Sex-specific growth in chicks of the sexually dimorphic Black-tailed Godwit

Loonstra, A. H. Jelle; Verhoeven, Mo A.; Piersma, Theunis

Published in:
Ibis

DOI:
10.1111/ibi.12541

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2018

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the “Taverne” license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.
Sex-specific growth in chicks of the sexually dimorphic Black-tailed Godwit

A. H. JELLE LOONSTRA,1* MO A. VERHOEVEN1 & THEUNIS PIERSMA1,2
1Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands
2Department of Coastal Systems and Utrecht University, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB, Den Burg, Texel, The Netherlands

Sexual size dimorphism (SSD) is common in birds and has been linked to various selective forces. Nevertheless, the question of how and when the sexes start to differentiate from each other is poorly studied. This is a critical knowledge gap, as sex differences in growth may cause different responses to similar ecological conditions. In this study, we describe the sex-specific growth – based on body mass and five morphometric measurements – of 56 captive Black-tailed Godwit Limosa limosa limosa chicks raised under ad libitum food conditions, and conclude that all six growth curves are sex-specific. Females are the larger sex in terms of body mass and skeletal body size. To test whether sex-specific growth leads to sex-specific susceptibility to environmental conditions, we compared the age-specific sizes of male and female chicks in the wild with those of Black-tailed Godwits reared in captivity. We then tested for a relationship between residual growth and relative hatching date, age, sex and habitat type in which the wild chicks were born. Early-hatched chicks were relatively bigger and in better condition than late-hatched chicks, but body condition and size were not affected by natal habitat type. Female chicks deviated more negatively from the sex-specific growth curves than male chicks for body mass and total-head length. This suggests that the growth of the larger females is more susceptible to limiting environmental conditions. On average, the deviations of wild chicks from the predicted growth curves were negative for all measurements, which suggests that conditions are limiting in the current agricultural landscape. We argue that in estimating growth curves for sexually dimorphic species, it is critical first to make accurate sex and age determinations.

Keywords: chick growth, environmental susceptibility, Gompertz growth curve, Limosa limosa limosa, logistic growth curve, sex-specific growth, waders.

Structural differences in size between males and females are observed in a wide range of animals (Fairbairn 1997). Sexual size dimorphism (hereafter: SSD) varies across taxa; the degree and direction of SSD varies among populations of the same species, among species, and among the broader groupings of birds, mammals and insects (Darwin 1871, Shine 1989, Weatherhead & Teather 1994, Stillwell et al. 2010). Variation in SSD has been linked to various selective forces, each of which has differential effects on the sexes: for example, fecundity selection leading to increased female size or sexual selection leading to increased male size (Székely et al. 2000, Serrano-Meneses & Székely 2006, Lislevand et al. 2009). If the costs of raising the two sexes differ due to different developmental patterns, such as SSD, the more expensive sex could experience a higher mortality rate under unfavourable environmental conditions, thereby affecting population dynamics (Benito & Gonzáles-Solis 2007). Although the pattern of SSD in adults has been examined in numerous studies, only a few studies have investigated the development of SSD (Cox & John-Alder 2007, Dietrich-Bischoff et al. 2008, Klenovšek &

*Corresponding author.
Email: a.h.j.loonstra@rug.nl
Kryštufek 2013, Lok et al. 2014). This is a real knowledge gap, as studies such as these might be able to explain SSD in an ecologically informed developmental sense (Stillwell et al. 2014, Chou et al. 2016).

SSD in adults has been observed to come about in three different ways, or any combination of these three. First, SSD can emerge during the prenatal phase, meaning that males and females differ in their embryonic growth rate. This can be caused by either inherited differences or differences in maternal investment between males and females (Cordero et al. 2000, Sellier 2000, Helle et al. 2013). Secondly, SSD can start to occur after hatch but before fledging, as a result of differences in the duration or rate of growth (Leigh & Shea 1995, Hasumi 2010, Zhang & Liu 2013, Lok et al. 2014). Thirdly, SSD can result from body-size-related differences in survival within or between differently sized males and females (Kersten & Brenninkmeijer 1995, Badyaev et al. 2001).

If variation in growth between individuals during a developmental stage is explained by inherited differences (including the effects of sex), the growth of different individuals may have different susceptibilities to similar environmental conditions (Richner 1991, Kalmbach et al. 2005). For instance, it is commonly assumed that the larger sex requires higher energetic demands to reach their adult size and may therefore be more sensitive to a shortage of resources (Anderson et al. 1993, Krijgsveld et al. 1998). This could result in a longer developmental time for the larger sex, an increase in mortality risk due to starvation or a greater likelihood of being predated (Manicom et al. 2014). To fully understand the degree of phenotypic plasticity in SSD, it is necessary to understand how and whether the sexes differ in their susceptibility to similar ecological conditions during the stage in which individuals grow (Badyaev 2002, Blanckenhorn 2005).

Here we examine sex-based growth differences of body mass and five different morphometric measurements in a shorebird, the Continental Black-tailed Godwit (Limosa limosa limosa). The Continental Black-tailed Godwit (hereafter: ‘Godwit’) is a medium-sized sexually dimorphic wader species. Although females are larger than males in body mass, wing, bill, total-head, tarsus and tarsus–toe length (Schroeder et al. 2008), sex-based differences in growth rate during the pre-fledging period have not yet been evaluated for Godwits (Beintema & Visser 1989). Using 56 captive-reared chicks, we were able to estimate sex-specific growth curves for body mass, and for the linear measurements of wing, bill, total-head, tarsus and tarsus–toe length. We then estimated the susceptibility of growth of the two sexes to relative hatch date and natal habitat type by comparing the measurements of wild Godwit chicks with the predictions based on the growth curves of captive-reared chicks. This enabled us to test whether the growth of females and males is affected differentially by similar ecological conditions. As Godwit chicks are precocial, and are guided and protected by their parents only during the pre-fledging period, the size and body condition of a chick during the pre-fledging period largely reflects the environmental conditions it has experienced.

**METHODS**

**Study population**

The study was conducted in south-west Friesland, The Netherlands (52°55’N, 5°25’E), during the breeding seasons of 2007–2010 and 2012–2016. The study area consists mostly of grassland that is managed primarily for dairy farming, along with some reserves for breeding meadow birds (Groen et al. 2012). Although the decline of Godwits in The Netherlands is ongoing (Kentie et al. 2016), our study area still holds a relatively high, and relatively stable, number of breeding Godwits (Groen et al. 2012, Kentie et al. 2017). To classify the management type and thus the quality of each field for Godwit chicks, we assigned fields into two classes on the basis of herb richness and the presence of foot drains (Groen et al. 2012, Kentie et al. 2013). In referring to these two habitat types, we use the names ‘meadows’ for fields that have been previously associated with relatively good growing conditions for Godwit chicks, and ‘monocultures’ for fields that were linked with poorer growing conditions (complete description in Kentie et al. 2013).

From 2007 to 2010 we studied Godwits in a 8780-ha area. In 2012 the study area was enlarged to 10 280 ha. Godwits are present in the study area from early March until late July (Gill et al. 2007). Nest initiation starts in the first week of April, and nesting attempts made after the failure of one or more previous nests can be observed until the first week of June (Senner et al. 2015). Precocial Godwit chicks hatch after an incubation
period of approximately 21 days and fledge when c. 25 days old (pers. obs.); after this period, chicks can be accompanied by their parents for another 1 or 2 weeks (pers. obs.).

**Chicks raised in captivity and in the wild**

To obtain standardized and repeated growth measurements of chicks, we reared Godwit chicks in captivity under ad libitum food conditions. We collected 64 eggs within our study area in 2016 and incubated them in an incubator (Heka STANDARD 9) at a temperature of 37.5 °C and a relative humidity of 55–60%. After successful hatching 56 chicks, we individually marked them with a plastic engraved flag with a unique code of three characters. Chicks were kept inside for 1 week, and 100-W infrared lamps were used to provide them with extra warmth during this period.

Chicks were housed in cages of 6.25 m², with individuals divided equally between eight cages. To prevent group effects, we shuffled the chicks between these cages every day in a random order. After the initial period of 1 week, the chicks spent every other day outside in a 2500-m² enclosure in a meadow from 08:00 to 17:00 h. Indoors, these chicks were fed a commercially obtained waterfowl food (Micro Lundi, Lundi, Verl, Germany) and occasionally live buffalo worms (Alphitobius diaperinus). In the outdoor enclosures, the chicks were able to behave and forage as they would in the wild. Water was made available ad libitum in shallow bowls both indoors and outdoors. Day length conditions inside were similar to the conditions outside. At ages greater than 35 days, the chicks were colour-ringed and released in the wild.

To compare our captive-raised chicks with wild chicks, we recaptured previously ringed hatchlings (1 day old) in the nest with a plastic diaper (C6). In the outdoor enclosures, the chicks were able to behave and forage as they would in the wild. Water was made available ad libitum in shallow bowls both indoors and outdoors. Day length conditions inside were similar to the conditions outside. At ages greater than 35 days, the chicks were colour-ringed and released in the wild.

**Body size measurements**

Body size and mass measurements of the captive-reared chicks were taken between 07:00 and 08:00 h. These measurements were performed every day during the first 25 days, and every other day thereafter. For chicks from 0 to 5 days, body mass was measured using an electronic scale (± 0.1 g); chicks older than 5 days were weighed to the nearest 1 g on a larger electronic scale. We also measured the following linear dimensions in both wild and captive chicks: bill length (exposed culmen, ± 0.1 mm), total-head length (± 0.1 mm), wing length (flattened and straightened, ± 1 mm), tarsus length (± 0.1 mm) and tarsus–toe length (tarsus plus mid-toe without claw, ± 1 mm).

**Molecular sex identification**

To determine the genetic sex of each chick we obtained a ~ 10-μL blood sample from the leg vein after hatching. When an older chick (> 6 days) was recaptured, we took the blood sample from the brachial vein. Blood was stored in individual 1.5-mL Eppendorf tubes containing 97% alcohol buffer, and frozen at –80 °C as soon as possible. The genetic sexing techniques used are fully described in Schroeder et al. (2010).

**Statistical analysis**

All statistical analyses were performed using R (version 3.3.0, R Development Core Team 2016). For body mass and each morphometric measurement of the captive raised chicks, we assessed whether growth was best described by one of the two models typically used to describe avian growth: the Gompertz growth model, \( y_t = y_\infty \times \exp\left(-\exp\left(-k \times (t - T_i)\right)\right) \), and the logistic growth model, \( y_t = y_\infty/(1 + \exp\left(-k(t - T_i)\right)) \) (Ricklefs 1968, Tjørve & Tjørve 2010). In these formulas, \( y_t \) is value of the trait at age \( t \), \( y_\infty \) is the asymptotic value of the biometric trait, \( t \) is the age (in days), \( k \) is the growth coefficient and \( T_i \) is the age (in

<table>
<thead>
<tr>
<th>Biometric measurement</th>
<th>Sex</th>
<th>Body mass</th>
<th>Wing</th>
<th>Bill</th>
<th>Total-head</th>
<th>Tarsus</th>
<th>Tarsus-toe</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>114</td>
<td>107</td>
<td>110</td>
<td>109</td>
<td>78</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>90</td>
<td>87</td>
<td>89</td>
<td>86</td>
<td>78</td>
<td></td>
</tr>
</tbody>
</table>

**Table 1. Sample sizes of recaptured male and female Godwit chicks in the wild from 2007–2010 and 2012–2015.**
days) at the point of inflection. For both growth models we also evaluated sex differences in $y_{\infty}$, $k$ and $T_i$.

To test for an effect of sex on $y_{\infty}$, $k$ and $T_i$ of the captive-raised chicks we used non-linear mixed models (nlme package) (Lindstrom & Bates 1990, Pinheiro & Bates 2000, Pinheiro et al. 2012). We included chickID as a random effect, to account for pseudoreplication (Pinheiro & Bates 2000). However, models including a random effect for all three different growth parameters ($y_{\infty}$, $k$ and $T_i$) did not converge. A closer examination of the correlation between the estimated random effects revealed that they were highly correlated and that the model was overfitted (negative variances of the random effects).

Exploratory analyses showed that the convergence problems were solved when individuals were only allowed to vary randomly for asymptotic size ($y_{\infty}$). We therefore decided to only include a random effect for the asymptotic growth parameter ($y_{\infty}$). We then tested, using both growth functions (Gompertz and logistic), for an effect of sex on $y_{\infty}$, $k$ and $T_i$. As a result, we compared 16 different models. Models with $< 2 \Delta AIC_c$, and with the fewest parameters were considered to be the most parsimonious (Burnham & Anderson 2002, Arnold 2010).

**Comparing the growth of wild recaptured chicks with the fitted growth functions**

Secondly, we compared the linear and mass measurements of the recaptured wild chicks with the predicted value given by the best growth model, which was found on the basis of the captive raised chicks (see above). To do this, we calculated the residuals by subtracting the observed measurement from the predicted value. We then determined the relative difference of these residuals by comparing them with the predicted value of the measurement. Similar to Kentie et al. (2013), we assumed that the habitat type (‘meadow’ or ‘monoculture’) in which a chick hatched (natal habitat) is also the habitat type in which the chick grew up. To test whether hatching date influenced the growth of chicks, we calculated the difference between individual hatch date and the annual mean hatch date in our study area (hereafter relative hatching date). To statistically control for the unmeasured year to year variations in the phenology of arthropods (Reneerkens et al. 2016), we included year as an interaction in our models.

We tested whether the relative growth of chicks recaptured in the wild (relative to the predicted value of the captive-reared chicks) was affected by natal habitat type, year, relative hatching date, age (in days), sex and the interactions age \times sex, relative hatching date \times sex, relative hatching date \times year, year \times natal habitat type, age \times natal habitat type and natal habitat type \times relative hatching date. We did this by fitting linear mixed-effects models using the package lme4 (Bates et al. 2015).

As some chicks were recaptured more than once, we included chickID as a random effect. Unfortunately, in many wild recaptured chicks wing lengths were not measured, which precluded estimates of the interaction between year and relative hatch day, and year and natal habitat type. We started the analysis with a full model for each separate biometric measure, including all effects and their interactions. Subsequently, a stepwise backward procedure was followed to find the minimal adequate model (MAM) in which terms were deleted in order of decreasing $P$-value (Quinn & Keough 2005). All reported 95% confidence intervals for parameters that are included in the MAM were calculated with a parametric bootstrap (1000 iterations). The goodness-of-fit was calculated according to Xu (2003). We checked and confirmed the normality of the residuals by visually inspecting their QQ-plots (Miller 1986).

**RESULTS**

**Growth curves**

Based on the 26 females and 30 males that were raised in captivity, growth of the tarsus and tarsus-toe length were best described by a logistic growth curve, whereas bill, total-head, wing length and body mass were best described by a Gompertz growth curve (for model selection results, see Table 2 and Supporting Information Table S1). There was considerable support for growth differences between males and females for body mass (removing the sex effects for body mass led to a $\Delta AIC_c$ of 78.31) and all five linear body size measurements (tarsus $\Delta AIC_c = 207.77$, bill $\Delta AIC_c = 64.53$, tarsus-toe $\Delta AIC_c = 235.79$, wing $\Delta AIC_c = 38.57$, total-head $\Delta AIC_c = 171.97$; Fig. 1, Tables 2 and Table S1). Females had larger asymptotic values for all linear and mass
where a value of 0.00 corresponds to a weight of 0.00.

The most parsimonious model is shown in bold (i.e. the model with the fewest parameters among the supported models; AICc < 2). We only show the top five models; all models are shown in Supporting Information Table S1. aTesting the effect of sex on \( y_{oo}, k, T_i \) or no effect (–). bNo. of parameters in the model. cAICc weight, where a value of 0.00 corresponds to a weight of 0.00 – 4. dMinimum (-2logL) value observed. eMinimum AICc value observed.

Growth of recaptured wild chicks

The average deviation from the predicted growth for all measurements ranged from -16.0% for body mass to -5.7% for total-head length. There was no effect of natal habitat type, nor was there a significant interaction between natal habitat type and any of the other predictor variables used to model the amount of deviation from the predicted body mass and the five morphometric measurements (Table 4). There was also no evidence for an effect of age on the deviation in body mass (Table 4). However, recaptured females deviated on average 4.60% (95% CI -1.10 to -7.83%) more from the expected body mass than recaptured males (Fig. 2a, Table 4). Furthermore, residual body mass of chicks was negatively correlated with relative hatching date, but the extent differed between years (Fig. 2b, Table 4). In other words, early-hatched chicks were relatively heavier than late-hatched chicks. The deviation in wing length was negatively correlated with relative hatching date only, with chicks hatched later deviating more from the predicted length (relative hatch date: \( \beta = -0.51\% \), 95% CI -0.84 to -0.14) (Table 4).

The most parsimonious model for bill length growth included a negative correlation with age, revealing that the negative deviation from the predicted bill length increased with age (\( \beta = -0.35\% \), 95% CI -0.47 to -0.28%) (Table 4). Furthermore, the deviation in bill length of recaptured chicks was negatively correlated with relative hatching date (Table 4). For total-head length, we found a
Figure 1. Estimated growth curves for body mass, wing length, bill length, total-head length, tarsus length and tarsus–toe length based on the most parsimonious model in Table 2. The black line represents for each biometric measurement the growth for females and the grey line for males. Points represent the measurements of the captive-raised chicks, grey points represent females and open grey points represent males.

Table 3. Parameter estimation (mean ± se) of the growth curves (Gompertz or logistic) for bill, total-head, tarsus, tarsus–toe, wing length and body mass, based on the most parsimonious model in Table 2.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Growth function</th>
<th>Fixed effects</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>Gompertz</td>
<td>$y_0$</td>
<td>363 ± 7</td>
<td>298 ± 8</td>
<td>0.0737 ± 0.001</td>
<td>0.0737 ± 0.001</td>
<td>14.89 ± 0.17</td>
<td>13.98 ± 0.13</td>
</tr>
<tr>
<td>Bill</td>
<td>Gompertz</td>
<td>$k$</td>
<td>161 ± 5</td>
<td>147 ± 3</td>
<td>0.032 ± 0.0012</td>
<td>0.030 ± 0.0012</td>
<td>26.91 ± 0.80</td>
<td>26.91 ± 0.80</td>
</tr>
<tr>
<td>Total-head</td>
<td>Gompertz</td>
<td>$T_t$</td>
<td>181 ± 4</td>
<td>163 ± 5</td>
<td>0.034 ± 0.0008</td>
<td>0.029 ± 0.001</td>
<td>13.6 ± 0.66</td>
<td>9.00 ± 0.80</td>
</tr>
<tr>
<td>Tarsus</td>
<td>Logistic</td>
<td>$y_0$</td>
<td>84.9 ± 0.7</td>
<td>77.1 ± 0.9</td>
<td>0.142 ± 0.001</td>
<td>0.142 ± 0.001</td>
<td>3.38 ± 0.05</td>
<td>2.33 ± 0.08</td>
</tr>
<tr>
<td>Tarsus–toe</td>
<td>Logistic</td>
<td>$k$</td>
<td>131 ± 0.9</td>
<td>121 ± 1.2</td>
<td>0.127 ± 0.001</td>
<td>0.127 ± 0.001</td>
<td>-1.05 ± 0.07</td>
<td>-2.24 ± 0.08</td>
</tr>
<tr>
<td>Wing</td>
<td>Gompertz</td>
<td>$T_t$</td>
<td>221 ± 2.3</td>
<td>211 ± 2.9</td>
<td>0.098 ± 0.001</td>
<td>0.097 ± 0.001</td>
<td>13.62 ± 0.07</td>
<td>13.62 ± 0.07</td>
</tr>
</tbody>
</table>

© 2017 British Ornithologists' Union
significant interaction between sex and age: the positive deviation from the predicted length decreased slightly with age for males ($\beta = -0.01\%$, 95% CI $-5.50$ to $2.83\%$), and also decreased with age for females ($\beta = -0.59\%$, 95% CI $-5.83$ to $1.63\%$). Also, we found a negative effect of relative hatching date (Table 4). Relative residual tarsus length was negatively influenced by relative hatching date ($\beta = -0.20\%$, 95% CI $-0.33$ to $-0.05\%$), but positively influenced by the age of a chick (age: $\beta = 0.20\%$, 95% CI $-0.06$ to $0.34\%$) (Table 4). This suggests that any relative negative deviation decreased with age. Tarsus-toe length, which includes the length of the tarsus, was only negatively influenced by the relative hatching date ($\beta = -0.24\%$, 95% CI $-0.32$ to $-0.12\%$) (Table 4f).

**DISCUSSION**

**Development of sexual size dimorphism**

Our results show that a large part of the observed SSD in adult Continental Black-tailed Godwits develops during the pre-fledging period (Fig. 1). Males and females differed only slightly in their morphology at hatching, but differences between the sexes in wing, bill, total-head, tarsus, tarsus-toe length and body mass slowly increased during the pre-fledging period (Table 5). Differences in asymptotic values between males and females at the time of fledging were most pronounced in total-head and body mass, whereas the SSD for all estimated asymptotic values in most cases resembled the degree of SSD observed in adults (Table 5). However, asymptotic values of total-head, bill and wing length do not resemble the length of these structures in adult Godwits, indicating that birds still show growth after fledging (Fig. 1, Table 3) (Schroeder et al. 2008).

As the degree of SSD increased during the pre-fledging period, females must either grow faster than males, or show growth for a longer period. We found evidence for the first mechanism, as the maximum growth rates of females were higher than those of males for body mass and all five morphometric measurements. Assuming that there are no countervailing sex differences in the actual energetic costs of increasing body mass or structural size, this suggests that the energy demands during the pre-fledging period are higher for females than for males. However, we note that different metabolic rates or activity levels caused by different hormone levels could actually lead to the smaller sex having higher energy demands (Ros 1999, Eising et al. 2003). Therefore, to determine
whether female chicks require more energy during the pre-fledging phase, direct metabolic measurements are necessary (Vedder et al. 2005). We found that the growth curves for body mass and size were influenced by the sex of an individual. As suggested by Anderson et al. (1993), it is of crucial importance to calculate the inherited body size (e.g. as determined by sex) of an individual at a given age when inferring information about relative chick growth. Our results suggest that the use of non-sex-specific growth curves for Godwits provided by Beintema and Visser (1989) resulted in overestimates of female growth in later studies (Beintema 1994, Schekkerman & Boele 2009b, Schekkerman et al. 2009a, Kentie et al. 2013). Overestimations of body mass and structural size resulting from the use of non-sex-specific growth curves are likely to increase when the survival probabilities of males and females differ between habitat types. This could result in the selective disappearance of individuals with lower condition indexes, causing an overestimation of the condition index of chicks that are still alive and available for recapture (Kersten & Breninkimeijer 1995, Ruthrauff & McCaffery 2005).

We also show that the relative deviation in body mass and size in wild chicks were influenced by their environment. As a result, none of these measurements are suitable for estimating age (contra: Beintema & Visser 1989). Future studies on the growth of Godwit chicks should therefore include the genetic sexing of individuals (see discussion in Piersma & van der Velde 2009), and also the measured age of a chick to correctly estimate relative growth rate.

### Environmental susceptibility of growth

In line with the growing body of evidence that the larger sex is more vulnerable to poor growth conditions (Nager et al. 2000, Velando 2002, Müller et al. 2005), we found that the deviation from the predicted values of body mass and total-head length in wild recaptured chicks was higher in females than in males. However, we did not find an effect of sex on the deviation in growth of bill,

---

**Table 4.** Results of mixed models examining the effect of relative hatching date (noted as HD), age, sex, year (noted as y), natal habitat type (noted as: NH) and their interactions on the standardized residuals with the growth curve on body mass and body size (wing, bill, total-head, tarsus and tarsus-toe length).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Intercept</th>
<th>Age</th>
<th>Sex</th>
<th>HD</th>
<th>y2008 b</th>
<th>y2009</th>
<th>y2010</th>
<th>y2012</th>
<th>y2013</th>
<th>y2014</th>
<th>y2015</th>
<th>NH</th>
<th>Age × Sex</th>
<th>HD × Sex</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>-25.57***</td>
<td>-0.16</td>
<td>4.60*</td>
<td>-0.49*</td>
<td>3.43</td>
<td>-4.40</td>
<td>11.99</td>
<td>-2.87</td>
<td>11.88</td>
<td>-2.55**</td>
<td>13.23</td>
<td>4.33</td>
<td>-0.54</td>
<td>-0.09</td>
</tr>
<tr>
<td>Wing length</td>
<td>-12.08***</td>
<td>0.18</td>
<td>-3.07</td>
<td>-0.51***</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.56</td>
<td>-0.19</td>
<td>-0.23</td>
</tr>
<tr>
<td>Bill length</td>
<td>-3.24**</td>
<td>-0.35***</td>
<td>1.76</td>
<td>-0.16*</td>
<td>-1.46</td>
<td>-3.07</td>
<td>4.17</td>
<td>-4.02</td>
<td>4.47</td>
<td>-1.46</td>
<td>4.38</td>
<td>1.74</td>
<td>0.10</td>
<td>-0.16</td>
</tr>
<tr>
<td>Total-head length</td>
<td>-0.59*</td>
<td>-0.47***</td>
<td>6.05**</td>
<td>-0.19***</td>
<td>-2.44</td>
<td>-4.48</td>
<td>-2.13</td>
<td>-2.06</td>
<td>3.40</td>
<td>-3.03</td>
<td>2.32</td>
<td>1.09</td>
<td>0.60***</td>
<td>-0.02</td>
</tr>
<tr>
<td>Tarsus</td>
<td>-14.36***</td>
<td>0.20**</td>
<td>1.23</td>
<td>-0.20**</td>
<td>-2.18</td>
<td>-5.08</td>
<td>-1.60</td>
<td>-1.51</td>
<td>2.79</td>
<td>-2.94</td>
<td>1.79</td>
<td>1.10</td>
<td>-0.12</td>
<td>0.098</td>
</tr>
<tr>
<td>Tarsus-toe</td>
<td>-7.54***</td>
<td>0.09</td>
<td>0.45</td>
<td>-0.24***</td>
<td>-1.86</td>
<td>-2.42</td>
<td>2.79</td>
<td>-1.60</td>
<td>2.57</td>
<td>-1.32</td>
<td>0.04</td>
<td>1.26</td>
<td>-0.15</td>
<td>-0.04</td>
</tr>
</tbody>
</table>

Estimates of non-significant terms are from the last model before simplification. Variables that are maintained in the minimum adequate model after stepwise backward model selection are in bold. The effect size is noted as \( R^2 \). \(^*\)Reference level for sex is female. \(^\dagger\)Reference level for year is 2007. \(^\ddagger\)Reference level for natal habitat type is ‘monoculture’. \(^\star\)Significant at the 0.05 probability level. \(^**\)Significant at the 0.01 probability level. \(^***\)Significant at the 0.001 probability level.
tarsus, tarsus-toe or wing length. This indicates that different body sizes may be affected by environmental context in different ways. This in turn corroborates the idea that structural growth generally shows a less plastic response to limiting energetic conditions during development than does body mass (Schew & Ricklefs 1998, Moe et al. 2004, 2005). In precocial birds, this difference in the response of structural growth to limiting conditions could be more pronounced; a developmental delay in one of these structures (wing, tarsus, tarsus-toe) could delay the moment of fledging, thus potentially increasing mortality through starvation or predation.

We did not find a relationship between natal habitat type and the deviation of chick body mass, despite the fact that arthropods, the food of Godwit chicks, are more abundant in the meadow habitat type (Schekkerman & Beintema 2007, Schekkerman & Boele 2009b), in which Kentie et al. (2013) measured the fastest growth. However, Godwit chicks are highly mobile and may move up to several kilometres in the course of the pre-fledging period (Schekkerman et al. 2009a). Especially in the increasingly fragmented landscape of our study area (Groen et al. 2012), it is likely that chicks use both meadows and monocultures during development. To better interpret habitat use, chick growth and movements should be monitored on finer spatiotemporal scales than we have been able to. The fact that all the measurements of wild Godwit chicks deviated negatively from the predicted size of the captive Godwits chicks, which were not limited by food availability, suggests that wild chicks are hampered in their growth. Further studies on the growth rates of wild Godwit chicks are required to establish the nature of any such growth limitations.

In this study we standardized the deviation in size of recaptured chicks with the expected size at a certain age, but similar relative deviations in growth might have different consequences at different ages. If the amounts of ‘reserve’ nutrients stored increase with age, an older chick would have more resources to cover a period of food limitation, whereas similar incidents could be lethal for younger chicks. The opposite could be true for the linear dimensions, which only grow during a restricted period. In such cases, food limitations during and after this period would have different implications for the individual, as the older individuals would not be able to have any form of compensatory growth (Metcalfe & Monaghan 2001).
While we have shown that sex and several environmental conditions affect the growth of Godwit chicks differentially, we cannot confirm that the observed deviations from expected size are maintained into adulthood. Birds may still show compensatory growth after fledging (Pienkowski & Minton 1973, Davies et al. 1988, Larsson & Forslund 1991). Even if size deviations that started to emerge during the pre-fledging period are maintained in a later phase, selective mortality can nevertheless cause the disappearance of certain individuals in the population (van Gils et al. 2016). Further studies should therefore investigate whether the survival probabilities of Godwit chicks and adults are size-dependent. In any case, if the degree of SSD or the structural size of an individual is influenced by variation in food resources, the use of linear measurements to identify sex of individuals should be replaced by genetic sexing.

We are grateful to the land management organizations ‘It Frysk Gea’ and ‘Staatsbosbeheer’ and the private landowners for granting us access to their properties. We thank our field crews from 2007 onwards and volunteers of local birding communities for locating nests and helping to catch and measure chicks in the field, data which have been curated by Jos Hooijmeijer and Rosemarie Kentie. We are especially grateful for the repeated measurements of the chicks in captivity to Bernice Brands, Livia de Felici, Wiebe Kaspersma, Manon Mulder, Tom Remmerswaal, Nina Schouten, Esmée Schutgens and Kyra Vervoorn. We thank Marco van der Velde, Yvonne Verkuil and Julie Thumloup for comments on the draft and for editing the text. This study was funded by the former Netherlands Ministry of Agriculture, the Province of Friesland, and the Spinoza Premium 2014 awarded to T.P. by the Netherlands Organization for Scientific Research. The work was done under licence numbers 6350A, 6350G and 6350H following the Dutch Animal Welfare Act Articles 9 and 11.

REFERENCES


Table 5. Sexual size dimorphism (SSD) in captive-raised Godwit hatchlings.

<table>
<thead>
<tr>
<th></th>
<th>Females n = 26</th>
<th>Males n = 30</th>
<th>SSD of captive raised hatchlings</th>
<th>SSD of estimated $y_{co}$</th>
<th>SSD of adult Godwits</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>sd</td>
<td>Range</td>
<td>Mean</td>
<td>sd</td>
</tr>
<tr>
<td>Body mass</td>
<td>28.9</td>
<td>1.90</td>
<td>25.1–32.4</td>
<td>28.4</td>
<td>2.09</td>
</tr>
<tr>
<td>Wing</td>
<td>18.4</td>
<td>2.24</td>
<td>15–23</td>
<td>18.2</td>
<td>1.88</td>
</tr>
<tr>
<td>Bill</td>
<td>16.9</td>
<td>0.84</td>
<td>14.8–19.1</td>
<td>16.4</td>
<td>0.99</td>
</tr>
<tr>
<td>Total-head</td>
<td>39.6</td>
<td>1.26</td>
<td>37.7–42.2</td>
<td>38.9</td>
<td>1.10</td>
</tr>
<tr>
<td>Tarsus</td>
<td>37.7</td>
<td>1.63</td>
<td>35.0–41.5</td>
<td>37.0</td>
<td>1.85</td>
</tr>
<tr>
<td>Tarsus-toe</td>
<td>76.6</td>
<td>2.92</td>
<td>72–82</td>
<td>75.1</td>
<td>3.07</td>
</tr>
</tbody>
</table>

Reported are means with standard deviations and comparison of SSD. SSD was calculated as female size divided by male size; body mass in grams, length in millimetres. SSD of chicks is based on the estimated $y_{co}$ from the chick growth data and SSD of adult birds is based on data obtained from Schroeder et al. (2008).
Sex-specific growth in Godwit chicks


Received 20 January 2017; revision accepted 20 September 2017.

Associate Editor: Ruedi Nager

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Detailed description of all models of Gompertz and logistic growth curves for body mass, tarsus, bill, tarsus–toe, wing and total-head length testing for an effect of sex on the different growth parameters.