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Sex-specific growth and effects of hatching condition in the reversed sexually size-dimorphic great skua

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Abstract

Increased environmental sensitivity of the larger sex has been reported in several size-dimorphic vertebrate species. It is generally assumed that this is due to a higher energy demand of the larger sex, thus increasing susceptibility to food shortage. However, sex-specific growth rates might act to reduce discrepancies in energy demands of differently sized chicks. To test these ideas, we compared growth of male and female chicks in a reversed size-dimorphic seabird, the great skua *Stercorarius skua*, for which a higher mortality rate of female chicks has been shown. We used chick growth data of mass, tarsus and wing from unmanipulated nests, as well as from an egg removal experiment in which chicks hatched from smaller eggs and in poor body condition. Experimental chicks were raised by either of two groups of parents with differing condition. We fitted logistic growth curves to the data using non-linear mixed models. In the experimental treatments growth was only impaired in the group which was raised by poor condition parents, which underlines the importance of parental quality for chick development. At the end of the nesting period, great skua chicks exhibited a comparable degree of size dimorphism as is found in adults, although neither sex had reached final adult size. Despite females reaching larger asymptotic values, timing of growth was not different between the sexes. However, we found a sex-specific effect of hatching condition: improved hatching condition correlated with faster growth of mass and tarsus in females, but did not affect male growth. The instantaneous growth rates suggest that females face higher energetic demands during growth, especially in the latter part of chick development when size-dimorphism is most apparent. However, vulnerability appears to be connected to circumstances during early development, a time at which the dimorphism is not yet apparent in terms of size or weight. We propose that nutritional constraints during early life negatively affect the development of structures or processes that are necessary to sustain high growth rates later. We found no evidence that growth rates are adapted in order to reduce differences in sex-specific offspring cost in this size dimorphic species. (360 words)

Introduction

Body size is a main descriptive for every species, and it is tightly related to physiological, morphological and ecological characteristics of organisms. Across vertebrate species, body size is correlated with physiological and life history characteristics, such as metabolic rate, age at maturity, and longevity (Gaillard et al. 1989; Speakman 2005; Stearns 1984). Also within species size varies between individuals and leads to differences in physiology and fitness (Blanckenhorn 2000; Wikelski & Romero 2003). This may be most striking in the consistent size differences between males and females of species which exhibit sexual size dimorphism. Sexual size dimorphism represents the norm rather than the exception, as it is found in the majority of vertebrate species (Fairbairn et al. 2007).

In order to achieve different final sizes some aspect of growth must vary between males and females. Divergent development of the sexes might start as early as the embryo stage (Blanco et al. 2003; Krackow 1990). Any variation in growth is likely to affect the “cost” of an offspring: energetically, in time spent raising it, in the “quality” of organism that is produced, or in predation risk. In several size-dimorphic vertebrate species it has been shown that the larger sex exhibits a higher mortality rate during ontogeny (Clutton-Brock et al. 1985; Griffiths 1992; Roskaft & Slagsvold 1985; Teather & Weatherhead 1988). These studies mostly included species with larger males, and it has been suggested that male-specific aspects of phenotype other than size lead to this increased vulnerability (Folstad & Karter 1992; Potti & Merino 1996). However, recent studies on sexually size dimorphic birds with larger females have strengthened the argument that sex-specific vulnerability is indeed mostly connected to larger size *per se* (Kalmbach & Benito 2007; Kalmbach et al. 2005; Torres & Drummond 1997).

What is still not clear, however, is why the larger sex is more vulnerable. Generally, it is assumed that the larger sex needs more energy to grow to its larger size, and this higher energy requirement renders the chicks more sensitive to a shortage of resources (Clutton-Brock et al. 1985; Griffiths 1992; Teather & Weatherhead 1994). However, sex differences in timing of growth might act to reduce the disparity in energy requirements inferred from size alone. The modulation of energetic demands by sex-specific growth could be one reason why studies on sexually size-dimorphic species have rarely found results in support of Fisher’s (1930) sex ratio predictions (Gowaty 1991; Richter 1983; but see Richner 1991).

Reaching different sizes at fledging can be achieved by relative variation of different aspects of growth between the sexes (Richner 1991). In short, given a certain size that is to be reached, the time taken to complete development and the daily rate of increment are the two

main factors that determine the shape of growth. A particular form of growth exhibited by one sex is followed by distinct consequences for energy requirement in relation to the other sex. Richter (1983) and Rofstad (1986) for example argued that the smaller sex grows as rapidly as the larger one, resulting in earlier development, which would render the chick energetically more expensive than expected simply on the basis of its final size. By contrast, Richner (1991) showed that equal growth rates of the larger and smaller sex only occur in exceptional cases, whereas in the majority of sexually size-dimorphic species the larger chick grows at a higher absolute rate than the smaller one. Thus, growth patterns can tell us more about the energy needs during development than the extent of size dimorphism at the time of fledging, and might provide insight into the mechanism for size-dependent offspring vulnerability.

In the present study, we investigated sex-specific growth of nestlings of the great skua, *Stercorarius skua*. Adult great skuas exhibit female-biased sexual size-dimorphism and female chicks exhibit higher mortality than male chicks (Kalmbach et al. 2005). Survival of daughters was particularly poor when they hatched with very low body mass, while sons' survival was not related to mass at hatching. This suggests that male and female chicks experience different demands during development, which might be related to the size dimorphism found in adult birds. In addition to presenting the growth patterns of male and female chicks from natural broods, we used chicks from an egg removal experiment (Kalmbach et al. 2005) in order to investigate sex-specific effects of low hatch weight on development.

Methods

Field procedures

The study was carried out between May and August 2000 on the island of Foula, Shetland (60°08'N, 2°05'W). Breeding success of great skuas in Shetland in 2000 was moderately good and fairly typical for this species in recent years (around 0.8 chicks fledged per pair) but with some indications of shortage of preferred food (Mavor et al. 2001), so our observations were made in a fairly typical season. We followed the growth of 81 chicks from 51 un-manipulated great skua broods plus 56 chicks from an egg removal and cross-fostering experiment (see Kalmbach et al. 2005). Great skuas normally lay clutches of two eggs. In the un-manipulated group, 21 nests had single-chick broods and 30 hatched two chicks. There was no effect of hatching order on chick sex and no combination of offspring sexes in a two-chick brood was more frequent than expected by chance.

In 55 experimental pairs, laying of additional eggs was induced by continuous egg removal until the production of a sixth egg. The sixth egg was then left with the parents to be raised. Several pairs produced a seventh egg, which was also left, resulting in four experimental broods with two hatchlings. The fourth eggs of the extended laying sequences were incubated and raised singly by foster parents, who themselves had only laid the normal clutch of two eggs. All chicks hatching from fourth, sixth and seventh eggs are referred to as experimental chicks, from fourth eggs only as foster chicks, and from sixth and seventh eggs as removal chicks.

The three treatments differed between each other on two levels. On the parental level, females differed in body condition. In the control and foster group females had produced the normal clutch of two eggs, while removal mothers had laid six or seven eggs which negatively affected their body condition (see Kalmbach et al. 2004). On the level of the egg, both the foster and the removal group chicks hatched from eggs smaller than in unmanipulated clutches of two eggs (Kalmbach et al. 2005).

Nest checks were carried out every two days, and more frequently around the expected time of hatching. At hatching or on the following day, chicks were marked by painting individual combinations of toenails until they were old enough to be ringed with a metal ring. A small blood sample (ca. 50 µl) was taken from each chick for molecular sexing. Chicks were measured every two to three days, at each occasion taking a measure of their body mass, wing and tarsus length. Body condition at hatching was calculated as a body mass index (BMI) correcting mass for size. As a measure of size we used wing*tarsus length, which provided a better fit than each of the two parameters on their own. Chicks were defined as fledglings at 38 days old. At that age they are already very mobile, and start flying at around 40 days.

Growth models

To describe the growth patterns in numerical terms, logistic growth curves of the form

$$y = A / 1 + e^{(-k*(age - t_i))}$$

were fitted to the data for body mass, wing and tarsus with age in days after hatching. Parameters estimated by the curve fitting procedure were A = asymptotic size, k = growth constant, which is inversely proportional to the time taken between hatching and fledging, and t_i = inflection point, which represents the time of maximum growth. We also fitted the other two commonly used functions to describe avian growth, the Gompertz and the Van Bertalanffy curves (Starck & Ricklefs 1998). However, the fit of the logistic growth curve

was the best for all three measurements (mass, wing and tarsus), and in the following analyses we therefore only used logistic growth models.

When estimating the logistic growth parameters it is important to remember that the estimates for A , k , and t_i are inter-dependent. Particularly for chicks which do not survive until fledging this can lead to erroneous estimates, as too few data points are available to produce a reliable estimate of the asymptotic value, and therefore also of k , and t_i . Depending on the question of the study, different approaches can be followed to deal with this problem. In our study we initially included all chicks in the growth analysis, and tested for differences in growth parameters between chicks alive and chicks which had died before fledging age. When we found significant differences we continued the analysis only with those chicks alive around fledging age.

The instantaneous growth rate represents the daily mass increment for a given age, and was calculated as

$$\text{growth rate} = k * y_t * (1 - y_t / A)$$

with y_t = mass at age t . We based the calculation of the sex-specific instantaneous growth rates on the logistic growth curves obtained from chicks which were alive at fledging age.

Data analysis

All growth data were analyzed with non-linear mixed effects models using the nlme function in the open source software R (Ihaka & Gentleman 1996; Pinheiro & Bates 2000). Initially we included a nested random effect: individuals nested within biological mother. However, the nested random effect did not change the model estimates compared to models in which a simple random effect on the level of the individual was included. This is probably due to the fact that only few chicks in the dataset shared a biological mother. The final models (mass, wing, tarsus) showed the best fit when we included random effects for all three growth parameters (A , k , t_i).

As fixed effects we estimated A , k , and t_i and modeled their dependence on having survived to fledging age, treatment, sex, hatching condition and the interactions of sex with treatment and condition, using the 'fixed' argument to the nlme function. We carried out backward model selection by stepwise removal of the least significant parameter (based on F-tests), starting with the interactions (Crawley 2002).

Due to the fact that hatching condition was not available for all chicks we used two datasets of different sizes for the analyses: one where only those chicks were included for which hatching condition was available ($n = 95$, of which $n = 49$ were alive at fledging), and

one with all chicks included ($n = 134$, of which $n = 78$ alive at fledging). The larger dataset was used to estimate sex-specific growth parameters without including effects of hatching condition.

For comparative use, we also present data on sizes of adult male and female great skuas, which were caught and ringed during the years 1999 to 2001. All adult birds were caught during incubation. Weights of birds which were part of an experiment were not included.

Results

Growth of chicks and survival until fledging

Growth parameters of chicks which survived until fledging age and those that died at some point beforehand differed for all three measures of size, i.e. body mass, wing length and tarsus length. The factor “alive at fledging age” had a highly significant influence on the predicted final value of mass (+ 110g, SE 20.4), wing (-28.5 mm, SE 7.8) and tarsus (-2.3 mm, SE 0.6; all $p \leq 0.0003$). The fate of chicks before fledging also affected the estimation of the growth constant k and inflection point t_i for wing and tarsus: all four coefficients indicated slower growth for chicks which did not survive the whole nestling period (wing k : -0.011, SE 0.002, t_i : +3.1, SE 0.7; tarsus k : -0.022, SE 0.003, t_i : +1.4, SE 0.3; all $p < 0.0001$).

However, due to the inter-dependence of the three parameters (A , k , t_i) of the logistic growth curve and the difficulties of estimating asymptotic values when chicks died before reaching the age at which the growth curve flattens, the parameter estimates of the models have to be considered with caution. For example, structural growth was estimated to be slower in chicks which died during the nestling phase, but at the same time the final sizes were predicted to have been larger. This prediction of larger final sizes is more likely due to the constraints of the logistic model rather than a true biological effect. Despite the uncertainties about the real effect of the fate “having died” on growth, our models clearly show that there is a qualitative difference between growth of surviving and non-surviving chicks. In the following analysis we only included chicks which could be measured until around fledging age.

Sex-specific growth

Sex-related differences in growth were most noticeable in body mass, to a lesser extent for wing length, and were only very slight for tarsus (Fig. 1). In the final model, a sex effect predicting higher values for females was present for the asymptotic values of all three

measures, but not for the growth constant or the age at the inflection point (Table 1a-c). The results were similar when using the larger data set for a model where hatching condition was not included. Asymptotic body mass and wing length were larger for females ($p = 0.0001$ and $p = 0.0024$ respectively), while females had a slightly higher growth constant for tarsus length ($p = 0.0253$) but not a larger asymptotic tarsus size. Although the absolute differences in body mass, wing and tarsus length between the sexes are largest at the end of the nestling phase, the differences in daily increments are most pronounced around the ages of the inflection point (Fig. 1, right column).

Effects of treatment on growth

Since we pooled chicks from different treatments in the analysis, treatment was included in all models as a main factor. It had significant or near significant effects on the growth parameters of all three measures (Table 1a-c). While chicks in natural and foster nests did not differ from each other in their growth patterns, those from the removal treatment exhibited slightly altered growth. Tarsi of removal chicks grew more slowly than in the other two treatment groups, as the time of the inflection point was only reached around one day later. The estimated asymptotic size of the wings was around 1 cm shorter than for control chicks. By contrast, removal chicks appeared to have a higher mass growth rate than chicks from the other two groups. Taken together, while structural growth seemed to be impaired in removal chicks, mass growth was not negatively affected by the treatment.

Eggs in the two experimental groups were smaller than in non-experimental nests, and consequently hatchlings were also smaller in experimental nests. This was true for all three measures at hatch – wing length, tarsus and body mass (Table 2). Experimental chicks were not just lighter because they were smaller – both experimental groups also hatched in poorer condition, which reflects body mass adjusted for size (Table 2). While hatching condition and size of foster chicks was most similar to removal chicks, their growth pattern was more similar to the heavier and larger chicks from non-experimental nests. Therefore poor hatching condition and small size of removal chicks on its own can not explain the difference in growth patterns with non-experimental nests, as this was not found for foster chicks.

Effect of hatching condition on growth

Although hatching condition correlated with treatment, condition index values overlapped between treatments, with the largest range being found in the foster group (Table 2). This can explain why there was a small additional effect of hatching condition on the asymptotic wing

size and on the age at inflection point of tarsus growth, even when including treatment in the same model (Table 1b+c). However, the strongest influence of hatching condition was observed in an interaction with sex on the time of maximal mass growth and the tarsus growth constant (Table 1a+c). The better the hatching condition of females, the faster they increased mass or tarsus, while there was no significant relationship between growth and hatching condition for males (Fig. 2). These sex-specific effects are not a consequence of differing starting points for males and females, as neither sex was larger or in better condition at hatch (Table 3).

Discussion

The female-biased sexual size dimorphism which is found in adult great skuas (Catry et al. 1999, Table 4) is reflected in the development of the chicks. Even though hatching at the same weight and size, daughters reached a higher fledging mass and grew longer wings than sons. The asymptotic tarsus size was only slightly different between the sexes, and tarsus length also differs little between male and female adult great skuas (Furness 1987, this study). The extent of size dimorphism exhibited by nestlings near the time of fledging was very similar to that seen in adults – around 10 % for mass and 2 % or less for wing and tarsus.

As great skua chicks did not show a detectable sexual size dimorphism at hatch, but females were larger and heavier by the end of the nestling period, we expect females to either grow at a higher rate than males or to grow for a longer period. The parameters t_i and k of the logistic growth curve are both indicators of timing, and they were not different between the sexes in the final model for any of the three variables (mass, wing, tarsus) we measured. We found no evidence that the smaller sex reaches its final size at an earlier age than the larger one and would therefore grow at a faster relative rate and be more expensive than expected from its size alone (Richter 1983; Ricklefs 1979; Teather & Weatherhead 1994). Rather, the fact that females grew at higher absolute rates than males during at least parts of the nestling period supports the assumption that females, the larger sex, indeed have higher energetic demands during development, due both to larger size and higher growth demands (Anderson et al. 1993; Krijgsveld et al. 1998; Weathers 1992). However, the energetic cost of increasing weight or structural size by a given amount might differ between the sexes. Differences in basal metabolic rates between sexes or in activity levels could lead to an equal absolute increase being more costly for the smaller sex, particularly when the males are smaller, as in the great skua. Male chicks generally exhibit higher levels of testosterone and of activity, both factors which can contribute to increased energy demands per unit weight (Eising &

Groothuis 2003; Ros 1999; Wikelski et al. 1999); (but see Eising et al. 2003). Although our results indirectly suggest that female great skua chicks have higher energetic demands during development, direct metabolic measurements are needed to verify this conclusion (Riedstra et al. 1998; Vedder et al. 2005).

Higher energy demands are assumed to be a main factor contributing to increased vulnerability of the larger sex (Clutton-Brock et al. 1985). Although the difference in daily energy consumption is probably largest around the time of maximum growth, some studies found that the larger sex is also more sensitive to conditions at the beginning of development, when size dimorphism is still negligible (Kruuk et al. 1999; Lindström 1999). In a previous analysis of chick survival in great skuas, we showed that female chicks exhibited a higher mortality rate, and the risk of dying was increased by low hatch weight for females but not for males (Kalmbach et al. 2005). The fact that hatching in poor condition lead to slow growth in female but not male great skua chicks is further evidence that the larger sex is less able to mitigate difficult starting conditions. This in turn indicates that within a single species the developmental program of the larger sex is more tightly constrained than of the smaller one. In great skuas, as in other species with sexual size dimorphism, there can be a considerable size overlap between the sexes, and same-sized males and females exist. The fundamental question that remains is whether a potential male and female, which are genetically the same size, are equally vulnerable to poor conditions. Put differently: would poor hatching condition delay growth of a genetically small female equally much as of a genetically large female? This question can only be tackled with pedigree knowledge and predicting genetic sizes of individuals (see Weatherhead & Dufour 2005).

The sex-specific effect of hatching condition was present for mass and tarsus growth of great skua chicks but not for wing length. Structural growth, and particularly wing length, generally shows a less plastic response to varying feeding conditions during development than body mass. While organ sizes are quickly reduced as a consequence of food deprivation, growth of bone structures and feathers is maintained at normal rates for much longer (Benowitz-Fredericks et al. 2006; Moe et al. 2004; Moe et al. 2005; Schew & Ricklefs 1998). Particularly wings are crucial for successful fledging, and a delay in feather development will delay fledging age and increase exposure to predation risk. Maintaining the potential for feather development is considered to be energetically very costly, and poorly grown feathers affect flight ability and are less durable (Lindstrom et al. 1993; Murphy 1996; Swaddle et al. 1996). The fact that hatching condition did not delay wing growth in females is probably less

due to wings being a cheap structure to build, but rather to them being very important to be built well and on time.

Chicks in both our experimental groups had to cope with reduced resource availability already during embryonic development, as they hatched from smaller eggs than in unmanipulated clutches. However, these disadvantaged starting conditions did not affect timing of growth and final sizes of those chicks which were raised by parents in good body condition (i.e. the "foster" group). Only the additional disadvantage of being raised by physically stressed parents altered the growth pattern: structural growth was impaired while body mass increase was accelerated. This is further evidence that the production of replacement eggs is costly for parents, not only because it affects their own body condition, but also in terms of parental rearing ability (Monaghan et al. 1998; Nager et al. 2000). The link between extra egg production, maternal body condition, and rearing abilities is underlined by the fact that being raised by parents which had not laid additional eggs (in the "foster" group) could apparently compensate for reduced resource availability during embryonic development.

The analysis of hatching condition and growth across all treatments coupled with our earlier results on sex-specific effects of hatch weight on survival (Kalmbach et al. 2005) clearly show that great skua daughters are more sensitive to early conditions than sons. In the removal group of the current experiment, as well as in a previous egg removal experiment, we found that the primary or hatching sex ratio in the later eggs of extended laying sequences was skewed in favour of males (Kalmbach et al. 2005; Kalmbach et al. 2001). Given that male development and survival are less affected by low hatch weight, producing sons rather than daughters under circumstances when mothers are in poor condition and unable to lay large eggs could be a strategy to maximise offspring survival and quality (Kruuk et al. 1999; Nager et al. 1999; Nager et al. 2000).

For vertebrate species with sexual size dimorphism there is a growing body of circumstantial evidence that the larger sex is more sensitive to poor rearing conditions (Kruuk et al. 1999; Muller et al. 2005; Nager et al. 2000; Velando 2002). This might result in increased mortality, depressed growth or other quality differences between the differently sexed offspring (Kalmbach & Benito 2007). Although the main reason cited for this differential environmental sensitivity is higher energetic requirements in order to grow larger, studies like ours show that the sensitivity can be determined by circumstances which act before differences in energy requirements become apparent. This suggests that between individuals of the same species energy and resource allocation are varied from early

development on, in relation to the size that is to be reached by the organism. Basically, the “hardware” that is needed to achieve faster growth at a later stage has to be built at the beginning of life. Despite sufficient energy supply at a later stage, growth might be impaired if the necessary structures could not be established during early development (Bech & Ostnes 1999; Ricklefs 2003).

Differences in allocation to various organs can be expected to occur during post-hatch growth too. Standard growth measurements are usually not detailed enough to pick these up. Body mass is a general indicator of visceral growth, but cannot provide details about the mass of different organs, which might play a crucial role in energy budgets (Bech & Ostnes 1999; Moe et al. 2004). *In vivo* magnetic resonance imaging presents a non-destructive opportunity to determine organ sizes, although it is logistically difficult to apply in field studies (Czisch et al. 2001). Within the non-destructive framework, studies which directly measure energy consumption, as well as those which investigate physiological correlates of growth, such as oxidative damage, are alternative approaches to gain better insights into the connection between early development, sex-specific growth patterns, energy requirements and offspring sensitivity.

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Table 1. Final growth models for mass, wing and tarsus of great skua chicks. Models were fitted as non-linear mixed effects models, with random factors on the level of the individual for A , k and t_i . Only data of chicks which survived until fledging age are included in the models. * indicate significant values. The coefficients for “sex” are for females in reference to males. Similarly, treatment effects for “foster” and “removal” are in contrast to unmanipulated nests.

dependent	growth parameter	variable	value	SE	p-value	
a) mass	A	(intercept)	1097.0	20.3	0.0000*	
		sex	93.0	32.6	0.0045*	
	k	(intercept)	0.1532	0.0029	0.0000*	
		treatment “foster”	0.0018	0.0036	0.6141	
		treatment “removal”	0.0087	0.0036	0.0163*	
		<i>treatment</i>			0.07	
	t_i	(intercept)	17.84	0.25	0.0000*	
		sex	0.25	0.28	0.3815	
		condition	0.06	0.04	0.0820	
		sex*condition	-0.19	0.05	0.0002*	
n = 49 chicks; observations = 815; random effects: positive-definite						
b) wing	A	(intercept)	345.55	1.63	0.0000*	
		sex	6.76	2.15	0.0017*	
		treatment “foster”	-1.49	2.34	0.5251	
		treatment “removal”	-9.42	3.00	0.0017*	
		<i>treatment</i>			<.0001*	
	k	(intercept)	0.1158	0.0009	0.0000*	
	t_i	(intercept)	26.12	0.28	0.0000*	
	n = 49 chicks; observations = 811; random effects: positive-definite					
	c) tarsus	A	(intercept)	70.71	0.40	0.0000*
			sex	1.38	0.70	0.0495*
k		(intercept)	0.1202	0.7035	0.0000*	
		sex	0.0016	0.0021	0.4417	
		condition	-0.0007	0.0003	0.0052	
		sex*condition	0.0016	0.0004	0.0000*	
t_i		(intercept)	5.68	0.18	0.0000*	
		treatment “foster”	-0.28	0.35	0.4206	
		treatment “removal”	0.87	0.32	0.0065*	
		<i>treatment</i>			0.0208*	
n = 49 chicks; observations = 808; random effects: positive-definite						

Table 2. Size measures at hatch for chicks from different treatment groups. The p-values refer to the contrast of each experimental group with non-experimental chicks. The last column gives the p-values of post-hoc tests comparing the two experimental treatments with each other.

	non- experimental chicks	foster chicks	removal chicks	foster vs. removal post-hoc
Body mass at hatch (in g)	67.4 ± 0.97 (68)	59.0 ± 1.07 (25) <i>p</i> < 0.0001	56.9 ± 0.84 (28) <i>p</i> < 0.0001	<i>p</i> = 0.136
Wing at hatch (in mm)	23.8 ± 0.21 (43)	22.8 ± 0.24 (25) <i>p</i> = 0.0009	23.0 ± 0.21 (29) <i>p</i> = 0.0047	<i>p</i> = 0.518
Tarsus at hatch (in mm)	26.0 ± 0.14 (48)	25.6 ± 0.18 (25) <i>p</i> = 0.0441	24.8 ± 0.18 (29) <i>p</i> < 0.0001	<i>p</i> = 0.0071
Hatching condition index	2.11 ± 0.83 (44)	- 1.32 ± 1.21 (24) <i>p</i> = 0.0077	- 2.30 ± 0.50 (28) <i>p</i> = 0.0004	<i>p</i> = 0.432

Table 3. Size measures at hatch for male and female chicks. P-values refer to ANOVA tests.

	males	females	<i>p</i>
Body mass at hatch (in g)	62.2 ± 0.82	64.6 ± 1.34	0.112
Wing at hatch (in mm)	23.4 ± 0.20	23.2 ± 0.18	0.649
Tarsus at hatch (in mm)	25.5 ± 0.13	25.65 ± 0.18	0.548
Hatching condition index	- 0.16 ± 0.63	0.10 ± 0.98	0.825

Table 4. Biometric measurements of male and female adult great skuas from Foula, Shetland, caught between 1999 and 2001. Result of t-test comparing male and female measurements. Length of sternum was measured with two fingers on the mid-point of the two clavicles, and is therefore referred to as sternum index. Asterixes indicate significant

size differences between the sexes after sequential Bonferroni correction of the t-test results.

	males	females	t	p	
Mass (g)	1298.8 ± 88.6 (26)	1436.8 ± 77.4 (80)	7.615	0.000	*
Tarsus (mm)	70.4 ± 2.3 (16)	70.8 ± 2.2 (94)	0.614	0.541	
Wing (mm)	419.6 ± 8.7 (37)	428.0 ± 7.9 (123)	5.498	0.000	*
Sternum - index (mm)	90.8 ± 4.6 (25)	94.8 ± 3.6 (122)	4.777	0.000	*
Head-bill (mm)	111.3 ± 2.6 (25)	112.4 ± 2.6 (120)	1.798	0.074	

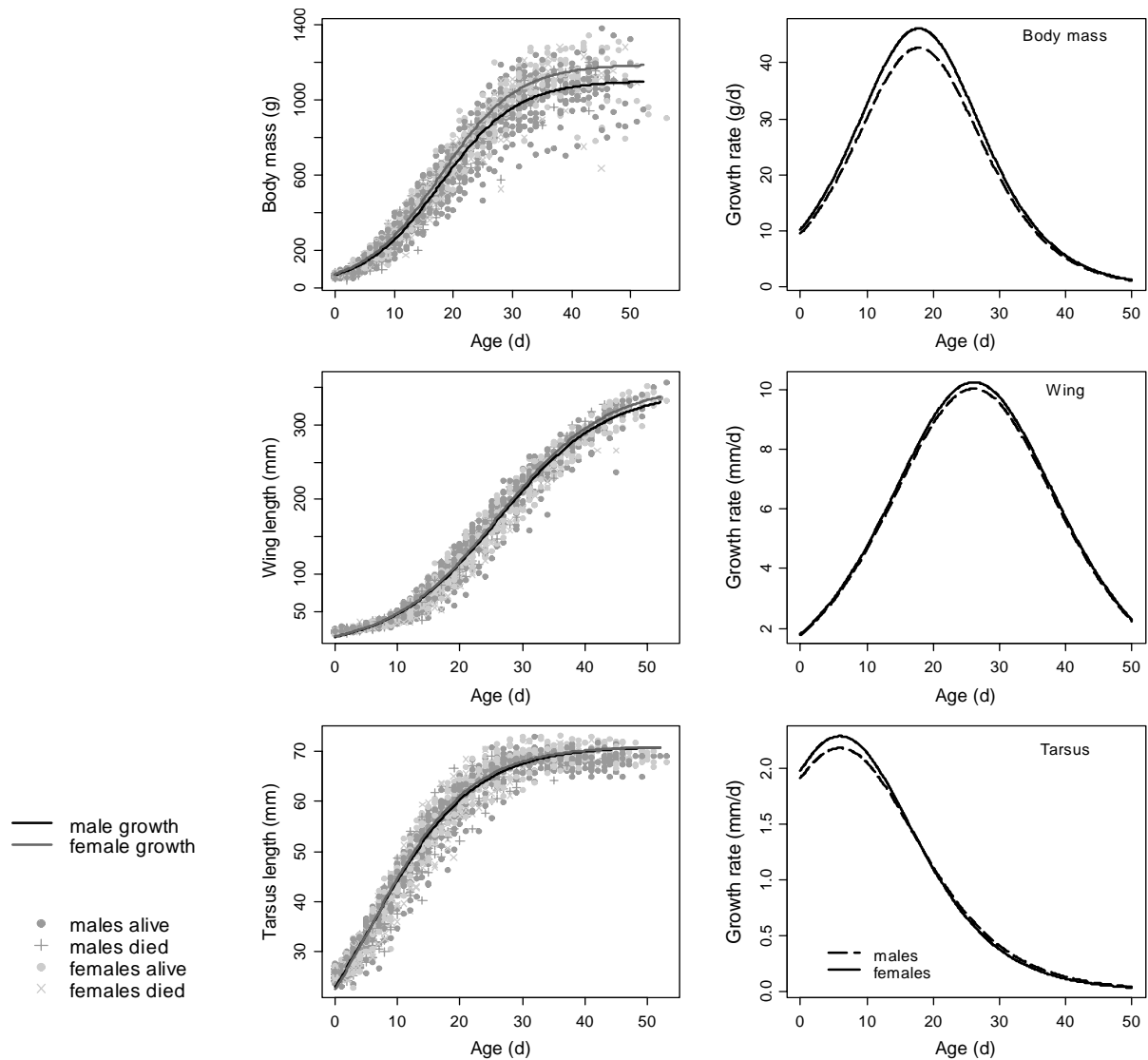


Figure 1. Growth of body mass, wing and tarsus from hatching to fledging age for male and female chicks of the great skua. The left column represents original data and fitted logistic growth curves. Data points of all chicks that were measured are represented – those which were still alive at fledging age (round symbols) and those which died at some point between hatching and fledging age (cross symbols). Since growth patterns differed significantly between those chicks which reached fledging age and those that did not, the growth curves are based only on the surviving chicks (see also text). The right column represents the respective instantaneous growth rate, i.e. the daily increment at a given age.

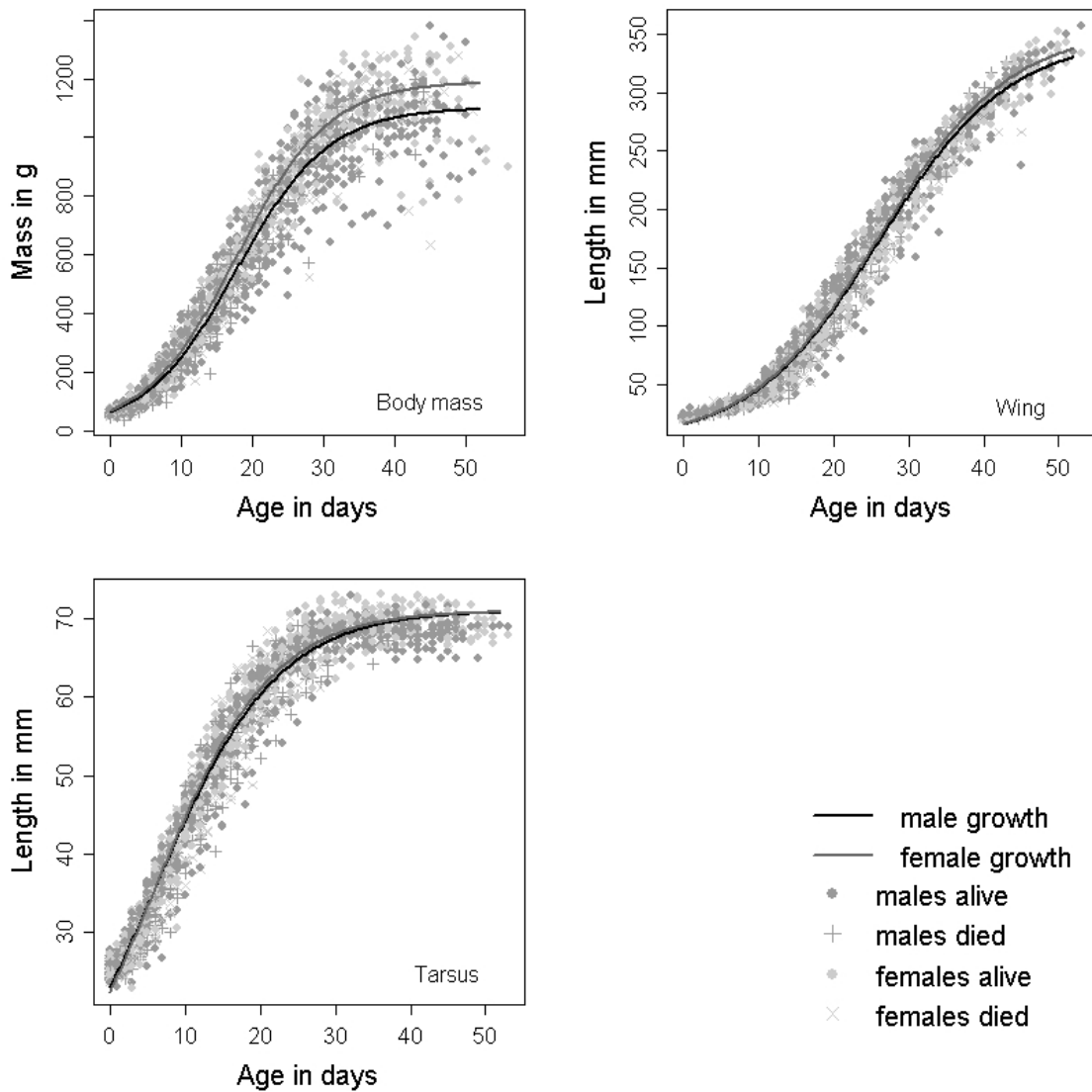


Figure 1. Growth of body mass, wing and tarsus from hatching to fledging age for male and female chicks of the great skua. Data points of all chicks that were measured are represented – those which were still alive at fledging age (round symbols) and those which died at some point between hatching and fledging age (cross symbols). Since growth patterns differed significantly between those chicks which reached fledging age and those that did not, the growth curves are based only on the surviving chicks (see also text).

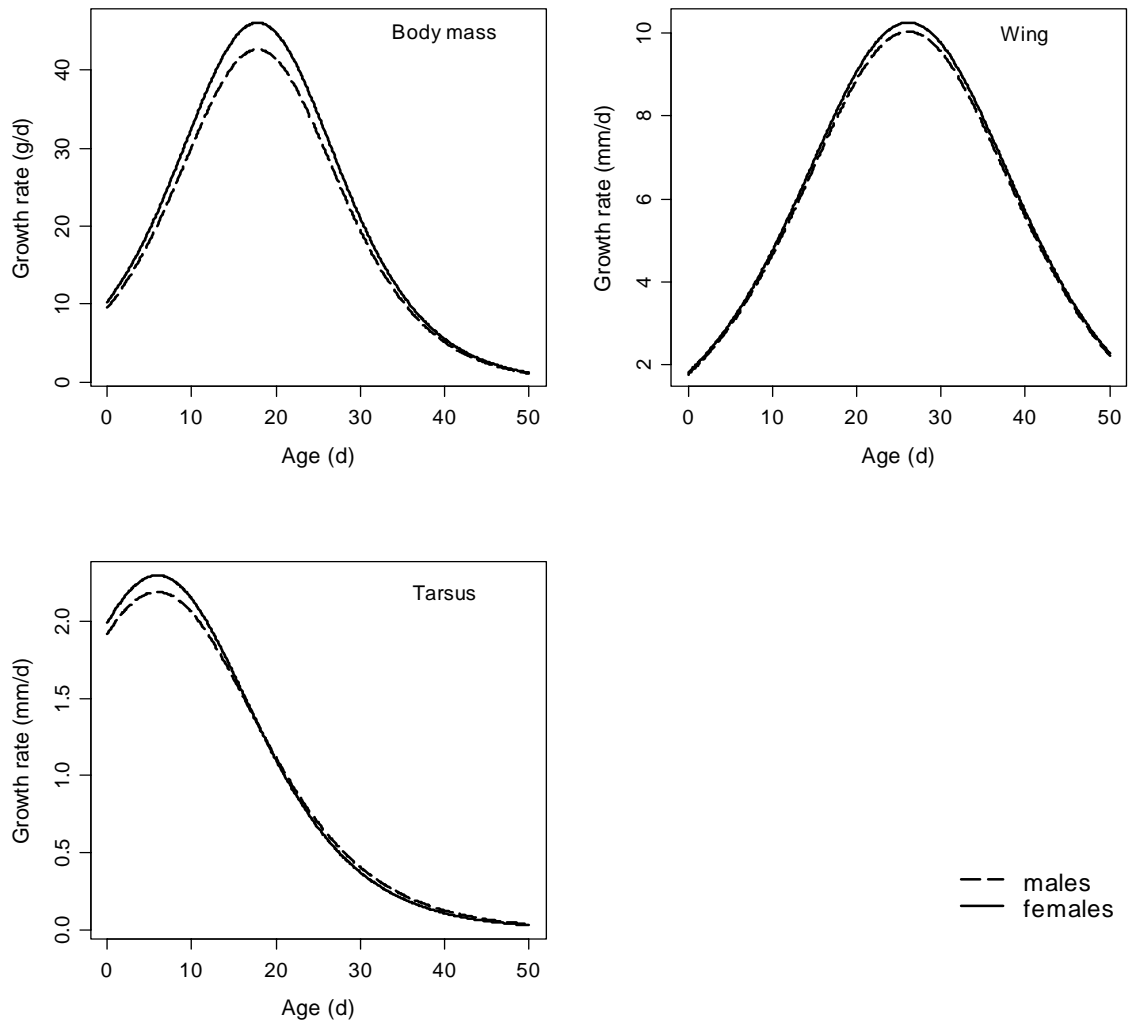


Figure 2. Instantaneous growth rates of body mass, wing and tarsus for male and female great skua chicks, based on the sex-specific logistic growth curves from fig. 1.

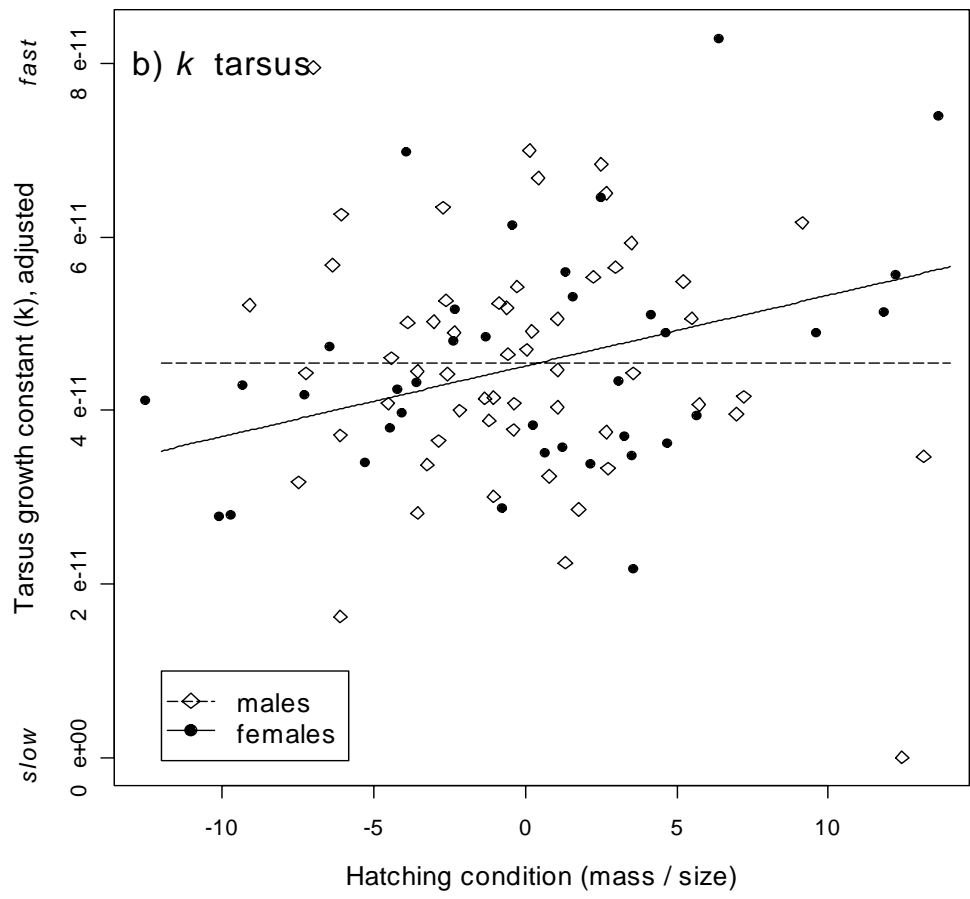
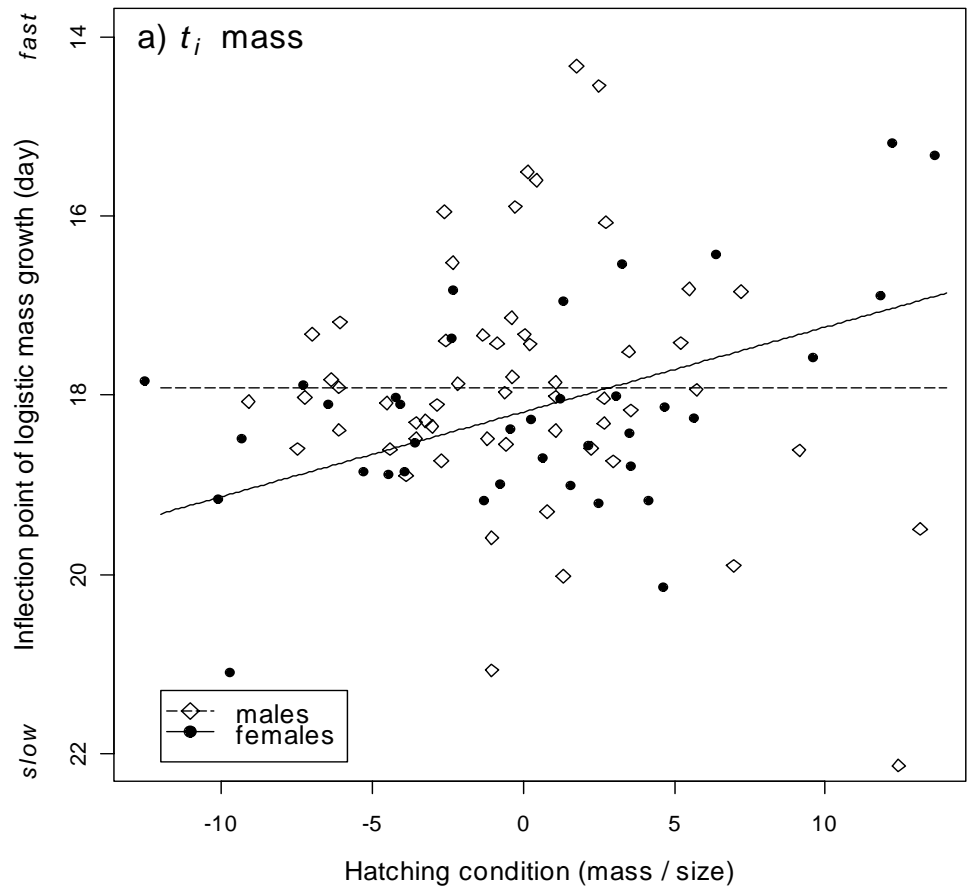


Figure 3. Relationship of growth parameters with hatching condition for male and female great skua chicks. **a)** Inflection point of mass growth; for males this relationship was not significant, and the line is drawn at the mean value; note that the values of the y-axis go from large to small in order to represent the slow / fast direction in the same way as for part b) of the graph; **b)** growth constant of tarsus growth, adjusted by subtracting the lowest value of the sample from each individual value; for males this relationship was not significant, and the line is drawn at the mean value.