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Uwarunkowania proporcji płci w lęgach rybitwy białowąsej *Chlidonias hybrida*

Agata Banach

Rozprawa doktorska

Promotor

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Determinants of sex ratio in broods of Whiskered Tern *Chlidonias hybrida*

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Doctoral thesis

Supervisor

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Spis treści

Streszczenie

Proporcja płci stanowi istotny element historii życiowej gatunku, stąd też jest częstym tematem zainteresowania naukowców. Odchylenie od najpowszechniejszej w przyrodzie proporcji 1:1 wśród potomstwa pojawia się w sytuacji, gdy koszty wychowania syna i córki różnią się między sobą lub zysk ewolucyjny zależy od płci potomka. Na koszt wychowania potomstwa wpływa między innymi dynamika wzrostu oraz osiągana masa i wymiary ciała. Dlatego sugeruje się, że proporcja płci wśród osobników młodocianych powinna być wychylona w kierunku płci mniejszej u gatunków wykazujących dymorfizm płciowy pod względem wielkości jeszcze przed osiągnięciem samodzielności.

Obiektem badawczym w niniejszej pracy była rybitwa białowąsa *Chlidonias hybrida*. Gatunek ten charakteryzuje się największym spośród rybitw dymorfizmem płciowym pod względem wielkości (dorosłe samce w zależności od badanej cechy są od 3 do 10% większe od samic). Dodatkowo występuje u nich unikalny wśród rybitw system opieki rodzicielskiej – praktycznie wszystkie samice opuszczają lęgi jeszcze przed usamodzielnieniem się młodych, pozostawiając opiekę nad nimi samcowi. Stąd też sukces lęgowy w większej mierze zależy od jakości samca niż samicy. Badania były prowadzone w koloniach lęgowych na stawach karpiowych w Dolinie Górnej Wisły. Miały na celu analizę (1) parametrów wzrostu piskląt (w tym wykazanie, czy dymorfizm płciowy pod względem wielkości objawia się już na etapie pisklęcym) oraz czynników na nie wpływających; (2) proporcji płci na etapie klucia jaj oraz osiągnięcia przez pisklęta zdolności do lotu na poziomie populacji oraz czynników wpływających na powyższe proporcje; (3) śmiertelności piskląt w zależności od płci oraz czynników wpływających na prawdopodobieństwo przeżycia.

Uzyskane wyniki wykazały, że dymorfizm płciowy pod względem wielkości rozwija się już na etapie pisklęcym. Na etapie klucia długość całkowita głowy była większa u samców niż u samic, natomiast na etapie osiągnięcia lotności przez pisklęta już trzy z czterech mierzonych parametrów wykazywało istotne różnice pomiędzy osobnikami różnych płci. Oprócz osiąganych wymiarów, różnice międzypłciowe dotyczyły również dynamiki wzrostu – najistotniejsze dotyczyły maksymalnego tempa wzrostu masy ciała, wyższej u samców niż u samic (**Banach i in. 2021)**. Pomimo sugerowanego przez powyższe wyniki wyższego kosztu wychowania samców niż samic, nie wykazano odchyleń w proporcji płci na poziomie populacji zarówno na etapie klucia piskląt jak i osiągnięcia przez nie zdolności do lotu. Także żaden z analizowanych czynników nie miał wpływu na proporcję płci na etapie klucia. Proporcja płci na etapie uzyskania zdolności do lotu była zależna od objętości jaj – proporcja samic w lęgu była pozytywnie skorelowana ze średnią objętością jaj.

Wśród osobników, które padły ofiarą drapieżnictwa było istotnie więcej samic niż samców, natomiast udział samców i samic wśród osobników znalezionych jako martwe w gnieździe był równy. Jednak ogólna śmiertelność piskląt była na tyle mała, że prawdopodobieństwo przeżycia pisklęcia do okresu osiągnięcia zdolności do lotu nie było zależne od jego płci. Jedynym czynnikiem modyfikującym przeżywalność była wielkość lęgu – wraz ze wzrostem liczby piskląt w lęgu spadało prawdopodobieństwo przeżycia okresu pisklęcego (**Banach i in. 2024**).

Summary

Sex ratio is an important part of the life history of a species, hence it is also a frequent topic of interest of scientists. Deviation from the parity, which is the most common in nature, occurs when the cost of raising offspring depends on their sex, or when sons and daughters bring different fitness. The cost of raising offspring depends, among other things, on the dynamics of growth and the body mass and size achieved. Therefore, the sex ratio among juveniles should be skewed towards the smaller sex in species showing sexual size dimorphism (SSD) already before independence.

The studied species was the Whiskered Tern *Chlidonias hybrida*. This species is characterized by the greatest sexual size dimorphism among terns (adult males are from 3 to 10% larger than females). In addition, Whiskered Tern exhibit a parental care system unique to terns - almost all females desert before the juveniles become independent, leaving the care of the offspring to the male. Hence, breeding success depends more on the quality of the male than the female. The study was conducted in breeding colonies on carp ponds in the Upper Vistula Valley. The aim of this study was to analyse (1) growth parameters of chicks (including checking whether SSD is already present in the nestling period) and factors affecting them; (2) hatching (HSR) and fledging sex ratio (FSR) at the population level and the factors affecting the above ratios; (3) sex-specific chick mortality and the factors affecting the probability of survival.

The results showed that SSD was already developing at the chick stage. At the hatching, the total head length was greater for males than for females, while at the fledging already 3 of the 4 measured parameters showed significant sex-dependent differences. In addition to the achieved dimensions, intersex differences were also related to the growth dynamics - the most significant concerned the maximum growth rate of body mass, higher in males than in females (**Banach et al. 2021**). Despite the higher cost of rearing males than females, suggested by the above results, there was no deviation from parity in HSR and FSR at the population level. Also, none of the analysed factors affected HSR. Analysis of the effect of hatching success on the HSR also suggests that the sex ratio does not differ from the sex ratio at the egg-laying stage. FSR was dependent on the volume of eggs - the proportion of females in the brood was positively correlated with the average volume of eggs. Among individuals that died and disappeared during the nesting period, there were more females than males - such a correlation applied to chicks that fell victim to predation, and was not observed among individuals found dead in the nest. However, overall chick mortality was so low that the sex of the individual did not significantly affect the probability of chick survival.

The only factor modifying survival was the size of the brood - as the number of chicks in a brood increased, the probability of survival to flight decreased (**Banach et al. 2024**).

Publikacje wchodzące w skład rozprawy doktorskiej

Banach A, Neubauer G, Flis A, Ledwoń M (2021) Sex-specific growth of nestlings of the Whiskered Tern *Chlidonias hybrida*, a species with sexual size dimorphism and female brood desertion. J Ornithol 162:1035–1047. https://doi.org/10.1007/s10336-021-01911-y

Journal of Ornithology, IF (1,3), 5-letni Impact Factor (1,5), MEiN: 140
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Banach A, Flis A, Kusal B, Łożyńska H, Ledwoń M (2024) Sex ratio and sex-specific chick mortality in a species with moderate sexual size dimorphism and female brood desertion. J Ornithol, https://doi.org/10.1007/s10336-024-02182-z

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1. Wstęp

Proporcja płci (stosunek liczby samców do liczby samic), zarówno w populacji jak i w obrębie potomstwa danego osobnika, jest istotnym elementem historii życiowej (West 2009; Guillon 2016; Booksmythe i in. 2017). W przyrodzie najczęściej liczba samców nie różni się istotnie od liczby samic. W sytuacji, w której zarówno wychowanie córki, jak i syna wymaga takich samych nakładów energii oraz wiąże się z porównywalnymi zyskami ewolucyjnymi (liczba potomków w kolejnych pokoleniach), rodzice powinni w równym stopniu inwestować w potomstwo, niezależnie od jego płci (Fisher 1930). W konsekwencji proporcja płci w obrębie potomstwa danego osobnika jest losowa, i w skali populacji dąży do proporcji 1:1. Jeśli jednak koszty wychowania bądź zysk z posiadania syna lub córki nie są równe, rodzice powinni przekierować inwestycję w płeć generującą mniejsze koszty lub dającą większe zyski – w zależności od własnej kondycji oraz warunków środowiskowych (Trivers i Willard 1973).

Sugeruje się, że samice ptaków są zdolne do kontroli proporcji płci w lęgu (Sheldon i in. 1999; Pike i Petrie 2003; Rutkowska i Badyaev 2008; Gam i in. 2011; Tagirov i Rutkowska 2013). Umożliwia to heterogametyczność samic oraz fakt, że w czasie mejozy następującej przed owulacją i zapłodnieniem może dochodzić do segregacji chromosomów płci (Rutkowska i Badyaev 2008). W związku z powyższym, samice potencjalnie są w stanie regulować proporcję płci potomstwa tak, by zapewnić sobie jak największy zysk ewolucyjny.

Na poziomie populacji nierówna proporcja płci bywa związana z występowaniem dymorfizmu płciowego pod względem wielkości, zwykle z większą produkcją osobników płci mniejszej (Teather i Weatherhead 1988; Kalmbach i in. 2001; Benito i González-Solís 2007). Wynika to z tego, że większe osobniki (najczęściej samce) zazwyczaj osiągają większe rozmiary ciała niż samice jeszcze w okresie pisklęcym jako efekt wyższego tempa wzrostu (Velando 2002; Müller i in. 2007; Bogdanova i Nager 2008; Kalmbach i in. 2009; Bosman i in. 2016; Požgayová i in. 2018) bądź dłuższej fazy szybkiego wzrostu związanej z wyższym poziomem metabolizmu (Velando i in. 2000), co oznacza dla rodziców wyższy koszt spowodowany koniecznością dostarczenia większej ilości pokarmu (Slagsvold i in. 1986; Teather i Weatherhead 1988; Stamps 1990; Magrath i in. 2007; lecz patrz Torres i Drummond 1999). Różnica w wielkości pomiędzy osobnikami odmiennej płci może skutkować śmiertelnością związaną z płcią, a w konsekwencji w zmianach proporcji płci w czasie. Z jednej strony osobniki płci większej, ze względu na wyższe tempo wzrostu, bywają bardziej wrażliwe na niedobór pokarmu (Teather i Weatherhead 1989; Griffiths 1992), co skutkuje ich zwiększoną śmiertelnością i przesunięciem proporcji płci w stronę płci mniejszej (Teather i Weatherhead 1988; Kalmbach i in. 2001; Benito i González-Solís 2007). Z drugiej strony, w sytuacji, gdy dostęp do pokarmu zależny jest od wielkości i związanej z nią siły osobnika – to przedstawiciele płci mniejszej (najczęściej samice) przegrywają konkurencję o pokarm z większym rodzeństwem i wykazują zwiększoną śmiertelność (Bortolotti 1986; Edwards i Collopy 1983; Anderson i in. 1993; lecz patrz Drummond i in. 1991). Także w obliczu niedoboru pokarmu, gdy istotne są rezerwy osobnicze, obserwuje się większą przeżywalność osobników płci większej (Kernsten i Brenninkmeijer 1995; Eberhart-Phillips i in. 2017).

Wspomniana powyżej nierówna śmiertelność w zależności od płci osobnika w trakcie rozwoju i wynikające z niej zmiany proporcji płci w obrębie lęgu w czasie powodują, że konieczne jest badanie proporcji płci na różnych etapach życia osobnika. W przypadku osobników młodocianych zazwyczaj wyróżnia się trzy kategorie proporcji płci: pierwotna (w czasie składania jaj, ściśle związana z segregacją chromosomów podczas mejozy), na etapie klucia oraz na etapie uzyskania zdolności do lotu (proporcja płci wśród podlotów). Zmiany w proporcji płci pomiędzy etapem składania jaj a klucia powoduje zróżnicowana wrażliwość embrionów w zależności od płci na zanieczyszczenia środowiskowe (Fry i Toone 1981; Erikstad i in. 2009) czy stężenie hormonów płciowych w jajach (Krackow 1999; Pérez i in. 2006). Zróżnicowana śmiertelność wśród piskląt o odmiennej płci wynika głównie z rozważanych powyżej zależności związanych z dymorfizmem płciowym pod względem wielkości.

Co istotne, różnica w wielkości piskląt w zależności od płci i idąca za nią przewaga osobników płci większej również może ujawniać się na różnych etapach rozwoju. W niektórych przypadkach jest obserwowana już u świeżo wyklutych piskląt, jako wynik różnego tempa wzrostu embrionów w zależności od płci (Cordero i in. 2000), co może być związane ze zróżnicowaną depozycją hormonów i składników pokarmowych w jajach (Petrie i in. 2001). Częściej jednak ujawnia się dopiero na etapie pisklęcym (Jordi i Arizaga 2016; Loonstra i in. 2018) czy nawet później (Magrath i in. 2007). Stąd też badania nad czynnikami wpływającymi na proporcję płci w tym okresie u ptaków wykazujących dymorfizm płciowy pod względem wielkości powinny być poprzedzone badaniami sprawdzającymi, czy różnice te objawiają się jeszcze przed osiągnięciem lotności piskląt.

Większość gatunków rybitw (ptaków należących do rzędu siewkowych Charadriiformes) wykazuje dymorfizm płciowy pod względem wielkości – samce są zazwyczaj większe od samic (Ledwoń 2011; Lisnizer i in. 2014), choć zwykle różnice te nie są duże. Największe różnice w wielkości pomiędzy dorosłymi osobnikami w tej grupie ptaków wykazuje rybitwa białowąsa (*Chlidonias hybrida*) – samce osiągają wymiary od 3 do 10% większe od samic, w zależności od mierzonej cechy (Ledwoń 2011). Odzwierciedla się to w zajmowanych przez płcie odmiennych niszach pokarmowych: samce, jako cięższe i bardziej predysponowane tym do nurkowania za ofiarą, specjalizują się w polowaniu na ryby, żaby czy kijanki, natomiast samice chwytają mniejsze kręgowce oraz ważki czy inne owady (Betleja 2003; Ledwoń 2010; Gwiazda i Ledwoń 2015, 2016; Gwiazda i in. 2017; Ledwoń i Neubauer 2017). Skutkuje to sporą dysproporcją w kaloryczności pokarmu dostarczanego pisklętom (samce dostarczają potomstwu ok. 25% więcej kalorii niż samice). Dodatkowo, gatunek ten wykazuje unikalny wśród rybitw system opieki rodzicielskiej – niemal wszystkie samice opuszczają lęgi i partnera przed usamodzielnieniem się młodych, w tym aż 52% jeszcze przed osiągnięciem zdolności do lotu przez pisklęta (Ledwoń i Neubauer 2017).

Takie odwrócenie ról płciowych przy wychowaniu młodych może wynikać z liczebnościowej przewagi samców w populacji (Kosztolányi i in. 2011), umożliwiającej samicom ponowne przystąpienie do lęgu z kolejnym samcem. Zjawisko to jest obserwowane u innego gatunku z rzędu siewkowych, sieweczki morskiej *Anarhynchus alexandrinus* (Amat i in. 1999; Székely i in. 2004; Eberhart-Phillips i in. 2017, 2018). Co istotne, nierówna proporcja płci u tego gatunku występuje już na etapie wylotu z gniazda, czyniąc ją dobrym prognostykiem proporcji płci wśród dorosłych osobników (Székely i in. 2004; Eberhart-Phillips i in. 2017). Proporcja płci wśród dorosłych rybitw białowąsych nie jest znana, jednak na chwilę obecną nie ma przesłanek wskazujących na znaczne odchylenie proporcji w którąkolwiek stronę: obserwacje wykazały, że samice po dezercji rzadko przystępują do ponownego lęgu (Ledwoń i in. 2023), a nietypowo duże lęgi, tworzone przez pary samiczo-samicze wynikające z niedoboru samców, również są spotykane sporadycznie (Betleja i in. 2007). Niemniej, rozpoznanie nierówności w proporcji płci wśród młodych osobników mogłoby wskazywać na nierówną proporcję płci w populacji dorosłych (Szczys i in. 2001; Kosztolányi i in. 2011; Székely i in. 2014a, b; Nisbet i in. 2016).

2. Cele i hipotezy badawcze

Celem niniejszej rozprawy jest rozpoznanie czynników mogących wpływać na: proporcję płci w lęgach rybitwy białowąsej na etapie klucia piskląt oraz osiągnięcia przez nie zdolności do lotu, śmiertelność oraz wielkość piskląt w zależności od płci. Spodziewano się, że dymorfizm płciowy pod względem wielkości rozwija się już w okresie pisklęcym. W związku z tym przewidywano również pojawienie się zależnej od płci wrażliwości na niekorzystne warunki środowiskowe skutkującej nierówną śmiertelnością piskląt w zależności od płci. Wynikający z rozwoju dymorfizmu płciowego pod względem wielkości różny koszt wychowania potomstwa powinien skłaniać samice do modyfikacji proporcji płci na etapie składania jaj w zależności od doświadczanych warunków środowiskowych.

Realizację powyższych celów podzielono na poniższe zadania badawcze:

1. Analiza parametrów wzrostu piskląt w zależności od płci osobnika oraz dodatkowych czynników środowiskowych i matczynych mogących na nie wpływać (**Banach i in. 2021**).
2. Analiza proporcji płci na etapie klucia oraz osiągnięcia zdolności do lotu na poziomie populacji oraz czynników środowiskowych i matczynych mogących na nie wpływać (**Banach i in. 2024**).
3. Analiza śmiertelności piskląt w zależności od płci z uwzględnieniem przyczyny śmierci oraz czynników środowiskowych i matczynych wpływających na prawdopodobieństwo przeżycia do momentu osiągnięcia lotności (**Banach i in. 2024**).

Przystępując do badań postawiono następujące hipotezy badawcze:

1. Dymorfizm płciowy pod względem wielkości rozwija się już w okresie pisklęcym (**Banach i in. 2021**).
2. W związku z różnicami w parametrach wzrostu pomiędzy osobnikami różnej płci występuje zależna od płci wrażliwość na niekorzystne warunki środowiskowe skutkująca nierówną śmiertelnością piskląt różnej płci (**Banach i in. 2024**).
3. Wynikający z rozwoju dymorfizmu płciowego pod względem wielkości różny koszt wychowania potomstwa skłania samice do modyfikacji proporcji płci w zależności od doświadczanych warunków środowiskowych (**Banach i in. 2024**).
4. Wraz z postępem sezonu, zwiększeniem wielkości lęgu oraz zmniejszeniem objętości jaj dochodzi do pogorszenia parametrów wzrostu: obniżenia maksymalnego tempa wzrostu oraz osiąganej asymptoty, opóźnienia i wydłużenia fazy szybkiego wzrostu poszczególnych parametrów biometrycznych. Efekt ten powinien dotyczyć w szczególności masy ciała (**Banach i in. 2021**).
5. Wraz z postępem sezonu oraz zwiększeniem wielkości lęgu proporcja płci, zarówno na etapie klucia jak i osiągnięcia zdolności do lotu, jest przechylona w stronę płci mniej kosztownej – czyli samic (**Banach i in. 2024**).
6. Prawdopodobieństwo przeżycia piskląt spada wraz z postępem sezonu, zmniejszeniem objętości jaj oraz ze zwiększeniem wielkości lęgu. Śmiertelność jest zależna od płci – większa wśród samic niż samców (**Banach i in. 2024**).

3. Materiały i metody

3.1. Procedury terenowe

Badania terenowe były prowadzone w ciągu czterech sezonów lęgowych, w latach 2016-2019, w dziewięciu koloniach lęgowych rybitwy białowąsej, na pięciu kompleksach stawów karpiowych, w Dolinie Górnej Wisły, w Małopolsce (50°00′ N 19°30′ E). Prace terenowe obejmowały cały okres lęgowy rybitw, od połowy maja do początku września. Około połowy okresu inkubacji gniazda były ogradzane plastikową siatką, by uniemożliwić pisklętom opuszczanie gniazd przed osiągnięciem zdolności do lotu (rybitwy są półzagniazdownikami). Jaja były mierzone suwmiarką celem wyliczenia ich objętości. Dodatkowo, od 2017 roku, jaja były znakowane wodoodpornym flamastrem – celem skorelowania wymiarów jaj z płcią wyklutych z nich piskląt oraz sukcesem klucia jaja. Możliwe to było jedynie w niektórych przypadkach: gdy pisklęta kluły się asynchronicznie oraz gdy wszystkie pisklęta w gnieździe były tej samej płci (**Banach i in. 2024**). Wszystkie pisklęta zaraz po wykluciu były znakowane indywidualnie numerowanymi stalowymi obrączkami ornitologicznymi oraz pobierano im niewielką próbkę krwi do analiz molekularnych. Dokładna data klucia osobnika była określana na podstawie obecności mokrych piór na świeżo wyklutym pisklęciu bądź oznak klucia na jaju podczas poprzedniej kontroli oraz długości skrzydła i masy ciała osobnika (Paillisson i in. 2008; **Banach i in. 2021**). W gniazdach wyznaczonych do monitoringu parametrów wzrostu (w czterech koloniach w latach 2016-2017) pisklęta w czasie kontroli miały mierzone cztery cechy biometryczne: długość całkowitą głowy (DCG), długość skoku, długość skrzydła oraz masę ciała. Pisklęta były mierzone dwa do trzech razy w tygodniu, co dawało zwykle po pięć lub sześć pomiarów każdej cechy na pisklę (**Banach i in. 2021**). Pisklęta osiągały zdolność do lotu ok. 20-23 dnia życia. Zniknięcie osobnika z gniazda przed tym okresem uznawano za wynik drapieżnictwa („upolowane”). Inne przyczyny śmiertelności (choroby, wygłodzenie, wychłodzenie lub utonięcie) klasyfikowano jako „martwy w gnieździe”. Wiek piskląt w momencie śmierci wyznaczano na środkowy dzień pomiędzy ostatnim stwierdzeniem żywego pisklęcia a dniem stwierdzenia zniknięcia bądź znalezienia martwego osobnika w gnieździe.

3.2. Molekularna analiza płci

Płeć piskląt określano na podstawie genu CHD zlokalizowanego na chromosomach płci (Dubiec i Zagalska-Neubauer 2006; Goławski i in. 2016). Wyizolowane DNA amplifikowano w reakcji PCR z użyciem dwóch zestawów starterów: F2550 i R2718 oraz P2, P8 i P0. Produkty reakcji rozdzielano elektroforetycznie na żelu agarozowym. Obecność jednego prążka oznaczała samca, dwóch – samicę. Każda próbka była testowana przynajmniej dwa razy. Nie udało się określić płci 52 z 1694 obserwowanych osobników – ze względu na brak lub słabą jakość próbki krwi (**Banach i in. 2021**, **Banach i in. 2024)**.

3.3. Analizy statystyczne

Parametry wzrostu danego osobnika wyliczane były poprzez dopasowanie co najmniej czterech pomiarów danej cechy biometrycznej, mierzonej od wyklucia pisklęcia do osiągnięcia zdolności do lotu, do funkcji logistycznej o wzorze $y = A/(1 + B \times \exp^{(-k \times t)})$, gdzie y to pomiar długości całkowitej głowy, skoku lub skrzydła bądź masy ciała w t-dniu życia, A – asymptota (spodziewany wymiar ostateczny danej cechy), B – punkt przegięcia, k – stała wzrostu (wskazująca na długość fazy szybkiego wzrostu). Dodatkowo wyliczano maksymalne tempo wzrostu ze wzoru $g_{max} = k \times A/4$ (Richner 1989, 1991). Parametry wzrostu wyliczono dla 270 osobników (**Banach i in. 2021**).

Porównanie wielkości samców i samic w pierwszym dniu życia, w 21 dniu życia (tuż przed wylotem z gniazda), wartości asymptoty (wyliczonej z funkcji logistycznej, dla każdego z analizowanych piskląt), a także wśród osobników dorosłych (pomiary do porównania wzięte z Ledwoń 2011) dla każdej mierzonej cechy biometrycznej, wykonano przy pomocy testu t. Wartość dymorfizmu płciowego pod względem wielkości była liczona jako proporcja wielkości samców i samic, wyrażona jako procent różnicy w wielkości (**Banach i in. 2021**).

Proporcja płci na etapie klucia (N=1642) oraz wylotu z gniazda (N=1245) oraz wśród piskląt, które nie dożyły do wylotu (N=230, także z podziałem na „martwe w gnieździe” oraz „upolowane”) była wyliczana z użyciem testu Chi^2 (**Banach i in. 2024**).

Wpływ czynników środowiskowych oraz matczynych na parametry wzrostu, proporcję płci na etapie klucia oraz wylotu z gniazda, przeżywalność oraz sukces klucia testowano z użyciem modeli liniowych z efektami mieszanymi. Następnie przeprowadzano selekcję modeli z użyciem kryterium informacyjnego Akaikego (AIC). Do dalszych analiz brano uśrednione wyniki z modeli z $\Delta AIC<2$ (Zuur i in. 2009, **Banach i in. 2021**, **Banach i in. 2024**).

Model globalny dla analizy wpływu płci i innych czynników na parametry wzrostu przyjmował postać: Y = PŁEĆ x ŚREDNIA OBJĘTOŚĆ JAJ + PŁEĆ x DATA KLUCIA + PŁEĆ x WIELKOŚĆ LĘGU + PŁEĆ x PROPORCJA PŁCI W LĘGU + *KOLONIA(GNIAZDO).* Zmienna zależna Y to wartość parametru wzrostu danego osobnika (analizowano cztery parametry dla czterech cech biometrycznych – w sumie 16 analiz). Wielkość prób badawczych w poszczególnych analizach nieco się różniła, najmniejsza dla DCG, mierzonego tylko w 2016 roku: N=147, dla masy ciała, długości skoku i skrzydła wynosiła odpowiednio: 260, 262 i 270 (**Banach i in. 2021**).

Model globalny dla analizy proporcji płci na etapie klucia miał postać: PŁEĆ = LICZBA PISKLĄT + DATA KLUCIA + ŚREDNIA OBJĘTOŚĆ JAJ + SUKCES KLUCIA + *ROK(KOLONIA(GNIAZDO)).* SUKCES KLUCIA był czynnikiem kategorycznym, przyjmującym wartość "1" – gdy z wszystkich jaj w lęgu wykluły się pisklęta bądź "0" – przynajmniej z jednego jaja w lęgu nie wykluło się pisklę. Czynnik ten testował różnicę w proporcji płci pomiędzy lęgami z pełnym sukcesem klucia a tymi bez pełnego sukcesu – jeśli jego wpływ okazałby się istotny, oznaczałoby to występowanie różnicy pomiędzy proporcją płci na etapie składania jaj oraz klucia, co wskazywałoby na śmiertelność embrionów zależną od płci. Wielkość próby wynosiła 1472 (**Banach i in. 2024**).

Model globalny dla analizy wpływu poszczególnych czynników na PŁEĆ PODLOTA miał podobną postać: PŁEĆ PODLOTA = LICZBA PODLOTÓW + DATA KLUCIA + ŚREDNIA OBJĘTOŚĆ JAJ + *ROK(KOLONIA(GNIAZDO)),* z tą różnicą, że uwzględniano liczbę piskląt żywych do momentu wylotu z gniazda oraz nie analizowano SUKCESU KLUCIA (N=1102, **Banach i in. 2024**).

Analiza PRZEŻYWALNOŚCI w okresie pisklęcym zawierała interakcję poszczególnych czynników liniowych z PŁCIĄ – miało to na celu sprawdzenie, czy wpływ analizowanych czynników zależy od płci pisklęcia. Model globalny miał postać: PRZEŻYWALNOŚĆ = DATA KLUCIA x PŁEĆ + ŚREDNIA OBJĘTOŚĆ JAJ x PŁEĆ + LICZBA PISKLĄT x PŁEĆ + *ROK(KOLONIA(GNIAZDO)).* PRZEŻYWALNOŚĆ przyjmowała wartość "1" dla pisklęcia, które przeżyło do momentu osiągnięcia lotności bądź "0" dla osobnika, który został znaleziony martwy bądź zniknął przed czasem wylotu z gniazda (N=1317, **Banach i in. 2024**).

Dzięki numerowaniu jaj możliwe było przeprowadzenie analizy wpływu objętości danego jaja oraz innych czynników na PŁEĆ pisklęcia. Model globalny był niemal identyczny jak przy poprzedniej analizie proporcji płci na etapie klucia, jedynie z uwzględnieniem DOKŁADNEJ zamiast ŚREDNIEJ OBJĘTOŚCI JAJ: PŁEĆ = LICZBA PISKLĄT + DATA KLUCIA + DOKŁADNA OBJĘTOŚĆ JAJA + SUKCES KLUCIA + *ROK(KOLONIA(GNIAZDO))* (N=545, **Banach i in. 2024**).

Ostatnia analiza sprawdzała wpływ DOKŁADNEJ OBJĘTOŚCI JAJA oraz LICZBY JAJ w lęgu i DATY KLUCIA najstarszego w LĘGU pisklęcia na SUKCES KLUCIA JAJA. Model globalny przyjmował postać: SUKCES KLUCIA = DOKŁADNA OBJĘTOŚĆ JAJA + LICZBA JAJ + DATA KLUCIA LĘGU + *ROK(KOLONIA(GNIAZDO))* (N=246, **Banach i in. 2024**).

Wszystkie analizy statystyczne były przeprowadzone w R 3.6.1, 3.6.3 lub 4.1.1 (R Core Team 2019, 2020, 2021). Uwzględniono poziom istotności testów statystycznych 0,05. W żadnej z analiz nie pojawił się problem współliniowości czynników wyjaśniających – współczynnik korelacji w żadnym przypadku nie przekraczał 0,3 (**Banach i in. 2021**; **Banach i in. 2024**).

4. Wyniki

Dymorfizm pod względem wielkości ujawniał się już na etapie pisklęcym (**Banach i in. 2021).** Tuż po wykluciu samce miały istotnie większą od samic długość całkowitą głowy (DCG). Wskutek wyższego maksymalnego tempa wzrostu masy ciała, samce tuż przed osiągnięciem zdolności do lotu osiągały masę ciała średnio aż o 13% wyższą niż samice – był to najwyższy z obserwowanych poziom dymorfizmu płciowego w parametrach biometrycznych mierzonych na różnych etapach rozwoju. Na etapie wylotu piskląt z gniazda także długość skoku oraz DCG była istotnie wyższa u samców niż u samic, przy czym długość skoku osiągała maksymalne wymiary już w okresie pisklęcym, natomiast DCG rosła także po osiągnięciu zdolności do lotu. Różnica w długości skrzydła między osobnikami różnej płci pojawiała się dopiero po wylocie z gniazda (**Banach i in. 2021**).

Proporcja płci na etapie klucia na poziomie populacji nie wykazywała odchyleń od stosunku 1:1. Pośród piskląt, które nie dożyły wylotu z gniazda, więcej było samic niż samców. Co ciekawe, różnica dotyczyła jedynie piskląt, które zniknęły z gniazda (padły ofiarą drapieżnictwa), pośród piskląt martwych w gnieździe (głównie w wyniku głodu, chorób) nie wykazano takiej zależności. Pomimo większej śmiertelności wśród samic niż samców, proporcja płci na etapie uzyskania lotności również nie odbiegała od równości (**Banach i in. 2024**).

Sukces klucia jaj w lęgu nie wpływał istotnie na płeć piskląt, co sugeruje brak różnic pomiędzy proporcją płci na etapie składania jaj oraz klucia (**Banach i in. 2024**).

Wielkość lęgu negatywnie wpływała na parametry wzrostu piskląt (**Banach i in. 2021)**. Ponadto w większych lęgach była niższa przeżywalność piskląt. Śmiertelność ta jednak nie była związana z płcią, stąd brak wpływu wielkości lęgu na proporcję płci podlotów, nie miała ona także wpływu na proporcję płci na etapie klucia. Również liczba jaj w zniesieniu nie wpływała na sukces klucia jaj (**Banach i in. 2024**).

Data klucia miała negatywny wpływ na parametry wzrostu długości całkowitej głowy i skoku (**Banach i in. 2021**). Data klucia nie miała jednak żadnego wpływu na proporcję płci (zarówno na etapie klucia jak i osiągnięcia zdolności do lotu) ani na przeżywalność piskląt.

Nie wykazano żadnego związku między średnią objętością jaj a żadnym z parametrów wzrostu piskląt (**Banach i in. 2021**). Czynnik ten nie miał też wpływu na proporcję płci na etapie klucia ani na przeżywalność piskląt. Jednak wraz ze wzrostem średniej objętości jaj zwiększała się proporcja samic osiągających zdolność do lotu (**Banach i in. 2024**). Analizy z uwzględnieniem dokładnej objętości jaj nie wykazały wpływu tego czynnika ani na płeć pisklęcia ani na sukces klucia jaja (**Banach i in. 2024**).

5. Dyskusja

Niniejsze badania wykazały, że pisklęta rybitwy białowąsej, wskutek zależnych od płci różnic w parametrach wzrostu, rozwijają dymorfizm płciowy pod względem wielkości jeszcze przed osiągnięciem zdolności do lotu (**Banach i in. 2021**). Na etapie klucia dymorfizm płciowy obserwowany był jedynie w długości całkowitej głowy, natomiast na etapie wylotu z gniazda już trzy z czterech mierzonych cech biometrycznych były większe u samców w porównaniu do samic. Na tym etapie jedynie długość skrzydła nie wykazywała różnic międzypłciowych - to z kolei czyni ją pomocną przy wyznaczaniu wieku piskląt niezależnie od płci przez cały okres pisklęcy (Paillisson i in. 2008; **Banach i in. 2021**).

Największy dymorfizm płciowy pod względem wielkości był obserwowany w przypadku masy ciała piskląt na etapie wylotu z gniazda, przy czym różnica ta malała po osiągnięciu zdolności do lotu (**Banach i in. 2021**). Większa masa ciała samców wśród podlotów obserwowana była także u innych gatunków rybitw, i to niezależnie od kierunku dymorfizmu płciowego pod względem wielkości wśród osobników dorosłych. U rybitwy krótkodziobej *Gelochelidon nilotica*, u której dorosłe samce mają masę ciała ok. 4% wyższą od samic, jako pisklęta wykazują wyższe tempo wzrostu i osiągają wyższą masę ciała niż samice (Villegas i in. 2013). Także u rybitwy rzecznej (*Sterna hirundo*) samce w czasie wylotu z gniazda osiągały masę ciała o ok. 5% większą niż samice (Becker i Wink 2003), chociaż wśród osobników dorosłych różnice w masie są nieistotne bądź to samice są nieco cięższe od samców (Fletcher i Hamer 2003; Becker i Ludwigs 2004; Nisbet i in. 2007). Wskazuje to na lepszą kondycję i zgromadzenie większych rezerw w postaci tłuszczu bądź mięśni przez samce niż samice rybitw rzecznych, prawdopodobnie jako wynik skuteczniejszego zdobywania pokarmu od rodziców bądź nawet preferencji rodziców w karmieniu synów przed córkami (Becker i Wink 2003). Skutkuje to koniecznością nadrobienia wzrostu masy ciała przez samice dopiero w okresie po wylocie z gniazda. Podobnie jest u rybitwy białowąsej – chociaż dymorfizm płciowy pod względem masy ciała występuje zarówno u podlotów jak i u dorosłych osobników, to młode samce osiągają masę ciała równą masie dorosłych samców już na etapie wylotu z gniazda, natomiast masa samic na tym etapie stanowi jedynie ok. 94% docelowej masy ciała (**Banach i in. 2021**).

Pojawienie się dymorfizmu płciowego pod względem wielkości już na etapie pisklęcia, a także wyższe tempo wzrostu – zwłaszcza masy ciała osobników jednej płci, jest powszechnie wiązane ze zróżnicowanym kosztem wychowania potomstwa w zależności od jego płci (Klaassen i in. 1992; Vedder i in. 2005; Magrath i in. 2007; lecz patrz Müller i in. 2007). Samce rybitwy białowąsej wykazywały wyższe tempo wzrostu oraz osiągały większą masę ciała jeszcze przed uzyskaniem zdolności do lotu. Także wymiary liniowe związane ze wzrostem kośćca (skok oraz DCG) były większe u samców niż u samic (**Banach i in. 2021**). Wskazuje to na potencjalnie wyższe koszty wychowania synów niż córek, związane z koniecznością dostarczenia większej ilości pokarmu.

W związku z wynikającymi z powyższych wyników potencjalnymi różnicami w nakładach na wychowanie potomków różnej płci, można było się spodziewać wyższej śmiertelności samców i przesunięcia proporcji płci w kierunku samic (Gonzáles-Solis i in. 2005; Müller i in. 2005). W badanej populacji nie wykryto jednak odchylenia od normy w proporcji płci zarówno na etapie klucia, jak i wylotu z gniazda. Także żaden z badanych czynników nie wpływał na proporcję płci na etapie klucia, jednak odsetek samic na tym etapie był pozytywnie skorelowany ze średnią objętością jaj w lęgu. Ponadto wyniki analiz pokazały, że proporcja płci na etapie składania jaj nie różniła się od tej na etapie klucia, co wskazuje na śmiertelność embrionów niezależną od płci (**Banach i in. 2024**). Można zatem wnioskować, że w tej populacji samice nie dostosowują proporcji płci zarodków ani depozycji w jajach składników mogących modyfikować przeżywalność embrionów w zależności od płci, bądź robią to w odpowiedzi na czynniki nie uwzględnione w niniejszych badaniach.

Analiza czynników mogących wpływać na przeżywalność piskląt wykazała istotny wpływ wielkości lęgu – wraz ze wzrostem liczby wyklutych piskląt spadało prawdopodobieństwo przeżycia do wylotu. Co więcej, chociaż nie wykryto związku przeżywalności z płcią pisklęcia, to wśród piskląt, które nie dożyły wylotu z gniazda, był większy odsetek samic niż samców. Powyższa, pozorna niezgodność wynika zapewne ze stosunkowo niewielkiej śmiertelności piskląt, stąd ogólny wpływ płci na przeżywalność jest niewielki (**Banach i in. 2024**). Analiza przyczyny śmiertelności ujawniła, że wśród piskląt, które padły w gnieździe (głównie w wyniku głodu, wychłodzenia czy chorób) nie było odchyleń w proporcji płci. Taka zależność mogłaby wskazywać na nierówną opiekę rodzicielską lub zależną od płci wrażliwość na niesprzyjające warunki. Natomiast pośród piskląt, które zniknęły z gniazda, zdecydowanie przeważały samice. Co ciekawe, zniknięcia miały miejsce głównie w pierwszym tygodniu życia piskląt, natomiast śmiertelność w gnieździe była równo rozłożona na cały okres pisklęcy. Wskazuje to na większą podatność samic na drapieżnictwo, zwłaszcza w większych lęgach (**Banach i in. 2024**). Możliwe, że w obliczu zagrożenia ze strony drapieżnika, takiego jak żaby, nawet niewielka przewaga w wielkości (a zapewne i sile) samców nad samicami powoduje, że to samice częściej padają ofiarą tego drapieżnika.

Wielkość lęgu wpływała negatywnie także na parametry wzrostu długości skrzydła, DCG oraz skoku. Co ciekawe, nie wykryto związku pomiędzy wielkością lęgu a wzrostem masy ciała (**Banach i in. 2021**), choć taki efekt jest powszechnie spotykany (Horak 2003; Müller i in. 2005; Bogdanova i Nager 2008; Gilliland i in. 2016). Może to wynikać z ogólnie dużego poziomu zmienności w parametrach wzrostu masy ciała (**Rycina 1.d, Banach i in. 2021**), co sprawiło, że ewentualne różnice nie były do wychwycenia przy niniejszej wielkości próby badawczej. Niewykluczone również, że zwiększona śmiertelność w większych lęgach doprowadziła do dopasowania liczby piskląt do optymalnej wielkości lęgu (Vedder i in. 2017, 2019). Jako że największa śmiertelność obserwowana jest w pierwszym tygodniu życia piskląt (**Banach i in. 2024**), kluczowym dla wzrostu skoku, nie dziwi wpływ początkowej wielkości lęgu na ten wymiar ciała. Chociaż wielkość lęgu bywa pozytywnie skorelowana z proporcją mniejszej płci wśród wyklutych piskląt (Lessells i in. 1996; Benito i in. 2013; Bukaciński i in. 2020), w przypadku rybitwy białowąsej nie wykryto takiego związku – być może wskutek dość stałej wielkości lęgu: aż 73% piskląt pochodziło z lęgów z trzema wyklutymi pisklętami. Raportowany powyżej wpływ wielkości lęgu na śmiertelność piskląt nie był zależny od płci, stąd też nie dziwi brak wpływu tego czynnika na proporcję płci na etapie uzyskania zdolności do lotu (**Banach i in. 2024**).

Powszechnie uznaje się, że wraz z postępem sezonu następuje pogorszenie warunków środowiskowych. Co więcej, osobniki w słabszej kondycji lub z mniejszym doświadczeniem zwykle przystępują do lęgów później (Ludwigs i Becker 2002; Dittmann i Becker 2003). W związku z tym wzrost piskląt (Bogdanova i Nager 2008; Loonstra i in. 2018), a także odsetek osobników płci o większych rozmiarach ciała w lęgu (Genovart i in. 2003; Wojczulanis-Jakubas i in. 2013; Minias 2016) bywa negatywnie skorelowany z datą klucia. Faktycznie, niniejsze badania również wykazały negatywny wpływ daty klucia na parametry wzrostu długości skoku i całkowitej długości głowy (**Banach i in. 2021**). Jednak wbrew przewidywaniom, nie wykryto związku pomiędzy proporcją płci a datą klucia zarówno na etapie klucia, jak i wylotu z gniazda (**Banach i in. 2024**). Jest to o tyle zaskakujące, że wcześniejsze badania nad rybitwą białowąsą wykazały taką zależność (Minias 2016). Trzeba jednak wziąć poprawkę na różnice w warunkach środowiskowych, w jakich były przeprowadzane te dwa badania. Możliwe, że obfitość pokarmu na stawach karpiowych spowodowała brak istotnego pogorszenia warunków do odchowania młodych pod koniec sezonu lęgowego, dzięki czemu samice nie decydowały się na modyfikację pierwotnej proporcji płci, a niewielka śmiertelność i brak wpływu postępu sezonu na przeżywalność piskląt nie wywołały odchylenia w proporcji płci na etapie osiągnięcia zdolności do lotu. Ponadto, chociaż zmiany proporcji płci w lęgach wraz z postępem sezonu są dość powszechnie raportowane, nie występują zawsze, np. u blisko spokrewnionej rybitwy rzecznej (Benito i in. 2013) czy u innych gatunków ptaków siewkowych (Ležalová i in. 2005; Que i in. 2019).

Wzrost objętości jaj może wiązać się ze zwiększeniem proporcji osobników płci mniejszej, dzięki czemu zyskują one przewagę w konkurowaniu o pokarm ze swoim większym rodzeństwem (Anderson i in. 1997; Cordero i in. 2001), jednak nie zawsze występuje taka zależność (Cichoń i in. 2003). Ponadto, wielkość jaja może zwiększać przeżywalność osobnika (Krist 2011) poprzez wpływ na masę świeżo wyklutego pisklęcia (Arnold i in. 2006). Niniejsze badania nie wykazały jednak żadnego wpływu średniej objętości jaj na wielkość piskląt w pierwszym dniu życia ani na żaden z parametrów wzrostu którejkolwiek z badanych cech biometrycznych (**Banach i in. 2021**), a także na proporcję płci na etapie klucia czy przeżywalność piskląt (**Banach et al. 2024**). Zaobserwowano jedynie związek pomiędzy średnią objętością jaj a proporcją płci wśród podlotów, jednak nie wynikała ona z różnic w przeżywalności płci w okresie pisklęcym, gdyż interakcja płci ze średnią objętością jaj również nie wpływała istotnie na prawdopodobieństwo przeżycia (**Banach i in. 2024**). Limitacją powyższych wyników jest fakt użycia uśrednionej dla lęgu zamiast indywidualnej objętości jaj. Jednakże także analizy z uwzględnieniem dokładnej objętości jaj nie wykazały żadnego wpływu tego parametru na płeć wyklutego pisklęcia ani na zdolność jaja do wyklucia (**Banach i in. 2024**). Trzeba jednak wziąć pod uwagę, że próba badawcza uwzględniająca dokładną objętość jaj była znacznie mniejsza, a ponadto nie w pełni losowa, co wynikało z ograniczonej możliwości przypisania jaja o znanej objętości do konkretnego osobnika.

6. Podsumowanie

Uzyskane wyniki pozwalają na wysunięcie następujących wniosków na temat rozwoju dymorfizmu płciowego oraz proporcji płci i śmiertelności w lęgach rybitwy białowąsej:

1. Dymorfizm płciowy pod względem wielkości rozwijał się już na etapie pisklęcym. W momencie klucia różnica obserwowana była jedynie w długości całkowitej głowy, natomiast na etapie osiągnięcia lotności przez pisklęta, trzy z czterech mierzonych

parametrów biometrycznych osiągało wyższe wartości dla samców niż samic. Ponadto wykazano różnice międzypłciowe w dynamice wzrostu – najistotniejsze dotyczyły maksymalnego tempa wzrostu masy ciała, wyższej u samców niż u samic.

2. Spośród wszystkich analizowanych czynników istotny wpływ na parametry wzrostu miały wielkość lęgu oraz data klucia – obydwa wykazywały negatywny wpływ na wzrost długości całkowitej głowy, skoku oraz skrzydła.
3. Pomimo uwzględnienia dużej próby badawczej, nie wykazano odchylenia od równości proporcji płci na poziomie populacji na etapie klucia czy wylotu z gniazda.
4. Spośród wszystkich analizowanych czynników wpływ na proporcję płci miała jedynie objętość jaj – wraz ze wzrostem średniej objętości jaj wzrastała proporcja samic wśród piskląt osiągających zdolność do lotu.
5. Pośród piskląt, które nie dożyły osiągnięcia zdolności do lotu, więcej było samic. Różnica dotyczyła jedynie piskląt, które zniknęły z gniazda (padły ofiarą drapieżnictwa).
6. Prawdopodobieństwo przeżycia do momentu osiągnięcia zdolności do lotu było negatywnie skorelowane z liczbą piskląt w lęgu.

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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 = sex + egg volume + hatching date + brood size + sex ratio + sex × egg volume + sex × hatching date + sex × brood size + sex × sex ratio + *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 ΔAICc < 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

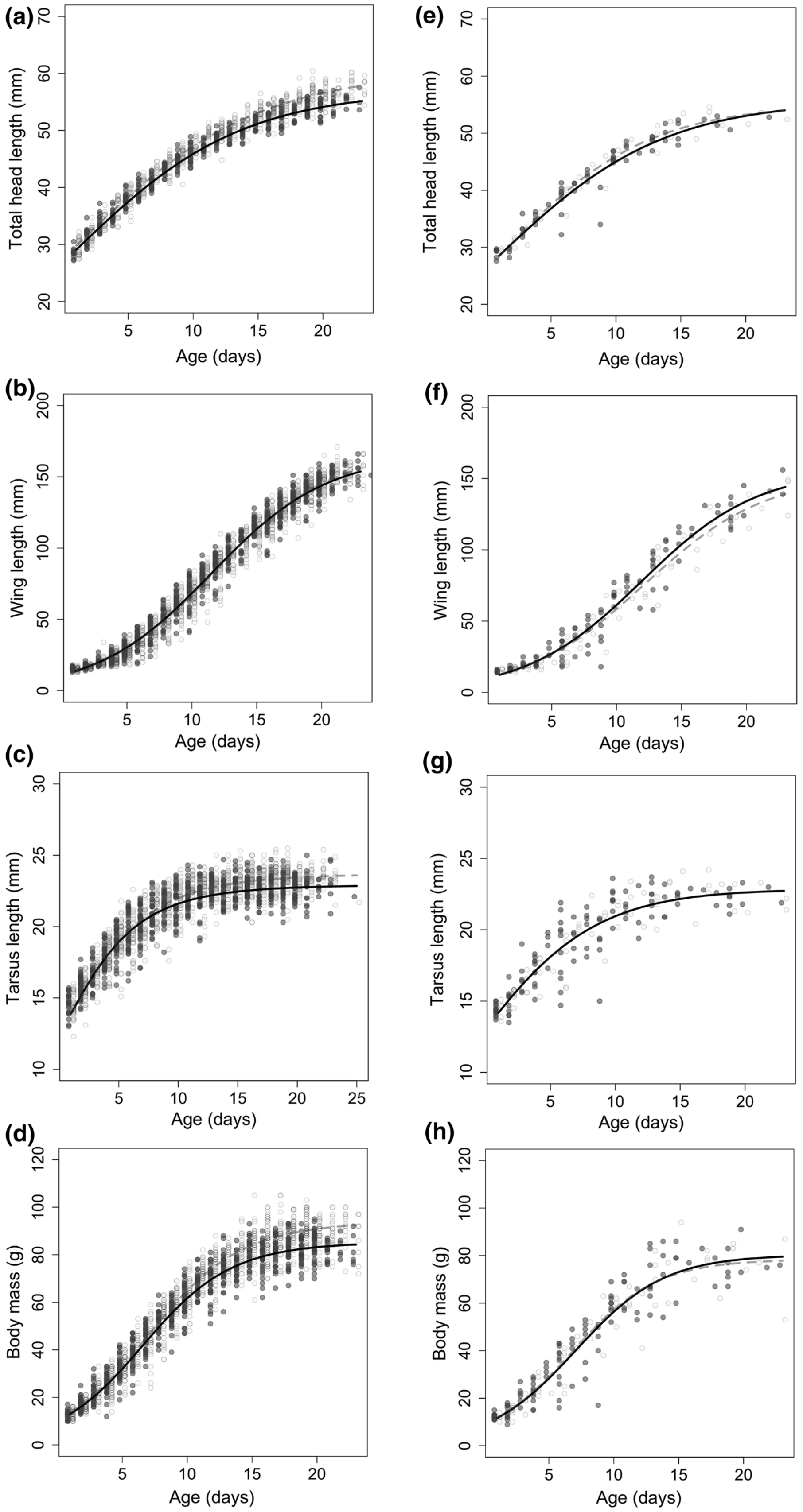

Table 3 Summary of sexual size dimorphism (SSD—the ratio of male and female dimensions or body mass) in particular body measurements recorded in the different growth stages

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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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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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 offspring 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 $\Delta AIC < 2$ 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 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.

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

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

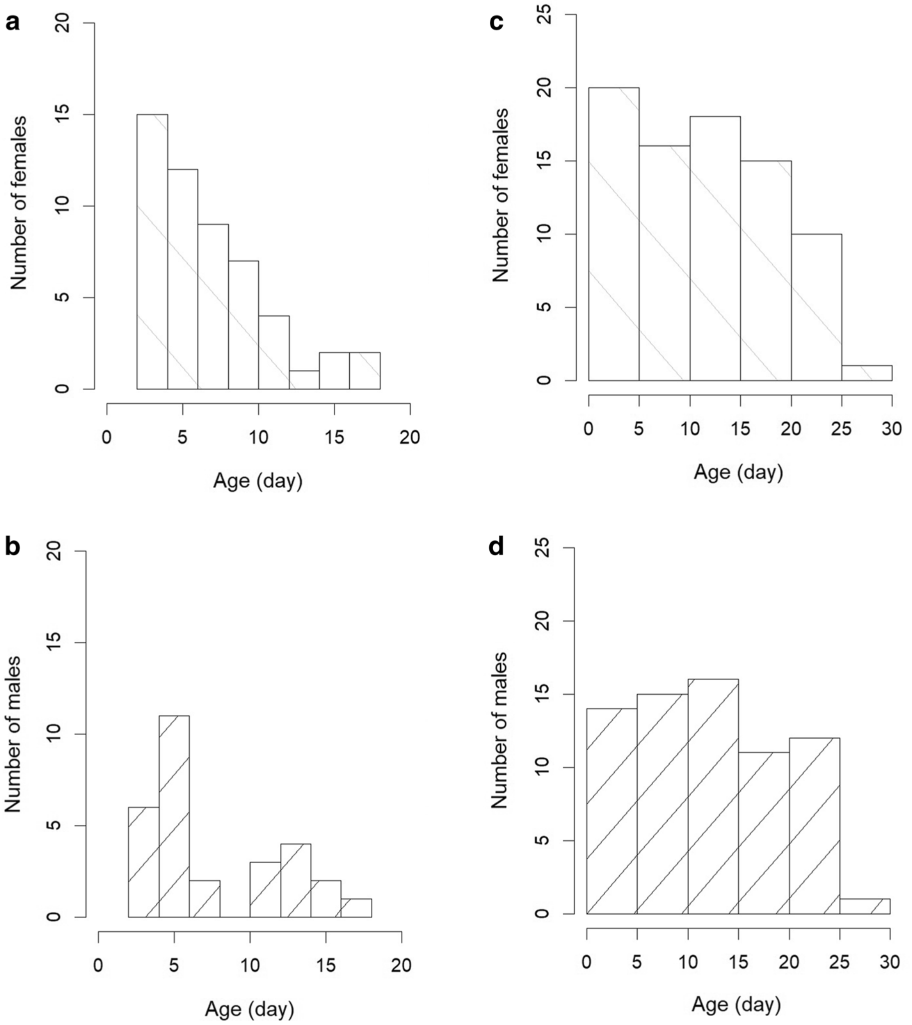

Fig. 1 Histograms of estimated age of **a** female and **b** male chicks at the time of disappearance from the nest (most probably killed and taken by a predator) and **c** female and **d** male chicks that were found dead in the nest (death due to disease, starvation, hypothermia, drowning)

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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Data availability Data are available on the Zenodo repository at https://zenodo.org/records/10679167

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Załączniki

Załączniki do publikacji

Banach A, Neubauer G, Flis A, Ledwoń M (2021) Sex-specific growth of nestlings of the Whiskered Tern *Chlidonias hybrida*, a species with sexual size dimorphism and female brood desertion. J Ornithol 162:1035–1047. https://doi.org/10.1007/s10336-021-01911-y

Supplementary Material:

Table S1. Summary of model validation. Growth parameters: A – asymptote, B – constant of integration, k – growth rate constant, g_{max} – maximum growth rate, No. of chicks – sample size of measured chicks included in the particular models, for testing the influence of factors on growth parameters; No. of models with ΔAICc <2 which were used for model-averaging Random effects - included in the global model, selection based on the Likelihood Ratio Tests of Nested Models.

Body measurement	Growth parameter	No. of chicks	No. of models with ΔAICc <2	Random effects	
				Nest	Colony
Total head length	A	145	5	x	
	B	145	8	x	
	k	145	4	x	
	g max	145	4	x	
Wing	A	250	6	x	x
	B	250	7	x	x
	k	250	7	x	x
	g max	250	11	x	x
Tarsus	A	243	8	x	
	B	243	35	x	x
	k	243	9	x	x
	g max	243	7	x	x
Body mass	A	241	6	x	x
	B	241	5	x	x
	k	241	5	x	

	g max	241	5	x

Table S2. Generalized linear mixed models used to explain variation in the growth parameters. All the models include the intercept and random effect of the nest; some models also include the random effect of the colony (omitted from this table; details in Table 1 in the main paper). Growth parameters: A – asymptote, B – constant of integration, k – growth rate constant, g_{max} – maximum growth rate.

Some growth parameters are on the log scale (log); Sex proportion – sex proportion of nestlings in the brood; ‘×’ stands for an interaction term; ‘+’ denotes the presence of a given effect in the model.

Model													
	Fixed effect												
Dependent variable	Hatch date	Brood size	Sex proportion	Sex	Egg volume	Hatch date × Sex	Brood size × Sex	Sex proportion × Sex	Egg volume × Sex	df	AICc	ΔAIC	ωAIC
A total head length	+		+	+		+				7	666.9	0.0	0.14
	+	+	+	+		+	+			9	667.0	0.0	0.14
	+			+		+				6	667.8	0.9	0.09
	+	+		+		+	+			8	668.6	1.6	0.06
	+		+	+	+	+				8	668.8	1.9	0.05
	+	+	+	+		+				8	668.9	2.0	0.05
	+		+	+		+		+		8	669.0	2.0	0.05
	+	+	+	+	+	+	+			10	669.1	2.1	0.05
	+	+	+	+		+	+	+		10	669.2	2.2	0.05
	+	+	+	+			+			8	669.9	3.0	0.03
	+			+	+	+				7	670.0	3.1	0.03

+	+		+		+				7	670.0	3.1	0.03
+	+		+	+	+	+			9	670.8	3.9	0.02
+	+	+	+	+	+				9	670.9	3.9	0.02
+		+	+	+	+		+		9	670.9	4.0	0.02
+	+		+			+			7	671.0	4.1	0.02
+	+	+	+		+		+		9	671.0	4.1	0.02
+		+	+	+	+			+	9	671.1	4.2	0.02
+	+	+	+	+	+	+	+		11	671.3	4.4	0.02
+	+	+	+	+	+	+		+	11	671.4	4.4	0.01
+	+	+	+			+	+		9	672.0	5.1	0.01
+	+	+	+	+		+			9	672.1	5.2	0.01
+			+	+	+			+	8	672.1	5.2	0.01
+	+		+	+	+				8	672.2	5.3	0.01
+	+	+	+	+	+		+		10	673.0	6.1	0.01
+	+		+	+	+	+		+	10	673.1	6.1	0.01
+	+	+	+	+	+			+	10	673.1	6.2	0.01
+		+	+	+	+		+	+	10	673.1	6.2	0.01
+	+		+	+		+			8	673.2	6.3	0.01
+	+	+	+	+	+	+	+	+	12	673.6	6.7	0.00
+	+	+	+	+		+	+		10	674.3	7.4	0.00
+	+	+	+	+		+		+	10	674.4	7.5	0.00
+	+		+	+	+			+	9	674.4	7.5	0.00
+		+	+						6	675.1	8.2	0.00

+	+	+	+	+	+		+	+	11	675.2	8.3	0.00
+	+		+	+		+		+	9	675.4	8.5	0.00
+			+						5	675.5	8.5	0.00
+	+	+	+	+		+	+	+	11	676.5	9.6	0.00
+		+	+				+		7	677.0	10.0	0.00
+		+	+	+					7	677.3	10.3	0.00
+	+	+	+						7	677.4	10.4	0.00
+	+		+						6	677.5	10.5	0.00
+			+	+					6	677.6	10.7	0.00
+		+	+	+			+		8	679.1	12.2	0.00
+	+	+	+				+		8	679.2	12.3	0.00
+		+	+	+				+	8	679.4	12.5	0.00
+	+	+	+	+					8	679.5	12.6	0.00
+	+		+	+					7	679.7	12.8	0.00
+			+	+				+	7	679.7	12.8	0.00
+		+	+	+			+	+	9	681.2	14.3	0.00
+	+	+	+	+			+		9	681.4	14.5	0.00
+	+	+	+	+				+	9	681.7	14.8	0.00
+	+		+	+				+	8	681.8	14.9	0.00
+	+	+	+	+			+	+	10	683.5	16.6	0.00
	+	+	+			+			7	686.4	19.5	0.00
	+		+			+			6	687.8	20.9	0.00
	+	+	+			+	+		8	688.5	21.6	0.00

	+	+	+	+	+			8	688.7	21.7	0.00
	+		+	+	+			7	689.9	23.0	0.00
	+	+	+	+	+		+	9	690.6	23.7	0.00
	+	+	+	+	+	+		9	690.8	23.9	0.00
	+		+	+	+		+	8	691.8	24.8	0.00
	+	+	+	+	+	+	+	10	692.5	25.6	0.00
			+					4	693.5	26.6	0.00
	+	+	+					6	693.6	26.7	0.00
	+		+					5	694.1	27.1	0.00
		+	+					5	694.2	27.3	0.00
	+	+	+			+		7	695.6	28.7	0.00
			+	+				5	695.6	28.7	0.00
	+	+	+	+				7	695.8	28.9	0.00
		+	+			+		6	696.1	29.2	0.00
	+		+	+				6	696.2	29.3	0.00
		+	+	+				6	696.4	29.5	0.00
			+	+			+	6	697.4	30.5	0.00
	+	+	+	+			+	8	697.6	30.7	0.00
	+	+	+	+		+		8	697.8	30.9	0.00
	+		+	+			+	7	697.9	31.0	0.00
		+	+	+			+	7	698.3	31.4	0.00
		+	+	+		+		7	698.3	31.4	0.00
+		+						5	698.9	32.0	0.00

		+	+	+	+		+	+	9	699.3	32.4	0.00
			+	+	+		+	+	8	699.9	33.0	0.00
	+		+		+				6	700.9	34.0	0.00
	+	+	+						6	701.1	34.1	0.00
	+	+	+		+				7	703.1	36.2	0.00
	+								4	716.7	49.8	0.00
	+	+							5	717.2	50.3	0.00
		+	+						5	718.4	51.5	0.00
	+				+				5	718.7	51.8	0.00
			+						4	719.0	52.1	0.00
	+	+			+				6	719.2	52.3	0.00
		+	+		+				6	720.6	53.7	0.00
			+		+				5	721.2	54.3	0.00
									3	731.5	64.6	0.00
					+				4	733.3	66.4	0.00
		+							4	733.5	66.6	0.00
		+			+				5	735.3	68.3	0.00
B total head length	+	+		+	+	+			8	-217.7	0.0	0.09
	+	+		+	+				7	-217.1	0.6	0.06
	+	+		+		+			7	-217.0	0.7	0.06
	+			+	+				6	-216.2	1.5	0.04
	+			+	+	+			7	-216.1	1.6	0.04
	+	+		+	+	+		+	9	-216.0	1.7	0.04

	+	+		+						6	-216.0	1.7	0.04
	+	+	+	+	+	+				9	-215.9	1.8	0.03
	+	+	+	+		+				8	-215.6	2.0	0.03
	+			+		+				6	-215.6	2.1	0.03
	+	+		+	+				+	8	-215.5	2.2	0.03
	+	+		+	+	+	+			9	-215.4	2.2	0.03
	+			+						5	-215.4	2.3	0.03
	+	+		+	+		+			8	-215.1	2.6	0.02
	+	+	+	+	+					8	-215.1	2.6	0.02
	+	+		+		+	+			8	-214.8	2.9	0.02
	+			+	+				+	7	-214.4	3.3	0.02
	+	+	+	+						7	-214.4	3.3	0.02
	+			+	+	+			+	8	-214.2	3.5	0.02
		+		+	+					6	-214.2	3.5	0.02
	+	+	+	+	+	+			+	10	-214.1	3.6	0.01
	+		+	+	+					7	-214.0	3.7	0.01
	+	+		+			+			7	-214.0	3.7	0.01
	+	+	+	+	+	+		+		10	-213.9	3.8	0.01
	+		+	+	+	+				8	-213.9	3.8	0.01
	+	+		+	+	+	+		+	10	-213.7	4.0	0.01
	+	+	+	+		+		+		9	-213.6	4.1	0.01
	+		+	+		+				7	-213.6	4.1	0.01
	+	+	+	+	+	+	+			10	-213.6	4.1	0.01

+	+		+	+		+		+	9	-213.4	4.3	0.01
+	+	+	+		+	+			9	-213.4	4.3	0.01
+	+	+	+	+				+	9	-213.4	4.3	0.01
+		+	+						6	-213.3	4.4	0.01
+	+	+	+	+			+		9	-213.3	4.4	0.01
+	+	+	+	+		+			9	-213.1	4.6	0.01
	+		+	+				+	7	-213.0	4.7	0.01
	+		+						5	-212.9	4.8	0.01
+	+	+	+	+	+		+	+	11	-212.5	5.1	0.01
+	+	+	+				+		8	-212.5	5.2	0.01
+	+	+	+			+			8	-212.4	5.3	0.01
	+	+	+	+					7	-212.4	5.3	0.01
	+		+	+		+			7	-212.3	5.4	0.01
+		+	+	+			+		8	-212.3	5.4	0.01
+		+	+	+				+	8	-212.2	5.5	0.01
+	+	+	+	+			+	+	10	-212.1	5.6	0.01
+		+	+	+	+		+		9	-212.0	5.7	0.01
+		+	+	+	+			+	9	-211.9	5.7	0.00
+	+	+	+	+	+	+		+	11	-211.8	5.9	0.00
+		+	+		+		+		8	-211.6	6.1	0.00
+	+	+	+	+	+	+	+		11	-211.6	6.1	0.00
	+	+	+						6	-211.6	6.1	0.00
+		+	+				+		7	-211.5	6.2	0.00

+	+	+	+	+		+		+	10	-211.4	6.3	0.00
+	+	+	+		+	+	+		10	-211.4	6.3	0.00
+	+	+	+	+		+	+		10	-211.2	6.5	0.00
	+	+	+	+				+	8	-211.0	6.6	0.00
	+		+	+		+		+	8	-211.0	6.7	0.00
	+		+			+			6	-211.0	6.7	0.00
+		+	+	+			+	+	9	-210.8	6.9	0.00
	+	+	+	+			+		8	-210.6	7.1	0.00
	+	+	+	+		+			8	-210.5	7.2	0.00
+	+	+	+			+	+		9	-210.4	7.2	0.00
+		+	+	+	+		+	+	10	-210.4	7.3	0.00
+	+	+	+	+	+	+	+	+	12	-210.2	7.5	0.00
+	+	+		+					7	-210.1	7.6	0.00
+	+	+	+	+		+	+	+	11	-209.9	7.7	0.00
	+	+	+	+			+	+	9	-209.9	7.8	0.00
	+	+	+			+			7	-209.7	8.0	0.00
	+	+	+				+		7	-209.7	8.0	0.00
+	+	+							6	-209.5	8.2	0.00
+				+					5	-209.3	8.4	0.00
+		+		+					6	-209.2	8.5	0.00
			+	+					5	-209.1	8.6	0.00
	+	+	+	+		+		+	9	-209.1	8.6	0.00
+	+			+					6	-208.6	9.1	0.00

		+	+	+	+	+	+		9	-208.6	9.1	0.00
	+		+						5	-208.5	9.1	0.00
				+					4	-208.3	9.4	0.00
		+	+	+	+	+	+	+	10	-207.8	9.9	0.00
		+	+	+		+	+		8	-207.7	9.9	0.00
				+	+			+	6	-207.6	10.1	0.00
	+								4	-207.6	10.1	0.00
			+	+	+				6	-207.0	10.7	0.00
	+	+							5	-206.7	11.0	0.00
		+	+		+				6	-206.7	11.0	0.00
			+	+					5	-206.2	11.5	0.00
		+	+						5	-206.0	11.7	0.00
			+	+	+			+	7	-205.4	12.3	0.00
			+	+	+		+		7	-205.3	12.4	0.00
		+			+				5	-204.7	13.0	0.00
			+	+			+		6	-204.4	13.3	0.00
			+	+	+		+	+	8	-204.3	13.4	0.00
		+							4	-202.6	15.1	0.00
					+				4	-201.8	15.8	0.00
			+		+				5	-201.3	16.4	0.00
			+						4	-200.5	17.2	0.00
									3	-200.2	17.5	0.00
k total head	+	+		+		+			7	-777.2	0.0	0.15

length	+	+		+		+	+			8	-776.3	0.9	0.09
	+	+	+	+			+			8	-776.0	1.2	0.08
	+	+		+	+		+			8	-775.2	2.0	0.06
	+	+	+	+		+	+			9	-775.2	2.0	0.05
	+	+		+		+				7	-775.0	2.2	0.05
	+	+		+	+	+	+			9	-774.2	3.0	0.03
	+			+		+				6	-774.2	3.1	0.03
	+	+	+	+			+	+		9	-774.0	3.3	0.03
	+	+	+	+	+		+			9	-773.9	3.4	0.03
	+		+	+		+				7	-773.8	3.4	0.03
	+	+								5	-773.8	3.4	0.03
	+	+	+	+		+				8	-773.6	3.6	0.02
	+	+		+	+		+		+	9	-773.2	4.0	0.02
	+	+	+							6	-773.1	4.1	0.02
	+	+	+	+		+	+	+		10	-773.1	4.1	0.02
	+	+		+						6	-773.0	4.2	0.02
	+	+	+	+	+	+	+			10	-772.9	4.3	0.02
	+	+		+	+	+				8	-772.8	4.4	0.02
	+		+							5	-772.2	5.0	0.01
	+	+		+	+	+	+		+	10	-772.2	5.1	0.01
	+			+	+	+				7	-772.1	5.2	0.01
	+	+	+	+	+		+		+	10	-771.9	5.4	0.01
	+	+			+					6	-771.8	5.4	0.01

+	+	+	+	+		+	+		10	-771.8	5.4	0.01
+		+	+		+		+		8	-771.8	5.4	0.01
+	+	+	+		+		+		9	-771.6	5.6	0.01
+		+	+	+	+				8	-771.6	5.7	0.01
+	+	+	+						7	-771.4	5.8	0.01
+	+	+	+	+	+				9	-771.4	5.9	0.01
+			+						5	-771.3	6.0	0.01
+									4	-771.2	6.0	0.01
+	+		+	+					7	-771.0	6.2	0.01
+	+	+		+					7	-770.9	6.3	0.01
+	+	+	+	+	+	+		+	11	-770.9	6.3	0.01
+	+	+	+	+	+	+	+		11	-770.8	6.4	0.01
+	+		+	+	+			+	9	-770.8	6.5	0.01
+		+	+						6	-770.6	6.7	0.01
+		+		+					6	-770.0	7.2	0.00
+			+	+	+			+	8	-769.9	7.3	0.00
+	+	+	+	+		+	+	+	11	-769.6	7.6	0.00
+	+	+	+				+		8	-769.6	7.7	0.00
+		+	+	+	+		+		9	-769.5	7.7	0.00
+		+	+	+	+			+	9	-769.4	7.8	0.00
+				+					5	-769.4	7.9	0.00
+	+	+	+	+	+		+		10	-769.3	7.9	0.00
+	+	+	+	+	+			+	10	-769.3	7.9	0.00

+			+	+					6	-769.3	8.0	0.00
+	+	+	+	+					8	-769.2	8.0	0.00
+	+		+	+				+	8	-768.9	8.3	0.00
+		+	+				+		7	-768.7	8.5	0.00
+	+	+	+	+	+	+	+	+	12	-768.6	8.6	0.00
+		+	+	+					7	-768.4	8.8	0.00
+	+	+	+	+			+		9	-767.4	9.8	0.00
+		+	+	+	+		+	+	10	-767.3	10.0	0.00
+	+	+	+	+				+	9	-767.2	10.0	0.00
+	+	+	+	+	+		+	+	11	-767.1	10.1	0.00
+			+	+				+	7	-767.1	10.1	0.00
+		+	+	+			+		8	-766.5	10.7	0.00
+		+	+	+				+	8	-766.3	11.0	0.00
+	+	+	+	+			+	+	10	-765.2	12.1	0.00
+		+	+	+			+	+	9	-764.3	13.0	0.00
	+		+			+			6	-760.5	16.7	0.00
	+	+	+			+			7	-759.7	17.5	0.00
		+							4	-759.1	18.1	0.00
									3	-758.9	18.3	0.00
			+						4	-758.8	18.4	0.00
	+		+	+		+			7	-758.8	18.4	0.00
	+	+	+	+		+			8	-757.8	19.5	0.00
		+	+						5	-757.7	19.5	0.00

+	+	+		+	+		8	-757.7	19.5	0.00
			+				4	-757.2	20.0	0.00
	+		+				5	-757.1	20.1	0.00
		+	+				5	-757.0	20.2	0.00
+							4	-757.0	20.2	0.00
+	+						5	-757.0	20.2	0.00
+		+					5	-756.8	20.4	0.00
+		+	+	+		+	8	-756.6	20.7	0.00
	+	+			+		6	-755.8	21.4	0.00
	+	+	+				6	-755.7	21.5	0.00
+	+	+	+	+	+		9	-755.7	21.5	0.00
+	+	+					6	-755.5	21.7	0.00
+	+	+	+	+		+	9	-755.5	21.7	0.00
+			+				5	-755.3	21.9	0.00
+	+		+				6	-755.0	22.2	0.00
+		+	+				6	-754.9	22.3	0.00
		+	+			+	6	-754.9	22.4	0.00
	+	+	+		+		7	-753.8	23.4	0.00
+	+	+			+		7	-753.6	23.6	0.00
+	+	+	+				7	-753.5	23.7	0.00
	+	+	+			+	7	-753.5	23.7	0.00
+	+	+	+	+	+	+	10	-753.4	23.8	0.00
+		+	+			+	7	-752.7	24.5	0.00

			+	+	+			+	+	8	-751.6	25.6	0.00
		+	+	+	+			+		8	-751.6	25.6	0.00
		+	+	+	+				+	8	-751.2	26.0	0.00
		+	+	+	+			+	+	9	-749.3	27.9	0.00
g_{max} total head length	+	+		+			+			7	-83.8	0.0	0.18
	+	+		+		+	+			8	-82.4	1.4	0.09
	+	+		+	+		+			8	-82.1	1.8	0.07
	+	+		+		+				7	-81.9	1.9	0.07
	+	+	+	+			+			8	-81.8	2.1	0.06
	+	+		+						6	-81.2	2.6	0.05
	+	+								5	-80.7	3.2	0.04
	+	+		+	+	+	+			9	-80.5	3.3	0.03
	+	+		+	+		+		+	9	-80.5	3.3	0.03
	+	+	+	+		+	+			9	-80.4	3.4	0.03
	+	+		+	+	+				8	-79.9	3.9	0.02
	+	+	+	+	+		+			9	-79.9	4.0	0.02
	+	+	+	+		+				8	-79.8	4.0	0.02
	+	+	+	+			+	+		9	-79.6	4.2	0.02
	+	+		+	+					7	-79.3	4.5	0.02
	+	+	+	+						7	-79.1	4.8	0.02
	+	+		+	+	+	+		+	10	-78.9	4.9	0.02
	+	+	+							6	-78.8	5.0	0.01
	+	+			+					6	-78.7	5.2	0.01

+			+		+				6	-78.5	5.4	0.01
+	+	+	+	+	+	+			10	-78.4	5.5	0.01
+	+	+	+	+		+		+	10	-78.3	5.5	0.01
+	+		+	+	+			+	9	-78.3	5.6	0.01
+	+	+	+		+	+	+		10	-78.2	5.6	0.01
+	+	+	+		+		+		9	-77.7	6.1	0.01
+	+	+	+	+		+	+		10	-77.7	6.1	0.01
+	+		+	+				+	8	-77.7	6.1	0.01
+	+	+	+	+	+				9	-77.7	6.1	0.01
+									4	-77.2	6.6	0.01
+		+	+		+				7	-77.2	6.7	0.01
+	+	+	+				+		8	-77.1	6.7	0.01
+	+	+	+	+					8	-77.1	6.7	0.01
+	+	+		+					7	-76.9	6.9	0.01
+	+	+	+	+	+	+		+	11	-76.8	7.1	0.01
+			+						5	-76.6	7.2	0.00
+			+	+	+				7	-76.5	7.3	0.00
+	+	+	+	+	+	+	+		11	-76.2	7.7	0.00
+	+	+	+	+	+			+	10	-76.0	7.8	0.00
+	+	+	+	+		+	+	+	11	-76.0	7.9	0.00
+	+	+	+	+	+		+		10	-75.6	8.2	0.00
+	+	+	+	+				+	9	-75.4	8.4	0.00
+				+					5	-75.3	8.5	0.00

+		+	+						6	-75.2	8.7	0.00
+	+	+	+	+			+		9	-75.2	8.7	0.00
+		+							5	-75.1	8.8	0.00
+		+	+		+		+		8	-75.1	8.8	0.00
+		+	+	+	+				8	-75.0	8.8	0.00
+			+	+					6	-74.8	9.0	0.00
+			+	+	+			+	8	-74.5	9.3	0.00
+	+	+	+	+	+	+	+	+	12	-74.4	9.4	0.00
+	+	+	+	+	+		+	+	11	-73.8	10.1	0.00
+	+	+	+	+			+	+	10	-73.3	10.6	0.00
+		+	+	+					7	-73.2	10.7	0.00
+		+	+				+		7	-73.2	10.7	0.00
+		+		+					6	-73.2	10.7	0.00
+		+	+	+	+			+	9	-73.1	10.7	0.00
+		+	+	+	+		+		9	-72.9	10.9	0.00
+			+	+				+	7	-72.9	11.0	0.00
+		+	+	+				+	8	-71.2	12.6	0.00
+		+	+	+			+		8	-71.2	12.7	0.00
+		+	+	+	+		+	+	10	-70.8	13.0	0.00
+		+	+	+			+	+	9	-69.0	14.8	0.00
	+		+			+			6	-68.3	15.5	0.00
									3	-68.0	15.9	0.00
			+						4	-67.3	16.6	0.00

+		+	+	+			7	-66.9	17.0	0.00
+	+	+		+			7	-66.5	17.3	0.00
+							4	-66.5	17.3	0.00
			+				4	-66.3	17.5	0.00
+		+					5	-66.1	17.8	0.00
	+						4	-65.9	18.0	0.00
		+	+				5	-65.7	18.1	0.00
	+	+					5	-65.6	18.2	0.00
+	+	+	+	+			8	-64.9	18.9	0.00
+			+				5	-64.8	19.0	0.00
+		+	+	+		+	8	-64.7	19.1	0.00
+		+	+				6	-64.5	19.3	0.00
+	+	+		+	+		8	-64.4	19.4	0.00
+	+						5	-64.4	19.4	0.00
	+		+				5	-64.2	19.7	0.00
+	+	+					6	-64.1	19.7	0.00
	+	+	+				6	-63.9	20.0	0.00
	+	+			+		6	-63.7	20.2	0.00
		+	+			+	6	-63.6	20.2	0.00
+	+	+	+	+	+		9	-62.8	21.1	0.00
+	+	+	+	+		+	9	-62.7	21.1	0.00
+	+		+				6	-62.7	21.1	0.00
+	+	+	+				7	-62.4	21.4	0.00

		+		+	+				+	7	-62.4	21.5	0.00
		+	+	+				+		7	-62.2	21.7	0.00
			+	+	+			+		7	-61.9	21.9	0.00
			+	+	+				+	7	-61.7	22.1	0.00
		+	+	+	+		+	+	+	10	-60.5	23.3	0.00
		+	+	+	+			+		8	-60.4	23.4	0.00
		+	+	+	+				+	8	-60.2	23.6	0.00
			+	+	+			+	+	8	-59.7	24.2	0.00
		+	+	+	+			+	+	9	-58.2	25.6	0.00
A wing	+			+						6	1766.0	0.0	0.09
	+									5	1766.2	0.3	0.08
	+			+		+				7	1766.5	0.5	0.07
				+						5	1767.3	1.3	0.04
	+		+							6	1767.4	1.4	0.04
										4	1767.7	1.8	0.04
	+	+		+						7	1768.0	2.0	0.03
	+		+	+						7	1768.0	2.1	0.03
	+	+								6	1768.1	2.1	0.03
	+			+	+					7	1768.1	2.1	0.03
	+				+					6	1768.3	2.3	0.03
	+		+	+		+				8	1768.5	2.5	0.02
	+	+		+		+				8	1768.6	2.6	0.02
	+			+	+	+				8	1768.6	2.6	0.02

		+							5	1768.7	2.7	0.02
	+		+						6	1769.3	3.3	0.02
		+	+						6	1769.3	3.3	0.02
+	+		+			+			8	1769.3	3.4	0.02
			+	+					6	1769.4	3.4	0.02
+	+	+							7	1769.5	3.5	0.02
	+								5	1769.5	3.5	0.02
+	+		+		+	+			9	1769.5	3.5	0.01
+		+		+					7	1769.5	3.5	0.01
				+					5	1769.7	3.7	0.01
+		+	+				+		8	1770.1	4.1	0.01
+	+	+	+						8	1770.1	4.1	0.01
+	+			+					7	1770.1	4.1	0.01
+	+		+	+					8	1770.1	4.2	0.01
+		+	+	+					8	1770.2	4.2	0.01
+			+	+				+	8	1770.2	4.2	0.01
+		+	+		+		+		9	1770.6	4.6	0.01
+	+	+	+		+				9	1770.7	4.7	0.01
+		+	+	+	+				9	1770.7	4.7	0.01
	+	+							6	1770.7	4.7	0.01
+	+		+	+	+				9	1770.7	4.8	0.01
+			+	+	+			+	9	1770.7	4.8	0.01
		+		+					6	1770.8	4.8	0.01

	+		+			+			7	1770.8	4.8	0.01
		+	+				+		7	1771.3	5.3	0.01
	+	+	+						7	1771.3	5.3	0.01
	+		+	+					7	1771.3	5.3	0.01
			+	+				+	7	1771.4	5.4	0.01
		+	+	+					7	1771.4	5.4	0.01
	+			+					6	1771.4	5.4	0.01
+	+	+	+			+			9	1771.5	5.5	0.01
+	+		+	+		+			9	1771.5	5.5	0.01
+	+	+	+		+	+			10	1771.6	5.6	0.01
+	+	+		+					8	1771.6	5.6	0.01
+	+		+	+	+	+			10	1771.6	5.7	0.01
+	+	+	+				+		9	1772.2	6.2	0.00
+		+	+	+			+		9	1772.2	6.3	0.00
+	+		+	+				+	9	1772.3	6.3	0.00
+	+	+	+	+					9	1772.3	6.3	0.00
+		+	+	+				+	9	1772.3	6.3	0.00
+	+	+	+		+		+		10	1772.8	6.8	0.00
+		+	+	+	+		+		10	1772.8	6.8	0.00
	+	+		+					7	1772.8	6.8	0.00
+		+	+	+	+			+	10	1772.8	6.8	0.00
+	+	+	+	+	+				10	1772.8	6.9	0.00
	+	+	+			+			8	1772.9	6.9	0.00

+	+		+	+	+			+	10	1772.9	6.9	0.00
	+		+	+		+			8	1772.9	6.9	0.00
	+	+	+				+		8	1773.3	7.3	0.00
	+		+	+				+	8	1773.4	7.4	0.00
		+	+	+			+		8	1773.4	7.4	0.00
	+	+	+	+					8	1773.4	7.4	0.00
		+	+	+				+	8	1773.4	7.5	0.00
+	+		+	+		+		+	10	1773.6	7.6	0.00
+	+	+	+			+	+		10	1773.6	7.6	0.00
+	+	+	+	+		+			10	1773.6	7.6	0.00
+	+	+	+	+	+	+			11	1773.7	7.8	0.00
+	+	+	+		+	+	+		11	1773.7	7.8	0.00
+	+		+	+	+	+		+	11	1773.7	7.8	0.00
+	+	+	+	+			+		10	1774.3	8.4	0.00
+		+	+	+			+	+	10	1774.4	8.4	0.00
+	+	+	+	+				+	10	1774.4	8.4	0.00
	+		+	+		+		+	9	1774.9	8.9	0.00
+	+	+	+	+	+		+		11	1774.9	9.0	0.00
+		+	+	+	+		+	+	11	1774.9	9.0	0.00
	+	+	+			+	+		9	1775.0	9.0	0.00
+	+	+	+	+	+			+	11	1775.0	9.0	0.00
	+	+	+	+		+			9	1775.0	9.0	0.00
	+	+	+	+			+		9	1775.5	9.5	0.00

		+	+	+	+				+	9	1775.5	9.5	0.00
			+	+	+			+	+	9	1775.5	9.5	0.00
	+	+	+	+	+		+		+	11	1775.7	9.8	0.00
	+	+	+	+	+		+	+		11	1775.8	9.8	0.00
	+	+	+	+	+	+	+		+	12	1775.9	9.9	0.00
	+	+	+	+	+	+	+	+		12	1775.9	9.9	0.00
	+	+	+	+	+			+	+	11	1776.5	10.6	0.00
		+	+	+	+		+		+	10	1777.1	11.1	0.00
		+	+	+	+		+	+		10	1777.1	11.1	0.00
	+	+	+	+	+	+		+	+	12	1777.1	11.2	0.00
		+	+	+	+			+	+	10	1777.6	11.6	0.00
	+	+	+	+	+		+	+	+	12	1777.9	12.0	0.00
	+	+	+	+	+	+	+	+	+	13	1778.1	12.1	0.00
		+	+	+	+		+	+	+	11	1779.2	13.2	0.00
B wing (log)	+	+		+	+	+			+	10	-639.7	0.0	0.06
	+	+		+	+	+				9	-639.4	0.3	0.05
	+			+	+	+				8	-638.8	0.9	0.04
	+	+		+		+				8	-638.8	0.9	0.04
	+			+	+	+			+	9	-638.4	1.3	0.03
	+	+		+	+	+	+			10	-638.3	1.4	0.03
	+	+		+	+	+	+		+	11	-638.2	1.5	0.03
	+	+	+	+	+	+			+	11	-637.6	2.1	0.02
	+			+		+				7	-637.5	2.2	0.02

				+					5	-637.5	2.2	0.02
	+		+	+				+	8	-637.5	2.2	0.02
+	+		+		+	+			9	-637.4	2.3	0.02
			+	+					6	-637.3	2.4	0.02
+	+	+	+	+	+				10	-637.3	2.4	0.02
+		+	+	+	+				9	-637.2	2.5	0.02
			+	+				+	7	-637.2	2.5	0.02
+	+		+	+				+	9	-637.1	2.6	0.02
	+		+	+		+			8	-637.0	2.7	0.02
+		+	+	+	+			+	10	-637.0	2.7	0.02
	+		+	+		+		+	9	-637.0	2.7	0.02
	+		+	+					7	-637.0	2.8	0.02
+				+					6	-636.9	2.8	0.02
	+			+					6	-636.7	3.0	0.01
+	+	+	+		+				9	-636.7	3.0	0.01
+	+		+	+					8	-636.6	3.1	0.01
+			+	+					7	-636.6	3.1	0.01
+	+		+	+		+			9	-636.5	3.2	0.01
+	+			+					7	-636.4	3.3	0.01
+			+	+				+	8	-636.4	3.3	0.01
+	+		+	+		+		+	10	-636.4	3.3	0.01
+	+	+	+	+	+	+			11	-636.2	3.5	0.01
+	+	+	+	+	+		+	+	12	-636.2	3.5	0.01

+	+	+	+	+	+	+		+	12	-636.1	3.6	0.01
+	+		+						7	-636.1	3.6	0.01
	+		+						6	-636.1	3.6	0.01
		+	+	+				+	8	-636.0	3.8	0.01
		+	+	+					7	-635.8	3.9	0.01
			+						5	-635.8	3.9	0.01
	+		+			+			7	-635.7	4.0	0.01
	+	+	+	+				+	9	-635.6	4.1	0.01
									4	-635.6	4.2	0.01
+		+	+		+				8	-635.5	4.2	0.01
+	+		+			+			8	-635.5	4.2	0.01
+		+	+	+	+		+	+	11	-635.5	4.2	0.01
		+		+					6	-635.5	4.3	0.01
+			+						6	-635.4	4.3	0.01
+	+	+	+		+	+			10	-635.3	4.4	0.01
+	+								6	-635.3	4.4	0.01
	+								5	-635.2	4.5	0.01
+		+	+	+					8	-635.2	4.5	0.01
+									5	-635.2	4.5	0.01
+		+	+	+				+	9	-635.2	4.5	0.01
+	+	+	+	+	+		+		11	-635.2	4.5	0.01
+	+	+	+	+				+	10	-635.2	4.5	0.01
+		+	+	+	+		+		10	-635.2	4.5	0.01

	+	+	+	+		+		+	10	-635.1	4.6	0.01
	+	+	+	+		+			9	-635.1	4.6	0.01
	+	+	+	+					8	-635.0	4.7	0.01
+		+		+					7	-634.9	4.8	0.01
+	+	+	+	+					9	-634.7	5.0	0.01
	+	+		+					7	-634.7	5.1	0.00
+	+	+	+		+		+		10	-634.6	5.2	0.00
+	+	+	+	+		+			10	-634.5	5.2	0.00
+	+	+	+	+		+		+	11	-634.5	5.2	0.00
+	+	+	+	+	+	+	+	+	13	-634.5	5.3	0.00
		+	+	+			+	+	9	-634.4	5.3	0.00
+	+	+		+					8	-634.3	5.4	0.00
	+	+	+	+			+	+	10	-634.1	5.6	0.00
+	+	+	+	+	+	+	+		12	-634.1	5.7	0.00
	+	+	+						7	-633.9	5.8	0.00
+	+	+	+						8	-633.9	5.8	0.00
		+	+						6	-633.8	5.9	0.00
		+	+	+			+		8	-633.8	5.9	0.00
+	+	+	+	+			+	+	11	-633.8	5.9	0.00
+		+	+	+			+	+	10	-633.7	6.0	0.00
	+	+							6	-633.7	6.0	0.00
+	+	+							7	-633.7	6.0	0.00
		+							5	-633.6	6.1	0.00

		+	+	+			+			8	-633.6	6.1	0.00
	+		+	+						7	-633.5	6.2	0.00
	+		+	+		+		+		9	-633.4	6.3	0.00
	+	+	+	+			+			9	-633.3	6.4	0.00
		+	+	+	+		+	+	+	11	-633.3	6.4	0.00
	+		+	+	+			+		9	-633.2	6.5	0.00
	+		+							6	-633.2	6.5	0.00
	+	+	+	+		+	+	+		11	-633.1	6.6	0.00
		+	+	+	+		+	+		10	-633.0	6.7	0.00
		+	+	+	+			+		9	-633.0	6.8	0.00
	+	+	+	+	+		+	+	+	12	-632.8	6.9	0.00
	+	+	+	+	+			+		10	-632.7	7.1	0.00
	+	+	+	+	+		+	+		11	-632.4	7.3	0.00
		+	+	+				+		8	-631.8	7.9	0.00
	+	+	+	+				+		9	-631.8	7.9	0.00
			+	+				+		7	-631.7	8.0	0.00
		+	+	+			+	+		9	-631.4	8.3	0.00
	+		+	+				+		8	-631.4	8.3	0.00
	+	+	+	+			+	+		10	-631.2	8.5	0.00
k wing		+								5	-1373.2	0.0	0.10
										4	-1372.2	0.9	0.06
	+	+								6	-1371.9	1.3	0.05
		+			+					6	-1371.9	1.3	0.05

	+	+					6	-1371.9	1.3	0.05
	+		+				6	-1371.3	1.9	0.04
	+	+		+			7	-1371.2	2.0	0.04
+							5	-1371.1	2.0	0.04
+	+	+					7	-1370.7	2.5	0.03
				+			5	-1370.7	2.5	0.03
+	+			+			7	-1370.4	2.7	0.03
		+					5	-1370.3	2.9	0.02
			+				5	-1370.2	3.0	0.02
	+		+	+			7	-1370.1	3.1	0.02
+	+		+				7	-1370.0	3.1	0.02
+	+	+		+			8	-1369.9	3.3	0.02
	+		+		+		7	-1369.9	3.3	0.02
	+	+	+				7	-1369.7	3.4	0.02
+				+			6	-1369.4	3.7	0.02
+		+					6	-1369.2	4.0	0.01
	+	+	+	+			8	-1369.1	4.1	0.01
+			+				6	-1369.1	4.1	0.01
		+		+			6	-1368.9	4.3	0.01
+	+		+		+		8	-1368.7	4.4	0.01
+	+		+	+			8	-1368.7	4.5	0.01
			+	+			6	-1368.6	4.5	0.01
	+	+	+			+	8	-1368.6	4.6	0.01

+	+	+	+						8	-1368.6	4.6	0.01
	+		+	+		+			8	-1368.5	4.7	0.01
	+	+	+			+			8	-1368.3	4.8	0.01
		+	+						6	-1368.2	5.0	0.01
+	+		+		+				8	-1368.1	5.1	0.01
	+		+	+				+	8	-1367.9	5.2	0.01
+	+	+	+	+					9	-1367.7	5.4	0.01
	+	+	+	+			+		9	-1367.7	5.5	0.01
+		+		+					7	-1367.6	5.5	0.01
	+	+	+	+		+			9	-1367.4	5.7	0.01
+			+	+					7	-1367.4	5.8	0.01
+	+	+	+				+		9	-1367.3	5.8	0.01
+	+	+	+			+			9	-1367.3	5.8	0.01
+			+		+				7	-1367.3	5.9	0.01
+	+		+	+		+			9	-1367.2	6.0	0.01
+		+	+						7	-1367.1	6.1	0.00
		+	+				+		7	-1367.0	6.2	0.00
	+	+	+			+	+		9	-1366.9	6.2	0.00
	+	+	+	+				+	9	-1366.9	6.2	0.00
+	+		+		+	+			9	-1366.9	6.3	0.00
		+	+	+					7	-1366.7	6.4	0.00
+	+		+	+	+				9	-1366.7	6.5	0.00
			+	+				+	7	-1366.6	6.5	0.00

+	+		+	+				+	9	-1366.5	6.6	0.00
+	+	+	+		+				9	-1366.5	6.7	0.00
	+		+	+		+		+	9	-1366.3	6.9	0.00
+	+	+	+	+			+		10	-1366.3	6.9	0.00
+	+	+	+	+		+			10	-1366.2	7.0	0.00
	+	+	+	+		+	+		10	-1365.9	7.3	0.00
+		+	+				+		8	-1365.8	7.4	0.00
+	+	+	+			+	+		10	-1365.8	7.4	0.00
+	+	+	+	+	+				10	-1365.6	7.5	0.00
+			+	+	+				8	-1365.6	7.6	0.00
	+	+	+	+			+	+	10	-1365.6	7.6	0.00
+	+	+	+	+				+	10	-1365.5	7.6	0.00
+		+	+	+					8	-1365.5	7.7	0.00
		+	+	+			+		8	-1365.4	7.8	0.00
+	+	+	+		+	+			10	-1365.4	7.8	0.00
+			+	+				+	8	-1365.3	7.8	0.00
	+	+	+	+		+		+	10	-1365.3	7.9	0.00
+	+		+	+	+	+			10	-1365.3	7.9	0.00
+		+	+		+				8	-1365.3	7.9	0.00
+	+	+	+		+		+		10	-1365.3	7.9	0.00
+	+		+	+		+		+	10	-1365.0	8.2	0.00
		+	+	+				+	8	-1364.8	8.4	0.00
+	+	+	+	+		+	+		11	-1364.5	8.6	0.00

+	+		+	+	+			+	10	-1364.5	8.6	0.00
+	+	+	+	+	+	+			11	-1364.2	9.0	0.00
+	+	+	+	+	+		+		11	-1364.2	9.0	0.00
+	+	+	+	+			+	+	11	-1364.1	9.0	0.00
+		+	+	+			+		9	-1364.1	9.1	0.00
+	+	+	+	+		+		+	11	-1364.0	9.1	0.00
+		+	+		+		+		9	-1364.0	9.2	0.00
+	+	+	+		+	+	+		11	-1363.8	9.4	0.00
+		+	+	+	+				9	-1363.7	9.5	0.00
	+	+	+	+		+	+	+	11	-1363.7	9.5	0.00
+			+	+	+			+	9	-1363.5	9.6	0.00
+		+	+	+				+	9	-1363.5	9.7	0.00
+	+	+	+	+	+			+	11	-1363.4	9.7	0.00
		+	+	+			+	+	9	-1363.3	9.9	0.00
+	+		+	+	+	+		+	11	-1363.1	10.1	0.00
+	+	+	+	+	+	+	+		12	-1362.5	10.7	0.00
+	+	+	+	+		+	+	+	12	-1362.3	10.8	0.00
+		+	+	+	+		+		10	-1362.2	10.9	0.00
+	+	+	+	+	+		+	+	12	-1362.0	11.2	0.00
+	+	+	+	+	+	+		+	12	-1362.0	11.2	0.00
+		+	+	+			+	+	10	-1361.9	11.2	0.00
+		+	+	+	+			+	10	-1361.6	11.5	0.00
+	+	+	+	+	+	+	+	+	13	-1360.3	12.9	0.00

	+		+	+	+	+		+	+	11	-1360.1	13.1	0.00
g_{max} wing		+	+							6	319.2	0.0	0.07
		+	+		+					7	319.6	0.4	0.06
		+		+						6	319.6	0.4	0.05
		+	+	+						7	319.7	0.6	0.05
		+	+	+	+					8	320.3	1.1	0.04
	+	+	+							7	320.3	1.1	0.04
	+	+	+		+					8	320.5	1.3	0.04
	+	+		+						7	320.6	1.5	0.03
	+	+	+	+						8	320.9	1.7	0.03
		+	+	+				+		8	320.9	1.8	0.03
		+		+	+					7	321.0	1.9	0.03
	+	+	+	+	+					9	321.2	2.0	0.02
		+		+			+			7	321.5	2.3	0.02
		+	+	+			+			8	321.6	2.4	0.02
		+	+	+	+			+		9	321.7	2.5	0.02
	+	+		+	+					8	321.9	2.8	0.02
	+	+	+	+				+		9	322.0	2.8	0.02
		+								5	322.0	2.9	0.02
				+						5	322.0	2.9	0.02
		+	+	+	+		+			9	322.3	3.1	0.01
	+	+		+		+				8	322.3	3.1	0.01
	+	+	+	+		+				9	322.3	3.2	0.01

	+	+	+	+				+	9	322.4	3.3	0.01
+	+	+	+	+			+		10	322.5	3.4	0.01
+	+		+			+			8	322.6	3.4	0.01
+	+	+	+	+	+				10	322.6	3.4	0.01
+	+	+	+			+			9	322.8	3.6	0.01
		+							5	322.9	3.7	0.01
	+	+	+			+	+		9	322.9	3.7	0.01
+	+								6	323.0	3.8	0.01
	+		+	+		+			8	323.0	3.8	0.01
	+		+	+				+	8	323.2	4.0	0.01
+	+	+	+	+		+			10	323.2	4.1	0.01
									4	323.3	4.1	0.01
+	+	+	+	+				+	10	323.3	4.2	0.01
+			+						6	323.4	4.3	0.01
+	+	+	+		+		+		10	323.4	4.3	0.01
		+	+						6	323.5	4.3	0.01
+	+		+	+	+				9	323.6	4.4	0.01
	+	+	+	+		+	+		10	323.8	4.6	0.01
	+			+					6	323.8	4.6	0.01
			+	+					6	323.8	4.7	0.01
	+	+	+	+			+	+	10	323.8	4.7	0.01
+	+		+	+		+			9	323.9	4.8	0.01
+	+	+	+	+	+		+		11	324.0	4.8	0.01

+	+	+	+			+	+		10	324.0	4.9	0.01
+	+		+	+				+	9	324.1	4.9	0.01
+	+		+		+	+			9	324.3	5.1	0.01
+		+							6	324.3	5.2	0.01
		+		+					6	324.4	5.2	0.01
+	+	+	+		+	+			10	324.4	5.2	0.01
	+	+	+	+		+		+	10	324.4	5.3	0.00
+									5	324.6	5.4	0.00
+	+			+					7	324.6	5.5	0.00
+	+	+	+	+		+	+		11	324.7	5.5	0.00
+	+	+	+	+			+	+	11	324.7	5.5	0.00
		+	+				+		7	324.7	5.6	0.00
+	+	+	+	+	+	+			11	324.7	5.6	0.00
+	+	+	+	+	+			+	11	324.8	5.6	0.00
+		+	+						7	324.9	5.8	0.00
		+	+	+					7	325.0	5.9	0.00
	+		+	+		+		+	9	325.1	6.0	0.00
+			+	+					7	325.1	6.0	0.00
				+					5	325.2	6.1	0.00
+			+		+				7	325.3	6.1	0.00
+	+	+	+	+		+		+	11	325.4	6.3	0.00
+	+	+	+		+	+	+		11	325.6	6.4	0.00
+	+		+	+	+	+			10	325.7	6.5	0.00

+	+		+	+	+			+	10	325.7	6.6	0.00
+		+		+					7	325.7	6.6	0.00
			+	+				+	7	325.8	6.7	0.00
	+	+	+	+		+	+	+	11	325.9	6.8	0.00
+	+		+	+		+		+	10	326.1	7.0	0.00
+		+	+				+		8	326.1	7.0	0.00
+	+	+	+	+	+		+	+	12	326.1	7.0	0.00
+	+	+	+	+	+	+	+		12	326.2	7.0	0.00
		+	+	+			+		8	326.4	7.2	0.00
+		+	+	+					8	326.4	7.3	0.00
+				+					6	326.5	7.3	0.00
+		+	+		+				8	326.8	7.6	0.00
+	+	+	+	+		+	+	+	12	326.8	7.7	0.00
+	+	+	+	+	+	+		+	12	326.9	7.8	0.00
		+	+	+				+	8	327.0	7.8	0.00
+			+	+	+				8	327.0	7.9	0.00
+			+	+				+	8	327.2	8.0	0.00
+		+	+	+			+		9	327.7	8.6	0.00
+	+		+	+	+	+		+	11	327.9	8.7	0.00
+		+	+		+		+		9	328.0	8.8	0.00
+		+	+	+	+				9	328.3	9.1	0.00
+		+	+	+				+	9	328.4	9.2	0.00
+	+	+	+	+	+	+	+	+	13	328.4	9.2	0.00

			+	+	+			+	+	9	328.5	9.4	0.00
	+			+	+	+			+	9	329.1	9.9	0.00
	+		+	+	+	+		+		10	329.6	10.4	0.00
	+		+	+	+			+	+	10	329.9	10.7	0.00
	+		+	+	+	+			+	10	330.2	11.1	0.00
	+		+	+	+	+		+	+	11	331.7	12.6	0.00
A tarsus	+	+		+	+					7	604.7	0.0	0.09
	+	+		+						6	604.7	0.0	0.09
	+	+	+	+	+					8	604.8	0.1	0.08
	+	+		+	+				+	8	605.7	1.0	0.05
	+	+	+	+						7	605.9	1.2	0.05
	+	+	+	+	+				+	9	606.0	1.4	0.04
	+	+		+			+			7	606.5	1.8	0.03
	+	+		+	+		+			8	606.7	2.0	0.03
	+	+		+		+				7	606.7	2.0	0.03
	+	+		+	+	+				8	606.7	2.1	0.03
	+	+	+	+	+		+			9	606.8	2.1	0.03
	+	+	+	+	+			+		9	606.8	2.1	0.03
	+	+	+	+	+	+				9	606.9	2.2	0.03
		+		+	+					6	607.4	2.7	0.02
		+		+						5	607.6	2.9	0.02
	+	+	+	+			+			8	607.6	3.0	0.02
	+	+		+	+	+			+	9	607.8	3.1	0.02

+	+		+	+		+		+	9	607.8	3.1	0.02
	+	+	+	+					7	607.8	3.1	0.02
+	+	+	+		+				8	608.0	3.3	0.02
+	+	+	+				+		8	608.0	3.3	0.02
+	+	+	+	+		+		+	10	608.1	3.5	0.02
+	+	+	+	+	+			+	10	608.2	3.5	0.02
+	+	+	+	+			+	+	10	608.2	3.5	0.01
+	+		+		+	+			8	608.4	3.8	0.01
	+		+	+				+	7	608.5	3.9	0.01
+	+		+	+	+	+			9	608.7	4.0	0.01
+	+	+	+	+		+	+		10	608.8	4.1	0.01
+	+	+	+	+	+	+			10	608.8	4.2	0.01
+	+	+	+	+	+		+		10	608.9	4.3	0.01
	+	+	+						6	609.0	4.3	0.01
	+	+	+	+				+	8	609.2	4.5	0.01
	+		+			+			6	609.3	4.7	0.01
	+		+	+		+			7	609.3	4.7	0.01
+	+	+	+		+	+			9	609.7	5.0	0.01
+	+	+	+			+	+		9	609.8	5.1	0.01
	+	+	+	+		+			8	609.8	5.1	0.01
	+	+	+	+			+		8	609.8	5.1	0.01
+	+		+	+	+	+		+	10	609.8	5.1	0.01
+	+	+	+		+		+		9	610.1	5.4	0.01

	+	+	+	+	+	+	+		+	11	610.2	5.6	0.01
	+	+	+	+	+		+	+	+	11	610.3	5.6	0.01
	+	+	+	+	+	+		+	+	11	610.3	5.7	0.01
		+		+	+		+		+	8	610.6	5.9	0.00
		+	+	+			+			7	610.7	6.0	0.00
	+	+	+	+	+	+	+	+		11	610.9	6.2	0.00
		+	+	+				+		7	611.0	6.4	0.00
		+	+	+	+		+		+	9	611.2	6.5	0.00
		+	+	+	+			+	+	9	611.3	6.6	0.00
		+	+	+	+		+	+		9	611.7	7.0	0.00
	+	+	+	+		+	+	+		10	611.8	7.1	0.00
	+	+	+	+	+	+	+	+	+	12	612.4	7.7	0.00
		+	+	+			+	+		8	612.8	8.1	0.00
		+	+	+	+		+	+	+	10	613.3	8.7	0.00
	+			+						5	616.7	12.1	0.00
				+						4	616.7	12.1	0.00
				+	+					5	617.9	13.2	0.00
	+			+	+					6	618.0	13.4	0.00
	+			+		+				6	618.6	13.9	0.00
			+	+						5	618.8	14.1	0.00
	+		+	+						6	618.8	14.2	0.00
				+	+				+	6	619.8	15.1	0.00
	+			+	+	+				7	619.9	15.3	0.00

+			+	+			+	7	619.9	15.3	0.00
		+	+	+				6	619.9	15.3	0.00
+		+	+	+				7	620.1	15.5	0.00
+		+	+		+			7	620.7	16.1	0.00
		+	+			+		6	620.9	16.2	0.00
+		+	+			+		7	620.9	16.3	0.00
+			+	+	+		+	8	621.8	17.2	0.00
		+	+	+			+	7	621.9	17.2	0.00
		+	+	+		+		7	622.0	17.3	0.00
+		+	+	+	+			8	622.0	17.4	0.00
+		+	+	+			+	8	622.1	17.4	0.00
+		+	+	+		+		8	622.2	17.6	0.00
+		+	+		+	+		8	622.9	18.2	0.00
		+	+	+		+	+	8	624.0	19.3	0.00
+		+	+	+	+		+	9	624.0	19.3	0.00
+		+	+	+	+	+		9	624.2	19.5	0.00
+		+	+	+		+	+	9	624.2	19.5	0.00
+		+	+	+	+	+	+	10	626.2	21.5	0.00
+	+	+		+				7	628.5	23.8	0.00
+	+	+						6	629.9	25.2	0.00
	+	+		+				6	630.9	26.2	0.00
	+	+						5	632.4	27.7	0.00
+	+							5	640.3	35.6	0.00

		+							4	641.4	36.7	0.00
			+						4	641.5	36.9	0.00
	+		+						5	641.9	37.2	0.00
	+	+			+				6	641.9	37.2	0.00
			+		+				5	642.4	37.7	0.00
		+			+				5	642.9	38.2	0.00
	+		+		+				6	642.9	38.2	0.00
									3	645.3	40.6	0.00
	+								4	645.8	41.1	0.00
					+				4	647.1	42.4	0.00
	+				+				5	647.7	43.0	0.00
B tarsus (log)	+	+	+						7	-412.3	0.0	0.03
	+	+	+	+	+		+		10	-412.3	0.0	0.03
		+	+	+	+		+		9	-412.1	0.2	0.03
		+	+		+				7	-412.1	0.2	0.03
	+	+	+		+				8	-412.1	0.2	0.03
		+	+						6	-412.0	0.3	0.02
	+	+	+	+	+	+	+	+	12	-412.0	0.3	0.02
			+	+	+		+		8	-411.9	0.4	0.02
	+	+	+	+	+		+	+	11	-411.8	0.4	0.02
	+	+	+	+			+		9	-411.7	0.5	0.02
	+	+	+	+	+	+	+		11	-411.7	0.5	0.02
			+		+				6	-411.7	0.5	0.02

	+	+	+	+		+	+	10	-411.7	0.6	0.02
			+	+				6	-411.7	0.6	0.02
+	+	+	+		+	+		10	-411.7	0.6	0.02
+		+	+	+		+		9	-411.6	0.7	0.02
	+	+	+	+	+	+	+	11	-411.5	0.8	0.02
+			+	+				7	-411.4	0.9	0.02
+	+	+	+					8	-411.3	0.9	0.02
	+	+	+	+	+	+		10	-411.3	1.0	0.02
+		+		+				7	-411.3	1.0	0.02
	+	+	+			+		8	-411.2	1.0	0.02
	+	+	+	+				8	-411.2	1.0	0.02
+	+	+	+	+				9	-411.2	1.1	0.02
	+	+	+					7	-411.0	1.2	0.02
+	+		+	+				8	-411.0	1.3	0.01
	+		+	+				7	-410.9	1.4	0.01
		+	+	+		+	+	9	-410.9	1.4	0.01
	+	+	+		+	+		9	-410.8	1.4	0.01
		+	+	+				7	-410.8	1.4	0.01
+		+	+	+		+	+	10	-410.5	1.7	0.01
		+						5	-410.5	1.8	0.01
+	+	+	+		+			9	-410.5	1.8	0.01
+		+	+	+				8	-410.4	1.9	0.01
+		+						6	-410.3	2.0	0.01

				+					5	-410.2	2.1	0.01
+	+	+	+	+	+		+		11	-410.2	2.1	0.01
+	+	+	+	+	+	+	+	+	13	-410.2	2.1	0.01
+				+					6	-410.1	2.2	0.01
+	+	+	+		+	+	+		11	-410.0	2.2	0.01
	+	+	+			+			8	-410.0	2.2	0.01
+	+	+	+	+		+			10	-410.0	2.3	0.01
			+	+				+	7	-410.0	2.3	0.01
+	+	+	+	+	+	+	+		12	-410.0	2.3	0.01
+	+		+	+		+			9	-409.9	2.4	0.01
	+	+	+	+		+			9	-409.9	2.4	0.01
+	+	+	+		+		+		10	-409.8	2.5	0.01
		+	+				+		7	-409.7	2.5	0.01
+		+	+				+		8	-409.7	2.5	0.01
+	+	+	+	+	+		+	+	12	-409.7	2.5	0.01
	+	+	+	+				+	9	-409.7	2.6	0.01
+			+	+				+	8	-409.6	2.6	0.01
+	+	+	+	+				+	10	-409.6	2.7	0.01
	+		+	+		+			8	-409.6	2.7	0.01
+	+		+	+				+	9	-409.6	2.7	0.01
	+		+	+				+	8	-409.5	2.7	0.01
+	+		+						7	-409.5	2.8	0.01
		+	+						6	-409.5	2.8	0.01

+		+	+	+	+		+		10	-409.5	2.8	0.01
+	+	+	+		+				9	-409.4	2.9	0.01
+		+	+						7	-409.3	3.0	0.01
+			+	+	+				8	-409.3	3.0	0.01
+			+						6	-409.2	3.1	0.01
+	+	+	+	+	+				10	-409.2	3.1	0.01
			+						5	-409.1	3.2	0.01
		+	+	+				+	8	-409.0	3.3	0.01
+	+		+			+			8	-409.0	3.3	0.01
	+		+						6	-409.0	3.3	0.01
+	+		+	+	+				9	-408.9	3.4	0.01
+	+			+					7	-408.8	3.4	0.01
+	+	+	+		+	+			10	-408.8	3.5	0.01
	+			+					6	-408.7	3.5	0.00
+	+		+	+		+		+	10	-408.7	3.6	0.00
+	+	+	+	+		+		+	11	-408.6	3.7	0.00
	+	+	+	+		+		+	10	-408.5	3.8	0.00
+		+	+	+				+	9	-408.5	3.8	0.00
	+		+	+		+		+	9	-408.4	3.8	0.00
+		+	+	+	+		+	+	11	-408.4	3.9	0.00
+		+	+	+	+				9	-408.3	4.0	0.00
	+		+			+			7	-408.2	4.1	0.00
+	+	+	+	+	+	+			11	-408.2	4.1	0.00

	+	+		+	+	+	+			10	-407.9	4.3	0.00
	+		+	+		+		+		9	-407.6	4.7	0.00
	+	+	+	+	+	+			+	11	-407.5	4.7	0.00
	+			+	+	+			+	9	-407.5	4.8	0.00
	+	+		+		+				8	-407.4	4.8	0.00
	+	+		+	+	+			+	10	-407.4	4.8	0.00
	+									5	-407.2	5.0	0.00
	+		+	+		+				8	-407.2	5.1	0.00
	+	+		+		+	+			9	-407.1	5.1	0.00
	+			+		+				7	-407.1	5.2	0.00
										4	-407.0	5.3	0.00
	+	+	+	+	+	+	+		+	12	-406.8	5.5	0.00
	+	+		+	+	+	+		+	11	-406.7	5.6	0.00
	+	+								6	-406.5	5.7	0.00
	+		+	+	+	+			+	10	-406.3	5.9	0.00
		+								5	-405.9	6.4	0.00
k tarsus			+	+				+		7	-605.6	0.0	0.07
										4	-605.6	0.0	0.07
				+						5	-605.5	0.1	0.07
			+	+						6	-605.1	0.5	0.06
		+	+	+			+	+		9	-603.8	1.8	0.03
			+							5	-603.8	1.8	0.03
		+		+						6	-603.7	1.9	0.03

	+						5	-603.7	1.9	0.03
				+			5	-603.6	2.0	0.03
		+	+	+		+	8	-603.6	2.0	0.03
+							5	-603.6	2.0	0.03
			+	+			6	-603.6	2.0	0.03
	+	+	+			+	8	-603.6	2.0	0.03
+		+	+			+	8	-603.6	2.1	0.03
	+		+		+		7	-603.5	2.1	0.02
+			+				6	-603.5	2.2	0.02
	+	+	+				7	-603.1	2.5	0.02
+		+	+				7	-603.1	2.5	0.02
		+	+	+			7	-603.1	2.6	0.02
	+	+	+		+		8	-602.6	3.0	0.02
	+		+	+			7	-601.9	3.7	0.01
+	+	+	+		+	+	10	-601.8	3.8	0.01
	+	+					6	-601.7	3.9	0.01
		+		+			6	-601.7	3.9	0.01
+		+					6	-601.7	3.9	0.01
	+			+			6	-601.7	3.9	0.01
	+	+	+	+	+	+	10	-601.7	3.9	0.01
+	+		+				7	-601.7	3.9	0.01
+	+						6	-601.6	4.0	0.01
+				+			6	-601.6	4.0	0.01

	+	+	+	+			+		9	-601.6	4.0	0.01
+			+	+					7	-601.5	4.1	0.01
		+	+	+			+	+	9	-601.5	4.1	0.01
+		+	+	+			+		9	-601.5	4.1	0.01
	+		+	+		+			8	-601.5	4.1	0.01
+	+	+	+				+		9	-601.5	4.1	0.01
			+	+				+	7	-601.5	4.2	0.01
+	+		+			+			8	-601.4	4.2	0.01
+		+	+		+		+		9	-601.4	4.2	0.01
+			+		+				7	-601.3	4.3	0.01
	+	+	+	+					8	-601.0	4.6	0.01
+	+	+	+						8	-601.0	4.6	0.01
+		+	+		+				8	-601.0	4.7	0.01
+		+	+	+					8	-601.0	4.7	0.01
		+	+	+				+	8	-600.9	4.7	0.01
+	+	+	+			+			9	-600.5	5.1	0.01
	+	+	+	+		+			9	-600.5	5.2	0.01
+	+		+	+					8	-599.8	5.8	0.00
	+		+	+				+	8	-599.8	5.8	0.00
+	+	+	+		+	+	+		11	-599.8	5.8	0.00
	+	+	+	+		+	+	+	11	-599.8	5.8	0.00
	+	+		+					7	-599.7	5.9	0.00
+	+	+							7	-599.7	6.0	0.00

+		+		+					7	-599.7	6.0	0.00
+	+			+					7	-599.6	6.0	0.00
+	+	+	+	+		+	+		11	-599.6	6.0	0.00
+	+		+		+				8	-599.5	6.1	0.00
	+	+	+	+			+	+	10	-599.5	6.1	0.00
+	+	+	+	+			+		10	-599.5	6.2	0.00
+		+	+	+			+	+	10	-599.4	6.2	0.00
+			+	+	+				8	-599.4	6.2	0.00
+	+		+	+		+			9	-599.4	6.2	0.00
+			+	+				+	8	-599.4	6.2	0.00
+	+		+		+	+			9	-599.4	6.2	0.00
+		+	+	+	+		+		10	-599.4	6.3	0.00
	+		+	+		+		+	9	-599.3	6.3	0.00
+	+	+	+		+		+		10	-599.3	6.3	0.00
	+	+	+	+				+	9	-598.9	6.7	0.00
+	+	+	+	+					9	-598.9	6.7	0.00
+	+	+	+		+				9	-598.9	6.8	0.00
+		+	+	+				+	9	-598.8	6.8	0.00
+		+	+	+	+				9	-598.8	6.8	0.00
+	+	+	+		+	+			10	-598.5	7.1	0.00
+	+	+	+	+		+			10	-598.4	7.3	0.00
	+	+	+	+		+		+	10	-598.3	7.3	0.00
+	+		+	+				+	9	-597.7	7.9	0.00

	+	+	+	+	+		+	+	+	12	-597.7	7.9	0.00
	+	+		+	+	+				9	-597.7	7.9	0.00
	+	+	+	+	+	+	+	+		12	-597.6	8.0	0.00
	+	+	+		+					8	-597.6	8.0	0.00
	+	+	+	+	+			+	+	11	-597.3	8.3	0.00
	+	+		+	+	+	+			10	-597.3	8.3	0.00
	+	+	+	+	+	+		+		11	-597.3	8.3	0.00
	+		+	+	+	+		+	+	11	-597.2	8.4	0.00
	+			+	+	+			+	9	-597.2	8.4	0.00
	+	+		+	+		+		+	10	-597.2	8.4	0.00
	+	+	+	+	+				+	10	-596.8	8.9	0.00
	+	+	+	+	+	+				10	-596.7	8.9	0.00
	+		+	+	+	+			+	10	-596.7	8.9	0.00
	+	+	+	+	+	+	+			11	-596.3	9.3	0.00
	+	+	+	+	+		+		+	11	-596.2	9.5	0.00
	+	+	+	+	+	+	+	+	+	13	-595.7	10.0	0.00
	+	+		+	+	+			+	10	-595.5	10.1	0.00
	+	+		+	+	+	+		+	11	-595.1	10.5	0.00
	+	+	+	+	+	+		+	+	12	-595.1	10.5	0.00
	+	+	+	+	+	+			+	11	-594.6	11.0	0.00
	+	+	+	+	+	+	+		+	12	-594.1	11.5	0.00
g_{max} tarsus										4	242.6	0.0	0.12
			+							5	244.0	1.3	0.06

			+				5	244.3	1.7	0.05
		+	+			+	7	244.3	1.7	0.05
+							5	244.6	2.0	0.04
		+	+				6	244.6	2.0	0.04
				+			5	244.6	2.0	0.04
	+						5	244.7	2.1	0.04
+		+					6	246.0	3.3	0.02
	+	+					6	246.0	3.4	0.02
		+		+			6	246.0	3.4	0.02
	+	+	+		+	+	9	246.1	3.4	0.02
			+	+			6	246.3	3.6	0.02
+			+				6	246.3	3.6	0.02
+		+	+			+	8	246.3	3.7	0.02
	+		+				6	246.4	3.7	0.02
		+	+	+		+	8	246.4	3.8	0.02
	+	+	+			+	8	246.4	3.8	0.02
	+		+		+		7	246.5	3.9	0.02
+				+			6	246.6	4.0	0.02
+		+	+				7	246.6	4.0	0.02
	+	+	+				7	246.7	4.0	0.02
+	+						6	246.7	4.1	0.02
		+	+	+			7	246.7	4.1	0.02
	+			+			6	246.7	4.1	0.02

	+	+	+			+			8	247.0	4.4	0.01
+	+	+							7	248.0	5.4	0.01
+	+	+	+			+	+		10	248.0	5.4	0.01
+		+		+					7	248.1	5.4	0.01
	+	+		+					7	248.1	5.5	0.01
	+	+	+	+		+	+		10	248.2	5.6	0.01
+			+	+					7	248.2	5.6	0.01
	+		+	+					7	248.3	5.7	0.01
+	+		+						7	248.4	5.7	0.01
+			+		+				7	248.4	5.7	0.01
			+	+				+	7	248.4	5.7	0.01
		+	+	+			+	+	9	248.4	5.8	0.01
+	+	+	+				+		9	248.4	5.8	0.01
+		+	+	+			+		9	248.4	5.8	0.01
+	+		+			+			8	248.5	5.8	0.01
+		+	+		+		+		9	248.5	5.8	0.01
	+	+	+	+			+		9	248.5	5.9	0.01
	+		+	+		+			8	248.6	6.0	0.01
+	+	+	+						8	248.7	6.1	0.01
+	+			+					7	248.7	6.1	0.01
+		+	+	+					8	248.8	6.1	0.01
+		+	+		+				8	248.8	6.1	0.01
	+	+	+	+					8	248.8	6.2	0.01

		+	+	+				+	8	248.8	6.2	0.01
+	+	+	+			+			9	249.0	6.4	0.00
	+	+	+	+		+			9	249.2	6.5	0.00
	+	+	+	+		+	+	+	11	250.0	7.4	0.00
+	+	+	+		+	+	+		11	250.1	7.4	0.00
+	+	+		+					8	250.1	7.5	0.00
+	+	+	+	+		+	+		11	250.2	7.6	0.00
+	+		+	+					8	250.4	7.7	0.00
+			+	+	+				8	250.4	7.7	0.00
+			+	+				+	8	250.4	7.8	0.00
+		+	+	+			+	+	10	250.5	7.8	0.00
	+		+	+				+	8	250.5	7.8	0.00
+	+		+		+				8	250.5	7.9	0.00
	+	+	+	+			+	+	10	250.5	7.9	0.00
+	+		+		+	+			9	250.5	7.9	0.00
+	+	+	+	+			+		10	250.6	7.9	0.00
+	+		+	+		+			9	250.6	7.9	0.00
+	+	+	+		+		+		10	250.6	8.0	0.00
+		+	+	+	+		+		10	250.6	8.0	0.00
	+		+	+		+		+	9	250.7	8.1	0.00
+	+	+	+		+				9	250.9	8.2	0.00
+	+	+	+	+					9	250.9	8.2	0.00
+		+	+	+				+	9	250.9	8.3	0.00

+		+	+	+	+				9	250.9	8.3	0.00
	+	+	+	+				+	9	251.0	8.3	0.00
+	+	+	+		+	+			10	251.1	8.5	0.00
+	+	+	+	+		+			10	251.2	8.5	0.00
	+	+	+	+		+		+	10	251.3	8.7	0.00
+	+	+	+	+		+	+	+	12	252.0	9.4	0.00
+	+	+	+	+	+	+	+		12	252.3	9.6	0.00
+	+		+	+	+				9	252.5	9.9	0.00
+	+		+	+				+	9	252.5	9.9	0.00
+			+	+	+			+	9	252.5	9.9	0.00
+	+	+	+	+			+	+	11	252.6	10.0	0.00
+		+	+	+	+		+	+	11	252.7	10.0	0.00
+	+		+	+	+	+			10	252.7	10.1	0.00
+	+		+	+		+		+	10	252.7	10.1	0.00
+	+	+	+	+	+		+		11	252.8	10.1	0.00
+	+	+	+	+				+	10	253.0	10.4	0.00
+	+	+	+	+	+				10	253.0	10.4	0.00
+		+	+	+	+			+	10	253.1	10.4	0.00
+	+	+	+	+	+	+			11	253.3	10.6	0.00
+	+	+	+	+		+		+	11	253.4	10.7	0.00
+	+	+	+	+	+	+	+	+	13	254.1	11.4	0.00
+	+		+	+	+			+	10	254.7	12.1	0.00
+	+	+	+	+	+		+	+	12	254.8	12.2	0.00

	+	+		+	+	+	+		+	11	254.9	12.2	0.00
	+	+	+	+	+	+			+	11	255.2	12.6	0.00
	+	+	+	+	+	+	+		+	12	255.5	12.8	0.00
A body mass				+						5	1706.4	0.0	0.13
			+	+						6	1707.8	1.5	0.06
	+			+						6	1708.2	1.8	0.05
		+		+						6	1708.3	1.9	0.05
				+	+					6	1708.3	1.9	0.05
				+	+				+	7	1708.3	2.0	0.05
			+	+	+				+	8	1709.2	2.8	0.03
	+			+		+				7	1709.2	2.9	0.03
		+	+	+						7	1709.5	3.1	0.03
			+	+	+					7	1709.6	3.2	0.03
	+		+	+						7	1709.6	3.3	0.03
			+	+				+		7	1709.9	3.5	0.02
	+			+	+					7	1710.1	3.8	0.02
	+	+		+						7	1710.2	3.8	0.02
		+		+	+					7	1710.2	3.8	0.02
	+			+	+				+	8	1710.2	3.8	0.02
		+		+			+			7	1710.4	4.0	0.02
		+		+	+				+	8	1710.4	4.1	0.02
	+		+	+		+				8	1710.6	4.2	0.02
			+	+	+			+	+	9	1710.8	4.5	0.01

	+	+	+	+				+	9	1711.0	4.6	0.01
+		+	+	+				+	9	1711.0	4.7	0.01
	+	+	+	+					8	1711.1	4.7	0.01
+			+	+	+			+	9	1711.1	4.7	0.01
+	+		+		+				8	1711.1	4.8	0.01
+			+	+	+				8	1711.2	4.8	0.01
+		+	+	+					8	1711.4	5.0	0.01
+	+	+	+						8	1711.4	5.1	0.01
	+	+	+				+		8	1711.6	5.2	0.01
	+	+	+			+			8	1711.6	5.3	0.01
		+	+	+			+		8	1711.6	5.3	0.01
+		+	+	+	+			+	10	1711.7	5.3	0.01
+		+	+				+		8	1711.7	5.4	0.01
+	+		+	+					8	1712.1	5.7	0.01
+	+	+	+		+				9	1712.2	5.8	0.01
+	+		+			+			8	1712.3	5.9	0.01
	+		+	+		+			8	1712.3	6.0	0.01
+	+		+	+				+	9	1712.3	6.0	0.01
+		+	+	+	+				9	1712.3	6.0	0.01
	+		+	+		+		+	9	1712.6	6.2	0.01
+		+	+	+			+	+	10	1712.7	6.3	0.01
	+	+	+	+			+	+	10	1712.7	6.3	0.01
+		+	+		+		+		9	1712.7	6.3	0.01

+	+	+	+	+				+	10	1713.0	6.6	0.00
+	+	+	+	+					9	1713.0	6.7	0.00
+	+		+	+	+				9	1713.1	6.7	0.00
	+	+	+	+			+		9	1713.1	6.8	0.00
	+	+	+	+		+		+	10	1713.2	6.8	0.00
+	+		+	+	+			+	10	1713.2	6.8	0.00
	+	+	+	+		+			9	1713.2	6.8	0.00
+	+		+		+	+			9	1713.2	6.9	0.00
+		+	+	+	+		+	+	11	1713.3	7.0	0.00
+	+	+	+	+	+			+	11	1713.4	7.1	0.00
+		+	+	+			+		9	1713.5	7.1	0.00
+	+	+	+				+		9	1713.5	7.2	0.00
+	+	+	+			+			9	1713.6	7.2	0.00
+	+	+	+	+	+				10	1713.7	7.3	0.00
	+	+	+			+	+		9	1713.8	7.4	0.00
+	+		+	+		+			9	1714.3	7.9	0.00
+	+	+	+		+	+			10	1714.3	7.9	0.00
+	+	+	+		+		+		10	1714.3	8.0	0.00
+		+	+	+	+		+		10	1714.4	8.1	0.00
+	+		+	+		+		+	10	1714.5	8.1	0.00
+	+	+	+	+			+	+	11	1714.6	8.3	0.00
	+	+	+	+		+	+	+	11	1714.8	8.5	0.00
+	+	+	+	+	+		+	+	12	1715.1	8.7	0.00

+	+	+	+	+			+		10	1715.1	8.7	0.00
+	+	+	+	+		+		+	11	1715.1	8.8	0.00
+	+		+	+	+	+			10	1715.2	8.8	0.00
+	+	+	+	+		+			10	1715.2	8.8	0.00
	+	+	+	+		+	+		10	1715.3	9.0	0.00
+	+		+	+	+	+		+	11	1715.3	9.0	0.00
+	+	+	+	+	+	+		+	12	1715.6	9.2	0.00
+	+	+	+			+	+		10	1715.7	9.3	0.00
+	+	+	+	+	+	+			11	1715.8	9.4	0.00
+	+	+	+	+	+		+		11	1715.8	9.5	0.00
+	+	+	+		+	+	+		11	1716.5	10.1	0.00
+	+	+	+	+		+	+	+	12	1716.8	10.4	0.00
+	+	+	+	+		+	+		11	1717.3	10.9	0.00
+	+	+	+	+	+	+	+	+	13	1717.3	11.0	0.00
+	+	+	+	+	+	+	+		12	1718.0	11.6	0.00
		+							5	1731.6	25.2	0.00
		+		+					6	1733.1	26.7	0.00
	+	+							6	1733.2	26.9	0.00
+		+							6	1733.3	27.0	0.00
	+	+		+					7	1734.4	28.1	0.00
+		+		+					7	1734.9	28.5	0.00
+	+	+							7	1735.1	28.7	0.00
+	+	+		+					8	1736.4	30.0	0.00

								4	1747.2	40.8	0.00
		+						5	1748.9	42.6	0.00
	+							5	1749.1	42.7	0.00
					+			5	1749.2	42.8	0.00
	+	+						6	1750.7	44.4	0.00
		+			+			6	1750.9	44.5	0.00
	+				+			6	1751.1	44.7	0.00
	+	+			+			7	1752.7	46.3	0.00
B body mass (log)		+		+	+			7	-367.2	0.0	0.09
		+		+	+		+	8	-366.5	0.7	0.06
				+	+			6	-366.0	1.2	0.05
	+	+		+	+			8	-365.7	1.5	0.04
		+			+			6	-365.2	1.9	0.03
		+	+	+	+			8	-365.2	2.0	0.03
		+		+	+	+		8	-365.1	2.1	0.03
	+	+		+	+		+	9	-365.0	2.2	0.03
					+			5	-364.9	2.2	0.03
				+	+		+	7	-364.7	2.5	0.03
		+		+				6	-364.6	2.6	0.02
		+	+		+			7	-364.4	2.8	0.02
		+	+	+	+		+	9	-364.4	2.8	0.02
		+		+	+	+	+	9	-364.3	2.9	0.02
	+			+	+			7	-364.2	3.0	0.02

+	+		+	+	+				9	-364.0	3.2	0.02
		+	+	+					7	-364.0	3.2	0.02
+	+			+					7	-363.7	3.4	0.02
+	+	+	+	+					9	-363.7	3.5	0.02
+	+		+	+		+			9	-363.6	3.6	0.02
+	+		+						7	-363.4	3.8	0.01
	+	+	+						7	-363.3	3.9	0.01
	+	+	+	+			+		9	-363.2	4.0	0.01
+				+					6	-363.1	4.0	0.01
		+		+					6	-363.1	4.1	0.01
+	+		+	+	+			+	10	-363.1	4.1	0.01
	+	+	+	+		+			9	-363.0	4.2	0.01
+	+	+		+					8	-362.9	4.3	0.01
+	+	+	+	+				+	10	-362.9	4.3	0.01
+	+		+	+		+		+	10	-362.8	4.3	0.01
	+	+	+	+			+	+	10	-362.8	4.4	0.01
+			+	+				+	8	-362.8	4.4	0.01
		+	+	+				+	8	-362.6	4.6	0.01
	+	+							6	-362.6	4.6	0.01
	+		+			+			7	-362.5	4.7	0.01
			+						5	-362.4	4.8	0.01
+			+	+	+				8	-362.3	4.9	0.01
	+	+	+	+		+		+	10	-362.2	5.0	0.01

+		+	+	+					8	-362.1	5.1	0.01
+	+	+	+						8	-362.1	5.1	0.01
		+	+	+			+		8	-362.0	5.1	0.01
+	+	+	+	+	+				10	-362.0	5.2	0.01
+	+		+	+	+	+			10	-361.9	5.3	0.01
	+								5	-361.8	5.4	0.01
+	+	+	+	+			+		10	-361.7	5.5	0.01
+	+		+		+				8	-361.7	5.5	0.01
+	+	+	+	+		+			10	-361.5	5.7	0.01
+	+	+							7	-361.4	5.8	0.01
+	+		+			+			8	-361.4	5.8	0.00
+	+	+	+	+			+	+	11	-361.3	5.9	0.00
+		+		+					7	-361.3	5.9	0.00
	+	+	+			+			8	-361.2	6.0	0.00
	+	+	+				+		8	-361.2	6.0	0.00
		+	+	+			+	+	9	-361.1	6.1	0.00
+	+		+	+	+	+		+	11	-361.1	6.1	0.00
+	+	+	+	+	+			+	11	-361.0	6.2	0.00
	+	+	+	+		+	+		10	-361.0	6.2	0.00
+			+	+	+			+	9	-360.8	6.4	0.00
+		+	+	+				+	9	-360.8	6.4	0.00
	+	+	+	+		+	+	+	11	-360.7	6.5	0.00
+	+	+	+	+		+		+	11	-360.7	6.5	0.00

+			+						6	-360.7	6.5	0.00
									4	-360.6	6.6	0.00
+	+								6	-360.6	6.6	0.00
+	+	+	+		+				9	-360.5	6.7	0.00
		+	+						6	-360.4	6.8	0.00
+		+	+	+			+		9	-360.2	7.0	0.00
+		+	+	+	+				9	-360.2	7.0	0.00
+	+	+	+			+			9	-360.0	7.2	0.00
+	+	+	+				+		9	-360.0	7.2	0.00
+	+	+	+	+	+		+		11	-360.0	7.2	0.00
+	+	+	+	+	+	+			11	-359.9	7.3	0.00
+	+		+		+	+			9	-359.8	7.4	0.00
		+							5	-359.7	7.5	0.00
+	+	+	+	+		+	+		11	-359.5	7.7	0.00
+	+	+	+	+	+		+	+	12	-359.4	7.7	0.00
+	+	+	+	+		+	+	+	12	-359.3	7.9	0.00
+		+	+	+			+	+	10	-359.2	8.0	0.00
	+	+	+			+	+		9	-359.1	8.1	0.00
+	+	+	+	+	+	+		+	12	-359.0	8.2	0.00
+									5	-359.0	8.2	0.00
+			+		+				7	-358.8	8.4	0.00
+		+	+	+	+			+	10	-358.7	8.5	0.00
+		+	+						7	-358.7	8.5	0.00

	+	+	+	+		+	+			10	-358.6	8.6	0.00
	+	+	+	+		+		+		10	-358.4	8.8	0.00
			+	+				+		7	-358.3	8.9	0.00
	+		+	+	+	+		+		10	-358.2	9.0	0.00
	+		+							6	-358.0	9.2	0.00
	+	+	+	+			+	+		10	-357.9	9.3	0.00
	+	+	+	+	+	+	+	+		12	-357.9	9.3	0.00
	+	+	+	+	+	+	+	+	+	13	-357.5	9.6	0.00
	+		+	+	+	+		+	+	11	-357.2	10.0	0.00
	+		+	+		+				8	-356.7	10.4	0.00
	+		+	+				+		8	-356.6	10.6	0.00
	+	+	+	+		+	+	+		11	-356.5	10.7	0.00
	+		+	+		+		+		9	-354.7	12.5	0.00
k body mass										3	-802.8	0.0	0.14
		+								4	-801.5	1.3	0.07
					+					4	-801.2	1.6	0.06
				+						4	-801.1	1.7	0.06
	+									4	-800.9	1.9	0.06
			+							4	-800.7	2.1	0.05
	+	+								5	-799.7	3.1	0.03
		+			+					5	-799.7	3.1	0.03
		+		+						5	-799.6	3.2	0.03
				+	+					5	-799.5	3.3	0.03

	+	+							5	-799.4	3.4	0.03
+				+					5	-799.3	3.5	0.02
+			+						5	-799.2	3.6	0.02
		+		+					5	-799.1	3.7	0.02
		+	+						5	-799.0	3.8	0.02
+		+							5	-798.8	4.0	0.02
			+	+				+	6	-798.4	4.4	0.02
	+		+			+			6	-798.3	4.5	0.01
+	+			+					6	-798.0	4.9	0.01
	+		+	+					6	-797.9	4.9	0.01
+	+		+						6	-797.8	5.0	0.01
	+	+	+						6	-797.7	5.1	0.01
+	+	+							6	-797.7	5.1	0.01
+			+	+					6	-797.6	5.2	0.01
	+	+		+					6	-797.6	5.2	0.01
		+	+	+					6	-797.4	5.4	0.01
+			+		+				6	-797.3	5.5	0.01
+		+		+					6	-797.2	5.6	0.01
+		+	+						6	-797.1	5.7	0.01
	+		+	+				+	7	-797.0	5.8	0.01
		+	+				+		6	-797.0	5.8	0.01
+			+	+				+	7	-796.5	6.3	0.01
+	+		+			+			7	-796.5	6.3	0.01

	+		+	+		+			7	-796.4	6.4	0.01
		+	+	+				+	7	-796.3	6.5	0.01
	+	+	+			+			7	-796.3	6.5	0.01
+	+		+	+					7	-796.1	6.7	0.01
+	+	+	+						7	-795.9	6.9	0.00
+	+		+		+				7	-795.9	6.9	0.00
+	+	+		+					7	-795.8	7.0	0.00
	+	+	+	+					7	-795.8	7.0	0.00
	+		+	+		+		+	8	-795.8	7.0	0.00
+			+	+	+				7	-795.7	7.1	0.00
	+	+	+				+		7	-795.6	7.2	0.00
+		+	+	+					7	-795.5	7.3	0.00
		+	+	+			+		7	-795.3	7.5	0.00
+	+		+	+				+	8	-795.3	7.5	0.00
+		+	+		+				7	-795.2	7.6	0.00
+		+	+				+		7	-795.0	7.8	0.00
	+	+	+	+				+	8	-794.9	7.9	0.00
+			+	+	+			+	8	-794.6	8.2	0.00
+	+		+	+		+			8	-794.6	8.2	0.00
		+	+	+			+	+	8	-794.5	8.3	0.00
+	+	+	+			+			8	-794.5	8.3	0.00
+	+		+		+	+			8	-794.4	8.4	0.00
+		+	+	+				+	8	-794.4	8.4	0.00

	+	+	+	+		+			8	-794.3	8.5	0.00
	+	+	+			+	+		8	-794.2	8.6	0.00
+	+		+	+	+				8	-794.1	8.7	0.00
+	+	+	+	+					8	-794.1	8.8	0.00
+	+		+	+		+		+	9	-794.0	8.8	0.00
+	+	+	+		+				8	-793.9	8.9	0.00
+	+	+	+				+		8	-793.8	9.0	0.00
	+	+	+	+			+		8	-793.7	9.1	0.00
	+	+	+	+		+		+	9	-793.6	9.2	0.00
+		+	+	+	+				8	-793.5	9.3	0.00
+		+	+	+			+		8	-793.4	9.4	0.00
+	+		+	+	+			+	9	-793.3	9.5	0.00
+	+	+	+	+				+	9	-793.2	9.7	0.00
	+	+	+	+			+	+	9	-793.1	9.7	0.00
+		+	+		+		+		8	-793.1	9.7	0.00
+		+	+	+			+	+	9	-792.6	10.2	0.00
+	+	+	+	+		+			9	-792.6	10.2	0.00
+	+		+	+	+	+			9	-792.5	10.3	0.00
+		+	+	+	+			+	9	-792.5	10.3	0.00
+	+	+	+			+	+		9	-792.5	10.4	0.00
+	+	+	+		+	+			9	-792.4	10.4	0.00
	+	+	+	+		+	+		9	-792.3	10.5	0.00
+	+	+	+	+	+				9	-792.0	10.8	0.00

		+	+	+	+		+	+	+	10	-792.0	10.8	0.00
	+	+	+	+	+			+		9	-792.0	10.9	0.00
	+	+		+	+	+	+		+	10	-791.9	10.9	0.00
	+	+	+	+	+		+		+	10	-791.9	10.9	0.00
	+	+	+	+		+		+		9	-791.8	11.0	0.00
	+		+	+	+	+		+		9	-791.5	11.3	0.00
	+	+	+	+	+			+	+	10	-791.3	11.5	0.00
	+	+	+	+	+	+			+	10	-791.2	11.6	0.00
	+		+	+	+	+		+	+	10	-790.7	12.1	0.00
	+	+	+	+	+		+	+		10	-790.5	12.3	0.00
	+	+	+	+	+	+	+			10	-790.4	12.4	0.00
	+	+	+	+		+	+	+		10	-790.3	12.5	0.00
	+	+	+	+	+		+	+	+	11	-790.3	12.5	0.00
	+	+	+	+	+	+		+		10	-789.9	12.9	0.00
	+	+	+	+	+	+	+		+	11	-789.7	13.1	0.00
	+	+	+	+	+	+		+	+	11	-789.3	13.5	0.00
	+	+	+	+	+	+	+	+		11	-788.3	14.5	0.00
	+	+	+	+	+	+	+	+	+	12	-788.1	14.7	0.00
g_{max} body mass										3	-802.8	0.0	0.14
		+								4	-801.5	1.3	0.07
					+					4	-801.2	1.6	0.06
				+						4	-801.1	1.7	0.06
	+									4	-800.9	1.9	0.06

		+						4	-800.7	2.1	0.05
+	+							5	-799.7	3.1	0.03
	+			+				5	-799.7	3.1	0.03
	+		+					5	-799.6	3.2	0.03
			+	+				5	-799.5	3.3	0.03
	+	+						5	-799.4	3.4	0.03
+				+				5	-799.3	3.5	0.02
+			+					5	-799.2	3.6	0.02
		+		+				5	-799.1	3.7	0.02
		+	+					5	-799.0	3.8	0.02
+		+						5	-798.8	4.0	0.02
			+	+			+	6	-798.4	4.4	0.02
	+		+			+		6	-798.3	4.5	0.01
+	+			+				6	-798.0	4.9	0.01
	+		+	+				6	-797.9	4.9	0.01
+	+		+					6	-797.8	5.0	0.01
	+	+	+					6	-797.7	5.1	0.01
+	+	+						6	-797.7	5.1	0.01
+			+	+				6	-797.6	5.2	0.01
	+	+		+				6	-797.6	5.2	0.01
		+	+	+				6	-797.4	5.4	0.01
+			+		+			6	-797.3	5.5	0.01
+		+		+				6	-797.2	5.6	0.01

+		+	+						6	-797.1	5.7	0.01
	+		+	+				+	7	-797.0	5.8	0.01
		+	+				+		6	-797.0	5.8	0.01
+			+	+				+	7	-796.5	6.3	0.01
+	+		+			+			7	-796.5	6.3	0.01
	+		+	+		+			7	-796.4	6.4	0.01
		+	+	+				+	7	-796.3	6.5	0.01
	+	+	+			+			7	-796.3	6.5	0.01
+	+		+	+					7	-796.1	6.7	0.01
+	+	+	+						7	-795.9	6.9	0.00
+	+		+		+				7	-795.9	6.9	0.00
+	+	+		+					7	-795.8	7.0	0.00
	+	+	+	+					7	-795.8	7.0	0.00
	+		+	+		+		+	8	-795.8	7.0	0.00
+			+	+	+				7	-795.7	7.1	0.00
	+	+	+				+		7	-795.6	7.2	0.00
+		+	+	+					7	-795.5	7.3	0.00
		+	+	+			+		7	-795.3	7.5	0.00
+	+		+	+				+	8	-795.3	7.5	0.00
+		+	+		+				7	-795.2	7.6	0.00
+		+	+				+		7	-795.0	7.8	0.00
	+	+	+	+				+	8	-794.9	7.9	0.00
+			+	+	+			+	8	-794.6	8.2	0.00

+	+		+	+		+			8	-794.6	8.2	0.00
		+	+	+			+	+	8	-794.5	8.3	0.00
+	+	+	+			+			8	-794.5	8.3	0.00
+	+		+		+	+			8	-794.4	8.4	0.00
+		+	+	+				+	8	-794.4	8.4	0.00
	+	+	+	+		+			8	-794.3	8.5	0.00
	+	+	+			+	+		8	-794.2	8.6	0.00
+	+		+	+	+				8	-794.1	8.7	0.00
+	+	+	+	+					8	-794.1	8.8	0.00
+	+		+	+		+		+	9	-794.0	8.8	0.00
+	+	+	+		+				8	-793.9	8.9	0.00
+	+	+	+				+		8	-793.8	9.0	0.00
	+	+	+	+			+		8	-793.7	9.1	0.00
	+	+	+	+		+		+	9	-793.6	9.2	0.00
+		+	+	+	+				8	-793.5	9.3	0.00
+		+	+	+			+		8	-793.4	9.4	0.00
+	+		+	+	+			+	9	-793.3	9.5	0.00
+	+	+	+	+				+	9	-793.2	9.7	0.00
	+	+	+	+			+	+	9	-793.1	9.7	0.00
+		+	+		+		+		8	-793.1	9.7	0.00
+		+	+	+			+	+	9	-792.6	10.2	0.00
+	+	+	+	+		+			9	-792.6	10.2	0.00
+	+		+	+	+	+			9	-792.5	10.3	0.00

+		+	+	+	+			+	9	-792.5	10.3	0.00
+	+	+	+			+	+		9	-792.5	10.4	0.00
+	+	+	+		+	+			9	-792.4	10.4	0.00
	+	+	+	+		+	+		9	-792.3	10.5	0.00
+	+	+	+	+	+				9	-792.0	10.8	0.00
	+	+	+	+		+	+	+	10	-792.0	10.8	0.00
+	+	+	+	+			+		9	-792.0	10.9	0.00
+	+		+	+	+	+		+	10	-791.9	10.9	0.00
+	+	+	+	+		+		+	10	-791.9	10.9	0.00
+	+	+	+		+		+		9	-791.8	11.0	0.00
+		+	+	+	+		+		9	-791.5	11.3	0.00
+	+	+	+	+			+	+	10	-791.3	11.5	0.00
+	+	+	+	+	+			+	10	-791.2	11.6	0.00
+		+	+	+	+		+	+	10	-790.7	12.1	0.00
+	+	+	+	+		+	+		10	-790.5	12.3	0.00
+	+	+	+	+	+	+			10	-790.4	12.4	0.00
+	+	+	+		+	+	+		10	-790.3	12.5	0.00
+	+	+	+	+		+	+	+	11	-790.3	12.5	0.00
+	+	+	+	+	+		+		10	-789.9	12.9	0.00
+	+	+	+	+	+	+		+	11	-789.7	13.1	0.00
+	+	+	+	+	+		+	+	11	-789.3	13.5	0.00
+	+	+	+	+	+	+	+		11	-788.3	14.5	0.00
+	+	+	+	+	+	+	+	+	12	-788.1	14.7	0.00

Table S3. Parameters (bootstrapped means and 95% confidence intervals) of the logistic models (A – asymptote, B – constant of integration, k – growth rate constant), fitted to the biometrics of individual Whiskered Terns which died during the nestling period, separately for males (M) and females (F), N – number of measured individuals used to estimate parameters, only individuals which died before fledging were used in the averaging.

Body measurement	sex	A ± SD	B ± SD	k ± SD	g_{max}	N
Total head length	M	55.38 ± 1.050	1.14 ± 0.057	0.172 ± 0.0143	2.38 ± 0.164	10
	F	56.17 ± 1.494	1.13 ± 0.044	0.152 ± 0.0145	2.13 ± 0.154	20
Tarsus	M	23.17 ± 0.416	0.76 ± 0.037	0.201 ± 0.0234	1.17 ± 0.121	22
	F	22.90 ± 0.278	0.76 ± 0.028	0.211 ± 0.0208	1.20 ± 0.107	36
Wing	M	152.1 ± 8.57	14.29 ± 1.166	0.219 ± 0.0150	8.32 ± 0.283	22
	F	157.0 ± 6.13	14.81 ± 0.882	0.224 ± 0.0116	8.79 ± 0.258	36
Body mass	M	79.07 ± 3.500	8.13 ± 0.783	0.309 ± 0.0281	6.08 ± 0.403	22
	F	80.54 ± 2.163	7.96 ± 0.596	0.291 ± 0.0156	5.85 ± 0.266	36

Załączniki do publikacji

Banach A, Flis A, Kusal B, Łożyńska H, Ledwoń M (2024) Sex ratio and sex-specific chick mortality in a species with moderate sexual size dimorphism and female brood desertion. J Ornithol, https://doi.org/10.1007/s10336-024-02182-z

Table S1. Generalized linear mixed model used to test the possible influence of factors on the sex of hatchlings (N=1472). 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. '+' denotes the presence of a given effect in the model. Model include the intercept and the random effect of nest, colony and year.

Intercept	Date	Hatchlings	Success	Volume	df	logLik	AIC	ΔAIC	ωAIC
-0.3047					4	-926.734	1861.5	0.00	0.245
-0.3067				-0.05446	5	-926.302	1862.6	1.14	0.139
-0.3433			+		5	-926.678	1863.4	1.89	0.095
-0.3045		0.007632			5	-926.725	1863.4	1.98	0.091
-0.3028	-0.007383				5	-926.731	1863.5	1.99	0.090
-0.3477			+	-0.05492	6	-926.239	1864.5	3.01	0.054
-0.3065		0.011540		-0.05532	6	-926.281	1864.6	3.10	0.052
-0.3056	-0.004108			-0.05437	6	-926.301	1864.6	3.13	0.051
-0.3519		-0.006873	+		6	-926.673	1865.3	3.88	0.035
-0.3414	-0.007810		+		6	-926.674	1865.3	3.88	0.035
-0.3026	-0.007837	0.007788			6	-926.721	1865.4	3.98	0.034
-0.3466	-0.004535		+	-0.05482	7	-926.238	1866.5	5.01	0.020
-0.3498		-0.001764	+	-0.05482	7	-926.238	1866.5	5.01	0.020
-0.3053	-0.004723	0.011640		-0.05522	7	-926.280	1866.6	5.09	0.019
-0.3499	-0.007524	-0.006677	+		7	-926.670	1867.3	5.87	0.013
-0.3487	-0.004476	-0.001655	+	-0.05472	8	-926.237	1868.5	7.01	0.007

Table S2. Generalized linear mixed models used to test the possible influence of factors on the sex of fledglings (N=1102). 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 include the intercept and the random effect of nest, colony and year.

Intercept	Date	Fledglings	Volume	df	logLik	AIC	ΔAIC	ωAIC
-0.1675			-0.1602	5	-755.955	1521.9	0.00	0.453
-0.1671		0.03083	-0.1631	6	-755.838	1523.7	1.77	0.187
-0.1637	-0.03827		-0.1594	6	-755.855	1523.7	1.80	0.184
-0.1632	-0.03924	0.03145	-0.1623	7	-755.733	1525.5	3.56	0.077
-0.1709				4	-759.154	1526.3	4.40	0.050
-0.1658	-0.04548			5	-759.022	1528.0	6.14	0.021
-0.1707		0.01596		5	-759.123	1528.2	6.34	0.019
-0.1655	-0.04612	0.01680		6	-758.987	1530.0	8.07	0.008

Table S3. Generalized linear mixed models used to test the possible influence of factors on the sex of chicks’ survival (N=1317). 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). ‘×’ stands for an interaction term; ‘+’ denotes the presence of a given effect in the model.Model include the intercept and the random effect of nest, colony and year.

Intercept	Date	Hatchlings	Sex	Volume	Date×Sex	Hatchlings×Sex	Volume×Sex	df	logLik	AIC	ΔAIC	ωAIC
2.175	0.2412	-0.2947	+	0.26710			+	9	-535.783	1089.6	0.00	0.143
2.208		-0.2956	+	0.26990			+	8	-537.018	1090.0	0.47	0.113
2.175	0.2375	-0.2831	+					7	-538.330	1090.7	1.10	0.083
2.212		-0.2843	+					6	-539.520	1091.0	1.47	0.068
2.180	0.2646	-0.3459	+	0.26140		+	+	10	-535.627	1091.3	1.69	0.061
2.170	0.2048	-0.2956	+	0.26750	+		+	10	-535.695	1091.4	1.83	0.057

2.218		-0.3512	+	0.27420		+	+	9	-536.816	1091.6	2.07	0.051
2.178	0.2338	-0.2927	+	0.10730				8	-537.862	1091.7	2.16	0.049
2.214		-0.2946	+	0.11260				7	-539.008	1092.0	2.45	0.042
2.176	0.2366	-0.3178	+			+		8	-538.240	1092.5	2.91	0.033
2.175	0.2008	-0.2842	+		+			8	-538.242	1092.5	2.92	0.033
2.213		-0.3204	+			+		7	-539.422	1092.8	3.28	0.028
2.329	0.2367	-0.2798						6	-540.493	1093.0	3.42	0.026
2.173	0.2062	-0.3486	+	0.27200	+	+	+	11	-535.494	1093.0	3.42	0.026
2.372		-0.2809						5	-541.702	1093.4	3.84	0.021
2.180	0.1989	-0.2935	+	0.10670	+			9	-537.782	1093.6	4.00	0.019
2.200	0.2161	-0.3345	+	0.10670		+		9	-537.805	1093.6	4.05	0.019
2.216		-0.3317	+	0.11290		+		8	-538.906	1093.8	4.25	0.017
2.335	0.2331	-0.2889		0.10080				7	-540.074	1094.1	4.58	0.014
2.180	0.1965	-0.3168	+		+	+		9	-538.150	1094.3	4.73	0.013
2.372		-0.2907		0.10620				6	-541.237	1094.5	4.91	0.012
2.161	0.2379		+	0.23990			+	8	-539.267	1094.5	4.97	0.012
2.194			+	0.24100			+	7	-540.531	1095.1	5.50	0.009
2.167	0.2340		+					6	-541.548	1095.1	5.53	0.009
2.179	0.1970	-0.3302	+	0.10700	+	+		10	-537.683	1095.4	5.80	0.008
2.199			+					5	-542.762	1095.5	5.96	0.007
2.169	0.2121		+	0.24540	+		+	9	-539.231	1096.5	6.90	0.005
2.169	0.2316		+	0.08347				7	-541.259	1096.5	6.95	0.004
2.201			+	0.08746				6	-542.444	1096.9	7.32	0.004
2.167	0.1997		+		+			7	-541.472	1096.9	7.38	0.004
2.320	0.2335							5	-543.675	1097.3	7.78	0.003
2.353								4	-544.908	1097.8	8.25	0.002
2.169	0.1988		+	0.08262	+			8	-541.189	1098.4	8.81	0.002
2.324	0.2312			0.07707				6	-543.424	1098.8	9.28	0.001
2.356				0.08138				5	-544.629	1099.3	9.69	0.001

Table S4. Generalized linear mixed models tested possible variation in the sex of hatchlings depending on exact egg volume and other factors (N=545). 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 include the Intercept and the random effect of nest, colony and year.

Intercept	Date	Hatchlings	Success	Volume	df	logLik	AIC	ΔAIC	ωAIC
0.95940			+		5	-310.068	630.1	0.00	0.213
0.97550			+	-0.2111	6	-309.668	631.3	1.20	0.117
-0.04818					4	-311.896	631.8	1.66	0.093
-0.09546		-0.37930			5	-310.930	631.9	1.72	0.090
0.84980		-0.08154	+		6	-310.042	632.1	1.95	0.081
0.96200	0.03368		+		6	-310.061	632.1	1.99	0.079
-0.05508				-0.1896	5	-311.571	633.1	3.01	0.047
-0.09695		-0.37290		-0.1795	6	-310.636	633.3	3.14	0.044
0.89960		-0.05620	+	-0.2080	7	-309.655	633.3	3.17	0.044
0.97800	0.03282		+	-0.2111	7	-309.661	633.3	3.19	0.043
-0.04818	0.01549				5	-311.895	633.8	3.65	0.034
-0.09547	0.01285	-0.37930			6	-310.929	633.9	3.72	0.033
0.85370	0.03148	-0.08031	+		7	-310.036	634.1	3.94	0.030
-0.05514	0.01565			-0.1897	6	-311.570	635.1	5.00	0.017
-0.09695	0.01258	-0.37290		-0.1796	7	-310.635	635.3	5.14	0.016
0.90350	0.03137	-0.05503	+	-0.2081	8	-309.650	635.3	5.16	0.016

Table S5. Generalized linear mixed models tested possible variation in the hatching success depending on exact egg volume and other factors (N=246). 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 include the Intercept and the random effect of nest, colony and year.

Intercept	Date	Eggs	Volume	df	logLik	AIC	ΔAIC	ωAIC
0.6208				4	-159.210	326.4	0.00	0.306
0.6235			0.1303	5	-158.749	327.5	1.08	0.179
0.6232		0.1111		5	-158.879	327.8	1.34	0.157
0.6208	-0.0004397			5	-159.210	328.4	2.00	0.113
0.6255		0.1057	0.1257	6	-158.449	328.9	2.48	0.089
0.6235	-0.0031360		0.1304	6	-158.749	329.5	3.08	0.066
0.6233	0.0239700	0.1164		6	-158.864	329.7	3.31	0.059
0.6255	0.0201400	0.1102	0.1251	7	-158.438	330.9	4.46	0.033

Oświadczenia współautorów

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Oświadczam, że w pracy

Banach A, Neubauer G, Flis A, Ledwoń M (2021) Sex-specific growth of nestlings of the Whiskered Tern *Chlidonias hybrida*, a species with sexual size dimorphism and female brood desertion. J Ornithol 162:1035–1047. https://doi.org/10.1007/s10336-021-01911-y

mój wkład polegał na: pomocy w przeprowadzeniu analiz statystycznych, przygotowaniu grafik przedstawiających wyniki analiz, współudziale w korekcie manuskryptu.

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