	48.64	< 0.001***
		Sex: male	0.00	0.00	0.20	0.839
		Brood size:3	0.00	0.01	0.29	0.773
		Egg volume	0.00	0.00	0.22	0.825
		Hatch date	0.00	0.00	0.15	0.884
	g_{max}	Intercept	6.61	0.18	36.35	< 0.001***
		Sex: male	0.42	0.11	3.86	< 0.001***
		Brood size:3	− 0.12	0.19	0.63	0.526
		Sex proportion	0.02	0.06	0.39	0.695
		Egg volume	0.00	0.03	0.14	0.893

Growth parameters: A—asymptote, B—constant of integration, k—growth rate constant, g_{max}—maximum growth rate. Coefficients and SE estimates of some growth parameters (log) are on the log scale. All the models include the random effect of the nest; some models also include the random effect of the colony (omitted from this table, details in Supplementary Material Table S1). For the full set of models, see Supplementary Material Table S2

than females as a result of their higher maximum growth rate. This difference became less apparent in adults since males are 7% heavier than females (Table 3). The lowest SSD was observed in wing length: the SSD of the wing in young birds was statistically significant only for the calculated asymptote (Table 3).

Discussion

Influence of sex on growth

Our results show that much of the SSD observed in adult Whiskered Terns occurs already during the nestling period (Fig. 1; Table 3). At hatching, sexes differed significantly only in total head length. SSD in total head length remained constant until fledging but then increased during the fledgling period since females completed their growth earlier, while it was still growing in males. The differences between the sexes in all body measurements increased as chicks become older (Fig. 1). SSD was the best marked in the final size (asymptote), which was higher in males for all body measurements (although in the analysis taking other factors into account, sex did not significantly influence the asymptote of wing length), but in most trait (except wing length) significant differences were already apparent on the 21st day of chick life—around the time of fledging (raw data, Table 3). Adults of Whiskered Tern, however, exhibit comparable SSD in both wing and tarsus length (Ledwoń 2011), whereas chicks at the end of the nestling period displayed SSD only in the latter trait: they had a fully grown tarsus whereas the wing was still growing after fledging. This slow growth of the wings, with almost no difference between the sexes, makes this trait particularly useful for ageing chicks (Paillisson et al. 2008, AB—unpublished data).

SSD was most pronounced in body mass. The biggest difference between sexes was observed close to fledging and later became less apparent (Table 3). Gull-billed Tern, in which adult males are ca 4% bigger than females, exhibits sex-dependent body mass growth with males growing faster and achieving a greater body mass (Villegas et al. 2013), similarly to what we recorded in the Whiskered Tern. Roseate Tern, the second tern species previously studied in this context, displays minimal SSD in adult body mass; it does

not exhibit any sex-related differences in body mass growth in chicks up to the 3rd day of life (Nisbet and Szczys 2001; Szczys et al. 2005), but such a disparity may occur in later stages of nestling growth (Villegas et al. 2013). Greater SSD and body mass in fledglings than in adults as we found in Whiskered Tern have also been reported for Common Tern (Becker and Wink 2003), a species with negligible SSD in adult body mass, or even a reversed SSD, where females are heavier than males (Fletcher and Hamer 2003; Becker and Ludwigs 2004; Nisbet et al. 2007). In Whiskered Tern, on average, males at fledging reached the adult mass while females reached only 94% of the adult female mass. Becker and Wink (2003) suggest that higher mass of Common Tern males during the last pre-fledging days could reflect better condition and more body reserves, laid down as extra fat or muscle tissues. Males being larger than females can be more successful in competing for food brought by parents or parents can favour sons over daughters. It indicates that females should exhibit catch-up growth of body mass after fledging.

In previous studies of tern species sex-dependent variations in the growth of measurements other than body mass were rarely tested (but see Becker and Wink 2003; Becker and Ludwigs 2004; Arnold et al. 2020). The increase in size traits during nestling growth is better known in other Charadriiformes, i.e. gulls (Larinae) and waders (Scolopacidae and Charadriidae). Some studies have documented SSD already at hatching: at this stage, SSD relates mainly to skeletal dimensions, especially the bill, as in the Whiskered Tern in this study (head plus bill measured); no differences in body mass between the sexes were observed (Bogdanova and Nager 2008; Dos Remedios et al. 2015; Loonstra et al. 2018). More often, differences in growth parameters were tested: in many cases, offspring of the larger sex had a higher maximum growth rate of body mass (as in our study) and linear size traits, or grew over a longer period (less commonly) achieving a higher asymptote (Müller et al. 2007; Bogdanova and Nager 2008; Dos Remedios et al. 2015; Bosman et al. 2016; Jordi and Arizaga 2016; Loonstra et al. 2018). This enables the sex to be identified by size traits even before fledging (Jordi and Arizaga 2016).

The increase in SSD during the nestling period and the higher maximum growth rate of the male body mass observed in Whiskered Tern are commonly associated with the higher energetic costs of care for offspring of the larger sex (Klaassen et al. 1992; Vedder et al. 2005; Magrath et al. 2007, but see Müller et al. 2007). The development of SSD during the nestling period suggests that males of the Whiskered Tern may be a more energy-demanding sex than females. This is important, as such a disparity may result in the higher mortality of the bigger sex if conditions are unfavourable or the parents less experienced (Gonzales-Solis et al. 2005; Müller et al. 2005). Nevertheless, in this study, we did not observe any sex-biased mortality and both hatchling and fledgling sex ratios were equal. This lack of differences in mortality between sexes may be due to food abundance in studied carp ponds and in consequence high chicks' survival rate (see below). Therefore, this issue requires a more comprehensive study.

Other factors

As expected, nestlings raised in smaller broods, where competition for food is less intense, exhibited enhanced growth parameters in comparison with larger broods: they grew faster (wing and total head length—the latter result is higher for females) and achieved greater size (tarsus). Surprisingly, brood size did not influence body mass growth, which is the most frequently demonstrated effect of this parameter (Horak 2003; Müller et al. 2005; Bogdanova and Nager 2008; Gilliland et al. 2016). Body mass growth exhibited the greatest variability among all the body measurements and because on our study site natural three-chick broods are more common, possible differences may not be perceptible. Moreover, the similar mass in larger and smaller broods may be due to superabundant food on carp ponds. The Whiskered Tern population breeding here is highly productive (Betleja 2003; Ledwoń and Neubauer 2017), not only due to food abundance but also because of low predation pressure and stable hydrological conditions. Furthermore, in originally larger broods we observed higher nestlings mortality, which occurred mostly during the first few days of life and resulted in brood reduction. This early mortality allows the brood size to be adjusted to the parent's ability to raise chicks (Vedder et al. 2017, 2019).

Frequently, nestling growth is negatively correlated with hatching date (Bogdanova and Nager 2008; Loonstra et al. 2018), as environmental conditions may deteriorate during a season. Likewise, individuals in poorer condition, and/or younger and/or less experienced, usually begin egg-laying later (Ludwigs and Becker 2002; Dittmann and Becker 2003). In our study, the progress of the season also had a negative impact on the growth of nestlings: they achieved a shorter tarsus, head grew more slowly and over a longer time, though date did positively influence the total head length asymptote of males. However, this last result may be a mathematical artefact: the correct calculation of the asymptote requires the inclusion of measurements made after the rapid growth phase. In our study, nestlings fledged at the same age throughout the season, but later in the season their heads and bills grew more slowly, and the last measurement of total head length before fledging was at the beginning of the slowdown of growth; this could lead to an overestimation of the asymptote. Females reached their final total head length earlier, so here we did not observe any increase in the total head length asymptote as the season progressed.

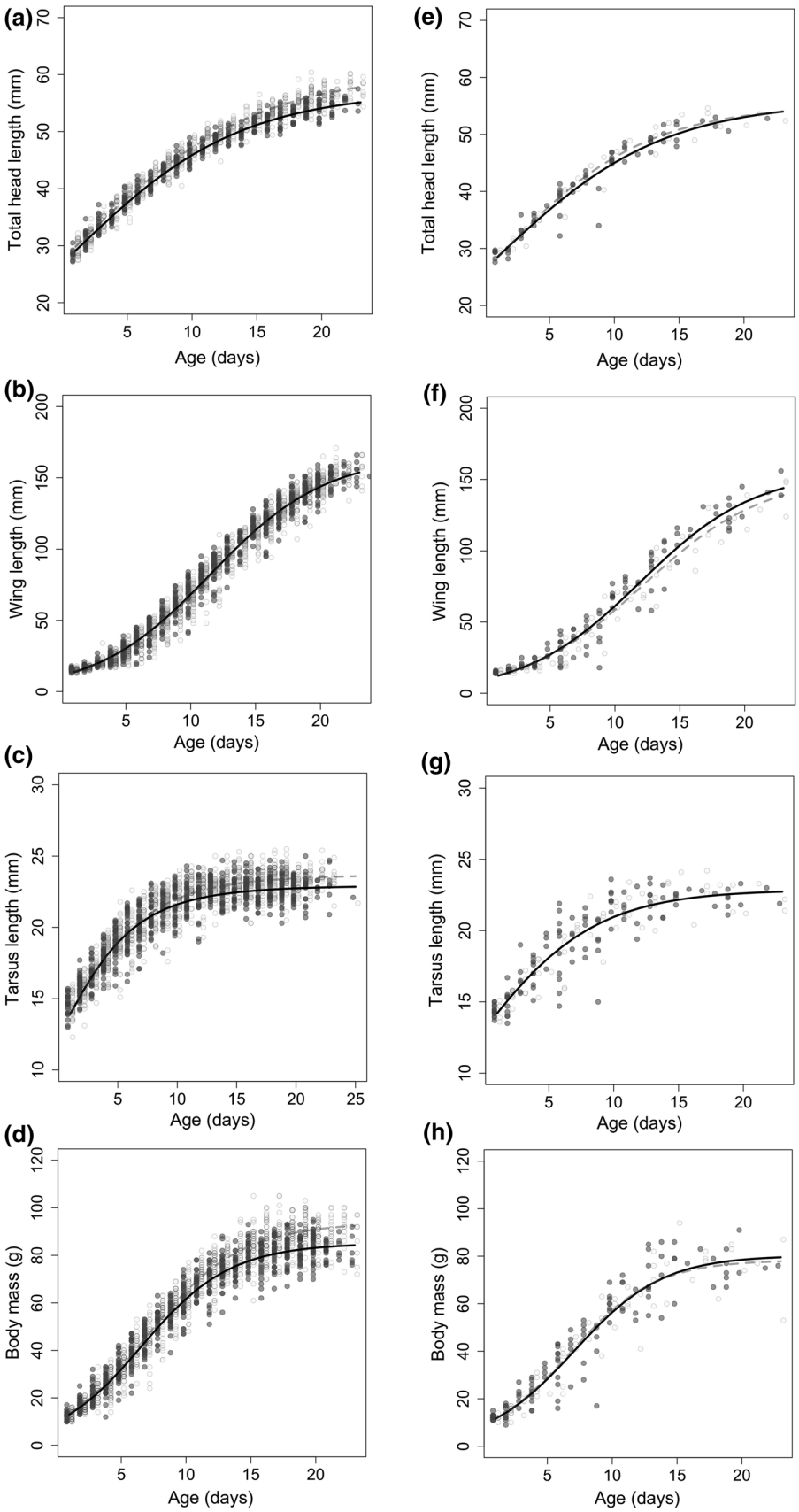


Fig. 1 Growth of Whiskered Tern nestlings successfully fledged (**a**–**d**) and had died before fledging (**e**–**h**): total head length (**a**, **e**), wing length (**b**, **f**), tarsus length (**c**, **g**), body mass (**d**, **h**) of females (solid points and lines) and males (open points and dotted lines). The points represent original measurements, lines are fitted logistic growth curves

Table 3 Summary of sexual size dimorphism (SSD—the ratio of male and female dimensions or body mass) in particular body measurements recorded in the different growth stages

Body measurements	Growth stage	Female				Male				Mean SSD	*t* test *p* value
		Mean	SD	*N*	Range	Mean	SD	*N*	Range		
Total head length	Hatch	28.55	0.82	13	27.2–30.5	29.65	1.43	24	27.5–32.2	1.04	0.006**
	Fledge	54.58	1.41	12	52.5–57.0	56.58	1.38	9	54.3–58.8	1.04	0.004**
	Asymptote	57.39	2.37	72	52.68–63.55	60.45	3.42	75	52.16–69.18	1.05	< 0.001***
	Adult	63.0	1.5	118	58.8–65.9	67.8	1.3	123	64.2–71.4	1.08	< 0.001***
Wing	Hatch	15.48	1.16	25	13–18	15.14	1.14	35	13–18	0.98	0.269
	Fledge	150.2	6.07	20	138–158	153.9	6.58	20	146–171	1.02	0.072
	Asymptote	166.1	9.25	131	138.0–190.1	168.6	9.75	139	134.6–206.8	1.01	0.034*
	Adult	230.4	5.3	64	217–243	237.6	5.2	86	226–253	1.03	< 0.001***
Tarsus	Hatch	14.6	0.74	25	13.0–15.7	14.51	0.82	34	12.3–16.0	0.99	0.682
	Fledge	22.73	1.06	19	20.7–25.0	23.32	0.68	20	21.9–24.5	1.03	0.047*
	Asymptote	23.13	0.84	129	21.0–25.35	23.77	0.99	133	21.62–27.89	1.03	< 0.001***
	Adult	22.8	0.9	103	18.9–24.6	23.5	0.9	107	21.0–26.6	1.03	< 0.001***
Body mass	Hatch	12.65	1.8	23	10–17	12.82	1.99	34	10.0–16.0	1.01	0.737
	Fledge	79.31	7.72	19	56–87	89.3	6.59	20	75–100	1.13	< 0.001***
	Asymptote	85.77	7.76	129	64.4–130.2	93.63	9.22	131	72.6–142.2	1.09	< 0.001***
	Adult	84.1	5.3	106	72–99	90.3	5.5	119	78–110	1.07	< 0.001***

Hatch—measurements on the 1st day of a nestling's life, Fledge—measurements on the 21st day of life, just before fledging, Asymptote—calculated from the logistic function fitted to the biometrics of individuals during the nestling period, *N*—number of individuals measured. Body measurements of adult birds were taken from Ledwoń (2011)

We found no effect of the egg volume on the chick growth parameters. However, previous studies of birds showed that in the majority of species, chick growth is dependent on egg size (Williams 1994). However, the potential limitation of our study is the fact that we used the average volume of the egg in the clutch instead of the volume of the egg from which the exact chick hatched, since we were not able to connect individual chicks with eggs. Furthermore, favourable food conditions in our study area could overcome the potential effect of egg volume on chick growth. Nevertheless, in broods with a brood reduction, there was a lower egg volume, which corresponds with findings in other bird species (review in Krist 2011).

Conclusions

We found that, in line with our expectations, SSD in Whiskered Tern, a species with moderate SSD in adults, also occurs during the nestling period. Close to fledging, males were larger than females in total head length, tarsus length, body mass, but not in wing length. Other factors affected the final size of both sexes in the same way: nestlings achieved a shorter tarsus length in bigger broods and as the season progressed. We found that at fledging, SSD was the most pronounced in body mass, as in adults. Since SSD is present in Whiskered Terns already at the chick stage, males may be more costly to raise than females. It could lead to higher mortality in bigger sex under unfavourable conditions and in consequence to skewed sex ratio. However, we did not find differences in mortality between the sexes, likely due to abundant food. In Whiskered Tern males, body size could have an impact on breeding success during the parental care of chicks and fledglings, since heavier males are better disposed to deliver larger prey items (Gwiazda and Ledwoń 2015, 2016). This could be of importance following female desertion when the male looks after the chicks on his own. Females can choose the best mate during mating flights, which enables them to assess male quality in terms of size and body mass (Wiącek 2004), the parameters which are impacted the most by the conditions experienced during the chick period.

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