ORIGINAL ARTICLE

Sex ratio and sex-specific chick mortality in a species with moderate sexual size dimorphism and female brood desertion

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Abstract

An equal sex ratio at the population level is the usual, evolutionarily stable condition. However, at the individual level, it may be adaptive for parents to manipulate the sex of their offspring, especially in species with sexual size dimorphism (SSD) when the costs and benefits of producing sons and daughters can vary. In this study, we investigated the hatching sex ratio (HSR) and fledging sex ratio (FSR) in the Whiskered Tern (*Chlidonias hybrida*). Despite the fact that SSD exists in Whiskered Terns already at the chick stage, HSR and FSR did not deviate from parity at the population level. We tested the dependence of HSR, FSR and the survival probability of males and females on the individual hatching date, average egg volume (in a clutch) and the number of nestlings. None of these factors influenced HSR. Survival probability was negatively correlated with the number of hatchlings. The proportion of females among the fledglings was positively correlated with the average egg volume per clutch. To better explore the effect of egg volume on the sex ratio, we tested the relationship between exact egg volume and hatchling sex or hatching success at the individual level; but despite the quite large sample size, our analyses failed to reveal any relationship. The sex ratio was equal among chicks that were found dead in a nest, mostly due to starvation, but more female than male chicks disappeared from nests (mostly due to predation), primarily in the first week of life. This indicates that females may be easier to predate, very likely by frogs hunting small chicks.

Keywords Sex ratio · Hatching sex ratio · Fledging sex ratio · Chick mortality · Survival probability · Whiskered Tern · *Chlidonias hybrida* · Egg volume

Zusammenfassung

Geschlechterverhältnis und geschlechtsspezifische Kükensterblichkeit bei einer Art mit schwach ausgeprägtem sexuellem Größendimorphismus und Brutverzicht der Weibchen

Ein ausgewogenes Geschlechterverhältnis auf Populationsebene ist der normale, evolutionär stabile Zustand. Aber auf individueller Ebene kann es für Eltern einen Anpassungsvorteil bedeuten, das Geschlecht ihrer Nachkommen zu beeinflussen, insbesondere bei Arten mit Größendimorphismus (SSD) der Geschlechter, bei denen die Kosten und Vorteile der Aufzucht von Söhnen und Töchtern unterschiedlich sein können. In dieser Studie untersuchten wir bei der Weißbart-Seeschwalbe (*Chlidonias hybrida*) das Geschlechterverhältnis beim Schlüpfen („hatching sex ratio ", HSR) und beim Ausfliegen („fledging sex ratio ", FSR). Trotz der Tatsache, dass der SSD bei den Weißbart-Seeschwalben schon im Kükenstadium besteht, blieben auf Populationsebene HSR und FSR gleichverteilt. Wir untersuchten die Abhängigkeit von HSR, FSR und der Überlebenswahrscheinlichkeit von Männchen und Weibchen vom individuellen Schlüpfdatum, dem durchschnittlichen

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Communicated by C. Barbraud.

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Eivolumen (innerhalb eines Geleges) und der Anzahl der Jungvögel. Keiner dieser Faktoren beeinflusste das HSR. Die Überlebenswahrscheinlichkeit korrelierte negativ mit der Anzahl der Küken. Der Anteil der weiblichen Küken korrelierte positiv mit dem durchschnittlichen Eivolumen innerhalb eines Geleges. Um eine mögliche Auswirkung vom Eivolumen auf das Geschlechterverhältnis genauer festzustellen, untersuchten wir für einzelne Tiere den Zusammenhang zwischen dem exakten Eivolumen und dem Geschlecht des Kükens und dem Schlüpferfolg; aber trotz der recht großen Stichprobe ergaben unsere Analysen keinen Zusammenhang. Das Geschlechterverhältnis war bei den tot im Nest aufgefundenen Küken ausgeglichen; diese waren zumeist verhungert, aber es verschwanden vor allem in der ersten Lebenswoche mehr weibliche als männliche Küken aus den Nestern (in der Regel als Beute von Raubtieren). Dies deutet darauf hin, dass die weiblichen Küken leichter zu erbeuten sind, höchstwahrscheinlich von Fröschen, die kleine Küken jagen.

Introduction

The sex ratio is an important life history trait at both the individual and population levels (West 2009; Guillon 2016; Booksmythe et al. 2017), and the offspring sex ratio can be mediated by both environmental and evolutionary processes (Gowaty 1993; Rosenfeld and Roberts 2004; Rutkowska and Badyaev 2008; Szász et al. 2012). Fisher (1930) attempted to explain the common occurrence of equal sex ratios in nature. He suggested that if both sons and daughters had the same cost (resource allocation) and benefits (fitness return) for parents, they should invest at the same level in both offspring sexes. Selection should, therefore, lead to an equal, evolutionarily stable sex ratio. However, if the cost–benefit ratios of producing sons and daughters are not equal, it may be adaptive for parents to manipulate offspring sex and selection would skew the sex ratio towards that of the sex with reduced costs and/or higher fitness (Trivers and Willard 1973).

In birds, females have the potential to control the sex of eggs because they are heterogametic and because the sex-determining division in avian meiosis occurs prior to ovulation and fertilization (Rutkowska and Badyaev 2008). There is increasing empirical evidence that females can control chromosomal segregation in relation to the social and environmental circumstances experienced at laying (Sheldon et al. 1999; Pike and Petrie 2003; Rutkowska and Badyaev 2008; Gam et al. 2011; Tagirov and Rutkowska 2013). Numerous studies have found several conditions that may influence the female sex allocation in eggs, such as parental condition (Nager et al. 2000; Velando 2002; Weimerskirch et al. 2005), mate attractiveness (Zielińska et al. 2010; Cantarero et al. 2018), clutch size (Lessells et al. 1996; Saino et al. 2002), hatching date (Cordero et al. 2001; Wojczulanis-Jakubas et al. 2013), laying order (Badyaev et al. 2002; Ležalová et al. 2005), food availability (Komdeur et al. 1997; Bukaciński et al. 2020), egg size (Anderson et al. 1997; Cordero et al. 2001; Krist 2011—meta-analysis) and maternal stress hormones (Love et al. 2005).

The sex ratio in young birds is usually studied at three different stages, although the exact boundaries of each stage have not been clearly defined (West 2009; see also the discussion in Kato et al. 2017): a primary stage (at laying), a secondary one (at birth, hatching sex ratio—HSR) and a tertiary one (the fledging stage, fledging sex ratio—FSR). However, the different mortalities of sons and daughters can cause shifts in the sex ratio between these stages (Griffiths 1992; Santoro et al. 2015). Differences in mortality between the sexes were found during both embryonic development (Cichoń et al. 2005; Kato et al. 2017) and the chick-rearing period (Nager et al. 2000; Szczys et al. 2001). This could have been due to the different sensitivities of male and female embryos to environmental pollutants (Fry and Toone 1981; Erikstad et al. 2009), hormonal factors and sex chromosome products (Chandra 1991; Krackow 1999; Pérez et al. 2006), selective provisioning by parents (Teather 1992) or the different vulnerability of the sexes to unfavourable rearing conditions (Nager et al. 2000; Kalmbach et al. 2005).

In birds, sexually size-dimorphic species have been intensively studied in terms of sex allocation and sex-dependent mortality, because a difference in size can lead to sex-specific effects on offspring survival, which might in turn promote the evolution of sex ratio biases (Myers 1978; Weatherhead and Teather 1991; Benito and González-Solís 2007; Eberhart-Phillips et al. 2017). In sexually size-dimorphic species, the larger sex (usually the male) is commonly assumed to be more costly for parents because of the higher growth and/or metabolic rates, and thus the overall greater energy needs or food intake during development (Slagsvold et al. 1986; Teather and Weatherhead 1988; Stamps 1990; but see Torres and Drummond 1999). In consequence, the sex ratio should be skewed towards the smaller sex because parents are expected to invest more in the cheaper sex (Fisher 1930). In addition, the bigger sex is more susceptible to mortality when food is scarce because of its increased nutrient needs resulting from faster growth rates (Teather and Weatherhead 1989; Griffiths 1992). Indeed, the offspring sex ratio in many bird species is skewed towards the production of the smaller sex in many sexually size-dimorphic species (Teather and Weatherhead 1988; Kalmbach et al. 2001; Benito and González-Solís 2007). In contrast, differential mortality among the smaller sex has been found in some circumstances. Higher mortality among smaller individuals was found in species where access to food depends on competitive abilities, because of the competitive advantages accruing from a larger size (Edwards and Collopy 1983;

Bortolotti 1986; Anderson et al. 1993; but see Drummond et al. 1991). Furthermore, having fewer reserves, the smaller sex may be less able to cope with periods of food scarcity (Kernsten and Brenninkmeijer 1995; Eberhart-Phillips et al. 2017).

To understand the mechanisms leading to a biased off-spring sex ratio, it is crucial to investigate successive changes in the sex ratio over different developmental stages based on large data sets. The Whiskered Tern (*Chlidonias hybrida*) is a sexually dimorphic bird, with moderate size differences between the sexes: adult males are 3–10% larger than females (Ledwoń 2011). This dimorphism is also evident at the nestling stage (Banach et al. 2021). At hatching, males are larger than females only in the total head length, but sexual size dimorphism (SSD) increases during the chicks' development and, close to fledging, most of the body measurements are larger in males than in females; the greatest differences in size between the sexes is in weight, that of females being only 89% of the male weight. Moreover, the maximum body mass growth rate is higher in males than in females. The occurrence of SSD during the nestling period and the higher maximum growth rate of body mass in males indicates that the costs of raising sons may be higher than of raising daughters. According to the above hypothesis, therefore, this can lead to a female-biased sex ratio. On the other hand, the males being larger are better able to prevail in the competition for food delivered by adults, and this will lead to higher female mortality, especially when food is scarce.

Among gulls and terns, the Whiskered Tern has a unique system of parental care. Almost all adult breeding females in this species desert during both the chick-rearing and post-fledging periods with as much as 52% of nests were deserted prior to fledging (Ledwoń and Neubauer 2017). It has been shown that that parental sex-role reversal may occur in populations that exhibit an extreme male-biased adult sex ratio (Kosztolányi et al. 2011). This situation was found in the related Kentish Plover (*Charadrius alexandrines*), where, as in the Whiskered Tern, the majority of females desert. Female Kentish Plovers have a higher probability than males of renesting after desertion owing to the male-biased adult sex ratio (Amat et al. 1999; Székely et al. 2004; Eberhart-Phillips et al. 2017, 2018). The unbalanced sex ratio in this species is manifested at fledging and continues during adulthood (Székely et al. 2004; Eberhart-Phillips et al. 2017). In contrast, deserting Whiskered Tern females rarely remate and renest (Ledwoń et al. 2023a), possibly because of the insufficient number of males. The adult sex ratio in the Whiskered Tern is not known. The female biased adult sex ratio is not indicated by the low proportion of super normal clutches that are formed by female–female pairs (Betleja et al. 2007). However biased sex ratio during the pre-fledging period may be indicative of an unbalanced adult sex ratio

(Szczys et al. 2001; Kosztolányi et al. 2011; Nisbet et al. 2016; but see Székely et al. 2014a, b).

The above characteristics make the Whiskered Tern a very good and an interesting model for testing some aspects of the sex allocation theory to study the sex ratio at different life stages and sex-specific chick mortality. Here, we investigated whether HSR, FSR and sex-specific chick mortality were biased and correlated with the ecological environment (hatching date, clutch size) and maternal traits (average egg size), over four consecutive years. As SSD in Whiskered Tern is apparent at the nestling stage, we generally expected sex-dependent mortality and in consequence an unbalanced sex ratio (see also above). We expected that as the season progresses—when less experienced parents start their clutches and environmental conditions may deteriorate—HSR and FSR will be female-biased, as parents should invest more in less-expensive offspring. Survival probability should be positively correlated with egg volume, in contrast to brood size with expected negative impact on chick survival—especially of the more sensitive sex.

Methods

Study site and field procedures

The data used in this study were collected during four breeding seasons 2016 to 2019 in nine Whiskered Tern colonies (Table 1) on five carp pond complexes (Spytkowice, Bugaj, Przeręb, Stawy Monowskie, Adolfin) in 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).

Nest monitoring started mostly during the first half of the incubation period and continued until the nestlings fledged. Colony inspections during the egg-laying period were kept to a minimum so as to prevent nest desertion. Eggs were measured with manual callipers to the nearest 0.1 mm and a few days before the expected hatching date nests were enclosed with plastic horticultural mesh to prevent nestlings from escaping from the nest site until they

Table 1 Number of monitored colonies, nests with at least one chick with known sex, hatchlings and fledglings with known sex in particular years

Year	Colonies	Nests	Hatchlings	Fledglings
2016	6	153	409	341
2017	4	213	515	384
2018	6	198	493	310
2019	1	81	225	210
All	9	645	1642	1245

could fly (for a detailed description of the enclosure, see Ledwoń et al. 2015 and Banach et al. 2021). Egg volumes (*v*) were calculated from the formula $v = k \times l \times b^2$, where *k*—volume coefficient, *l*—length, *b*—breadth ($k = 0.478$) (Hoyt 1979; Betleja 2003). First eggs in early colonies were laying around mid-May, last ones in the second half of July. Incubation lasted about 21 days, nestlings usually reached flight ability between 20 and 23 days of age (Betleja 2003; Banach et al. 2021). 85% of the nestlings hatched between 15th June and 20th July (median 30th June). At least one chick hatched in 645 of the monitored nests (Table 1), and chicks hatched from all the eggs in 475 nests. From 2017 onwards, eggs were distinguished with a waterproof marker so that the chick (or unhatched egg) could be linked with the exact egg volume (this was feasible in cases of asynchronous hatching, provided that the inspection fell within the hatching period—the chick usually emerges from the egg within 24 h after the appearance of the hatching star). Colonies were usually visited every 3–4 days (in a few cases more often, even three times a week, or less often, after the hatching period). Each newly hatched chick was ringed with an individually numbered steel ring, and a small sample of blood was taken from the tarsus vein for molecular sexing. The exact hatching date of individuals was determined from the presence of wet feathers after emergence from the egg (the first day of a chick's life), presence of hatching star during the previous inspection and on the basis of the hatchling's wing length and body mass (Paillisson et al. 2008; AB—unpublished data). An individual was classified as being alive at fledging if it was absent from the nest at the age of at least c. 20 days (considering the fledging wing length, Banach et al. 2021). Earlier disappearances were put down to predation. Other death causes (disease, starvation, and hypothermia) or drowning if the dead chick's body was found on the nest or right next to it, on the water (inside the enclosure) were grouped as "dead in the nest". Whiskered Terns, unlike passerine birds, do not carry their dead chicks outside the nest. The age of the chick at the time of death or disappearance was estimated as the age on the middle day between the last inspection during which the chick was alive and the first day on which the chick was found to be missing or dead. For logistical reasons or damage to the enclosure, we stopped inspecting seven nests before fledging. Moreover, in 51 nests we conducted a brood size manipulation experiment, which changed the conditions of chick development to the extent that they could not be included in the FSR or mortality analysis.

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, c. 20 μl was dried at 42 °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′-GTT ACT GAT TCG TCT ACG AGA-3′) and R2718 (5′-ATT GAA ATG ATC CAG TGC TTG-3′) (Fridolfsson and Ellegren 1999), and P2 (5′-TCT GCA TCG CTA AAT CCT TT-3′), P8 (5′-CTC CCA AGG ATG AGR AAY TG-3′) and P0 (5′-ATT GAG TTG GAA CCAGA-ICA-3′) (Griffiths et al. 1998; Han et al. 2009), also used in previous studies of the Whiskered Tern (Ledwoń 2011; Goławski et al. 2016; Banach et al. 2021). PCR products were separated on agarose gel. The presence of one band indicated a male, two bands—a female. Each sample was tested at least twice. If the result was not obvious (usually poor product quality), the PCR was repeated another two or four times (Banach et al. 2021). We were unable to determine the sex of 52 out of 1,694 individuals because of the lack or bad quality of a blood sample.

Statistical analysis

We investigated sex ratios at the population level among hatchlings and fledglings using the *Chi*^{2} test. The primary sex ratio (at laying) was tested indirectly in a subsequent analysis by testing whether HSR in broods with full hatching success differed from broods in which at least one egg failed to hatch.

The influence of environmental and maternal factors in all of the following analyses was tested using generalised linear mixed models (GLMM) with binomial distribution. The best random effects structure for each analysis was selected based on the lowest Akaike information criterion (AIC, if AIC comparison did not give a clear answer, we were guided in our choice by the best representation of the relationship between random factors). Model selections were performed using AIC by function *dredge* in the *MuMIn* library (Bartoń 2015). The coefficients of the models with ΔAIC < 2 were averaged and used for final inference (Zuur et al. 2009).

In the first GLMM analysis we investigated the relationship between HSR (sex of an individual)—dependent variable and several predefined factors. The global model took the form: sex ~ hatchlings + date + volume + success + nest ID/colony/year. The number of hatchlings in the nest, the date of individual hatching and the average volume of all the eggs in a clutch were continuous predictors, scaled prior to analysis. Nest ID, colony and year were categorical, random factors, nested hierarchically (nest in colony in year). The success of clutch hatching was a categorical fixed factor. Success 1 signifies that all eggs hatched successfully, 0 that at least one egg did not hatch (this predictor enables us to detect the difference between the primary sex ratio and HSR—if this has a statistically significant influence on a hatchling's sex, we may suspect increased

mortality among the embryos of one sex; we were unable to determine the sex of embryos from unhatched eggs, so inferring the sex ratio at the egg-laying stage could only be indirect). The hatching date was the exact hatching date of an individual (measured in days numbered from 1st June each year; 1st June = day 1). The number of successfully hatched hatchlings was from one to four (73.6% of individuals were from nests with three hatchlings, 22.3%—two hatchlings, 2.1%—one hatchling, and 2%—four hatchlings). The exact egg volume was known for only 12% of hatchlings, so the average egg volume was included in this analysis. A complete set of data (sex, hatching date, averaged egg volume, number of nestlings, hatching success) was obtained for 1472 hatchlings from 575 nests (the remaining 170 chick with known sex were from broods for which it was not possible to determine averaged egg volume—mainly broods found near the hatching time). 70 hatchlings included in this analysis (from 43 nests) came from nests where not all chicks had their sex determined.

In the second GLMM analysis, we investigated the relationship between FSR (sex of an individual)—dependent variable and several predefined factors. The global model took the form: sex ~ fledglings + date + volume + nest ID/colony/year. The number of fledglings in the nest, the date of individual hatching and the average volume of all the eggs in a clutch were continuous predictors, scaled prior to analysis. Nest ID, colony and year were categorical, random factors, nested hierarchically (Nest in colony in year). The number of fledgelings varied from one to four (53.8% individuals were from nests with three fledglings, and correspondingly 39.0%—two fledglings, 6.1%—one fledgling, 1.1%—four fledglings). A complete set of data (sex, hatching date, averaged egg volume, number of fledglings) was obtained for 1102 fledglings from 486 nests (the sample of fledglings is smaller than the number of hatchlings due to chick mortality and exclusion from analysis broods subjected to brood-size experiment). 19 fledglings from nine nests (included in analysis) came from nests where not all chicks alive to fledge had their sex determined.

In the third GLMM analysis, we investigated the relationship between nestling mortality (survive)—depended variable and several predefined variables. The global model took the form: survive ~ date*sex + volume*sex + hatchlings*sex + nest ID/colony/year. Survive was whether a chick survived to fledging (c. 20 days; survive 1—alive to fledging, 0—found dead in the nest or disappeared before fledging; 1317 individuals in the analysis). The individual hatching date, average egg volume and the number of hatchlings in the nest were continuous predictors, scaled prior to analysis. The sex of an individual was a categorical fixed factor. The interactions of sex with all the above predictors were also included in the model. nest ID, colony and year were categorical, random factors, nested hierarchically.

Difference in deviation in the sex ratios from parity among all chicks that did not survive to fledge on the population level ($n = 230$) and divided by specific categories: nestlings that died in the nest (as a results of disease, starvation, hypothermia, drowning: $n = 149$) and nestlings that were predated (individuals that disappeared from the nest: $n = 81$) were analysed using the Chi^2 test.

Egg numbering allowed us to link some eggs of known volume to certain chicks (it was possible in two circumstances—in part of nests with asynchronous hatching (182 individuals) or when all the chicks in the nest were of the same sex ($n = 363$)). In the fourth GLMM analysis, we tested the effect of exact egg volume and other predefined factors on the sex of individual chick (dependent variable). The global model took the form: sex ~ exact volume + date + hatchlings + success + nest ID/colony/year. The exact volume of egg, individual hatching date and number of hatchlings were the continuous predictors, scaled prior to analysis. The success of clutch hatching was a categorical fixed factor (see first GLMM analysis). Nest ID, colony and year were categorical, random factors, nested hierarchically. This analysis was similar to that previous of HSR, but took into account the exact egg volume instead of the clutch-averaged egg volume.

Egg numbering also made it possible to control the hatching success of individual eggs. The hatching success of an egg was the dependent variable in the fifth GLMM analysis. The global model took the form: hatching success ~ exact volume + hatch date + eggs + nest ID/colony/year. The exact volume of egg, hatch date of the earliest hatched chick in the clutch and number of eggs in the clutch were the continuous predictors, scaled prior to analysis. Nest ID, colony and year were categorical, random factors, nested hierarchically. The egg was classified as unhatched (hatching success = 0) when it disappeared without signs of hatching (a hatching star was not found during the last inspection) or it demonstrated signs of decay (e.g. unpleasant smell, lower weight). This analysis included only nests with at least one unhatched egg ($n = 80$ clutches) to test whether there was any variance within the clutch between the hatched ($n = 160$) and unhatched eggs ($n = 86$).

All the analyses were conducted in R 4.1.1 (R Core Team 2021). There was no problem with collinearity—the correlation coefficients between the covariates were ≤ 0.1 in all cases. The significance threshold was 0.05.

Results

At the population level, the sex ratio did not deviate from parity in either hatchlings (HSR) or fledglings (FSR, Table 2). Hatch success (on the clutch level) did not affect the hatchlings' sex, which suggests that embryo mortality is not sex-dependent and that the primary sex ratio (at laying)

is the same as HSR (Table 3, S1—see electronic supplementary material). The sex of hatchlings was not affected by any of tested factors (hatchlings number, hatching date, averaged egg volume). The sex of fledglings also was not affected by hatching date and the number of fledglings. However, the average volume of eggs had a significant influence on FSR: the greater the average egg volume, the higher the probability of more females than males fledging (Table 4, S2).

The survive probability on individual level was not affected by sex of nestling nor interaction of sex with any of other tested factors (hatching date, averaged egg volume, number of hatchlings). The only factor that influenced the survive probability was number of hatchlings: the higher the number of hatchlings in the nest, the lower the survive probability (Table 5, S3).

Analysis of the sex ratio at the population level among individuals that died and disappeared during the nestling period showed that more females than males failed to fledge (Table 2). Interestingly, the sex ratio deviated from parity only among nestlings that had disappeared from the nest (most probably killed and taken by a predator); there was no deviation among individuals found dead in the nest (death due to disease, starvation, hypothermia, drowning). Moreover, it was mainly the youngest chicks, in the first week of life, that fell victim to predators (Fig. 1a, b), whereas the number of chicks that died in the nest was independent of their age (Fig. 1c, d).

Despite a quite large sample size, analyses showed that the precise egg volume had no influence on the hatchling's sex (Table 6, S4) or on hatching success (Table 7, S5).

Discussion

This 4-year study allowed us to test for deviations of the offspring sex ratio in a large sample of Whiskered Tern broods. Contrary to our expectations, the primary (at laying, obtained indirectly), secondary (HSR) and fledging (FSR) sex ratios in this population did not differ significantly from

Table 2 Summary of sex ratio on population level

	Males	Females	Sex ratio	X^2	p value
Hatchlings	799	843	0.487	1.126	0.289
Fledglings	613	632	0.508	0.260	0.610
Dead	98	132	0.423	4.735	0.030*
Dead in nest	69	80	0.463	0.671	0.413
Disappeared	29	52	0.358	5.975	0.014*

Dead—all chicks that failed to fledge: this category included Dead in nest—death due to disease, starvation, hypothermia, drowning and disappeared—nestlings that had disappeared from the nest, most probably killed and taken by a predator. Females—number of females, males—number of males, sex ratio—proportion of males

Table 3 Model-averaged coefficients from generalized linear mixed models used to test the possible influence of factors on the sex of hatchlings ($N = 1472$)

	Coefficient	SE	Adjusted SE	z value	p value
Intercept	− 0.310	0.2554	0.2556	1.214	0.225
Volume	− 0.011	0.0348	0.0349	0.328	0.743
Success1	0.007	0.0572	0.0572	0.121	0.904
Hatchlings	0.001	0.0214	0.0215	0.049	0.961
Date	− 0.001	0.0350	0.0351	0.029	0.977

Hatchlings—number of hatchlings in the nest, date—individual hatching date, volume—averaged volume of all eggs in a clutch (above predictors were scaled prior to analysis), success—hatching success of eggs in a clutch: 1—all eggs hatched, 0—at least one egg in clutch did not hatch. Model includes the random effect of nest, colony and year. For the full set of models, see Supplementary Material Table S1

parity. Therefore, our research increases the number of studies describing a balanced sex ratio in young birds (review in Hasselquist and Kempenaers 2002; e.g. Ležalová et al. 2005; Dyrcz and Cichoń 2009; Czyż et al. 2012; Bonter et al. 2015; Bartlow et al. 2021). Papers reporting an unbalanced sex ratio are probably overrepresented in the literature, because such a result is considered more interesting and easier to publish. Moreover, publication bias towards significant results may distort our view of adaptive sex ratio manipulation (Hasselquist and Kempenaers 2002). An unbiased sex ratio may actually be more widespread among birds than the literature suggests.

In this population of Whiskered Terns, the primary and HSR did not differ either from each other or from parity. It seems that Whiskered Terns females either did not adjust the sex ratio or did so too weakly for this change to be detectable with our sample size. It is also possible that females manipulate the sex at laying in relation to factors not studied here, e.g. mate attractiveness or food availability. Manipulation of the chick sex ratio by females in this population may not offer benefits that are sufficient to outweigh the costs.

Table 4 Model-averaged coefficients from generalized linear mixed models used to test the possible influence of factors on the sex of fledglings ($N = 1102$)

|	Coefficient	SE	Adjusted SE	z value	p value
Intercept	− 0.167	0.1125	0.1126	1.480	0.139
Volume	− 0.161	0.0637	0.0638	2.518	0.012 *
Fledglings	0.07	0.0330	0.0331	0.212	0.832
Date	− 0.008	0.0437	0.0437	0.196	0.845

Fledglings—number of fledglings in the nest, date—individual hatching date, volume—averaged volume of all eggs in a clutch. All predictors were scaled prior to analysis. Model includes the random effect of nest, colony and year. For the full set of models, see Supplementary Material Table S2

Table 5 Model-averaged coefficients from generalized linear mixed models used to test the possible influence of factors on the sex of chicks' survival (N = 1317)

	Coefficient	SE	Adjusted SE	z value	p value
Intercept	2.187	0.2529	0.2532	8.639	<0.001 ***
Date	0.156	0.1703	0.1703	0.917	0.359
Hatchlings	− 0.298	0.1205	0.1206	2.469	0.013 *
SexM	0.371	0.1919	0.1921	1.930	0.054
Volume	0.190	0.1675	0.1676	1.136	0.256
Sex M × Volume	− 0.275	0.2388	0.2389	1.153	0.249
Sex M × Hatchlings	0.014	0.0777	0.0778	0.185	0.854
Sex M × Date	0.009	0.0723	0.0723	0.127	0.899

Sex—sex of individual (categorical factor), hatchlings—number of hatchlings in the nest, date—individual hatching date, volume—averaged volume of all eggs in a clutch (all above linear predictors were scaled prior to analysis). Model includes the random effect of nest, colony and year. For the full set of models, see Supplementary Material Table S3

Fig. 1 Histograms of estimated age of **a** female and **b** male chicks at the time of disappearance from the nest (most probably killed and taken by a predator) and **c** female and **d** male chicks that were found dead in the nest (death due to disease, starvation, hypothermia, drowning)
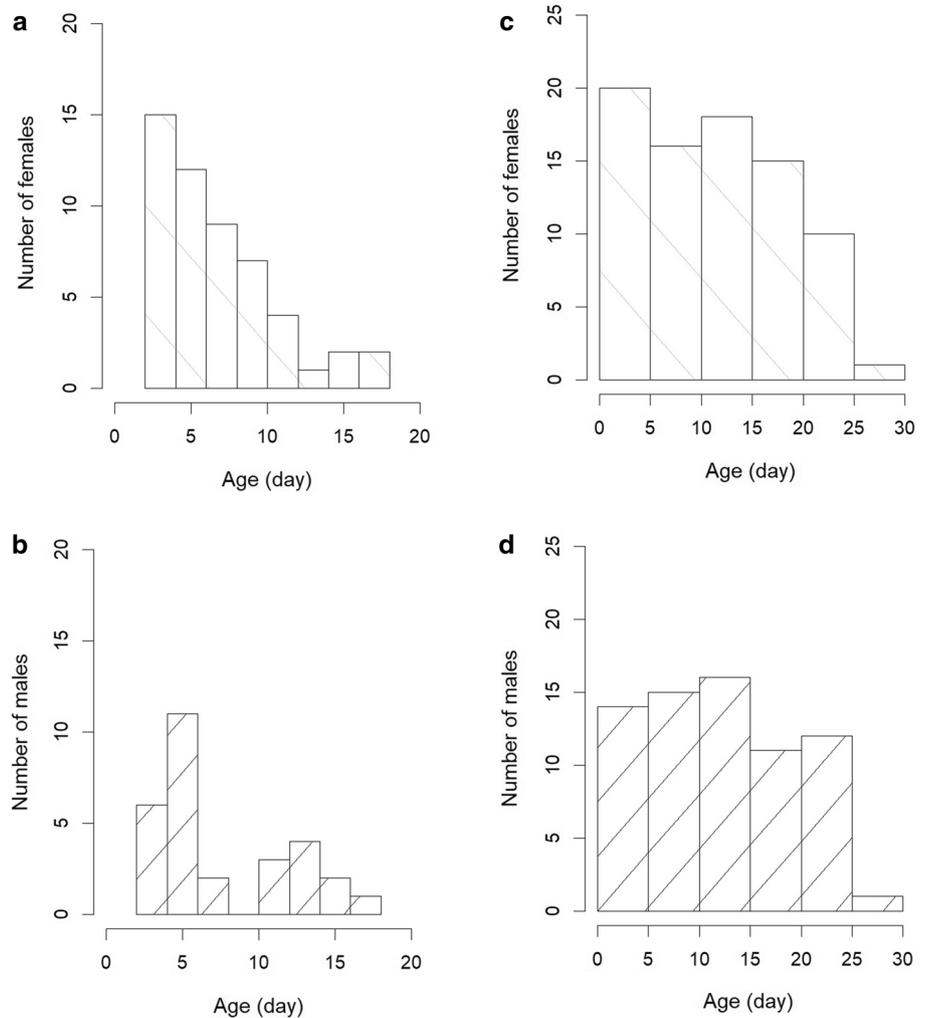
HSR can be adaptively skewed by mothers in response to ecological and environmental factors, as well as other elements like parental quality (reviews in Cockburn et al. 2002; Hasselquist and Kempenaers 2002; Alonso-Alvarez 2006). One of our main aims was to determine whether HSR of a sexually size-dimorphic species (females smaller than males) was influenced by breeding date, brood size and/or average egg volume. We found that none of these factors cause the deviation of HSR from parity. Sex manipulation according to laying date seems to be quite common (Cordero

Table 6 Model-averaged coefficients from generalized linear mixed models tested possible variation in the sex of hatchlings depending on exact egg volume and other factors ($N = 545$)

	Coefficient	SE	Adjusted SE	z value	p value
Intercept	0.669	0.7365	0.7376	0.907	0.365
Success 1	− 0.961	0.8825	0.8836	1.088	0.277
Volume	− 0.037	0.1271	0.1272	0.289	0.773
Hatchlings	− 0.060	0.2049	0.2051	0.295	0.768
Date	0.004	0.1023	0.1025	0.039	0.969

Hatchlings—number of hatchlings in the nest, date—individual hatching date, volume—exact egg volume (above predictors were scaled prior to analysis), Success—hatching success of eggs in a clutch: 1—all eggs hatched, 0—at least one egg in clutch did not hatch (categorical factor). Model includes the random effect of nest, colony and year. For the full set of models, see Supplementary Material Table S4

Table 7 Model-averaged coefficients from generalized linear mixed models tested possible variation in the hatching success depending on exact egg volume and other factors ($N = 246$)

	Coefficient	Std. Error	Adjusted SE	z value	p value
Intercept	0.622	0.1339	0.1345	4.623	< 0.001 ***
Volume	0.031	0.0866	0.0869	0.355	0.723
Eggs	0.023	0.0775	0.0777	0.297	0.766
Date	> 0.001	0.0517	0.0520	0.001	0.999

Date—hatching date of the earliest hatched chick in the clutch, volume—exact egg volume, eggs—number of eggs in the clutch. All predictors were scaled prior to analysis. Model includes the random effect of nest, colony and year. For the full set of models, see Supplementary Material Table S5

et al. 2001; Andersson et al. 2003; Husby et al. 2006; Bartlow et al. 2021). Although environmental conditions can deteriorate as the season progresses, individuals in poorer condition, and/or younger, and/or less experienced, usually begin laying eggs later. Therefore, females are expected to adjust the sex ratio towards the smaller sex (usually females) in late broods, less expensive to produce and rear, as some studies have shown (Genovart et al. 2003; Bonter et al. 2005; Wojczulanis-Jakubas et al. 2013; Minias 2016). That females may skew the sex ratio in late broods was found in Whiskered Terns breeding in central Poland (Minias 2016) but not in the closely-related Common Tern (*Sterna hirundo*) (Benito et al. 2013) or in some other Charadriiformes (Ležalová et al. 2005; Que et al. 2019). We did not assess food availability in relation to breeding season advancement in our population, but the high frequency of female desertion, also late in the breeding season, may be an indication of superabundant food on carp ponds (Ledwoń and Neubauer 2017). This allows males to increase their provisioning rates and to compensate at least partly for the desertion of their mates. In addition, male and female body condition did not appear to decrease during the breeding season (Ledwoń et al. 2023b), neither did brood size influence body mass growth in chicks (Banach et al. 2021). However, nestling growth was negatively correlated with hatching date, which may that condition or parental quality is deteriorating along with breeding season advancement. Overall, the probably good breeding conditions as regards food availability may mean that the costs of raising sons do not significantly exceed those of raising daughters, as a result of which female Whiskered Terns do not adjust the sex in their eggs towards the cheaper sex in relation to season advancement.

Some studies have shown that HSR is skewed towards the cheaper sex (usually females) in relation to clutch size (Lessells et al. 1996; Benito et al. 2013; Bukaciński et al. 2020). Furthermore, the number of the smaller sex increased with increasing egg volume, which may level the playing field in competition with their larger siblings (Anderson et al. 1997; Cordero et al. 2001), but this dependence is not always apparent (Cichoń et al. 2003). We found no connection between brood size, the egg volume averaged within the clutch or the exact egg volume and HSR. However, the latter result should be treated with some caution, as the sample was not fully random owing to the limitations in assigning chicks of known sex to an egg of known volume, while averaging egg volumes within a brood may have hidden potential differences that would only become apparent on a larger scale. Next, it is possible that the fairly constant size of the clutch (85% of hatchlings were from clutches with three eggs) did not give space to highlight the relationship between brood size and sex ratio. Nevertheless, it is difficult to unequivocally explain our results; again, we can only presume that food abundance and/or the similar costs of raising both sexes were acting towards an equal sex ratio.

FSR did not differ from parity in our population of Whiskered Terns, but one of the factors we examined—the average egg volume—did influence FSR: more females than males fledged from clutches with higher average egg volumes. Egg volume could influence individual survival (Krist 2011) by affecting hatchling weight (Arnold et al. 2006). However, our results showed no relationship between average egg volume in clutch and nestling survival. The only factor affecting chick survival was brood size. The chick was less likely to survive in nests with more siblings. Interestingly, there were no sex bias in mortality due to starvation, hypothermia or disease, indicating a shortage in parents' care abilities for their numerous offspring. Increased mortality was due to predation, with the highest percentage of disappearances observed among chicks in the first week of life. It is possible that the smaller Whiskered Tern females in bigger clutches facing the threat of a predator (such as frogs, which prey on young tern chicks: ML—unpublished data) were more

likely to loss in a life-saving competition with their bigger and probably stronger brothers and consequently fall prey to predators.

Even though we found that more females than males disappeared during the chick-rearing period, the difference in mortality between the sexes did not lead to a male-biased FSR. In species with SSD, the larger sex (males in the Whiskered Tern) is more susceptible to mortality under unfavourable conditions because of the greater energy demands or food intake during development (see the relevant references in literature in the Introduction). Males, on the other hand, being larger and probably stronger than females, can prevail in the competition for food or can more easily avoid being caught by a predator. This will lead to female-biased mortality, especially when food is scarce (literature in introduction). It seems that in this population, the above mechanisms lead to sex-biased mortality but not to a statistically significant unbalanced FSR owing to the relatively low overall chick mortality. This could be due to the abundance of food on the carp ponds (see above), but we did not study this in detail. Further studies should focus on food availability in relation to breeding season advancement.

In conclusion, our results suggest that the possible manipulation of the chick sex ratio by females in this Whiskered Tern population may not provide benefits sufficient to outweigh the costs. Hence, HSR did not exhibit any deviation from parity. Nevertheless, the egg volume did influence FSR—in broods with higher average egg volume, more females fledged than males. Despite the fact that SSD is present in Whiskered Terns already at the chick stage and that males may be more costly to raise than females, we found no differences in survival probability between the sexes and balanced FSR. As expected, in larger broods, chicks were less likely to survive (regardless of sex). Moreover, the youngest females (in first week of their live) were easier prey for predators than males. We would encourage sex ratios to be studied in different Whiskered Tern populations, especially in conditions where food is less abundant.

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