



## **Interpreting Variation in Growth of Eurasian Spoonbill Chicks: Disentangling the Effects of Age, Sex and Environment**

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# Interpreting variation in growth of Eurasian Spoonbill chicks: disentangling the effects of age, sex and environment

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Chick body condition can be a sensitive indicator of local environmental conditions and has been shown to be correlated with chick survival. Designing a reliable index of chick body condition for a given species from a single measurement point requires knowledge about the extent of variation in body size, about chick age and about the relative sensitivity of the growth of different biometric measures to variation in environmental conditions. To gain this knowledge, we describe sex-specific variation in growth of several morphometric measures and body mass of Eurasian Spoonbills *Platalea leucorodia*. We repeatedly measured 35 chicks that grew up in small colonies on the island of Schiermonnikoog to derive detailed growth curves until fledging (based on the 12 surviving chicks) and to assess the extent of reduction in growth of starved chicks measured at least twice ( $n = 11$ ) compared to those that survived. Growth curves until fledging were compared with biometric measurements of two to five week old chicks from (mostly) larger colonies of which hatching date was accurately estimated ( $n = 631$ ). Growth of all measures, except the eighth primary, was sex-specific, with the most pronounced sex effect on the asymptotic values of tarsus length and body mass: adult males were predicted to become 17% heavier than females and to have 22% longer tarsi than females. Body mass and tarsus growth tended to be more reduced under food deprivation than (head-)bill and eighth primary growth. As an index of chick body condition, we propose to use the proportional deviation in body mass from the predicted body mass for a given age and sex. To do so, measurements of nearly fledged Spoonbill chicks should include at least eighth primary length to estimate age, tarsus length to estimate sex, and body mass as a measure that integrates age, sex and environmental effects.

**Key words:** age estimation, body condition index, chick growth, developmental plasticity, Gompertz growth curve, hatching order, logistic growth curve, *Platalea leucorodia*, waterbirds

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Chick growth rate can be a sensitive indicator of local environmental conditions (Schew & Ricklefs 1998). Under favourable environmental conditions, chicks tend to grow faster and as a result fledge earlier, larger or heavier (Gebhardt-Henrich & Richner 1998). Collecting the necessary data to determine individual growth rates requires much effort, disturbance and

money (Benson *et al.* 2003). To use chick growth rates as an indicator of the environmental quality of breeding sites through time and space, more efficient methods of assessing chick growth rates would therefore be useful. As body mass growth has been shown to be sensitive to environmental conditions (Nilsson & Svensson 1996, Schew & Ricklefs 1998), an often used metric of chick

growth performance (or body condition, a term often used when specifically referring to body mass) from a single measurement point is the deviation in body mass from the predicted body mass, either for a given age (Beintema & Visser 1989, Hamer & Hill 1993, Bolton 1995, Quillfeldt *et al.* 2006, Schekkerman *et al.* 2009, Kentie *et al.* 2013) or for a given length of a morphometric measure (Beintema 1994, Benson *et al.* 2003). Indices of chick body condition have been shown to be correlated with pre- and post-fledging survival, as well as recruitment probability in a wide variety of species (e.g. de Kogel 1997, Gebhardt-Henrich & Richner 1998, van der Jeugd & Larsson 1998, Naef-Daenzer *et al.* 2001, Reid *et al.* 2003, Ruthrauff & McCaffery 2005). Which method is preferred, and which morphometric measure(s) should be used, depends on the extent of genetic and environmentally induced variation in chick body size.

If variation in chick body size for a given age is mostly genetic, chick body condition is preferably estimated as the residual body mass for a given length of a morphometric measure (or combination of measures) that accurately reflects body size. For example, in sexually size dimorphic species, the larger sex generally grows faster than the smaller sex (Anderson *et al.* 1993) and is therefore larger for a given age. This method requires that the morphometric measure accurately reflects the genetic component of the body size of an individual and that its growth is relatively insensitive to environmental conditions. When the morphometric measure does not reflect the genetic component of body size, the body condition of genetically larger individuals (e.g. the larger sex) will be overestimated. When growth of the morphometric measure is sensitive to environmental conditions, variation in body condition will be underestimated. If variation in chick body size for a given age is mostly induced by the environment (instead of genetic), chick body condition is preferably estimated as the residual body mass for a given age (known or estimated from morphometric measures). To investigate which method should preferably be used to estimate chick body condition for a given species, it is therefore important to assess variation in growth rates for several morphometric measures and body mass to determine (1) which measures may reflect the genetic component of body size (i.e. show a linear relationship with body mass and are sex-specific for sexually size dimorphic species), (2) which measures are accurate for predicting age (i.e. show little variation in growth) and (3) the sensitivity of growth of the different measures and body mass to poor environmental conditions.

As part of a long-term research effort on the population biology of Eurasian Spoonbills *Platalea leucorodia leucorodia* (e.g. Bauchau *et al.* 1998, Lok *et al.* 2009, 2011, 2013), we here describe variation in growth of Spoonbill chicks on the island of Schiermonnikoog. To avoid undesired disturbance of large colonies, we selected nests in small colonies to collect high-resolution growth data on individual chicks (the regularly measured chicks). Using the chicks that survived to at least 27 days ( $n = 12$ ), we estimated growth curves for several morphometric measures and body mass, to determine which measures most accurately predicted chick age, and which were sex-specific (as males are larger than females in Spoonbills). To investigate the sensitivity of the growth of different morphometric measures and of body mass to poor environmental conditions, we compared the growth of chicks shortly before they died (presumably of starvation) with the growth of surviving chicks. Growth of the regularly measured chicks was compared with biometric measures of 2- to 5-week old chicks from other (often earlier and larger) colonies where age was estimated from head-bill length within two weeks after hatching ( $n = 631$ ), using the head-bill growth curve estimated from the regularly measured chicks. Finally, we advise how to estimate the body condition of Spoonbill chicks of two to five weeks old (i.e. the age at which they can be colour-ringed).

## METHODS

### Study population

We studied the breeding population of Eurasian Spoonbills on the island of Schiermonnikoog, The Netherlands (53°29'N, 6°15'E), during the breeding seasons of 2006–2009. A total of 208, 232, 217 and 223 nests were counted during these years (including some re-nesting attempts), spread over 11 or 12 colonies (with inter-colony distances of 100 m to 3 km), varying in size from 1 to 60 nests. Most Spoonbills on Schiermonnikoog breed on the ground in saltmarsh habitat. Adult birds forage on small fish and shrimps in shallow fresh- and saltwater creeks in the vicinity of the colony (El-Hacen *et al.* 2014).

The breeding season of Spoonbills on Schiermonnikoog is long, with egg-laying occurring between late March and early July. Spoonbills usually lay an egg every second day and have a clutch size of three to four eggs (pers. obs., Cramp & Simmons 1977). Incubation usually starts one or two days after the first egg has been laid and causes asynchronous hatching, with the



**Figure 1.** Marking and measuring Spoonbill chicks.

- (A) Newly hatched chicks are marked with a coloured stain.
- (B) After one week, chicks are marked with a temporary label.
- (C) Measuring head-bill length with a calliper.
- (D) Measuring head-bill and head length with a special head-bill apparatus.
- (E) Measuring wing length on a newly hatched chick.
- (F) Measuring wing length on a 3-week old chick.



second, third and fourth chick in the nest hatching on average one, three and four days later than the first chick (pers. obs.). Incubation of the eggs takes 25 to 26 days ( $n = 4$ ) and the chicks are altricial (Cramp & Simmons 1977, Starck & Ricklefs 1998). Spoonbill chicks fledge when c. 35 days old, after which they are still fed by their parents for at least another month (Cramp & Simmons 1977).

### Growth measurements

The study area was scanned for new colonies every two weeks. For regular growth measurements, we selected colonies of three or four nests in 2006 and 2007, resulting in  $n = 35$  chicks from 11 nests (five in 2006 and six in 2007). When colonies were clearly established (i.e. clutches were completed and incubating birds would fly up only when approached closer than c. 50 m distance), nests were checked daily to determine the hatching date of each chick in the nest. After hatching, chicks were individually marked with a coloured stain (Figure 1A). When the joint between the tibia and the tarsus was thick enough (after one week), a uniquely labelled cotton band was attached with a stapler around the tibia of a chick (Figure 1B) which was again replaced by colour rings at the age of four to five weeks.

Chick growth parameters were measured every third day (with some exceptions, due to adverse weather), starting at the day of hatching (age 0). Recorded morphometric measures include the length of head-bill (also known as total-head, Sutherland *et al.* 2004; measured with a calliper for young chicks (Figure 1C) and with a special head-bill length ruler for chicks with a head-bill larger than 150 mm (Figure 1D)), bill (i.e. the length from the feather margin to the tip of the bill, measured with a calliper), right 'maximum' tarsus (for a detailed description of this measure, see Sutherland *et al.* 2004), right wing (from the wrist up to the longest primary, flattened and straightened, see Figure 1E, F) and right eighth primary feather (flattened and straightened, starting from the basis between the eighth and ninth primary feather up to the tip of the eighth primary feather;  $\pm 1$  mm). In addition, we measured body mass using 500, 1000 and 2500 g Pesola spring balances ( $\pm 1$ , 5 and 10 g, respectively), depending on the weight of the chick. We only started measuring the eighth primary feather halfway through the breeding season of 2006. As a result, the eighth primary of three (out of four) fledged male chicks was only measured from day 18 onward.

### Growth functions

For each biometric measure, we assessed whether its growth was best described by either of two classical growth functions (Ricklefs 1968) that are often applied to chick growth (Tjorve & Tjorve 2010): the logistic growth curve,  $y_t = y_\infty / (1 + \exp(-k(t - T_i)))$ , and the Gompertz growth curve,  $y_t = y_\infty \times \exp(-\exp(-k \times (t - T_i)))$ .  $y_t$  is the biometric response variable,  $t$  is the age (in days),  $y_\infty$  is the asymptotic value of the response variable,  $k$  is the growth rate constant and  $T_i$  is the age (in days) at the inflection point. The inflection point occurs at  $y(T_i) = y_\infty / 2$  for the logistic curve, and at  $y(T_i) = y_\infty / e$  for the Gompertz curve. Maximum growth rate ( $g_{\max}$ ) that occurs at the inflection point  $T_i$  is calculated as  $ky_\infty / 4$  for the logistic and  $ky_\infty / e$  for the Gompertz growth curve.

### Comparing the growth of the regularly measured chicks with a reference dataset

The growth of the regularly measured chicks was compared with data of reference chicks (often earlier hatched) of all other (mostly larger) colonies on Schiermonnikoog between 2007 and 2009. Using the head-bill growth curve estimated from the regularly measured chicks, the hatching date of the reference chicks was estimated from head-bill length within two weeks after hatching. When two to five weeks old, these reference chicks were colour-ringed and their head-bill, head (for which the special head-bill apparatus was used, Figure 1D; bill length was calculated from head-bill and head length), eighth primary length and body mass were measured.

Because chicks are no longer attached to their nest about three weeks after hatching, but congregate in crèches, chicks were individually marked with a uniquely labelled cotton band (Figure 1B) within two weeks after hatching. During this procedure, the length of the head-bill of each chick was measured. To minimize the period of disturbance no other measurements were taken. To prevent undesirable cooling of small chicks (<3 days old, when they are normally still being brooded by their parents) during this procedure, they were covered with a cloth.

We fitted growth curves based on the data of the reference chicks and compared these with the estimated curves based on the regularly measured chicks. In the absence of data of reference chicks younger than two weeks, head-bill length, bill length and body mass were fixed at 41.2 mm, 20.5 mm and 56.6 gram at hatching ( $t_0 = 0$ ), and the eighth primary length at 17.3 mm at the ninth day ( $t_0 = 9$ , which was the age at which all chicks had started growing this feather).

These were the mean values of the regularly measured chicks at these ages. With  $y$  fixed to  $y_0$  at  $t = t_0$ ,  $T_i$  can be calculated from  $y_\infty$  and  $k$  as  $T_i = \ln(-\ln(y_0/y_\infty))/k + t_0$ . Consequently, the estimated growth curves of the reference chicks are not entirely independent from that of the regularly measured chicks, not only because the measurements at age 0 are used, but also because their age at temporary banding is estimated from the estimated head-bill growth curve from the regularly measured chicks.

### Age estimation

To assess which morphometric measure most accurately predicted age, we rewrote the logistic and Gompertz growth curve with age ( $t$ ) as a function of biometric measurement  $y_t$ . For the logistic growth curve, this is  $t = -\ln(y_\infty/y_t - 1)/k + T_i$  and for the Gompertz curve this is  $t = -\ln(-\ln(y_t/y_\infty))/k + T_i$ . We predicted age using the estimates of the best-supported growth curves for each morphometric measure and calculated the deviation of the predicted age from the real age. Because differences in growth generally become more pronounced at later stages of chick growth and because chicks can only be colour-ringed when c. two weeks of age or older, we separately calculated the accuracy of age prediction from morphometric measures for chicks younger than 15 days and for chicks of 15 days or older.

### Environmental sensitivity of growth measures

To investigate the sensitivity of the growth of different morphometric measures and body mass to poor environmental conditions, we compared the growth of 11 chicks that were found dead in the nest (i.e. that presumably died of starvation, not predation) during the last measured 3-day growth interval prior to death with the growth in the same age interval of the chicks that survived to fledging.

### Molecular sexing

At the time the chick received its unique colour-ring combination, a blood sample of 10–80  $\mu$ l was taken from the brachial vein and stored in 96% ethanol. DNA was extracted from the blood and sex-specific DNA-fragments were replicated using primers 2550F/2718R (Fridolfsson & Ellegren 1999).

### Statistical analysis

To model growth of the regularly measured chicks, we used nonlinear mixed models (Lindstrom & Bates 1990, Pinheiro & Bates 2000). Because these chicks were repeatedly measured over time, there is pseudo-replica-

tion within chicks. Moreover, some nests contained more than one chick. To account for this, we modelled chicks within nests as a hierarchical random effect structure. In addition, a first-order regressive correlation structure was used to account for temporal autocorrelation within chicks (Box *et al.* 1994, Pinheiro & Bates 2000). To enable proper estimation of the random effects, we restricted the analyses to chicks that fledged (i.e. that could fly, when  $\geq 32$  days old). Most models with a hierarchical random effect structure imposed on all three model parameters ( $y_\infty$ ,  $k$  and  $T_i$ ) did not converge. Inspection of the parameter estimates of models that did converge showed that there was a strong correlation between the estimated random effects for  $y_\infty$ ,  $k$  and  $T_i$ . In addition, estimated variances of random effects were often negative, indicating that these models were overfitted (i.e. contained more parameters than could be estimated from the data). Some exploratory analyses showed that convergence problems (and most negative variance problems) were solved when nest was removed from the random effect structure and when individuals were only allowed to vary randomly with respect to their asymptotic size,  $y_\infty$ . Using this simplified random effect structure, we then tested for an effect of sex by comparing models with and without a sex effect on  $y_\infty$ ,  $k$  and  $T_i$ , resulting in  $2^3 = 8$  logistic and Gompertz growth models to be compared. Growth of the reference chicks was also modelled using non-linear mixed effects models. As many nests had more than one chick that survived to colour-ringing, we modelled random variation in  $y_\infty$  among nests.

The relative growth of measure  $i$  for each chick that died was calculated as (increase in measure  $i$  in the three-day age interval prior to death) / (mean increase in measure  $i$  during the same three-day age interval of chicks that survived to fledging). To assess whether the calculated relative growth rates of chicks that died varied between the different morphometric measures and body mass, linear mixed effects models were used. Because the different measures taken on the same chick are not independent, we modelled random variation around the intercept between chicks. In contrast to morphometric measures that can only increase or remain the same (although measurement errors resulted in some negative values as well), body mass can also decrease during an interval. Therefore, relative body mass growth was negative in some cases. To allow direct comparison of relative growth of body mass and other morphometric measures, while not selectively excluding measurement errors, we therefore did not log-transform the data.

Analyses were performed using R (version 2.13, R Development Core Team 2011) and package nlme for the analysis of linear and non-linear mixed effects models (Pinheiro *et al.* 2012). We visually checked for heteroscedasticity and trends in residuals. We found heteroscedasticity in the residuals of body mass for the regularly measured chicks, but not for the reference chicks. The reason for this heteroscedasticity was that variation in body mass increased with average body mass. However, correcting for this heteroscedasticity by modelling variance as a function of age (Pinheiro & Bates 2000) had the undesirable result that the heavier (older) chicks had less influence on the estimated curve and caused the asymptotic values to become poorly estimated. For this reason, we decided not to correct for the heteroscedasticity of body mass residuals.

Candidate models were run using maximum likelihood estimation and their relative support was evaluated based on the Akaike information criterion, corrected for small sample size ( $AIC_c$ , Akaike 1973, Burnham & Anderson 2002). We selected the most parsimonious model as the best description of the data, which is the model with the fewest parameters among the supported models (with  $\Delta AIC_c < 2$ ). Restricted maximum likelihood estimates are reported of the most parsimonious model for each measure.

RESULTS

Growth curves

Of the 35 regularly measured chicks, no, one, two and three chicks survived until fledging in respectively

three, four, three and one nests, resulting in 13 fledged chicks. Of the 22 chicks that died, 14 chicks (67%) died within the first 10 days and four chicks between 10 and 20 days. The remaining four chicks were between 20 and 30 days old when they were flooded during a storm tide (and probably drowned or died of hypothermia). This resulted in age-specific chick survival rates of 0.60 from 0 to 10 days after hatching, 0.81 from 10 to 20 days, 0.76 from 20 to 30 days and 1.00 from 30 days to fledging (between 33 and 39 days). For growth curve estimation, we excluded the thirdly hatched chick of the nest in which three chicks fledged, because this chick showed considerably reduced growth (see below and Figure 5). Based on the data of the remaining 12 fledged chicks, head-bill, bill, wing and eighth primary length and body mass were best described by a Gompertz growth curve, whereas tarsus length was best described by logistic growth (for model selection results, see online supplementary material, Table A1).

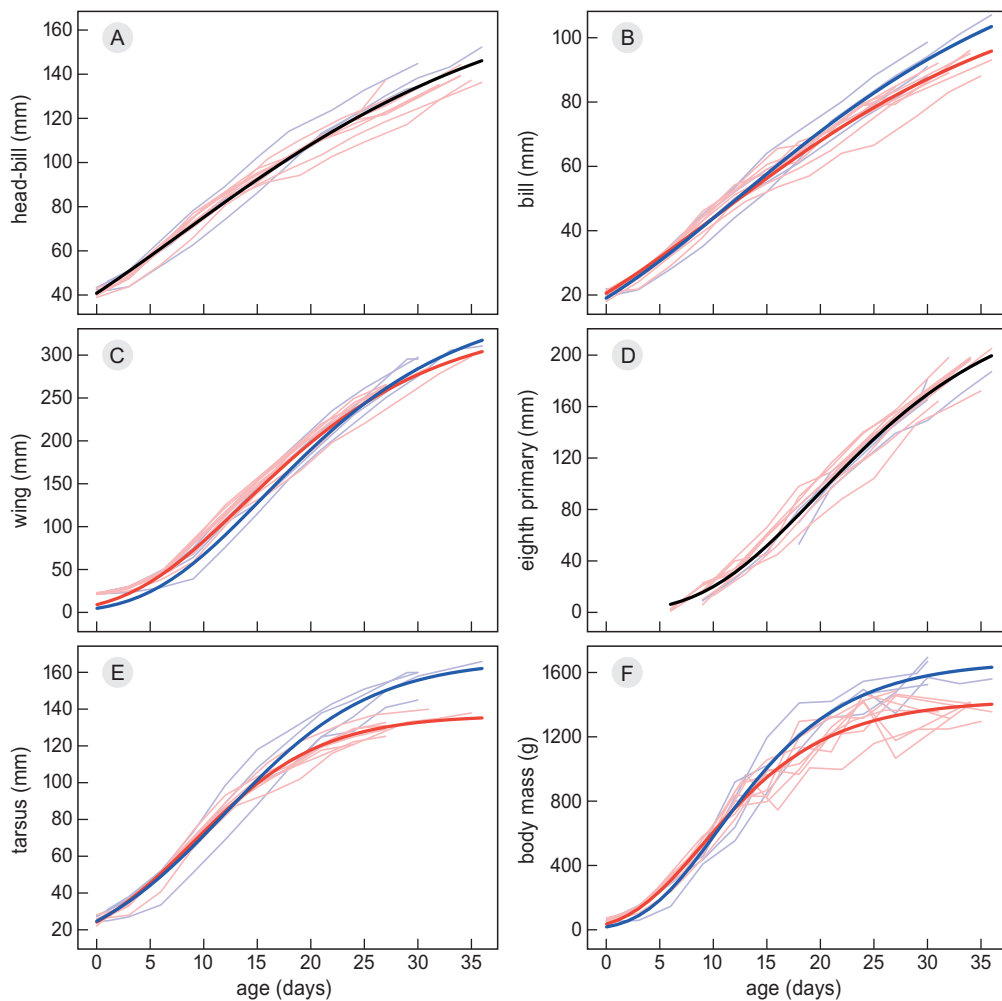
There was substantial support for differences in growth between males and females for bill, wing, tarsus and body mass (removing the sex effects increased  $AIC_c$  between 5.4 (for bill) and 33.4 (for tarsus)), but only minor support for a sex effect on  $y_\infty$  for head-bill ( $\Delta AIC_c = -0.53$ ) and  $T_i$  for eighth primary growth ( $\Delta AIC_c = -0.57$ ; Table 1, Table A1, Figure 2). Males had larger asymptotic values ( $y_\infty$ ) for bill, wing, tarsus and body mass than females and reached the inflection point ( $T_i$ , the age at which maximum growth occurs) at a later age. The most pronounced sex effects were found for tarsus and body mass: males were estimated to become 17% heavier than females and to have 22% longer tarsi (Table 1). For tarsus growth only,

**Table 1.** Parameter estimates (mean  $\pm$  SE) of the growth curves for five morphometric measures (head-bill, bill, wing, eighth primary and tarsus length (mm)) and body mass (g), based on the most parsimonious model for each measure (Table A1, in bold). Results are based on the regularly measured chicks ( $n = 8$  females and  $n = 4$  males).

Measure ( $y$ )	Growth curve	Fixed effects						Random effect (on $y_\infty$ )	
		$y_\infty$		$k$		$T_i$		$\sigma^2_{ind}$	$\sigma^2_{res}$
		Female	Male	Female	Male	Female	Male		
Head-bill	Gompertz	184 $\pm$ 5	184 $\pm$ 5	0.052 $\pm$ 0.002	0.052 $\pm$ 0.002	7.9 $\pm$ 0.6	7.9 $\pm$ 0.6	36	13
Bill	Gompertz	122 $\pm$ 4	135 $\pm$ 5	0.056 $\pm$ 0.003	0.056 $\pm$ 0.003	10.4 $\pm$ 0.7	12.1 $\pm$ 0.8	21	7
Wing	Gompertz	343 $\pm$ 10	366 $\pm$ 11	0.095 $\pm$ 0.004	0.095 $\pm$ 0.004	13.7 $\pm$ 0.4	15.6 $\pm$ 0.5	0	149
Eighth primary	Gompertz	247 $\pm$ 10	247 $\pm$ 10	0.095 $\pm$ 0.005	0.095 $\pm$ 0.005	19.7 $\pm$ 0.4	19.7 $\pm$ 0.4	265	38
Tarsus	Logistic	137 $\pm$ 2	167 $\pm$ 4	0.168 $\pm$ 0.007	0.146 $\pm$ 0.007	9.1 $\pm$ 0.3	12.0 $\pm$ 0.5	0*	29
Body mass	Gompertz	1434 $\pm$ 34	1676 $\pm$ 46	0.147 $\pm$ 0.007	0.147 $\pm$ 0.007	8.9 $\pm$ 0.27	10.4 $\pm$ 0.31	3629	6828

Logistic growth curve:  $y_t = y_\infty / (1 + \exp(-k \times (t - T_i)))$ ; Gompertz growth curve:  $y_t = y_\infty \times \exp(-\exp(-k \times (t - T_i)))$

\*This estimate should be interpreted with caution, as model convergence ceased when the estimated variance of the random effect became negative.



**Figure 2.** Estimated growth curves (in bold) for five structural size parameters: (A) head-bill, (B) bill, (C) wing, (D) eighth primary and (E) tarsus length and for (F) body mass based on the regularly measured chicks and the most parsimonious models (Table A1, in bold). Lines are only separately drawn for females (red) and males (blue) when the most parsimonious model contained a sex effect on one or more model parameters. The red and blue lines represent the actual growth of individual females ( $n = 8$ ) and males ( $n = 4$ ).

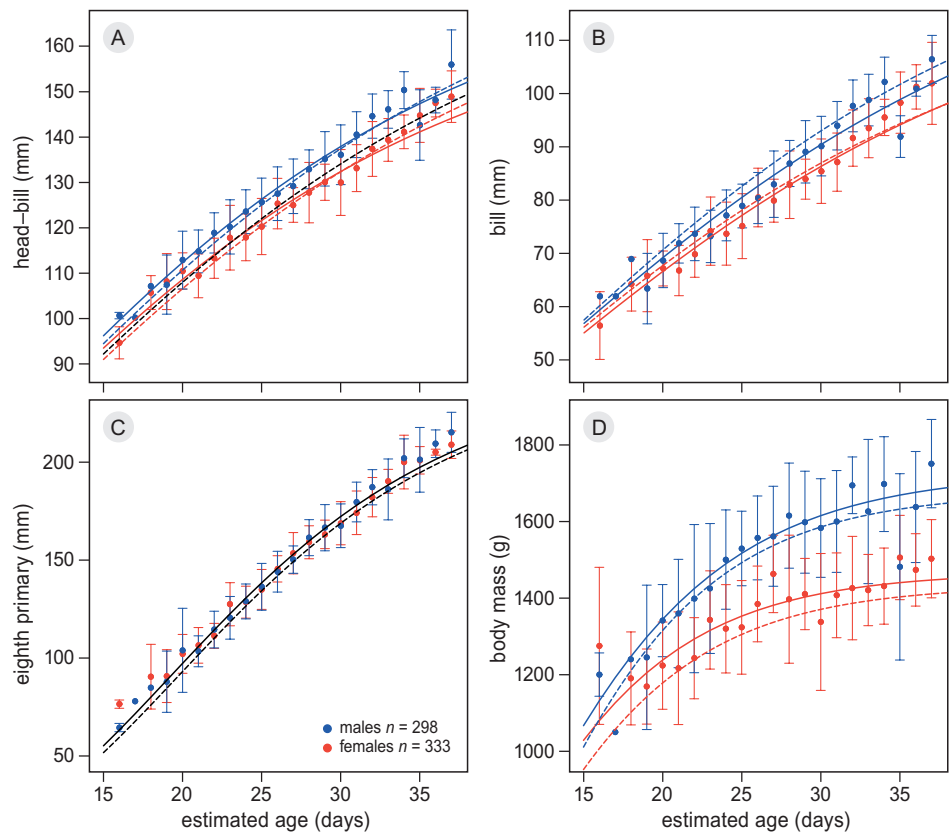
$k$  was lower for males than females. To achieve the same maximum growth rate  $g_{\max}$ , which occurs at  $T_1$  and is calculated as  $ky_{\infty}/4$  for logistic and  $ky_{\infty}/e$  for Gompertz growth,  $k$  should be lower when  $y_{\infty}$  is higher. This was the case for the growth of the tarsus, but not for bill, wing and body mass, implying faster maximum growth rates of these body measures in males than females.

#### Comparison of growth curves with reference chicks

Data and estimated growth curves of the reference chicks, with  $y_0$  fixed to that of the regularly measured chicks, are shown in Figure 3 (solid lines) and compared with the estimated growth of the regularly

measured chicks (dashed lines). While there was only minor evidence for a sex effect on head-bill growth for the regularly measured chicks ( $\Delta AIC_c = -0.53$ , Table A1; the sex-specific curves are shown in Figure 3A), there was substantial evidence for a sex effect for the reference dataset. In both datasets, a sex effect was supported for bill and body mass growth, but not for eighth primary growth. The estimated growth curves of the regularly measured chicks reasonably resembled that of the reference chicks, most closely for the eighth primary and the least for body mass: body mass was consistently lower for the regularly measured chicks than for the reference chicks.





**Figure 3.** (A) Head-bill length, (B) bill length, (C) eighth primary length and (D) body mass of reference chicks, plotted against age, estimated from the head-bill length measured within two weeks after hatching (using the growth curve parameters for head-bill from Table 1). Results are based on  $n = 333$  female (red) and  $n = 298$  male (blue) reference chicks. The dotted lines show the growth curves estimated from the regularly measured chicks (to allow better comparison of head-bill growth, the sex-specific curves are also drawn) and the solid lines the growth curves for the reference chicks, estimated from the most parsimonious model for each growth parameter (Table A2, in bold), with head-bill, bill and mass at hatching (age = 0) fixed at the mean of the regularly measured chicks (41.2 mm, 20.5 mm and 56.6 gram, respectively) and the eighth primary fixed at 17 mm when 9 days old (this was the first day that all regularly measured chicks had started growing this feather). Solid lines are only separately drawn for the sexes when there was substantial support for a sex effect on one or more model parameters.

**Table 2.** Accuracy of age estimation (i.e. the mean deviation from the true age) of the regularly measured first and second chicks that survived until fledging using the growth curve estimates in Table 1. Accuracy is calculated for chicks younger than 15 days, and for chicks of 15 days or older. For each growth period, the two most accurate estimators of age are shown in bold.

	<15 days	≥15 days
Head-bill	<b>0.73</b>	1.52
Bill*	0.83	1.57
Wing*	1.64	<b>1.07</b>
Eighth primary	1.37	<b>1.26</b>
Tarsus*	<b>0.66</b>	1.89
Body mass*	0.83	4.41

\*Accounting for sex effect

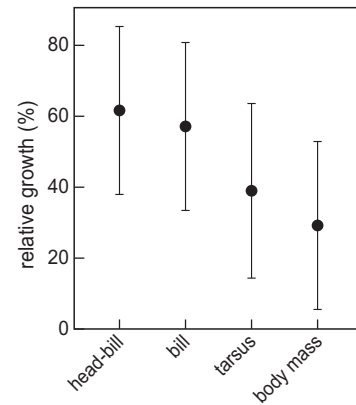
**Age estimation**

The age of the regularly measured chicks was more accurately estimated from morphometric measures when younger than 15 days rather than older (Table 2). For chicks younger than 15 days, head-bill and tarsus length were the best predictors, whereas at older ages (i.e. at the age when chicks are colour-ringed), wing and eighth primary length were better predictors of age. We also assessed which morphometric measures were most accurate for predicting age of the reference chicks at colour-ringing by comparing the estimated hatching date based on head-bill length within two weeks after hatching (using the estimates in Table 1) with the hatching date estimated from head-bill length and/or eighth primary during colour-ringing (using the estimates in Table 3). This revealed that the eighth

**Table 3.** Parameter estimates (mean  $\pm$  SE) of the Gompertz curves for three morphometric measures (head-bill, bill and eighth primary length (mm)) and body mass (g). Results are based on reference chicks ( $n = 333$  females and  $n = 298$  males) of which age was accurately estimated from head-bill length when younger than two weeks (see Table 2).

	Fixed effects				Random effects		Derived parameters			
	$\gamma_{\infty}$		$k$		$\sigma^2_{\text{nest}}$	$\sigma^2_{\text{res}}$	$T_i$		$g_{\text{max}}$	
	Female	Male	Female	Male			Female	Male	Female	Male
Head-bill	171 ± 3	180 ± 3	0.057 ± 0.001	0.057 ± 0.001	23	23	6.2 ± 0.3	6.8 ± 0.3	3.6 ± 0.0	3.8 ± 0.0
	125 ± 3	133 ± 3	0.053 ± 0.002	0.053 ± 0.002	35	21	11.3 ± 0.6	11.9 ± 0.6	2.4 ± 0.0	2.6 ± 0.0
Bill	247 ± 3	247 ± 3	0.095 ± 0.001	0.095 ± 0.001	578	98	19.3 ± 0.2	19.3 ± 0.2	8.7 ± 0.0	8.7 ± 0.0
Eighth primary	1467 ± 19	1729 ± 22	0.148 ± 0.006	0.13 ± 0.004	6391	12,251	8.0 ± 0.3	9.4 ± 0.3	79.7 ± 2.3	83.0 ± 1.7
Body mass										

For accurate estimation of early growth (despite the lack of data)  $\gamma_0$  was fixed at the mean size of the regularly measured chicks at  $t_0$ , being respectively 41.2 mm, 20.5 mm and 56.6 g for head-bill, bill and body mass at  $t_0 = 0$  and 17.3 mm for the eighth primary at  $t_0 = 9$ .  $T_i$  was calculated as  $\ln(-\ln(\gamma_0/\gamma_{\infty}))/k + t_0$  and the maximum growth rate ( $g_{\text{max}}$ , which occurs at  $T_i$ ) as  $ky_{\infty}/e$ . Standard errors for  $T_i$  and  $g_{\text{max}}$  were calculated using the Delta method (Cox 1998).



**Figure 4.** Growth of different biometric measures of chicks during the last 3-day interval before they died ( $n = 11$ ), relative to that of similar-aged chicks that survived until fledging. Dots and error bars represent estimated means and 95% confidence intervals of the mixed-effects ANOVA.

primary length most closely resembled the hatching date as estimated from head-bill at young ages (mean deviation = 1.18 days), compared with a deviation of 1.91 days when using sex-specific head-bill length.

#### Environmental sensitivity of growth measures

A total of 11, presumably starved, chicks had been measured at least twice before they died, enabling a comparison of their growth with that of surviving chicks. All starved chicks that died were less than 15 days old, with the last measured growth interval between age 0 and 3 ( $n = 5$ ), age 3 and 6 ( $n = 2$ ), age 6 and 9 ( $n = 3$ ) and age 9 and 12 ( $n = 1$ ). Because the eighth primary only starts growing somewhere between age 6 and 10 (Figure 2D), we only had data on eighth primary growth from three of the chicks that died. Similarly, the wing hardly grows during the first six days. Therefore, we excluded the wing and eighth primary from this analysis. The starved chicks showed reduced growth in all morphometric measures and body mass during their last measured growth interval, calculated as a percentage relative to the growth during the same age interval of the first or second chicks that survived to fledging ( $n = 12$ ; Figure 4). Yet, the extent of this reduction varied for the different measures, with a reduction of 40–45% for head-bill and bill growth, compared to 60–70% for tarsus and body mass growth. The overall difference between the four measures was close to the 5%- significance level ( $L = 7.33$ ,  $df = 4$ ,  $P = 0.06$ ) and a pairwise comparison among the measures showed that only the difference between the reduction in head-bill growth versus body mass was

significant ( $t = -2.37$ ,  $P = 0.02$ ). This indicates that body mass growth, closely followed by tarsus growth, is compromised most under severe food deprivation.

DISCUSSION

We have estimated growth curves for several morphometric measures and for the body mass of Spoonbill chicks born on the island of Schiermonnikoog. We reported growth curves from hatching to fledging for 12 chicks (from eight nests) that were measured every third day. Their growth was compared with biometric measurements of 631 chicks at colour-ringing (2–5 weeks old) in three consecutive years (2007–2009) of which age was accurately predicted from head-bill length within two weeks after hatching. In general, growth of the regularly measured chicks and the reference chicks was reasonably similar. Growth of the head-bill of the regularly measured chicks closely resembled the head-bill growth of female reference chicks (Figure 3A), which could be explained by the fact that this curve was based on more females ( $n = 8$ ) than males ( $n = 4$ ). We found some evidence for a sex effect on the  $y_{\infty}$  of head-bill length for the regularly measured chicks (Table A1; 182 and 188 mm for females and males) which provided very similar curves as those estimated for the reference chicks (Figure 3A). The body mass growth of the regularly measured chicks was slower than that of the reference chicks, suggesting that the former were in relatively poor condition (see below). Body mass growth was similar to that measured for African Spoonbill chicks *Platalea alba* (Kopij 1997).

Our results showed that growth was sex-specific for head-bill, bill and wing length and especially for tarsus length and body mass. Males were estimated to become 17% heavier than females and to have 22% longer tarsi. The more pronounced sex effect on body mass growth compared to several other morphometric measures was also found in chicks of the sexually size-dimorphic European Shag *Stictocarbo aristotelis* (Velando *et al.* 2000). That the differences in (especially) body mass and tarsus length between males and females were already evident prior to fledging, suggests that male Spoonbill chicks have higher daily nutritional demands and hence require more food than female chicks during the pre-fledging phase (e.g. Anderson *et al.* 1993, Krijgsveld *et al.* 1998). A comparison with biometric measurements on adult birds confirms that the wing and eighth primary length only subtly differ between the sexes. It also points out that the models considerably underestimated adult male and female head-bill and bill length as well as the sexual size dimorphism in these measures (Table 4). This suggests that, while the Gompertz curve appears well able to describe the growth of head-bill and bill of Spoonbill chicks during the pre-fledging phase, it poorly predicts the growth during the post-fledging phase. When taking a closer look at Figure 3A and 3B, the growth curves appear unable to capture the long (head-)bills of the oldest chicks measured. The growth of the bill therefore seems to have a longer linear phase than can be captured by the Gompertz growth curve. Indeed, the full length of the bill is only attained after 3–6 months (Cramp & Simmons 1977). During this period, the difference in bill length between males and females also becomes more pronounced, as adult birds showed

Table 4. Comparison of  $y_{\infty}$  (in mm or grams) estimated from chick growth data with biometric data of adult birds.

	Estimated $y_{\infty}$			Measurements on adult birds						
	Females	Males	SSD	Females			Males			SSD
				Mean	Range	$n$	Mean	Range	$n$	
Head-bill	171	180	1.05	231	230–231	2	266	255–283	9	1.15
Bill	125	133	1.06	182	168–191	14	213	195–231	15	1.17
Wing	343	366	1.07	370	360–377	10	394	386–412	13	1.06
Eighth primary	247	247	1.00	252	252–252	1	262	255–273	3	1.04
Tarsus	137	167	1.22	131	123–141	19	149	140–163	24	1.14
Body mass	1467	1729	1.18	1650	1620–1680	2	1881	1730–1960	9	1.14

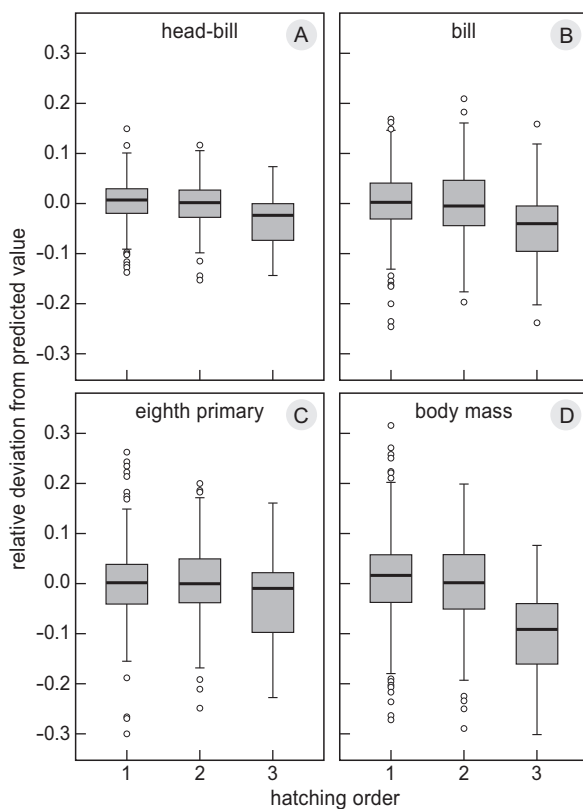
SSD = Sexual Size Dimorphism calculated as Male/Female. The estimated  $y_{\infty}$  of head-bill, bill, eighth primary length and body mass are from Table 3, and the  $y_{\infty}$  of wing and tarsus length are from Table 1. Adult data on head-bill length, eighth primary length and body mass are from incubating birds (2008–2012, Schiermonnikoog), whereas data on bill, wing and tarsus length come from museum specimens originating from the Netherlands (Cramp & Simmons 1977).

similar degrees of sexual size dimorphism in head-bill, bill, tarsus length and body mass (Table 4).

The estimated asymptotic values for body mass were also much lower than the actual body mass of incubating Spoonbills (Table 4), despite the fact that body mass already levelled off during the pre-fledging phase (Figures 2, 3). Given the enormous variation in body mass among chicks of the same age (Table 3), a potential explanation is that selective disappearance of the lighter chicks occurs after fledging. Alternatively, the lighter chicks gain additional weight after fledging in a way that is poorly predicted by an extrapolation of the estimated Gompertz growth curve.

Predicting age from morphometric measurements of chicks that survived to fledging (as sex was unknown of the chicks that died before fledging) was more accurate when done at young ages, probably because variation in growth becomes more pronounced at older ages, either due to structural size differences that become larger when chicks get larger, or because of the cumulative effect of variation in environmental conditions on growth. Age of young chicks was accurately estimated from head-bill or (sex-specific) tarsus length. However, as shown in Figure 4, tarsus growth is compromised more than head-bill growth under severe food deprivation, suggesting that tarsus length will likely be less accurate than head-bill length in predicting age of malnourished chicks. Therefore, we propose to use head-bill length instead of tarsus length to estimate age of chicks younger than two weeks old, using the parameter estimates in Table 1. The age of older chicks was more accurately estimated from the length of the wing or eighth primary feather (Table 2). That wing and eighth primary length poorly predicted age of chicks younger than 15 days old was explained by the fact that the flight feathers only start growing (on the outside) approximately one week after hatching, also explaining the delayed growth of the wing in the first week after hatching (Pearce-Higgins & Yalden 2002). This makes the eighth primary unsuitable and wing unreliable for predicting age of chicks younger than one week. After the initiation of external feather growth, wing length and eighth primary growth showed little variation, hence were good age predictors for older chicks. Estimated eighth primary growth curves were very similar for the regularly measured and the reference chicks, but because the curve of the reference chicks is based on a much larger dataset, we propose to use those estimates (Table 3) for age estimation of chicks older than 15 days. Wing length also appears to be an accurate age predictor of older chicks, but has unfortunately not been measured for the reference chicks.

To derive an estimate of chick growth performance from chick measurements at a single point in time, while accounting for genetic variation in body size, one should preferably correlate a measure of which the growth is very sensitive to environmental conditions (body mass, Figure 4; Nilsson & Svensson 1996, Schew & Ricklefs 1998) against a measure of which the growth is relatively insensitive to the environment and accurately describes the body size of an individual. In case of the Spoonbills, body mass and tarsus growth were more strongly reduced during severe food deprivation than the growth of head-bill and bill (Figure 4). Because all regularly measured chicks that died of starvation were younger than 15 days old, the generality of this pattern for older chicks remains to be shown. As an indication of whether this differential allocation of energy under poor conditions is similar in older chicks, we additionally compared the relative deviation in head-bill, bill, eighth primary length and body mass of the reference chicks in relation to their hatching order (tarsus length was unfortunately not measured for the reference chicks). Later hatched chicks are often competitively inferior when begging for food and as a result may receive less food than their older siblings (e.g. Fujioka 1985). We assessed a chick's hatching order from its head-bill length, measured within 2 weeks after hatching, relative to that of its siblings. Figure 5 shows the relative deviations from the mean growth curves (solid lines in Figure 3, Table 3) for first, second and third chicks in the nest (the single nest where four chicks survived until colour-ringing was excluded, because it probably involved chicks from two nests). First and second chicks were of similar size and mass, whereas third chicks were smaller and much lighter than expected for their age (Figure 5). After correcting for the age difference, third chicks were still 10.8% lighter than first chicks (95% CI: 7.7–13.9%), compared to a difference of 4.6% (3.2–6.1%) in head-bill length, 5.7% (3.4–7.9%) in bill length and 4.4% (1.4–7.4%) in eighth primary length. Similar findings were reported for Marsh Tits *Parus palustris* where the youngest chicks in the nest had significantly slower tarsus growth, but not wing growth (Nilsson & Svensson 1996), and in Kestrels *Falco tinnunculus*, where enlarged broods showed reduced body mass growth but not wing growth (Dijkstra et al. 1990). That wing growth was relatively unaffected may be explained by differential selection on wing growth, as it determines whether chicks are able to fledge (i.e. fly) at the same time as their siblings, which will strongly determine their ability to keep competing for food from their parents. To conclude, among the measures taken



**Figure 5.** Relative deviation in (A) head-bill, (B) bill, (C) eighth primary and (D) body mass for first ( $n = 376$ ), second ( $n = 216$ ) and third ( $n = 35$ ) chicks in the nest. Relative deviation is calculated as the absolute deviation divided by the expected value using the (sex-specific) growth curves estimated for the reference chicks (Table 3, Figure 4). The whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box.

on Spoonbill chicks in this study, body mass growth was the most sensitive to environmental conditions (Figures 4, 5), and considerably differed between male and female Spoonbill chicks (Figures 2, 3). To use the deviation from the predicted body mass for a given morphometric measure as an index of chick growth performance, the growth of this morphometric measure should therefore be equally sexually dimorphic (potentially after a power correction) during the pre-fledging growth trajectory. The only measure that met these requirements, and hence produced a linear and sex-independent relationship when plotted against body mass on a log-log scale (therefore accounting for a potential power correction), was tarsus length. However, as tarsus growth was nearly as sensitive to environmental conditions as body mass growth (Figure 4), deviations from this relationship will poorly reflect growth performance.

As an alternative, we therefore propose to use the deviation from the expected body mass for a given age and sex as an index of body condition. To determine the expected body mass for a given age and sex, we propose to use the sex-specific growth curves for body mass based on the large dataset of reference chicks (Figure 3D) and to use relative rather than absolute deviations from the expected body mass (following Hamer & Hill 1993, Quillfeldt *et al.* 2006), as older and heavier chicks may vary more in body mass than younger and on average lighter chicks. For this method to apply, chick age and sex should be known, or at least reliably estimated. Being sex-unspecific and the most reliable age estimator of the reference chicks, we propose to measure the eighth primary to estimate age. As there was no overlap in tarsus length between the regularly measured male and female chicks older than 25 days (Figure 2E), sex determination based on tarsus length could be reliable, especially for older chicks. In fact, for the closely related Glossy Ibis *Plegadis falcinellus*, the combination of sex-specific tarsus length and sex-unspecific wing length resulted in 84% of chicks of 2–5 weeks old being correctly sexed (Figuerola *et al.* 2006). We therefore propose that, in order to derive an index of body condition of chicks at colour-ringing, tarsus length is included as a standard measurement, in addition to (at least) the eighth primary for age estimation, and body mass. This will eventually allow the evaluation of whether sex determination based on this combination of biometric measurements is reliable enough to replace relatively expensive and time-consuming (both in the field and in the lab) molecular assays.

The Spoonbill chick growth curves presented in this paper are based on a large number of chicks ( $n = 631$ ) born at different times of the season and in three different years, and as a result, will closely resemble the average chick growth in our study population. However, as our study population is restricted to the island of Schiermonnikoog, one may wonder whether the results of this study are applicable to other breeding colonies in The Netherlands and to other populations of Eurasian Spoonbills in Europe (and Asia). When applying our methods to estimate chick age and body condition in another population, it is assumed that this population does not genetically differ from our study population with respect to chick growth rates and asymptotic body size. In case of the Wadden Sea area, very little genetic differentiation was found between colonies (Piersma *et al.* 2012). Therefore, our results can be readily applied throughout the Wadden Sea area to allow inter-colonial comparisons of timing of breed-



ing and chick body condition. To judge if our methods can also be applied to other populations of Eurasian Spoonbills, we propose that it is first checked whether the eighth primary length of known age chicks fall onto our estimated curve. If so, our methods are expected to be valid, if not, they will be biased. To achieve unbiased estimates of chick age and body condition for such genetically differentiated populations, population-specific growth curves for eighth primary length, tarsus length (assuming that this allows reliable sex determination) and body mass should be derived.

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## SAMENVATTING

De conditie van een kuiken kan een gevoelige graadmeter zijn voor lokale voedselomstandigheden en is vaak een goede voorspeller voor de overlevingskans na het uitvliegen. Om een betrouwbare maat te krijgen voor de conditie van kuikens van een bepaalde soort moeten we weten hoeveel variatie in lichaamsgrootte er kan bestaan, hoe de leeftijd kan worden geschat en hoe gevoelig de groei van verschillende lichaamsmaten is bij slechte lokale omgevingsomstandigheden. Om deze kennis te vergaren hebben we gekeken naar de geslachtsspecifieke variatie in de groei van verschillende lichaamsmaten en het gewicht van Lepelaars *Platalea leucorodia*. We hebben 35 kuikens die opgroeiden in kleine kolonies op Schiermonnikoog, elke drie dagen gemeten om gedetailleerde groeicurven tot uitvliegen te bepalen (gebaseerd op de 12 kuikens die zijn uitgevlogen) en om te bepalen in welke mate de groei van verhongerde kuikens ( $n = 11$ ) was vertraagd ten opzichte van die van de overlevende kuikens. De groeicurven hebben we vervolgens vergeleken met metingen aan twee tot vijf weken oude kuikens uit (vooral) grotere kolonies uit 2007–2009 waarvan de uitkomstdatum nauwkeurig kon worden geschat ( $n = 631$ ). De groei van alle maten, met uitzondering van de achtste grote slagpen, verschilde tussen mannetjes en vrouwtjes, met de grootste verschillen voor de asymptotische waarden voor tarsuslengte en lichaamsgewicht. Volwassen mannetjes worden 17% zwaarder dan vrouwtjes, en krijgen 22% langere tarsi. Bij ernstig voedseltekort was de toename in lichaamsgewicht en groei van de tarsus relatief lager dan de groei van de (kop-) snavel en de achtste grote slagpen. Als index voor de conditie van een lepelaarkuiken stellen we voor om de relatieve afwijking in lichaamsgewicht ten opzichte van het voorspelde gewicht voor een gegeven leeftijd en geslacht te gebruiken. Om de conditie te kunnen schatten van de kuikens die van kleurringen worden voorzien (als ze 2–5 weken oud zijn) stellen we daarom voor om ten minste de achtste grote slagpen te meten voor de leeftijdsbepaling, de tarsus voor de geslachtsbepaling en het lichaamsgewicht als een maat die de invloeden van leeftijd, geslacht én omgeving omvat.

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## APPENDIX

**Table A1.** Model selection results of logistic and Gompertz growth curves for five morphometric measures (head-bill, bill, wing, eighth primary and tarsus length) and body mass, testing for a sex effect on each growth parameter ( $y_{\infty}$ ,  $k$ ,  $T_i$ ). Results are based on the data of the regularly measured chicks ( $n = 12$ ). The number of parameters of each model ( $K$ ) is composed of the fixed effects parameters and three additional parameters: the variance components ( $\sigma^2_{\text{ind}}$  and  $\sigma^2_{\text{res}}$ ) and the autocorrelation coefficient. The most parsimonious model (i.e. the model with the fewest parameters among the supported models;  $\Delta AIC_c < 2$ ) is shown in bold.

Head-bill						Bill					
Shape	Sex effects	$K$	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight	Shape	Sex effects	$K$	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight
Gompertz	$y_{\infty}$	7	2.51	0.00	0.25	<b>Gompertz</b>	<b><math>y_{\infty}, T_i</math></b>	<b>8</b>	<b>1.08</b>	<b>0.00</b>	<b>0.41</b>
<b>Gompertz</b>	<b>–</b>	<b>6</b>	<b>5.27</b>	<b>0.53</b>	<b>0.19</b>	Gompertz	$y_{\infty}, k, T_i$	9	0.00	1.22	0.22
Gompertz	$y_{\infty}, T_i$	8	1.29	1.04	0.15	Gompertz	$K$	7	5.53	2.18	0.14
Gompertz	$K$	7	3.85	1.34	0.13	Gompertz	$y_{\infty}, k$	8	4.51	3.44	0.07
Gompertz	$y_{\infty}, k, T_i$	9	0.00	2.05	0.09	Gompertz	$y_{\infty}$	7	7.19	3.84	0.06
Gompertz	$y_{\infty}, k$	8	2.40	2.15	0.08	Gompertz	$k, T_i$	8	5.53	4.45	0.04
Gompertz	$T_i$	7	5.27	2.76	0.06	Gompertz	–	6	11.00	5.43	0.03
Gompertz	$k, T_i$	8	3.68	3.43	0.04	Gompertz	$T_i$	7	9.44	6.09	0.02
Logistic	$y_{\infty}$	7	13.69	11.18	0.00	Logistic	$y_{\infty}, T_i$	8	20.40	19.32	0.00
Logistic	–	6	16.54	11.79	0.00	Logistic	$K$	7	24.22	20.88	0.00
Logistic	$y_{\infty}, T_i$	8	12.62	12.37	0.00	Logistic	$y_{\infty}$	7	24.47	21.13	0.00
Logistic	$K$	7	14.95	12.44	0.00	Logistic	$y_{\infty}, k$	8	22.31	21.23	0.00
Logistic	$y_{\infty}, k$	8	13.25	13.00	0.00	Logistic	$y_{\infty}, k, T_i$	9	20.39	21.62	0.00
Logistic	$T_i$	7	16.51	14.00	0.00	Logistic	–	6	28.32	22.74	0.00
Logistic	$k, T_i$	8	14.53	14.28	0.00	Logistic	$k, T_i$	8	24.11	23.03	0.00
Logistic	$y_{\infty}, k, T_i$	9	12.59	14.65	0.00	Logistic	$T_i$	7	27.84	24.50	0.00
–2logL = 614.46 $AIC_c$ = 631.87						–2logL = 561.79 $AIC_c$ = 580.03					
Wing						Eighth primary					
Shape	Sex effects	$K$	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight	Shape	Sex effects	$K$	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight
<b>Gompertz</b>	<b><math>y_{\infty}, T_i</math></b>	<b>8</b>	<b>1.70</b>	<b>0.00</b>	<b>0.48</b>	Gompertz	$T_i$	7	1.31	0.00	0.24
Gompertz	$y_{\infty}, k, T_i$	9	0.00	0.67	0.34	<b>Gompertz</b>	<b>–</b>	<b>6</b>	<b>4.23</b>	<b>0.57</b>	<b>0.18</b>
Gompertz	$k, T_i$	8	5.52	3.82	0.07	Gompertz	$K$	7	2.15	0.84	0.16
Gompertz	$T_i$	7	8.29	4.27	0.06	Gompertz	$y_{\infty}, k$	8	0.09	1.20	0.13
Gompertz	–	6	12.91	6.60	0.02	Gompertz	$k, T_i$	8	0.98	2.09	0.09
Gompertz	$K$	7	10.69	6.67	0.02	Gompertz	$y_{\infty}$	7	3.51	2.20	0.08
Gompertz	$y_{\infty}$	7	11.66	7.63	0.01	Gompertz	$y_{\infty}, T_i$	8	1.31	2.42	0.07
Gompertz	$y_{\infty}, k$	8	10.67	8.97	0.01	Gompertz	$y_{\infty}, k, T_i$	9	0.00	3.59	0.04
Logistic	$y_{\infty}, k, T_i$	9	14.17	14.84	0.00	Logistic	–	6	31.66	27.99	0.00
Logistic	$y_{\infty}, T_i$	8	17.53	15.83	0.00	Logistic	$y_{\infty}$	7	30.75	29.44	0.00
Logistic	$T_i$	7	27.68	23.65	0.00	Logistic	$T_i$	7	31.35	30.05	0.00
Logistic	$k, T_i$	8	26.36	24.66	0.00	Logistic	$K$	7	31.61	30.30	0.00
Logistic	–	6	33.18	26.87	0.00	Logistic	$y_{\infty}, k$	8	30.42	31.53	0.00
Logistic	$K$	7	31.14	27.11	0.00	Logistic	$y_{\infty}, T_i$	8	30.75	31.86	0.00
Logistic	$y_{\infty}$	7	31.62	27.60	0.00	Logistic	$k, T_i$	8	31.36	32.47	0.00
Logistic	$y_{\infty}, k$	8	30.87	29.17	0.00	Logistic	$y_{\infty}, k, T_i$	9	29.80	33.39	0.00
–2logL = 719.65 $AIC_c$ = 738.78						–2logL = 581.68 $AIC_c$ = 598.37					

Table A1. Continued

Tarsus						Body mass					
Shape	Sex effects	<i>K</i>	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight	Shape	Sex effects	<i>K</i>	$\Delta(-2\log L)$	$\Delta AIC_c$	Akaike weight
<b>Logistic</b>	<b><math>y_\infty, k, T_i</math></b>	<b>9</b>	<b>0.00</b>	<b>0.00</b>	<b>0.78</b>	<b>Gompertz</b>	<b><math>y_\infty, T_i</math></b>	<b>8</b>	<b>0.00</b>	<b>0</b>	<b>0.71</b>
Logistic	$y_\infty, T_i$	8	4.80	2.48	0.22	Gompertz	$y_\infty, k, T_i$	9	0.00	2.30	0.23
Logistic	$y_\infty$	7	24.00	19.39	0.00	Logistic	$y_\infty, T_i$	8	5.97	5.97	0.04
Logistic	$y_\infty, k$	8	23.40	21.07	0.00	Logistic	$y_\infty, k, T_i$	9	5.70	8.01	0.01
Logistic	$T_i$	7	26.32	21.72	0.00	Gompertz	$y_\infty$	7	12.31	10.04	0.00
Logistic	$k, T_i$	8	24.88	22.56	0.00	Gompertz	$y_\infty, k$	8	11.16	11.15	0.00
Gompertz	$y_\infty, k, T_i$	9	26.41	26.41	0.00	Gompertz	$k, T_i$	8	12.21	12.21	0.00
Gompertz	$y_\infty, T_i$	8	29.42	27.10	0.00	Gompertz	$T_i$	7	14.94	12.67	0.00
Logistic	–	6	40.22	33.37	0.00	Logistic	$y_\infty, k$	8	12.74	12.74	0.00
Gompertz	$T_i$	7	39.60	35.00	0.00	Logistic	$y_\infty$	7	16.11	13.85	0.00
Logistic	<i>K</i>	7	40.08	35.48	0.00	Gompertz	<i>K</i>	7	16.21	13.94	0.00
Gompertz	$k, T_i$	8	38.04	35.72	0.00	Gompertz	–	6	22.12	17.62	0.00
Gompertz	$y_\infty, k$	8	42.09	39.77	0.00	Logistic	<i>K</i>	7	20.50	18.24	0.00
Gompertz	$y_\infty$	7	49.10	44.49	0.00	Logistic	$k, T_i$	8	18.71	18.71	0.00
Gompertz	–	6	59.17	52.32	0.00	Logistic	$T_i$	7	21.24	18.97	0.00
Gompertz	<i>K</i>	7	58.15	53.54	0.00	Logistic	–	6	26.61	22.11	0.00

–2logL = 648.06  
AIC<sub>c</sub> = 667.61

–2logL = 1493.25  
AIC<sub>c</sub> = 1565.81

**Table A2.** Model selection results to investigate sex-specific growth of reference chicks of which age was accurately estimated from head-bill length when younger than two weeks ( $n = 333$  females and  $n = 298$  males). A sex effect was assessed for the growth parameters  $y_\infty$  and  $k$  of the Gompertz growth curves for three morphometric measures (head-bill, bill and eighth primary length) and body mass.  $T_i$  was calculated from  $y_\infty$  and  $k$ , using the value set for  $y_0$ . The number of parameters ( $K$ ) is composed of the fixed effects parameters and the two variance components ( $\sigma^2_{\text{nest}}$  and  $\sigma^2_{\text{res}}$ ). The most parsimonious model for each measure is shown in bold.

	Sex effects	<i>K</i>	–2logL	$\Delta AIC_c$
<b>Head-bill</b>				
	<b><math>y_\infty</math></b>	<b>5</b>	<b>3922.11</b>	<b>0.00</b>
	$y_\infty, k$	6	3921.52	1.45
	$k$	5	3927.39	5.28
	–	4	4036.94	112.80
<b>Bill</b>				
	<b><math>y_\infty</math></b>	<b>5</b>	<b>3888.62</b>	<b>0.00</b>
	$y_\infty, k$	6	3887.66	1.08
	$k$	5	3891.30	2.68
	–	4	3950.08	59.42
<b>Eighth primary</b>				
	<b>–</b>	<b>4</b>	<b>4763.57</b>	<b>0.00</b>
	$y_\infty, k$	6	4760.39	0.89
	$y_\infty$	5	4763.42	1.88
	$k$	5	4763.58	2.04
<b>Body mass</b>				
	<b><math>y_\infty, k</math></b>	<b>6</b>	<b>7920.68</b>	<b>0.00</b>
	$y_\infty$	5	7926.43	3.71
	$k$	5	7993.79	71.07
	–	4	8155.69	230.94