Growth and energy expenditure of Wandering Albatross *Diomedea exulans* chicks

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Wandering Albatross *Diomedea exulans* chicks require 9–10 months to achieve adult body size at fledging, at which time they are also sexually size dimorphic. Because the developmental period spans the winter season, chicks must endure severe winter conditions and variability in provisioning effort by their parents. Thus chicks may adjust their rate of energy utilization to accommodate variations in provisioning, but this has not previously been studied. We followed longitudinally the changes in growth, body composition and oxygen consumption of 10 chicks from the end of the brooding period until fledging on the Crozet Islands. Body mass, culmen length and wing length were measured every 10 days and total body water (TBW) and resting metabolic rate (RMR) were measured monthly. Overall growth followed a logistic curve for all chicks, and sexual dimorphism in body mass appeared as early as the second month of measurements (males being heavier than females). Absolute TBW followed a logistic increase like that of body mass and was significantly higher in males owing to the difference in body mass. Conversely, mass-specific TBW (i.e. the proportion of body mass made up of water) did not differ significantly between male and female chicks. Absolute RMR peaked at $1.5 \times$ adult basal metabolism in midwinter when chicks achieved maximum body mass, but decreased to adult levels by the time chicks fledged. The decrease in absolute RMR following attainment of peak mass is atypical of most seabird chicks (Procellariiformes) and may be explained partly by a reduction in size of the gut when parents reduce provisioning effort. The changes in mass-specific RMR did not differ between sexes but male chicks, being heavier, had higher absolute oxygen consumption and therefore greater energy requirements.

The ontogeny of growth in birds is diverse among species. This diversity is characterized by a heterogeneous set of characters that may include behaviour, anatomical traits at hatching and growth rates after hatching (Nice 1962, Skutch 1976, Starck 1993, Starck & Ricklefs 1998). Differences in growth rates among species are presumed to represent adaptations to variability in the environment (Ricklefs *et al.* 1998). For example, Procellariiformes (albatrosses and petrels) have prolonged postnatal development, probably because parents experience difficulty acquiring resources in the pelagic environment (Lack 1968).

Wandering Albatrosses *Diomedea exulans*, the largest procellariiform species, forage far from the nesting colony and exploit patchy, ephemeral prey. They are also long-lived birds that sometimes experience periods of energy deficit during breeding when chick requirements are high (e.g. brooding stage; Weimerskirch & Lys 2000). Moreover, when food availability is insufficient to sustain the energy requirements of a brood, Wandering Albatrosses will abandon reproduction to avoid risking their own survival (Weimerskirch 1999). Slow chick growth reduces the pressure on adults to maintain high provisioning rates (Lack 1968, Ricklefs *et al.* 1998), and lowers the probability of chick starvation by reducing

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peak (but not necessarily total) metabolic requirements of the nestling (Ricklefs 1973). Nonetheless, hatchlings require 9–10 months to develop to adult body size at fledging (Tickell 1968), so they must endure the unpredictability of provisioning by adults (Weimerskirch & Lys 2000) and the harshness of winter conditions.

Adult Wandering Albatrosses are known to be sexually size dimorphic (Tickell 1968, Shaffer *et al.* 2001b), and chicks also exhibit sexual size dimorphism throughout the chick-rearing period and at fledging (Berrow *et al.* 1999, Weimerskirch *et al.* 2000, Shaffer *et al.* 2001b). Furthermore, the factors affecting survival from fledging to adulthood differ between the sexes. For male chicks, overall body size (i.e. structural size) at fledging seems to be the most critical factor affecting survival to maturity, whereas body condition at fledging is more important for survival than body size in female chicks (Weimerskirch *et al.* 2000). However, it is unclear whether these patterns of development for Wandering Albatross chicks are solely manifested by the differential parental investment of parents: males receive more food from their parents and are therefore more costly to rear (Weimerskirch *et al.* 2000), or possibly by sex differences in energy utilization in chicks, or both. So far, no study has examined the possible reasons for these developmental differences in growth and energy expenditure in a species with such a long development period. Therefore, we examined the growth and development of Wandering Albatross chicks by collecting longitudinal measurements of body size, body composition (i.e. total body water) and oxygen consumption (VO_2) of 10 chicks from the end of the brooding period to the end of the chick-rearing period. The aims of the study were to examine (1) how energy expenditure changes throughout the growth period and (2) whether growing male and female chicks differ in energy expenditure and body composition.

METHODS

Field study

The study was carried out on Ile de la Possession (46°25′S, 51°50′E), Crozet archipelago, south-western Indian Ocean from April to November 2000 at the colony of Baie du Marin (see colony descriptions in Weimerskirch & Jouventin 1987). After chicks hatch in mid-March, they are brooded alternately by both adults for approximately 30 days, and then left alone on the nest while both parents forage at sea (Tickell 1968). After mid-April, parents only visit the nest for brief periods of 6–12 h to feed the chick and then they return to sea (Weimerskirch & Lys 2000). This cycle continues for 8–9 months until chicks fledge in November/December

Ten chicks (four males and six females, of the same approximate age (±2 days)) were randomly chosen from a colony of about 50 nests at the end of the brooding period and measurements were then collected until the end of the chick-rearing period. Growth rates were measured every 10–12 days, and body composition and metabolic rate were assessed at the end of each month (every 21–30 days) from April to October. Chicks were transported in a crate at night to the nearby base (150–300 m from the nests) and allowed to settle in the metabolic chamber for 1 h. Measurements were collected for approximately 3 h, then chicks were returned to their nest in the colony before sunrise. All laboratory measurements were conducted after sunset to ensure that parents would not return to an empty nest, because Wandering Albatrosses nearly always return to the nest during local daylight hours (Weimerskirch & Lys 2000). In total, chicks were only away from their nest once a month, for about 5 h, from April to October.

Body measurements for assessment of growth

Body morphometrics were collected from chicks directly at the nest by the same person (G.M.) to ensure consistency in measurement technique. The culmen length, minimum bill depth and bill depth at the tip were measured using Vernier callipers, accurate to ±0.05 mm, and wing length was measured from the carpal joint to the tip of the primary using a tape measure accurate to ±0.5 mm. Body mass was measured by weighing chicks in a cloth sack, using a Salter spring balance accurate to ±50 g. The sex of each chick was determined using morphometric measurements collected during growth and at the time of fledging following Weimerskirch *et al.* (2000). According to the authors, 96% of the chicks are assigned correctly when using this method (Weimerskirch *et al.* 2000).

Tritiated water for estimating total body water (TBW)

Isotope dilution has commonly been used to measure

total body water in adults (e.g. Degen *et al*. 1981, Groscolas *et al*. 1991, Golet & Irons 1999) as well as in growing animals (Degen *et al*. 1991, 1992, Houser & Costa 2001). Prior to entering the metabolic chamber, chicks were weighed on a balance accurate to ±10 g, 2 mL of blood was collected from the brachial (wing) vein and the chicks were then given an intraperitoneal injection of 100 µCi (7.40 MBq/mL) of tritiated water (HTO) in 0.5 mL of sterile saline. The mass of the injected volume was determined by weighing the syringe (±0.01 g) before and after injection. We assumed that isotope equilibration time (Degen *et al*. 1981) for chicks was equivalent to that of adults, which was determined in a separate study (Shaffer *et al*. 2001a) to be around 120 min. Therefore, a post-equilibration sample of 2 mL of blood was collected 4 h after injection at the conclusion of the metabolic rate measurements.

All blood samples were collected with a 5-mL syringe, transferred to a vacutainer (B-D brand with no additives; Beckton-Dickinson, Franklin Lakes, NJ, USA), and centrifuged immediately after collection. Blood serum was transferred to 2-mL plastic screw cap vials (with silicon o-rings; Sarstedt, Inc., Germany) and frozen at –20 °C until analyses were performed in May 2001.

Tritiated body water in blood serum was obtained using the evaporative-freeze trap method of Ortiz *et al*. (1978). The average yield of tritiated water from the distillation of 150 µL of serum was approximately 140 mg. The distilled water was then suspended in 10 mL of Ecolite[+] scintillation cocktail (ICN Pharmaceuticals, Costa Mesa, CA, USA) and the specific activity measured in triplicate on a liquid scintillation counter (Beckman LS 6500, Beckman Coulter Inc., Fullerton, CA, USA).

All measurements of absolute total body water (in litres, L) were reduced by 4% to correct for the overestimate of total body water when using tritiated water compared with the dilution of oxygen-18 in body water (Speakman 1997). This assumption was verified in a separate study by Shaffer (2000), who determined that tritiated water overestimated TBW by 4% (range 3–6%) compared with TBW determined by the dilution of oxygen-18 in adult Wandering Albatrosses.

Oxygen consumption

Metabolic rates were determined using an open circuit respirometry system. Birds were placed in chambers of 100–180 L to accommodate the increasing body size of growing chicks. The metabolic chamber was placed in a large thermostatic box (Secasi, Secasi Technologies, Pessac, France) that controlled air temperature inside the chamber. The temperature inside the chamber was maintained at 5–10 °C, which was equivalent to the outside temperature. These temperatures are within the thermoneutral zone of Wandering Albatross chicks (lower critical temperature within 0 °C and –10 °C for 2-month-old chicks, K. Nadra, J.L. Rouanet & C. Duchamp pers. comm.). Airflow was adjusted to maintain chamber $O_2 > 20.5\%$ and moved through the chamber at a rate of 37–40 L/min. Subsamples of the exhaust air from the chamber were drawn continuously through columns of Drierite to trap moisture, then into a Servomex O_2 Analyser (Servomex France, Paris, France) to measure oxygen content and finally into a Uros 2 Hartman Braun infrared analyser to measure CO_2 content. There was a delay in the system of approximately 50 s between the time of a breath and a deflection in O_2 and CO_2 concentrations measured by the analysers. The fractional oxygen concentration of sampled air was averaged every 10 s and stored on a computer. Labtech Notebook 5.1.3 software (Labtech, Andover, MA, USA) was used to convert changes in fractional oxygen and carbon dioxide concentration to values of oxygen consumption (VO_2) and carbon dioxide production (VCO_2) using the methods of Depocas and Hart (1957). The entire system was calibrated using the N_2-dilution method (Fedak *et al*. 1981) and all gas measurements were corrected to standard temperature and pressure (STPD).

Chicks were allowed to settle in the chamber for 1 h to reach thermal equilibrium with the chamber air, before the start of each trial. Furthermore, chicks became habituated to the handling/manipulation and were therefore calm and generally quick to become quiescent during trials despite the equipment noise. Although metabolism was measured within the thermoneutral zone of chicks, it was not possible to ensure that chicks were post-absorptive (i.e. not digesting) because albatrosses and petrels retain stomach oil in their proventriculus when fasting (Warham 1990). However, chicks were weighed twice daily for several days preceding a trial to evaluate whether they had been fed. Trials were only conducted when it was possible to determine that a chick had not been fed for at least 24 h. Thus, for each chick, oxygen consumption was averaged over three 1-h periods and the minimum mean of the three was considered to

be the minimum resting metabolic rate (RMR) and was used in subsequent comparisons.

Statistics

Statistical analyses were performed using SYSTAT 9.0 (Wilkinson 1996) with a significance level of $P \leq 0.05$ for *t*-tests, paired *t*-tests, Mann–Whitney *U*-tests, ANOVAs and regression analyses. Repeated measures ANOVAs were used to test for the effect of the sex of the chick on (1) body mass, (2) body water content (absolute and relative) and (3) oxygen consumption (absolute and relative). Unless stated otherwise, all data are presented as means ± 1 sd.

RESULTS

Mass change, culmen length and wing growth

The overall mass growth curve for 10 Wandering Albatross chicks followed a typical logistic growth curve, with the most rapid increase occurring from April to July before the stabilization of body mass at the end of August (Fig. 1a). Sexual size dimorphism was apparent throughout the measurement period (repeated measures ANOVA: $F_{1,8} = 5.76$, $P = 0.043$), with males being heavier than females (115.0 ± 7.4% of the females' mass on average from April to October, Appendix 1).

The growth pattern of the culmen was similar to that of body mass, except that culmen length attained a plateau in late September (around 20 September, Fig. 1b). In addition, there was no significant influence of sex on culmen length (repeated measures ANOVA: $F_{1,8} = 1.34$, $P = 0.281$).

The rate of wing growth did not differ significantly between sexes until after the end of July (Fig. 1c). By the end of August, the difference in absolute growth between the sexes was significant (repeated measures ANOVA: $F_{1,8} = 9.55$, $P = 0.015$) with males exhibiting significantly longer wings (108.3 ± 2.8% of the females' wing length from September to October; Mann–Whitney *U*-tests for September and October, $U = 2.00$, $P = 0.033$ and $U = 0.00$, $P = 0.011$, respectively) than similarly aged females.

Changes in body composition

The change in absolute TBW followed a similar pattern to that of body mass (Fig. 2a). Furthermore, sex had a significant influence on absolute TBW (repeated measures ANOVA: $F_{1,8} = 8.80$, $P = 0.021$); however, body mass accounted for this difference because mass-specific TBW (i.e. percentage of body mass) did not differ significantly between the sexes (Fig. 2b, repeated measures ANOVA: $F_{1,8} = 0.15$, $P = 0.707$).

The relationship between absolute TBW and body mass was highly significant (Fig. 3a; $F_{1,67} = 1918$, $r^2 = 0.960$, $P << 0.001$). Mass-specific TBW (%) decreased significantly (paired *t*-test, $t = -6.59$, $df = 9$, $P << 0.001$) between April and October in both sexes: 52.2 ± 2.7% to 43.4 ± 4.6% for females and 50.9 ± 2.6% to 43.9 ± 3.4% for males (Fig. 2b and Appendix 1). Adult values for absolute and mass-specific TBW were recalculated from the literature (absolute TBW: females: 4.30 ± 0.29 L, males: 5.23 ± 0.16 L; mass-specific TBW: females: 47.8 ± 4.7%, males: 49.7 ± 4.9%, Shaffer *et al.* 2001a) and are also shown on Figure 2 for comparison with chicks. Levels of absolute TBW (Fig. 2a) for chicks at fledging
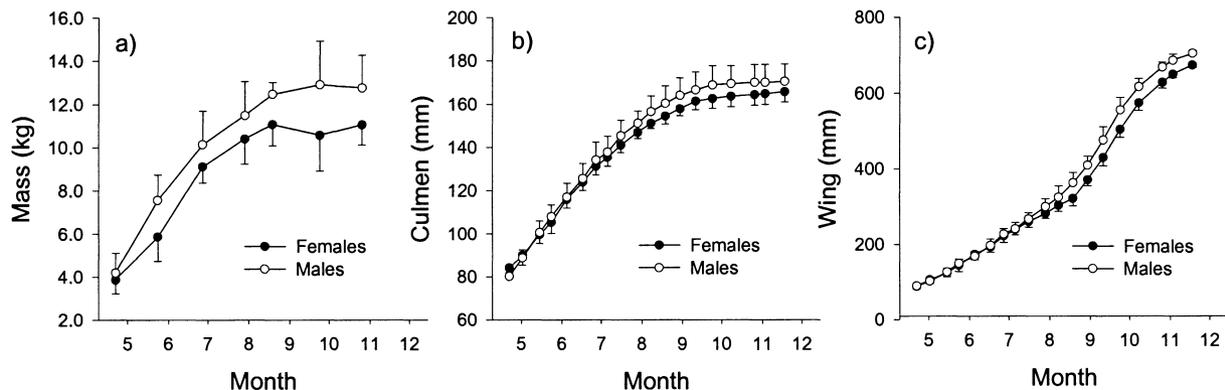

Figure 1. Growth curves as a function of time for four male and six female Wandering Albatross chicks for: (a) mass, (b) culmen length and (c) wing length, during the nestling period from April to November. Values are means ± 1 sdm.
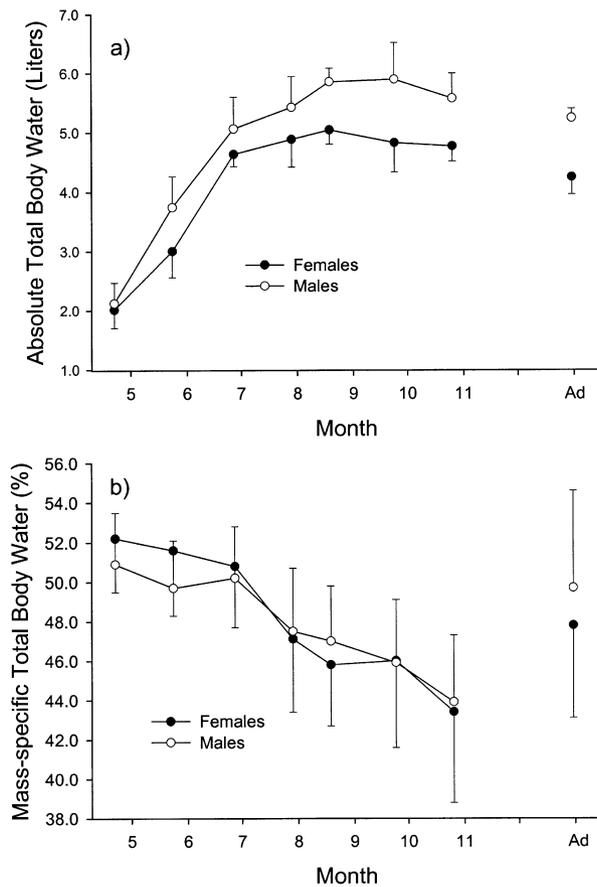
Figure 2. Ontogeny of (a) absolute total body water (TBW) and (b) mass-specific total body water of four male and six female Wandering Albatross chicks, during the nestling period from April to October. Adult values have been recalculated from the literature (Shaffer *et al.* 2001a) and added to the figure for comparison. Values are means ± 1 sdm.

Figure 3. Relationships between (a) total body water and body mass ($\log_{10}y = 0.86 \times \log_{10}x + 0.26$) and (b) absolute oxygen consumption and body mass ($\log_{10}y = 0.63 \times \log_{10}x + 1.10$) in growing Wandering Albatross chicks.

are similar to those of adults (*t*-test, $t = -0.95$, $df = 18$, $P = 0.353$) although, at the same time, chicks show lower mass-specific TBW than adults (Fig. 2b; *t*-test, $t = 2.739$, $df = 18$, $P = 0.013$).

Oxygen consumption

Mean absolute oxygen consumption increased with time until the end of July (Fig. 4a and Appendix 1), at which point metabolic rates were around 1.5 times higher than the adult basal level ($3318 \pm 852 \, \mathrm{mLO_2/h}$; Weimerskirch *et al.* 2002). After reaching a peak in July, mean oxygen consumption decreased in both sexes to reach the adult level at the end of October (Fig. 4a). When adjusting for the chick's body mass, mass-specific oxygen consumption essentially decreased throughout the growth
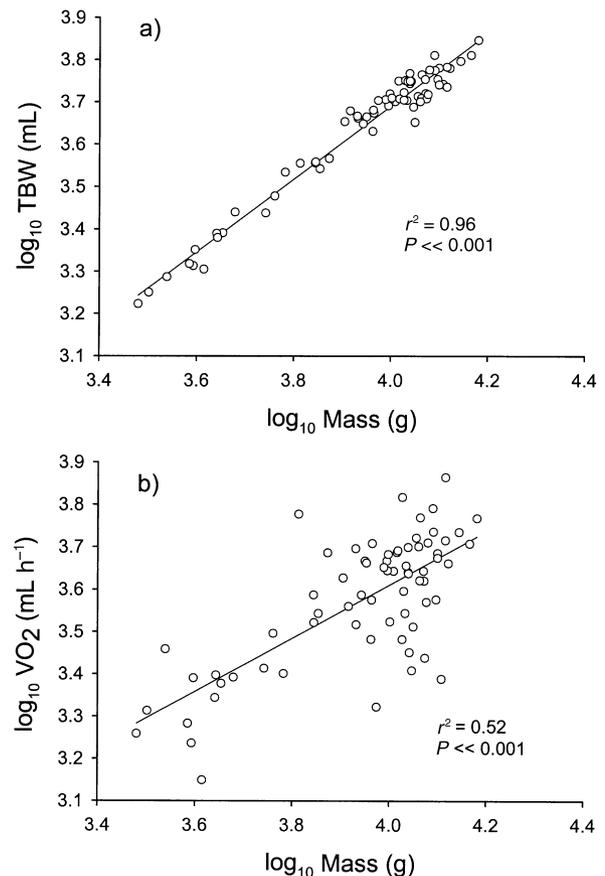
period (Fig. 4b). Mass-specific oxygen consumption was initially around 1.4 times higher than that of the adults in April and May and it declined progressively to 0.7 times the adult level in October (Fig. 4b). The reduction in metabolic rate below that of the adults in October corresponded to the time when chicks had the same absolute oxygen consumption but were heavier than adults.

The sex of the chick had a significant influence on absolute oxygen consumption (repeated measures ANOVA: $F_{1,8} = 17.42$, $P = 0.003$) but not on mass-specific oxygen consumption (repeated measures ANOVA: $F_{1,8} = 1.74$, $P = 0.223$). The difference in absolute oxygen consumption between male and female chicks was attributed to the difference in mass between the sexes (Fig. 4). In addition, the relationship between absolute oxygen consumption and body mass was highly significant (Fig. 3b; $F_{1,68}$
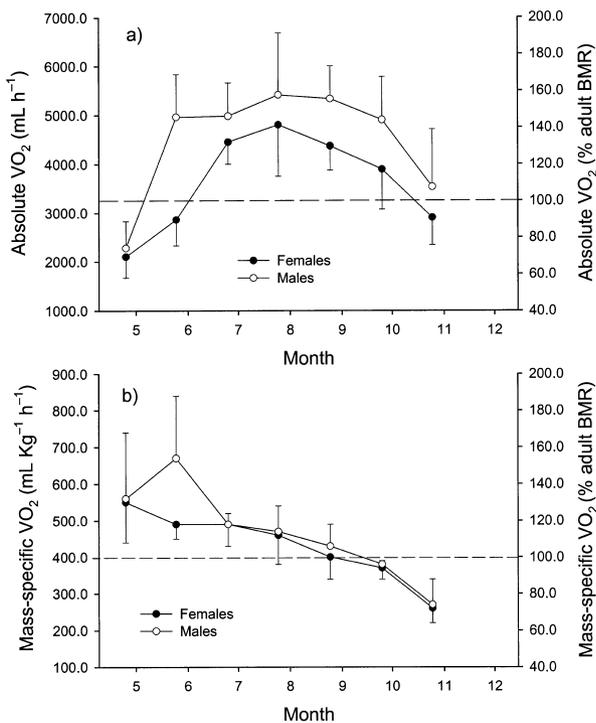
Figure 4. Ontogeny of (a) absolute oxygen consumption and (b) mass-specific oxygen consumption of four male and six female Wandering Albatross chicks, expressed as values and as a percentage of adult basal metabolic rate (BMR), during the nestling period from April to October. Values are means ± 1 sdm.

= 74.7, r^2 = 0.520, P << 0.001). Essentially, because they were heavier, male chicks had higher absolute rates of oxygen consumption than female chicks, but overall, mass-specific oxygen consumption did not differ between the sexes. May was the only month in which mass-specific oxygen consumption differed significantly between male and female chicks (Mann–Whitney, U = 0.00, P = 0.011). The mean mass-specific oxygen consumption for female chicks at that time was 490 ± 44 mL/kg/h compared with 670 ± 174 mL/kg/h for male chicks (Appendix 1).

DISCUSSION

The trend in absolute oxygen consumption of growing Wandering Albatross chicks followed a parabolic relationship with time during the periods when it was measured, and the maximum in absolute oxygen consumption was attained at the end of July, when chicks reached their asymptotic mass. After August, oxygen consumption decreased significantly whereas body mass remained approximately constant. This trend in oxygen consumption is atypical of seabirds,

which normally increase their oxygen consumption in the first part of growth and then maintain it until body mass declines prior to fledging (Grant & Whittow 1984, Brown 1988, Roby 1991, Gabrielsen *et al.* 1992, Weathers *et al.* 2000). Furthermore, our results confirm that sex differences in size and metabolism develop early during the growth of Wandering Albatross chicks. However, the difference in absolute oxygen consumption between the sexes seems to be attributed to body mass rather than to differences in energy utilization *per se* because metabolic rates were similar when adjusted for body mass differences. Regardless of this, the results support the conclusions of Weimerskirch *et al.* (2000) that male chicks are more 'costly' to rear because they are larger and have higher absolute metabolic rates.

Oxygen consumption throughout growth

In the present study, maximum oxygen consumption occurred concomitantly with the attainment of asymptotic body mass, which is probably related to the increase in maintenance costs (Ricklefs *et al.* 1980). Hence, as chicks grow, more energy is spent on maintenance metabolism. At peak body mass, oxygen consumption of chicks was approximately 150% of adult basal metabolism (Weimerskirch *et al.* 2002), which is consistent with results described in previous studies on other species (Grant & Whittow 1984, Chappell *et al.* 1989, Weathers *et al.* 2000). These studies indicate that growing chicks often attain higher absolute and mass-specific metabolic rates than adults, some as high as 300% of adult absolute basal metabolic rate (BMR) (Leach's Storm-Petrel, *Oceanodroma leucorhoa*, Ricklefs *et al.* 1980).

In contrast to studies on other seabird species (Grant & Whittow 1984, Brown 1988, Roby 1991, Gabrielsen *et al.* 1992, Weathers *et al.* 2000), Wandering Albatross chicks reduced their metabolic rate after attaining peak body mass. Unlike almost all other seabird species, Wandering Albatross chicks require 9–10 months to reach adult body size and development occurs during the austral winter (Tickell 1968). Despite the unpredictable nature of food resources during the winter season, parents maintain a relatively high provisioning effort until late winter (i.e. September; see Fig. 5, recalculated from Weimerskirch & Lys 2000), which corresponds to the period when chicks have reached asymptotic mass (Fig. 1a). After September, the parents lower the amount of food delivered to their brood (Fig. 5) and the absolute metabolic rate of the chick begins to decline.
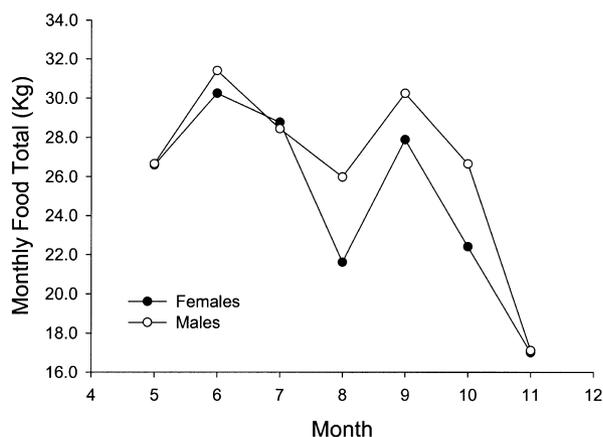
Figure 5. Changes in the average total quantity of food that Wandering Albatross chicks received per month throughout the nestling period from May to November. The data were recalculated from Weimerskirch and Lys (2000).

In a recent study on Northern Fulmar *Fulmarus glacialis* chicks, Phillips and Hamer (2000) demonstrated that the lean dry mass of liver, kidney and gut decreased as growth neared completion. Although they did not measure energy expenditure, they suggested that this recession allowed 'large energy savings to chicks because these organs are highly metabolically active' (Phillips & Hamer 2000). Piersma and Lindström (1997) have shown that organ sizes can be reduced rapidly if their use decreases. The reduction in provisioning rates during the latter part of the chick-rearing period would therefore cause a decrease in the size of the gut of the Wandering Albatross chicks, which may partly explain the decrease in RMR observed after August. If it is the case for Wandering Albatross chicks (as it was for Northern Fulmar), a decrease in the lean dry mass of the liver and kidney could also play a role in the reduction in RMR.

The low RMR at fledging would reduce energy requirements of chicks as they make the transition to self-feeding. Wandering Albatross chicks commonly remain on shore for several days or weeks after parents terminate provisioning; the young birds then depart on their own. A reduction in metabolic rate would undoubtedly prolong the utilization of body reserves that will carry them through until they develop adequate foraging skills. Our results show that the absolute oxygen consumption of adults and chicks is similar, even though chicks are heavier than adults at the time of fledging. This could be due to a difference in body composition between adults and chicks. Chicks store fat throughout growth, and Phillips and Hamer (1999) have demonstrated that Northern Fulmar chicks do not lose this fat before fledging. Chicks are therefore probably heavier than adults because they carry more fat, although at fledging they have attained similar levels of absolute oxygen consumption. Consequently, mass-adjusted metabolism is lower for chicks than for adults, a fact that may be important for chicks to survive the first stages of independence.

Sex differences in growth

Our results confirm that sexual size dimorphism appears early in development. For example, chick body masses differed significantly between sexes by the second measurement period (mid-May; Fig. 1a). The rate of increase to asymptotic mass was similar in the two sexes, indicating that birds of each sex required a similar length of time to attain adult size. However, given that fledgling body size differed between male and female chicks, overall growth rates of male chicks must be slightly higher early in development, as suggested by Weimerskirch *et al.* (2000). Smith and Arcese (1988) demonstrated that high provisioning rates early in the development of a chick can influence overall growth rates. It is therefore conceivable that Wandering Albatross parents invest more in male chicks early in development. However, as the rates of provisioning to male and female chicks were nearly equal from May to July (Fig. 5), the higher growth rate of male chicks could not have resulted from a difference in parental provisioning effort. Thus it appears that sex-specific differences in growth rate reflect intrinsic differences or constraints on the birds during development (Ricklefs 1969, Gebhardt-Henrich & Richner 1998).

In a similar manner to body mass, wing length (wrist to tip of primary) of male and female chicks diverged fairly early in development and the difference between the sexes was maintained throughout the growing period (Fig. 1c). The difference between the sexes appeared soon after the feathers began to grow in August (wing length of males was 13% larger than that of females) because male chicks started growing wing feathers earlier than females. However, once feather growth began in females, the difference between the sexes decreased (on average, wing length of males was only 8.3% higher than that of females from September to October). Ultimately, male Wandering Albatross chicks fledge with longer wings that have a greater surface area than those of

females (3% for wing span and 4% for wing area, Shaffer *et al.* 2001b).

Influence of sex on TBW and oxygen consumption

Given that body size influenced TBW, it is not surprising that absolute TBW exhibited a significant difference between male and female chicks early in development (Fig. 2a). Moreover, this difference was clearly related to body mass because mass-specific TBW (%) did not differ significantly between the sexes at any stage (Fig. 2b). According to Groscolas *et al.* (1991), body fat (%) is related to total body water (%) in adult seabirds according to the equation: Fat(%) = 100 – [TBW(%)/0.729]. Although it is unclear whether this relationship applies to growing chicks, the total change in mass-specific TBW (minus ~17%) suggests that body fat increased (i.e. mass-specific TBW decreases) as chicks neared fledging. Chicks at fledging also show lower values of mass-specific TBW than adults (Fig. 2b), and this suggests that they carry more fat. These results are consistent with those of Reid *et al.* (2000), who observed an increase in body fat in the latter stages of development in Grey-headed Albatross *Diomedea chrysostoma* chicks, and with those of Phillips and Hamer (1999) on Northern Fulmar chicks. Alternatively, the reduction in mass-specific TBW could be attributed to the increase in dry tissues such as feathers that contribute to overall body mass but not to body water.

Although absolute oxygen consumption differed between male and female chicks, the difference was again mainly due to body mass differences between the sexes. Indeed, when comparing mass-adjusted oxygen consumption (mL/kg/h), the sex of the chick did not have a significant influence except in May. During May, growth rates of male chicks increased slightly and, thenceforward, males were always heavier and had higher absolute oxygen consumption and TBW than did female chicks. As our sample was small and this difference was observed only in May, we are unsure whether the difference was due to measurement error or a statistical artefact. Furthermore, as mass-specific oxygen consumption and growth rates increase simultaneously, it is unclear whether the increase in mass-adjusted oxygen consumption (in May only) was the cause or the consequence of male chicks having slightly higher growth rates than female chicks. As suggested earlier, the slight increase in growth rates of males may have been due to some intrinsic difference between sexes.

If there were intrinsic differences in metabolism between the sexes, it could explain how males are able to achieve a larger body size early in development. However, additional studies should be performed to examine this issue more closely. Regardless of this, we are unaware of any study that has examined the sex differences in growth and energy utilization in seabird nestlings. Thus, investigations that examine the relative importance of sexual dimorphism on growth and development are warranted to clarify this point.

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Appendix 1.   Mean body mass, culmen and wing length, absolute and mass-specific total body water, absolute and mass-specific oxygen consumption ± sd for male and female chicks of Wandering Albatross. Values for male chicks are also expressed as a percentage of females' values for each month of the nestling period and the means over the entire period are calculated.

	April	May	June	July	August	September	October	Mean
Females, *n* = 6								
Mass (kg)	3.86 ± 0.63	5.86 ± 1.13	9.11 ± 0.74	10.40 ± 1.15	11.06 ± 0.97	10.56 ± 1.65	11.04 ± 0.92	
Culmen (mm)	84.0 ± 4.3	105.3 ± 5.1	131.2 ± 3.9	146.8 ± 2.8	154.3 ± 3.6	162.6 ± 4.5	164.2 ± 4.7	
Wing length (mm)	89.0 ± 7.7	143.7 ± 16.6	222.0 ± 17.1	281.3 ± 12.0	320.2 ± 18.9	502.8 ± 20.4	627.0 ± 15.2	
Absolute TBW (L)	2.01 ± 0.31	3.00 ± 0.44	4.63 ± 0.20	4.88 ± 0.46	5.04 ± 0.24	4.82 ± 0.49	4.76 ± 0.25	
Mass-specific TBW (%)	52.2 ± 2.7	51.6 ± 3.3	50.8 ± 3.1	47.1 ± 3.7	45.8 ± 3.1	46.0 ± 4.4	43.4 ± 4.6	
Absolute VO_2 (mL/h)	2101 ± 428	2857 ± 526	4454 ± 448	4804 ± 1050	4369 ± 495	3894 ± 820	2899 ± 563	
Mass-specific VO_2 (mL/kg/h)	551 ± 111	490 ± 44	491 ± 58	461 ± 80	398 ± 56	367 ± 30	262 ± 38	
Males, *n* = 4								
Mass (kg)	4.19 ± 0.91	7.54 ± 1.19	10.14 ± 1.55	11.48 ± 1.58	12.47 ± 0.54	12.90 ± 2.02	12.76 ± 1.50	
Mass (% females)	108 ± 24	129 ± 20	111 ± 17	110 ± 15	113 ± 5	122 ± 19	116 ± 14	116 ± 7
Culmen (mm)	80.1 ± 1.9	108.0 ± 5.4	134.1 ± 8.4	151.0 ± 5.9	160.2 ± 8.2	168.8 ± 8.8	169.9 ± 8.3	
Culmen (% females)	95 ± 2	103 ± 5	102 ± 6	103 ± 4	104 ± 5	104 ± 5	103 ± 5	102 ± 3
Wing length (mm)	89.5 ± 2.6	148.8 ± 11.4	227.0 ± 15.1	299.0 ± 20.8	361.5 ± 27.9	554.5 ± 34.0	666.8 ± 12.9	
Wing (% females)	101 ± 3	104 ± 8	102 ± 7	106 ± 7	113 ± 9	110 ± 7	106 ± 2	106 ± 4
Absolute TBW (L)	2.12 ± 0.35	3.74 ± 0.52	5.06 ± 0.54	5.42 ± 0.52	5.85 ± 0.23	5.89 ± 0.62	5.57 ± 0.42	
Absolute TBW (% females)	105 ± 17	125 ± 17	109 ± 12	111 ± 11	116 ± 5	118 ± 15	117 ± 9	115 ± 7
Mass-specific TBW (%)	50.9 ± 2.6	49.7 ± 2.4	50.2 ± 2.6	47.5 ± 3.2	47.0 ± 2.8	45.9 ± 3.2	43.9 ± 3.4	
Mass-specific TBW (% females)	97.6 ± 4.9	96.3 ± 4.7	98.7 ± 5.0	101 ± 7	103 ± 6	100 ± 7	101 ± 8	99.6 ± 2.2
Absolute VO_2 (mL/h)	2276 ± 546	4955 ± 872	4977 ± 677	5414 ± 1271	5332 ± 667	4902 ± 883	3530 ± 1178	
Absolute VO_2 (% females)	113 ± 27	179 ± 32	112 ± 15	111 ± 26	123 ± 15	129 ± 23	115 ± 39	126 ± 25
Mass-specific VO_2 (mL/kg/h)	560 ± 183	670 ± 174	493 ± 30	471 ± 72	429 ± 65	379 ± 10	274 ± 67	
Mass-specific VO_2 (% females)	102 ± 33	136 ± 35	99 ± 6	100 ± 15	109 ± 16	105 ± 3	101 ± 25	107 ± 13