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

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ABSTRACT

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.

INTRODUCTION

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 expen-

sive sex could experience a higher mortality rate under unfavourable environmental conditions, thereby affecting population dynamics (Benito & Gonzáles-Solís 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, Klenovsek & Krystufek 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°550 N, 5°250 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 100W infrared lamps were used to provide them with extra warmth during this period.

Chicks were housed in cages of 6.25m², 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 2500m² 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 of known age in the breeding seasons of 2007–2010 and 2012–2015, and measured their body size and mass. Wild chicks were uniquely marked as hatchlings (1 day old) in the nest with a plastic flag of the same type as those used on chicks raised in captivity. Between 2007–2010 and 2012–2015, we succeeded in recapturing 204 chicks of the 5102 chicks that had been ringed as hatchlings (Table 13.1).

Table 13.1. Sample sizes of recaptured male and female Godwit chicks in the wild from 2007–2010 and 2012–2015.

Sex	Biometric measurement					
	Body mass	Wing	Bill	Total-head	Tarsus	Tarsus-toe
Males	114	49	107	110	109	78
Females	90	43	87	87	89	86

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 ~ 10µL 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 1.5mL 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, $y_t = y_\infty \cdot \exp(-\exp(-k \cdot (t - T_i)))$, and the logistic growth model, $y_t = y_\infty / (1 + \exp(-k(t - T_i)))$ (Ricklefs 1968, Tjørve & Tjørve 2010). In these formulas, y_t is value of the trait at age t , y_∞ 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 days) at the point of inflection. For both growth models we also evaluated sex differences in y_∞ , k and T_i .

To test for an effect of sex on y_∞ , 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_∞ , 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_∞). We therefore decided to only include a random effect for the asymptotic growth parameter (y_∞). We then tested, using both growth functions (Gompertz and logistic), for an effect of sex on y_∞ , 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 sub-

tracting 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 · sex, relative hatching date · sex, relative hatching date · year, year · natal habitat type, age · natal habitat type and natal habitat type · 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*-

Table 13.2. Model selection results of Gompertz and logistic growth curves for body mass (a), tarsus (b), bill (c), tarsus-toe (d), wing (e) and total-head (f) lengths, testing for an effect of sex on the different growth parameters y_{∞} , k and T_i . Results are based on the biometric measurements obtained from hand-raised Godwits ($n = 56$). The most parsimonious model is shown in bold (i.e. the model with the fewest parameters among the supported models; $\text{AICc} < 2$). We only show the top five models; all models are shown in Supporting Information Table S1.

Growth function	Sex effects ^a	k^b	$\Delta(-2\log L)$	ΔAICc	Akaike weight ^c
(a) Body mass					
	y_{∞}, k, T_i	9	0.00	0.00	0.64
Gompertz	y_{∞}, T_i	8	1.57	1.15	0.36
Gompertz	y_{∞}, k	8	9.75	17.50	0.00
Gompertz	k, T_i	8	21.56	41.13	0.00
Gompertz	k	7	22.06	40.11	0.00
(-2logL) ^d = 6561.59; AICc^e = 13139.17					
(b) Tarsus					
Logistic	y_{∞}, T_i	8	0.00	0.00	1.00
Logistic	k, T_i	8	21.05	42.71	0.00
Logistic	T_i	7	24.71	48.03	0.00
Logistic	y_{∞}, k	8	84.70	170.00	0.00
Logistic	y_{∞}	7	84.76	168.13	0.00
(-2logL) ^d = 3772.95; AICc^e = 7559.29					
(c) Bill					
Gompertz	y_{∞}, k	8	0.00	0.00	1.00
Gompertz	k	8	20.08	11.04	0.00
Gompertz	y_{∞}	7	109.77	55.88	0.00
Logistic	y_{∞}, T_i	7	110.26	55.13	0.00
Logistic	y_{∞}, k, T_i	9	110.50	54.25	0.00
(-2logL) ^d = 3785.50; AICc^e = 6781.00					
(d) Tarsus-toe					
Logistic	y_{∞}, k, T_i	9	0.00	0.00	0.51
Logistic	y_{∞}, T_i	8	1.06	0.12	0.49
Logistic	k, T_i	8	24.25	46.50	0.00
Logistic	T_i	7	26.94	49.89	0.00
Logistic	y_{∞}, k	8	64.19	126.38	0.00
(-2logL) ^d = 4092.94; AICc^e = 8201.88					
(e) Wing					
Gompertz	y_{∞}, k	8	0.00	0.00	0.68
Gompertz	y_{∞}, k, T_i	9	0.23	1.55	0.31
Gompertz	k, T_i	8	4.65	9.31	0.00
Gompertz	T_i	7	10.78	19.57	0.00
Gompertz	y_{∞}, T_i	8	10.48	20.97	0.00
(-2logL) ^d = 3986.65; AICc^e = 7987.30					
(f) Total-head					
Gompertz	y_{∞}, k	9	0.00	0.00	1.00
Gompertz	T_i	7	22.20	40.39	0.00
Logistic	y_{∞}, T_i	8	60.67	119.32	0.00
Logistic	y_{∞}, k	8	74.29	146.58	0.00
Gompertz	y_{∞}	7	78.57	153.14	0.00
(-2logL) ^d = 3832.35; AICc^e = 7680.70					

^a Testing the effect of sex on y_{∞} , k , T_i or no effect (.). ^b No. of parameters in the model. ^c AICc weight, where a value of 0.00 corresponds to a weight of 0.004.

^d Minimum (-2logL) value observed. ^e Minimum AICc value observed.

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 13.2 and Supporting Infor-

mation 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 ΔAICc of 78.31) and all five linear body size measurements (tarsus ΔAICc = 207.77, bill ΔAICc = 64.53, tarsus-toe ΔAICc = 235.79, wing ΔAICc = 38.57, total-head ΔAICc = 171.97; Figure 13.1, Tables 13.2 and Table S1). Females had larger asymptotic values for all linear and mass measurements; the most pronounced differences between males and females were in body mass (21% heavier for females) and total-head length (11% larger for females) (Table 13.3, for model selection results, see Tables 13.2 and Table S1). As y_{∞} was higher for all different measurements in females, the growth coefficients (k) should all be lower to achieve the same maximum growth rates. However, k was either higher in females or equal between males and females, and as a result the maximum growth rates

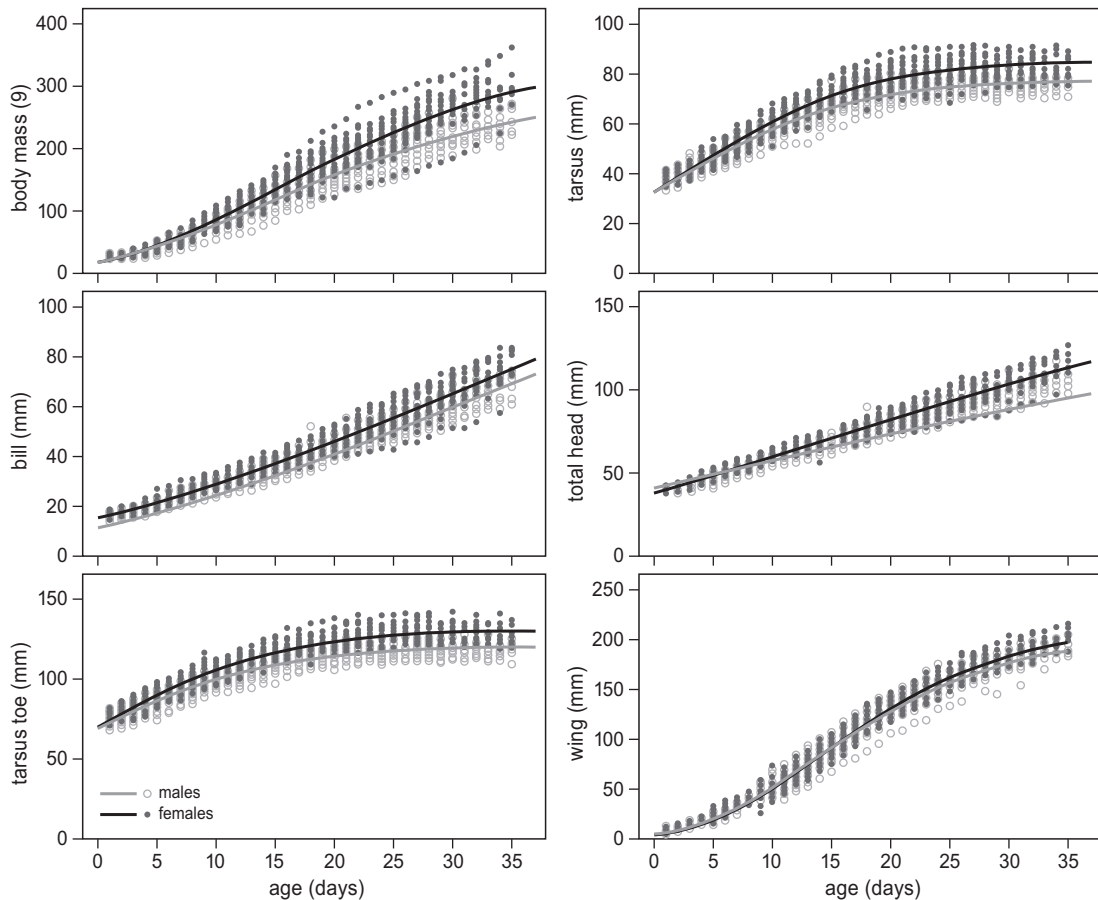


Figure 13.1. Estimated growth curves for body mass, wing length, bill length, total-head length, tarsus length and tarsus-toe length based on the most parsimonious model in Table 13.2. The black line represents for each biometric measurement the growth for females and the grey line for males. Points represent the measurements of the captive-raised chicks, grey points represent females and open grey points represent males.

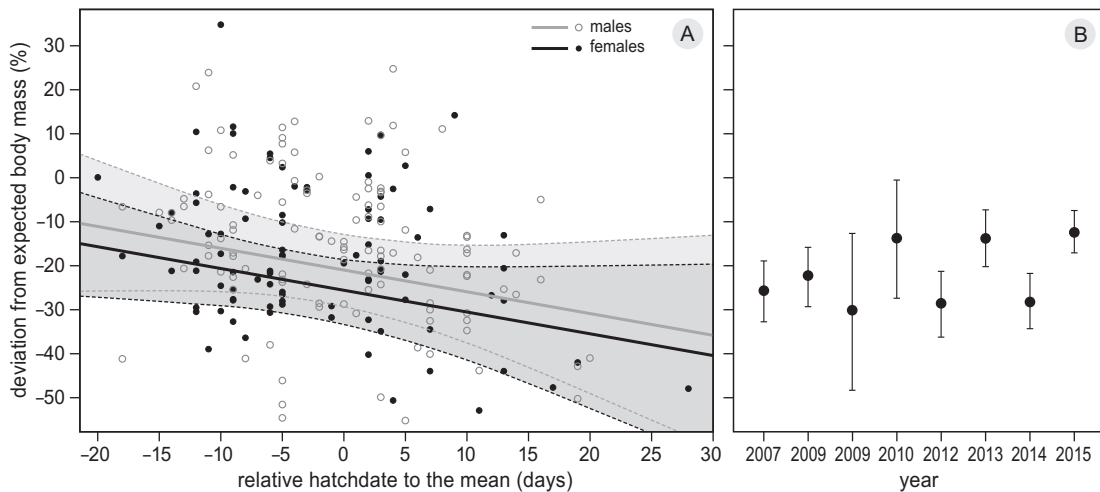


Figure 13.2. (A) Estimated relationship between the deviation in expected age-specific body mass and relative hatching date of wild recaptured chicks; the mean and 95% confidence intervals are shown for both males (grey lines) and females (black lines). Estimates refer to the reference year 2007. Open grey (males) and black (females) points are the actual deviation in body mass of recaptured Godwit chicks. (B) Estimated relationship between the deviation in expected body mass and year; mean and 95% confidence intervals are shown. Estimates refer to a relative deviation from the annual hatching date of 0 days.

were higher for females for all six measurements (Table 13.3). Nonetheless, females reached the inflection point (T_i , the age at which maximum growth occurs) at a later age for body mass, total-head, tarsus and tarsus-toe length (Table 13.3; for model selection results, see Table 13.2 and Table S1).

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 mor-

phometric measurements (Table 13.4). There was also no evidence for an effect of age on the deviation in body mass (Table 13.4). However, recaptured females deviated on average -4.60% (95% CI -1.10 to -7.83%) more from the expected body mass than recaptured males (Figure 13.2A, Table 13.4). Furthermore, residual body mass of chicks was negatively correlated with relative hatching date, but the extent differed between years (Figure 13.2B, Table 13.4). 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 13.4).

Table 13.3. Parameter estimation (mean \pm 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 13.2.

Measure	Growth function	Fixed effects					
		y_∞		k		T_i	
		Female	Male	Female	Male	Female	Male
Body mass	Gompertz	363.0 \pm 7.0	298.0 \pm 8.0	0.0737 \pm 0.0010	0.0737 \pm 0.0010	14.89 \pm 0.17	13.98 \pm 0.13
Bill	Gompertz	161.0 \pm 5.0	147.0 \pm 3.0	0.0320 \pm 0.0012	0.0300 \pm 0.0012	26.91 \pm 0.80	26.91 \pm 0.80
Total-head	Gompertz	181.0 \pm 4.0	163.0 \pm 5.0	0.0340 \pm 0.0008	0.0290 \pm 0.0010	13.60 \pm 0.66	9.00 \pm 0.80
Tarsus	Logistic	84.9 \pm 0.7	77.1 \pm 0.9	0.1420 \pm 0.0010	0.1420 \pm 0.0010	3.38 \pm 0.05	2.33 \pm 0.08
Tarsus-toe	Logistic	131.0 \pm 0.9	121.0 \pm 1.2	0.1270 \pm 0.0010	0.1270 \pm 0.0010	-1.05 \pm 0.07	-2.24 \pm 0.08
Wing	Gompertz	221.0 \pm 2.3	211.0 \pm 2.9	0.0980 \pm 0.0010	0.0970 \pm 0.0010	13.62 \pm 0.07	13.62 \pm 0.07

Table 13.4. 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). 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 .

Response variable	Fixed effects											
	Intercept	Age	Sex ⁽¹⁾	HD	y^{2008} (2)	y^{2009}	y^{2010}	y^{2012}	y^{2013}	y^{2014}	y^{2015}	
Body mass	<i>Estimate</i>	-25.57***	-0.16	4.60*	-0.49†	3.43	-4.40	11.99	-2.87	11.88	-2.55**	13.23
	<i>SE</i>	3.54	0.17	2.30	0.34	4.50	9.11	8.18	4.70	4.46	4.60	3.74
	$R^2 = 0.84$											
Wing length	<i>Estimate</i>	-12.08***	0.18	-3.07	-0.51***	--	--	--	--	--	--	--
	<i>SE</i>	1.27	0.25	2.32	0.16	--	--	--	--	--	--	--
	$R^2 = 0.97$											
Bill-length	<i>Estimate</i>	-3.24**	-0.35***	1.76	-0.16*	-1.46	-3.07	4.17	-4.02	4.47	-1.46	4.38
	<i>SE</i>	1.46	0.09	1.25	0.08	2.61	3.84	4.53	2.73	2.57	2.67	2.21
	$R^2 = 0.75$											
Total-head length	<i>Estimate</i>	-0.59†	-0.47***	6.05**	-0.19***	-2.44	-4.48	-2.13	-2.06	3.40	-3.03	2.32
	<i>SE</i>	2.08	0.10	2.05	0.05	1.62	2.43	2.89	1.70	1.60	1.66	1.35
	$R^2 = 0.94$											
Tarsus	<i>Estimate</i>	-14.36***	0.20**	1.23	-0.20**	-2.18	-5.08	-1.80	-1.51	2.79	-2.94	1.79
	<i>SE</i>	1.15	0.07	1.14	0.07	2.22	3.33	3.95	2.31	2.19	2.22	1.82
	$R^2 = 0.94$											
Tarsus-toe	<i>Estimate</i>	-7.54***	0.09	0.45	-0.24***	-1.86	-2.42	2.79	-1.60	2.57	-1.32	0.04
	<i>SE</i>	0.43	0.05	0.86	0.05	1.74	2.50	2.95	1.81	1.65	1.69	1.49
	$R^2 = 0.88$											

†Reference level for sex is female. ‡Reference level for year is 2007. §Reference level for natal habitat type is 'monoculture'.
 * Significant at the 0.05 probability level. ** Significant at the 0.01 probability level. *** Significant at the 0.001 probability level.

Response variable	Fixed effects										
	NH ⁽³⁾	Age * Sex	HD * Sex	HD * y^{2008}	HD * y^{2009}	HD * y^{2010}	HD * y^{2012}	HD * y^{2013}	HD * y^{2014}	HD * y^{2015}	
Body mass	<i>Estimate</i>	4.33	-0.54	-0.09	0.33	0.56	1.40	-0.65	-1.03*	-0.33	-0.10
	<i>SE</i>	2.51	0.39	0.29	0.49	1.11	0.79	0.53	0.55	0.44	0.43
	$R^2 = 0.84$										
Wing length	<i>Estimate</i>	1.56	-0.19	-0.23	--	--	--	--	--	--	--
	<i>SE</i>	2.14	0.47	0.36	--	--	--	--	--	--	--
	$R^2 = 0.97$										
Bill-length	<i>Estimate</i>	1.74	0.10	-0.16	0.36	0.46	0.15	-0.06	-0.56	-0.12	0.17
	<i>SE</i>	1.43	0.19	0.15	0.31	0.61	0.78	0.30	0.31	0.26	0.27
	$R^2 = 0.75$										
Total-head length	<i>Estimate</i>	1.09	0.60***	-0.02	0.10	0.39	0.62	-0.12	-0.32	0.04	0.12
	<i>SE</i>	0.95	0.12	0.10	0.18	0.39	0.35	0.19	0.19	0.15	0.15
	$R^2 = 0.94$										
Tarsus	<i>Estimate</i>	1.10	-0.12	0.098	-0.14	0.37	0.65	-0.41	-0.54	-0.13	-0.06
	<i>SE</i>	1.21	0.14	0.14	0.23	0.54	0.48	0.26	0.27	0.21	0.21
	$R^2 = 0.94$										
Tarsus-toe	<i>Estimate</i>	1.26	-0.15	-0.04	-0.001	-0.016	-0.014	-0.26	-0.46	-0.03	0.03
	<i>SE</i>	0.87	0.11	0.10	0.19	0.40	0.36	0.19	0.21	0.16	0.16
	$R^2 = 0.88$										

†Reference level for sex is female. ‡Reference level for year is 2007. §Reference level for natal habitat type is 'monoculture'.
 * Significant at the 0.05 probability level. ** Significant at the 0.01 probability level. *** Significant at the 0.001 probability level.

Table 13.4. Continued.

Response variable	Fixed effects									
	NH * γ^{2008}	NH * γ^{2009}	NH * γ^{2010}	NH * γ^{2012}	NH * γ^{2013}	NH * γ^{2014}	NH * γ^{2015}	Age * NH	NH * HD	
Body mass	<i>Estimate</i>	-5.71	-7.13	-29.29	-6.74	-9.60	-16.57	-14.58	0.58	0.21
	<i>SE</i>	9.98	13.76	15.46	10.73	9.95	10.31	9.20	0.35	0.37
	$R^2 = 0.84$									
Wing length	<i>Estimate</i>	--	--	--	--	--	--	--	-0.24	-0.13
	<i>SE</i>	--	--	--	--	--	--	--	0.47	0.35
	$R^2 = 0.97$									
Bill-length	<i>Estimate</i>	-4.39	2.26	-11.19	-6.26	-7.96	-14.28	-5.59	0.20	-0.03
	<i>SE</i>	5.91	8.04	10.42	6.10	5.68	5.83	5.33	0.23	0.15
	$R^2 = 0.75$									
Total-head length	<i>Estimate</i>	-1.65	1.27	-13.71	-5.91	-6.49	-5.30	-7.29	0.20	-0.09
	<i>SE</i>	3.66	5.08	9.38	3.88	3.66	4.00	3.39	0.12	0.13
	$R^2 = 0.94$									
Tarsus	<i>Estimate</i>	-2.14	-0.81	-28.72	1.68	-7.07	-1.75	-3.59	0.22	0.20
	<i>SE</i>	4.95	7.03	12.87	5.35	5.06	4.93	4.62	0.14	0.17
	$R^2 = 0.94$									
Tarsus-toe	<i>Estimate</i>	0.34	5.52	-8.49	0.44	-2.78	-1.18	-3.40	0.16	0.06
	<i>SE</i>	3.75	5.20	9.62	3.98	3.78	4.11	3.48	0.12	0.13
	$R^2 = 0.88$									

¹Reference level for sex is female. ²Reference level for year is 2007. ³Reference level for natal habitat type is 'monoculture'.
* Significant at the 0.05 probability level. ** Significant at the 0.01 probability level. *** Significant at the 0.001 probability level.

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 13.4). Furthermore, the deviation in bill length of recaptured chicks was negatively correlated with relative hatching date (Table 13.4). For total-head length, we found a 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 13.4). 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 13.4). 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 13.4).

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 (Figure 13.1). 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 13.5). 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 13.5). 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 (Figure 13.1, Table 13.3) (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 & Brenninkmeijer 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, Muller *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, 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

Table 13.5. Sexual size dimorphism in captive raised Godwit hatchlings. 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 mm. SSD of chicks are based on the estimated y_{∞} from the chick growth data and SSD of adult birds are based on data obtained from Schroeder *et al.* 2008.

	Females $n = 26$			Males $n = 30$			SSD of captive raised hatchlings	SSD of estimated y_{∞}	SSD of adult Godwits
	Mean	SD	Range	Mean	SD	Range			
Body mass	28.9	1.90	25.1 – 32.4	28.4	2.09	23.5 – 32.6	1.02	1.21	1.20
Wing	18.4	2.24	15 – 23	18.2	1.88	15 – 22	1.01	1.05	1.05
Bill	16.9	0.84	14.8 – 19.1	16.4	0.99	14.1 – 18.2	1.03	1.10	1.17
Total-head	39.6	1.26	37.7 – 42.2	38.9	1.10	36.7 – 40.7	1.02	1.11	1.13
Tarsus	37.7	1.63	35.0 – 41.5	37.0	1.85	33.4 – 40.7	1.02	1.10	1.10
Tarsus-toe	76.6	2.92	72 – 82	75.1	3.07	69 – 82	1.02	1.08	1.08

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 Godwit 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 (Metcalf & 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 devia-

tions 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.

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SUPPLEMENTARY MATERIAL

Table S1. Model selection results of Gompertz and logistic growth curves for body-mass (a), tarsus (b), bill (c), tarsus-toe (d), wing length (e), total-head (f) testing for an effect of sex on the different growth parameters y_{∞} , k , T_i . Results are based on the biometric measurements obtained from hand-raised Godwits ($n = 56$). The most parsimonious model is shown in bold (i.e. the model with the fewest parameters among the supported models; $\Delta AIC_c < 2$).

(a) Body mass						(b) Tarsus					
Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³	Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³
Gompertz	y_{∞}, k, T_i	9	0.00	0.00	0.64	Logistic	y_{∞}, T_i	8	0.00	0.00	1.00
Gompertz	y_{∞}, T_i	8	1.57	1.15	0.36	Logistic	k, T_i	8	21.05	42.71	0.00
Gompertz	y_{∞}, k	8	9.75	17.50	0.00	Logistic	T_i	7	24.71	48.03	0.00
Gompertz	k, T_i	8	21.56	41.13	0.00	Logistic	y_{∞}, k	8	84.70	170.00	0.00
Gompertz	k	7	22.06	40.11	0.00	Logistic	y_{∞}	7	84.76	168.13	0.00
Gompertz	T_i	7	22.75	41.49	0.00	Logistic	k	7	102.87	204.34	0.00
Gompertz	y_{∞}	7	26.86	49.73	0.00	Logistic	.	6	103.08	202.77	0.00
Gompertz	.	6	42.15	78.31	0.00	Gompertz	y_{∞}, k, T_i	9	130.27	263.15	0.00
Logistic	y_{∞}, k, T_i	9	97.67	195.33	0.00	Gompertz	y_{∞}, k	8	130.37	261.34	0.00
Logistic	y_{∞}, T_i	8	98.17	194.34	0.00	Gompertz	k, T_i	8	153.59	307.79	0.00
Logistic	y_{∞}, k	8	109.10	216.20	0.00	Gompertz	k	7	200.00	308.60	0.00
Logistic	k, T_i	8	118.48	234.96	0.00	Gompertz	T_i	7	207.93	414.45	0.00
Logistic	T_i	7	118.63	233.27	0.00	Gompertz	.	6	221.64	439.87	0.00
Logistic	k	7	123.06	242.10	0.00	Logistic	y_{∞}, k, T_i	9	775.77	1554.15	0.00
Logistic	y_{∞}	7	123.81	243.63	0.00	Gompertz	y_{∞}, k	8	843.91	1688.43	0.00
Logistic	.	6	138.99	271.97	0.00	Gompertz	y_{∞}	7	852.48	1733.57	0.00
(-2logL) ⁴ = 6561.59 AICc ⁵ = 13139.17						(-2logL) ⁴ = 3772.95 AICc ⁵ = 7559.29					
(c) Bill						(d) Tarsus-toe					
Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³	Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³
Gompertz	y_{∞}, k	8	0.00	0.00	1.00	Logistic	y_{∞}, k, T_i	9	0.00	0.00	0.51
Gompertz	k	7	20.08	11.04	0.00	Logistic	y_{∞}, T_i	8	1.06	0.12	0.49
Gompertz	y_{∞}	7	109.77	55.88	0.00	Logistic	k, T_i	8	24.25	46.50	0.00
Logistic	y_{∞}, T_i	8	110.26	55.13	0.00	Logistic	T_i	7	26.94	49.89	0.00
Logistic	y_{∞}, k, T_i	9	110.50	54.25	0.00	Logistic	y_{∞}, k	8	64.19	126.38	0.00
Gompertz	.	6	125.05	64.53	0.00	Gompertz	y_{∞}, k, T_i	9	72.69	145.38	0.00
Logistic	y_{∞}, k	8	126.79	63.40	0.00	Gompertz	y_{∞}, k	8	72.79	143.58	0.00
Logistic	k	7	144.03	73.01	0.00	Logistic	k	7	91.66	179.33	0.00
Logistic	k, T_i	8	145.77	72.89	0.00	Gompertz	k, T_i	8	97.41	192.83	0.00
Logistic	T_i	7	156.78	79.40	0.00	Logistic	y_{∞}	7	101.33	198.66	0.00
Logistic	y_{∞}	7	229.91	115.95	0.00	Logistic	.	6	120.89	235.79	0.00
Logistic	.	6	245.14	124.57	0.00	Gompertz	T_i	7	131.02	258.03	0.00
Gompertz	y_{∞}, k, T_i	9	2140.83	1069.41	0.00	Gompertz	y_{∞}, T_i	8	976.38	1950.76	0.00
Gompertz	y_{∞}, T_i	8	2143.26	1071.63	0.00	Gompertz	y_{∞}	7	995.70	1987.39	0.00
Gompertz	k, T_i	8	2150.90	1075.45	0.00	Gompertz	k	7	1310.95	2617.90	0.00
Gompertz	k	7	2255.10	1128.55	0.00	Gompertz	.	6	1444.72	2883.43	0.00
(-2logL) ⁴ = 3385.50 AICc ⁵ = 6781.00						(-2logL) ⁴ = 4092.94 AICc ⁵ = 8201.88					

Table S1. Continued.

(e) Wing						(f) Total-head					
Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³	Growth function	Sex effects ¹	k^2	$\Delta(-2\log L)$	ΔAIC_c	Akaike weight ³
Gompertz	y_∞, k	8	0.00	0.00	0.68	Gompertz	y_∞, k, T_i	9	0.00	0.00	1.00
Gompertz	y_∞, k, T_i	9	0.23	1.55	0.31	Gompertz	T_i	7	22.20	40.39	0.00
Gompertz	k, T_i	8	4.65	9.31	0.01	Logistic	y_∞, T_i	8	60.67	119.32	0.00
Gompertz	T_i	7	10.78	19.57	0.00	Logistic	y_∞, k	8	74.29	146.58	0.00
Gompertz	y_∞, T_i	8	10.48	20.97	0.00	Gompertz	y_∞	7	78.57	153.14	0.00
Gompertz	y_∞	7	19.07	36.14	0.00	Logistic	k	7	82.62	161.23	0.00
Gompertz	.	6	21.28	38.57	0.00	Logistic	T_i	7	87.62	171.25	0.00
Logistic	y_∞, T_i	8	57.86	115.72	0.00	Gompertz	.	6	88.99	171.97	0.00
Logistic	T_i	7	63.32	124.64	0.00	Logistic	y_∞	7	133.33	262.65	0.00
Logistic	k, T_i	8	62.76	125.53	0.00	Logistic	.	6	143.72	281.43	0.00
Logistic	y_∞, k	8	66.84	133.69	0.00	Gompertz	y_∞, k	8	923.70	283.39	0.00
Logistic	k	7	67.88	133.74	0.00	Gompertz	y_∞, T_i	8	924.17	286.33	0.00
Logistic	y_∞	7	76.46	150.91	0.00	Gompertz	k, T_i	8	927.22	287.43	0.00
Logistic	.	6	78.68	153.36	0.00	Logistic	y_∞, k, T_i	9	937.65	295.31	0.00
Logistic	y_∞, k, T_i	9	596.73	1195.45	0.00	Logistic	k, T_i	8	950.89	299.79	0.00
Gompertz	k	7	606.02	1210.05	0.00	Gompertz	k	7	1007.26	310.52	0.00
($-2\log L$) ⁴ = 3986.65 AICc ⁵ = 7987.30						($-2\log L$) ⁴ = 3832.35 AICc ⁵ = 7680.70					

¹ Testing the effect of sex on y_∞, k, T_i or no effect (.). ² No. of parameters in the model. ³ AIC_c weight, where a value of 0.00 corresponds to a weight of 0.004. ⁴ Minimum ($-2\log L$) value observed. ⁵ Minimum AIC_c value observed.