

# HISTORICAL GEOGRAPHIC DIFFERENCES IN GROWTH PARAMETERS OF WANDERING ALBATROSS *DIOMEDEA EXULANS* CHICKS

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## SUMMARY

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Offspring growth measurements provide an integrated measure of parental investment (foraging effort and success) and an indicator of offspring future survivorship. We present an average growth (mass) trajectory for Wandering Albatross *Diomedea exulans* chicks (n = 26) weighed at sub-Antarctic Macquarie Island during four breeding seasons between 1956 and 1962. Specified growth parameters were estimated using a nonlinear mixed model for an extension of the Gompertz model and, as an alternative, cubic smoothing splines within a linear mixed model. Both modelling approaches revealed that the chicks from Macquarie Island gained mass more slowly and reached a lower maximum mass than chicks weighed at Bird Island (South Georgia), the only other temporally aligned study for this species. After reaching maximum mass, chicks from Bird Island lost mass faster than Macquarie Island chicks, resulting in very similar fledging masses for chicks at both islands. One explanation for the different growth parameter estimates observed between the two islands is historical differences in productivity of foraging areas. The data presented here for Macquarie Island provide a baseline against which future studies could compare the effects of climate change and commercial fisheries on this long-lived and charismatic seabird species.

Key words: Wandering Albatross, *Diomedea exulans*, historical baseline data, chick growth, geographic differences

## INTRODUCTION

Early biological studies are of increasing value because they provide important baseline information against which contemporary studies can make comparisons and predictions regarding the effects of commercial fishing, climate change and pollutant loading. In the Southern Hemisphere, Macquarie Island (54°30'S, 154°55'E) is one of a handful of isolated oceanic island sites in the sub-Antarctic where studies of marine vertebrate predators have been conducted since the mid-1950s. Study species included the Southern Elephant Seal *Mirounga leonina*, the Royal Penguin *Eudyptes schlegeli*, the White-headed Petrel *Pterodroma lessoni* and Wandering Albatross *Diomedea exulans*, the focal species for this paper.

A small but stable population of 19 pairs of the endangered (Croxall & Gales 1998) Wandering Albatross breeds on Macquarie Island (Terauds 2002). Chick development is slow (approximately nine months) and includes a winter period when chicks are exposed to extreme weather conditions and high variability in parental care. Such a slow developmental rate likely reduces pressure on the parents to provide food and lowers the probability of the chick starving (Mabille *et al.* 2004). Typical smoothed growth curves for Procellariiforme chicks are similar to those of other vertebrates (Warham 1990); however, they differ in that the chicks experience a period of mass loss in the weeks before flying (Huin & Prince 2000, Weimerskirch & Lys 2000).

Nestling mass can be used as a measure of environmental variability because mass comprises a structural component (organs, muscle and

bone) and a storage component (adipose tissue, also known as fat) (Reid *et al.* 2000). It is the quantity of fat stored in fat-accumulating species that serves as a useful proxy for measuring adult foraging success (Boersma & Parrish 1998) between years and study sites. In so-called “normal to better” foraging years, chick tissue growth will reach a constant (maximum possible) and any differences from this maximum weight will therefore reflect insufficient/extra food (poorer/higher quality or quantity) supplied to the chick (Boersma & Parrish 1998). Maximum, or peak, weight corresponds to a time when weight no longer increases, thus providing an indication of mature weight or maximal theoretical weight for a given season/year (Maruyama *et al.* 1999). Boersma and Parrish (1998) used this approach to show that the wide range of observed growth rates, including mass gain, among individual Fork-tailed Storm-Petrels *Oceanodroma furcata* was in response to environmental variability. Environmental variability has also been implicated in Yellow-nosed Albatross *Thalassarche chlororhynchos* chick-provisioning parameters (Weimerskirch *et al.* 2001). Wandering Albatross are likely to respond in a similar fashion, since altered prey quality, distribution and abundance should produce changes in the provisioning ability of breeding adults and in the resulting offspring tissue composition (e.g., mass) (Montevicchi 1993).

This paper presents estimates of baseline growth parameters for 26 Wandering Albatross chicks weighed at Macquarie Island between 1956 and 1962, before large-scale commercial fisheries escalated during the 1960s (Nel *et al.* 2002). We extend the reverse Gompertz growth model proposed for Procellariiformes (Huin & Prince 2000) by using non-linear mixed models (NLMM) to

incorporate a random chick effect on the log-asymptote scale (Pinheiro & Bates 2000, Diggle *et al.* 2001, Davidian & Giltinan, 2003). As an alternative to the NLMM, we also fit cubic smoothing splines within a linear mixed model (LMM) (Verbyla *et al.* 1999, Candy & van den Hoff, 2010). The cubic smoothing splines may provide more flexibility in modelling growth trajectories than the NLMM, especially when multiple feeding–fasting cycles occur over time. Average parameter estimates from both modelling approaches for Macquarie Island chicks are then compared with chicks weighed at Bird Island (South Georgia) in 1963. The growth model estimates we present can be compared with current day and future measurements to understand whether regional differences in climate variation influence parental foraging and thus chick growth parameters and future survival potential.

## STUDY AREAS AND METHODS

This study of Wandering Albatross chick growth was undertaken at Macquarie Island over four winter seasons (1956, 1957, 1960 and 1962). Macquarie Island (54°30'S, 154°55'E) is located in the sub-Antarctic mid-way between the southern tip of Australia (Tasmania) and continental Antarctica. Wandering Albatrosses arrive at their breeding sites (Fig. 1) in November and the often single egg is laid in an elevated mud-nest during December and January. Incubation takes about 80 days (Tickell 1968), and hatchlings are brooded for 21–43 days. After brooding, the attending adult departs, and the chick remains alone in or near the nest, receiving intermittent feeds from either parent for the next 9–10 months until the chick attains fledging mass (Tickell 1968).

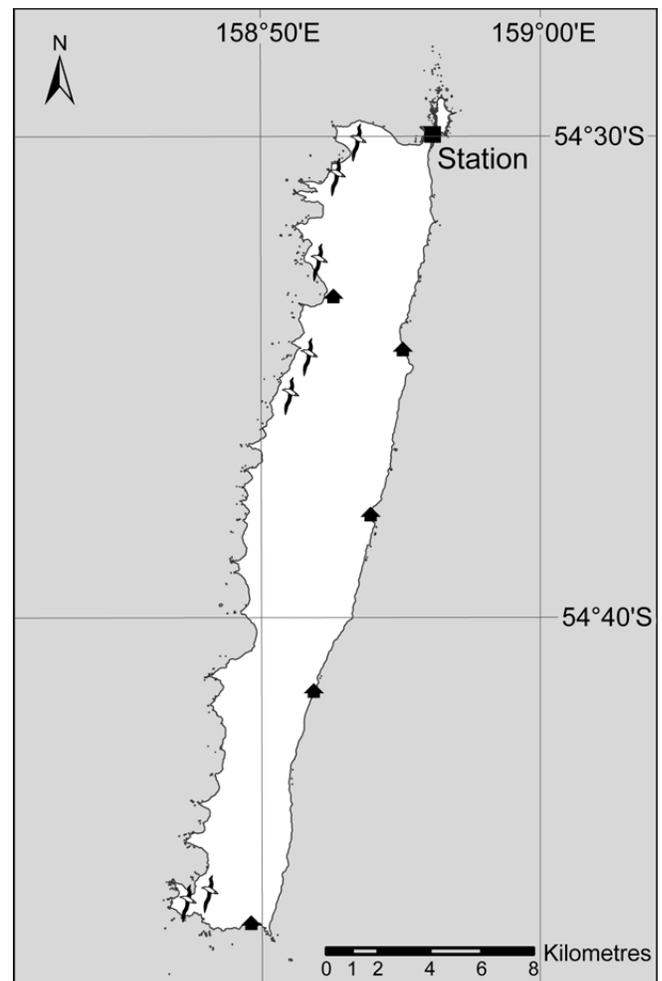
Twenty-six Wandering Albatross chicks were weighed opportunistically with a spring balance for as long as they were accessible during the nestling period. Sample sizes of chicks weighed were six in 1956, two in 1957, seven in 1960 and 11 in 1962. While 1962 was the year with the largest number of chicks sampled, these chicks were weighed only once or twice throughout the development period. In other years, chicks were weighed on 7–20 separate occasions. One-hundred and fifty-two individual weights were recorded and used in this study. The dataset incorporated values collected for chicks of both sexes, in poor to healthy condition and raised by experienced and inexperienced breeders. Data for five Wandering Albatross chicks weighed at Macquarie Island (1956) and published in Carrick *et al.* (1960) were included in the analyses. Where mass was recorded in pounds we converted it to kilograms.

The exact date of chick hatching is often missed because there is variation in the timing of egg laying, hatching and fledging for Wandering Albatross (Tickell 1968, Terauds 2002) and because “Wanderers” nest in remote areas of the island (Fig. 1). As the main objective of this study was to determine an average growth trajectory for Wanderer chicks to compare it with other studies, we needed to synchronise each individual chick’s timeline to a common starting (birth) date (Tickell 1968). From field observations of adult birds sitting on hatching chicks or brooding very small chicks with broken egg shell still in the nest (Australian Antarctic Division, unpublished biology log books), March 10<sup>th</sup> was selected as the hatching date common to all chicks weighed at Macquarie Island.

Masses for 15 Wandering Albatross chicks measured at Bird Island (54°00'S, 38°03'W) in 1963 were transcribed to an electronic database from Lance Tickell’s 1963/64 day-book. Hatching dates for

all birds were recorded and their mass then measured almost daily using a 30-pound ( $\pm 0.5$  ounces) dial scale. Birds over 30 pounds were weighed with the same balance fitted to a counterbalanced beam, thereby doubling the capacity but halving the accuracy. Chicks that were used in a cross-fostering experiment were excluded from the analyses (Tickell, pers. comm.).

Growth can be expressed as change in some morphological aspect (here, mass) of the subject as a function of time (age). Three equations have been widely used to model growth: the von Bertalanffy equation, the Gompertz equation and the logistic equation (Reiss 1989). These functions are particularly useful where growth shows a clear asymptote, but Wandering Albatross chicks experience a somewhat different growth pattern (Huin and Prince 2000). Theirs has a period of mass gain to a maximum, followed by a period of mass loss before chicks finally depart the nest (Carrick *et al.* 1960). Solved Gompertz equations have been used to provide growth parameters for comparison between years, individuals and colonies for this species (Weimerskirch *et al.* 2000, Terauds & Gales 2006). However, the shortfall in the Gompertz equation’s ability to fully describe albatross growth, especially the period of mass loss, led Huin & Prince (2000) to formulate a new equation that integrated this period into the model.



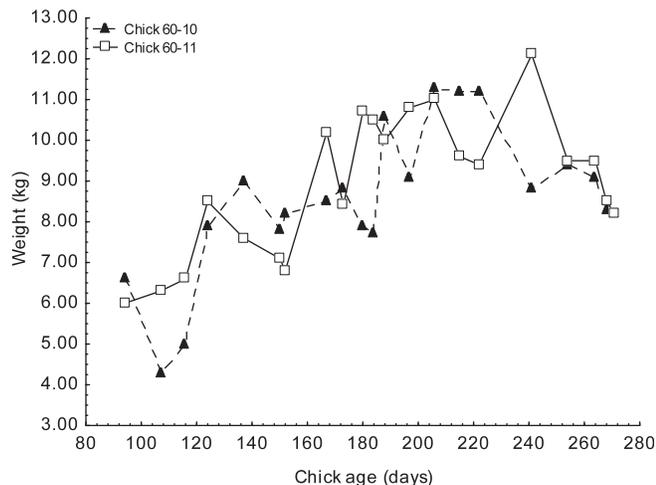
**Fig. 1.** Coastal outline of Macquarie Island showing the Wandering Albatross *Diomedea exulans* sites where chicks were weighed (1956–1962). The main research station is labeled, and remote field hut locations are shown.

We fitted this reverse Gompertz model (Huin & Prince 2000) with the extension that random chick effects were incorporated into the asymptote parameter using the *nlme* (Pinheiro & Bates 2000) library in R (R Development Core Team 2008) as given by:  $M_{ij} = \exp(A + \delta_i) \exp[-\exp\{\beta_1(t_{ij} - \tau_0)\} - \exp\{\beta_2(t_{ij} - \tau_1)\}] + \varepsilon_{ij}$  where  $M_{ij}$  is the mass (kg) of chick  $i$  measured at day  $t_{ij}$  where  $j = 1, \dots, n_i$ ; fixed parameters ( $A, \beta_1, \beta_2, \tau_0, \tau_1$ ) are to be estimated;  $\delta_i$  is the random chick effect on the log-asymptote,  $A$ , scale where these random effects are assumed to be normally distributed with zero expectation and variance  $\sigma_\delta^2$ ; and  $\varepsilon_{ij}$  is a within-chick residual error with variance  $\sigma^2$ . The resulting non-linear mixed model (NLMM) was fitted separately to the data for each island.

An alternative approach to modelling complex longitudinal profiles that are subject to variation among individuals is to use cubic smoothing splines as a component of a linear mixed model (LMM) (Verbyla *et al.* 1999, Candy & van den Hoff 2010). This approach relies more on the data to drive the shape of the estimated mass profile than assumed parametric models (as in the Gompertz equation), including parametric modifications such as that given by Huin and Prince (2000). Such an approach is helpful when there is imbalance in the data, as is the case here for Macquarie Island (MI), where mass was measured on fewer days within the growth period than in the Bird Island (BI) data set.

Splines were fitted using the *asreml* library (Gilmour *et al.* 1995, 1999) within R as the sum of fixed-effect linear components plus random-effect nonlinear components using every fifth day from day 1 to day 300 as “knot points” (Verbyla *et al.* 1999). The fixed effects of interest were ISLAND (MI versus BI), AGE and the interaction of ISLAND and AGE (i.e., separate slopes for the linear component of the cubic smoothing splines). To account for increasing variance of mass with time given the treatment combination, data were log-transformed so that the response variable fitted by the LMM was  $y = \log(\text{Mass})$ . Predictions on this scale,  $\hat{y}$ , could be back-transformed to give a predicted mass of  $\exp(\hat{y})$ .

A random effects linear mixed model (RE-LMM) included the terms AGE, ISLAND, ISLAND:AGE (i.e., separate slopes for each



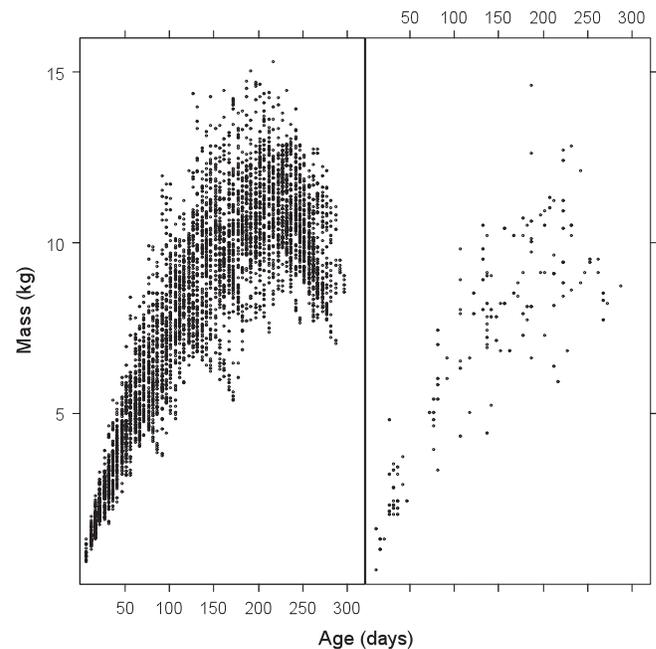
**Fig. 2.** Fluctuations in chick weight as a function of time for two Wandering Albatross chicks weighed at Macquarie Island during 1960. Chick weight was measured between ages 90 and 270 days. Periods of mass gain were interspersed with periods of mass loss until the chicks fledged.

island), and random terms BIRD\_ID and ISLAND:spl(AGE). The random term in the LMM (apart from spline terms) was BIRD\_ID (factor with 41 levels). Because of the high degree of imbalance in the Macquarie Island data, it was not possible to successfully incorporate an additional autoregressive error term in the above model; in a previous analysis, we had incorporated this additional error term in an LMM fitted to the Bird Island data alone (Candy & van den Hoff 2010).

Approximate standard errors of predicted mass were obtained as  $SE(\hat{y})\exp(\hat{y})$  where  $SE(\hat{y})$  is the standard error on the transformed scale. To determine statistical significance in the difference in average growth trajectory between islands, the standard error of the difference (SED) between islands was calculated for each knot point from the fitted RE-LMM using the predict function in the *asreml* library (Welham *et al.* 2004).

Indications of statistical significance level from the fit of the RE-LMM for the fixed effects were determined from sequential Wald tests (Welham & Thompson 1997) and for random effects, by calculation of a Z-statistic that is the ratio of the estimated random effect variance to its estimated standard error. These are used to provide only an approximation of significance level (e.g., Z-statistic greater than two was considered significant at the 5% probability level), since the true distribution of these statistics under null hypotheses is difficult to determine in theory; however, simulation studies show that they can be used with appropriate caution in practice (i.e., the Wald statistic can be anti-conservative, Welham & Thompson [1997]).

The fitted NLMM and RE-LMM provided four chick growth parameters: the rate of mass gain between 10% ( $t_{10}$ ) and 90% ( $t_{90}$ ) of maximum mass (g/day), the maximum mass (kg) reached, age at maximum mass (days) and rate (g/day) of mass loss between 100% ( $t_{100}$ ) and 85% ( $t_{85}$ ). These parameter estimates were obtained



**Fig. 3.** Mass observations for Wandering Albatross *Diomedea exulans* chicks weighed at Macquarie Island (right panel) in the South Pacific Ocean and at Bird Island (left panel) (1963 only) in the South Atlantic Ocean. Points for individual chicks are not joined to maintain clarity.

empirically from the fitted RE-LMM via the predict function using fine-scale (daily age steps from 1 to 300 days) predictions. Similarly, predictions obtained from the fitted reverse Gompertz NLMM were used to estimate these parameters with the exception of maximum mass, which was obtained analytically. Predicted average growth rate was estimated at  $1000 \cdot \{M(t_{100}) - M(t_{90})\} / (t_{90} - t_{10})$  where  $M(t_{90})$  is the predicted mass as age  $t_{90}$  and  $M(t_{100})$  is the predicted maximum mass. The corresponding formula was used for rate of mass loss. The confidence bounds for estimate of rate of mass gain were approximated as  $\pm 2 \cdot \text{SERG} \cdot 1000 \cdot M(t_{90}) / (t_{90} - t_{10})$ , where the SERG was calculated as the standard error of the difference in predicted log(mass) between ages corresponding to  $t_{90}$  and  $t_{10}$  for a given island. Similarly, approximate 95% confidence bounds for the estimated mean rate of mass loss were obtained as  $\pm 2 \cdot \text{SERG} \cdot 1000 \cdot M(t_{85}) / (t_{85} - t_{100})$ . These confidence bounds are based on estimates of the variance of relative growth (i.e.,  $\log\{M(t_{90})\} - \log\{M(t_{10})\}$ ) conditional on  $M(t_{90})$  or  $M(t_{85})$  in each of the above cases (Candy & van den Hoff 2010). The SERG is easily obtained from the fit of the LMM using the *asreml* library, but corresponding values for the NLMM are less conveniently calculated, since they are a complex function of parameter estimate variances and covariances.

**RESULTS**

At Macquarie Island the slow-growing Wandering Albatross nestlings took between 280–290 days to develop from hatchling to fledgling. Growth, measured as individual chick mass, followed a pattern of periods of mass gain punctuated by periods of mass loss (Figs. 2 & 3) until maximum mass was reached. Thereafter, chicks endured a period, just before fledging, when mass lost exceeded mass gained.

Macquarie Island nestlings gained mass more slowly between  $t_{10} - t_{90}$ , were 1 kg lighter at maximum mass and lost mass more slowly than chicks at Bird Island (Table 1). Age at maximum mass differed between breeding islands, but the estimates and direction of the difference depended on the model (Table 1).

The analysis of variance (ANOVA) results from the fit of the RE-LMM (sequential Wald tests, Welham & Thompson, 1997, Table 2) indicated that ISLAND was highly significant ( $P < 0.005$ ), considering the effect of ISLAND on all of the intercept, linear (i.e., ISLAND:AGE) and nonlinear (i.e., ISLAND:spl(AGE)) components.

**TABLE 1**  
Comparisons of the growth parameter estimates (and approximate 95% confidence limits [CL]) for Wandering Albatross chicks weighed at Macquarie (MI) and Bird (BI) islands predicted from the RE-LMM and NLMM (see Methods)

Model	Study site	Year	Sample size, no. chicks	Modelled maximum mass, kg (95% CL)	Mean growth rate, Mean mass loss rate,		Age at maximum mass, d
					g/d ( $t_{10}, t_{90}$ ) (95% CL)	g/d ( $t_{85}$ ) (95% CL)	
RE-LMM	MI	All	26	10.23 (9.72, 10.77)	51.9 (15, 172) (43.5, 60.3)	19.7 (279) (1.4, 40.8)	201
RE-LMM	BI	1963	15	11.15 (10.78, 11.54)	52.6 (11, 178) (50.1, 55.0)	41.2 (270) (32.9, 49.5)	229
NLMM	MI	All	26	9.827	49.0 (1, 159)	25.9 (279)	222
NLMM	BI	1963	15	10.838	57.7 (1, 150)	26.6 (279)	218

**TABLE 2**  
ANOVA and variance components for the RE-LMM for log(Mass)

Source	Degrees of freedom	Sum of squares	Wald statistic ( $\chi^2$ )	Probability
Intercept	1	111.1	6 101	< 0.001
AGE	1	439.7	24 154	< 0.001
ISLAND	1	0.2	12.5	0.0004
ISLAND:AGE	1	0.02	9.6	0.0019
		Variance	Standard Error	Z-statistic
BIRD_ID		0.0150	0.0042	3.595
ISLAND:spl(AGE)		0.5694	0.1444	3.941
residual variance		0.0182	0.0004	44.780

**TABLE 3**  
Parameter estimates ( $\pm$ SE) for reverse Gompertz growth model for Wandering Albatross chicks weighed at Macquarie (MI) and Bird (BI) islands, obtained from its fit as an NLMM

Study site (AIC)	Parameter estimate (SE)					
	A	$\beta_1$	$\beta_2$	$\tau_0$	$\tau_1$	$\sigma_\delta$
MI (502)	2.4388 (0.1386)	0.0141 (0.0029)	0.0296 (0.0236)	61.86 (11.22)	323.5 (30.1)	0.1164
BI (11 631)	2.4819 (0.0259)	0.0165 (0.0004)	0.0321 (0.0029)	52.99 (0.91)	323.8 (3.5)	0.0875
Pooled (12 136)	2.4149 (0.0240)	0.0165 (0.0004)	0.0321 (0.0029)	53.16 (0.91)	323.7 (3.5)	0.1188

Table 3 gives the parameter estimates for the fit of the reverse Gompertz model for each island separately and for the model fitted to the pooled data along with the corresponding Akaike's information criterion (AIC) produced by *nlme*.

Growth trajectories obtained from back-transformation of the predicted RE-LMM values are shown in Fig. 4. The confidence bounds were calculated to have widths corresponding to the exponential of twice the standard error of the difference (SED) between curves on the log scale. The SED was calculated for knot-points used for predicting mass. This gives approximate 95% confidence bounds on separation between the curves. Comparisons of fitted trajectories with SED bounds on the log-transformed scale (i.e., the appropriate scale for comparison) showed that the position of the curves relative to the bounds on the log scale was very similar to that seen in Figure 4.

Normal quantile–quantile plots demonstrated that the chick random effects estimates and residual errors from the fit of the RE-LMM are approximately normally distributed. Also, these residual errors (on the log scale), when plotted against age or fitted value, demonstrated that the assumption of homogeneity of variance on the log scale is reasonable.

Figure 5 shows a comparison between the predictions from the RE-LMM spline model and the fit of the reverse Gompertz NLMM for Bird Island chicks only. Average mass was obtained from predictions of the non-parametric LMM (i.e., RE-LMM with linear and spline age terms replaced with age as a factor, with levels for each age of measurement). The curves are similar, but the RE-LMM

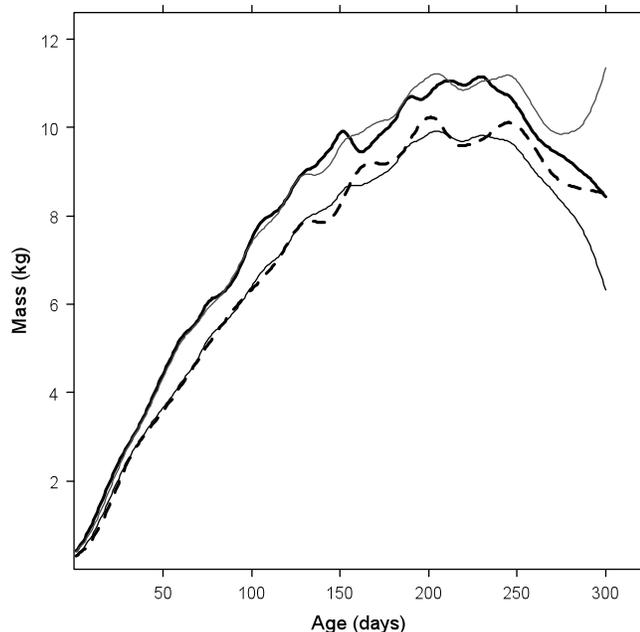
identified a period (around 150 days) of sustained mass loss, estimated at the aggregate population level. The Gompertz NLMM failed to detect this feature because it was smoothed over.

## DISCUSSION

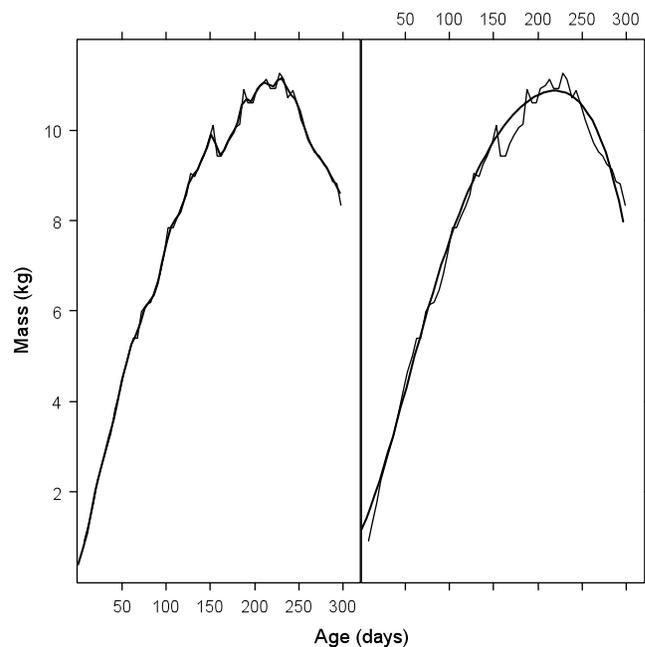
### Data caveats

Mass is more variable as a measure of growth than other structural body part measurements. Modelling albatross chick growth (mass gain over time) can be confounded by several factors: chick mass may be post-feeding rather than post-absorptive; chicks may ingest “ballast stones” and vegetation (Warham 1990); and some snow or rain-water can be retained in the chicks' feathers in wet weather (Tickell 1968). These effects are difficult to eliminate unless the birds are continually observed, which is unlikely in such remote localities, and are thus assumed to be consistent between colonies and islands.

The data for Macquarie Island also comprise both cross-sectional and longitudinal samples collected from both sexes, irrespective of parental breeding experience. Neither factor (sex or adult breeding experience) is considered to bias the growth data presented here. It is known that Wandering Albatross chicks are sexually dimorphic; the maximum mass of male chicks is greater than that of females (Weimerskirch *et al.* 2000, Mabile *et al.* 2004) but chick sex ratios were not biased (Weimerskirch *et al.* 2000). Thus, an average mass can be taken here to represent the chick population. Evidently, adult breeding experience does not influence the amount of food delivered to the developing chick (Weimerskirch *et al.* 2000) because inexperienced breeders are already experienced foragers



**Fig. 4.** Growth trajectory for Macquarie Island (dashed black line) and Bird Island (solid black line) Wandering Albatross *Diomedea exulans* chicks with predictions obtained from the fitted RE-LMM. The fine black lines represent confidence bounds centred on the midpoint between the curves, with width calculated as twice the standard error of the difference between predictions for the two islands. This provides an approximate 95% confidence limit test of the significance between the curves, with a significant difference indicated if the bounds do not envelop the two curves for particular ages.



**Fig. 5.** Predicted mean mass for each day of measurement for Bird Island Wandering Albatross *Diomedea exulans* chicks (fine black line) overlaid with predicted mean trajectory for the RE-LMM spline model (left panel, thick black line) and reverse Gompertz NLMM (right panel, thick black line). Note the dip in mass gain at about 150 days identified by the RE-LMM but smoothed over by the NLMM.

(Lequette & Weimerskirch 1990, Berrow *et al.* 2000). The growth data presented here therefore represents the mean mass for chicks surviving to each successive age class, regardless of their sex or parental experience. Modelled chick growth parameters, such as growth rates and maximum mass, can therefore be compared among individuals, years and breeding colonies.

### Geographic differences in growth parameters

The general shape of the modelled growth curve for Wandering Albatross chicks at Macquarie Island was consistent with that for chicks weighed at Bird Island (Fig. 4; Tickell 1968, Berrow *et al.* 2000) and at Île de la Possession (Weimerskirch *et al.* 2000). Comparisons with Île de la Possession birds were not made here because of decadal differences in sampling. Analysis of variance (ANOVA) for the LMM identified significant island-based differences in growth parameter estimates between Macquarie and Bird islands (Fig. 4, Table 2) where the sampling periods overlapped, a difference that was not clearly demonstrated by the reverse Gompertz NLMM model (Table 3). This was because the fitted NLMM does not account for differences across all parameters simultaneously. Comparing the AIC statistic between the pooled NLMM (modified reverse Gompertz model) and the sum of AIC statistics for the island-specific fits shows that this latter model is the most parsimonious, but only by a very small margin (12 133 versus 12 136; Table 3).

Chicks raised at Bird Island in 1963 reached a greater maximum mass than chicks at Macquarie Island between 1956 and 1962 (Table 1). The Bird Island chicks accumulated mass more rapidly, reach a greater maximum mass by approximately 10% relative to the Macquarie Island chicks (for both LMM and NLMM estimates). The LMM estimates indicated that this was followed by a more rapid loss mass for the Bird Island chicks, whereas this difference was only minor for the NLMM estimates. However, the average mass loss rate for the population of chicks on Macquarie Island chicks is quite uncertain, given the wide 95% confidence bounds on the estimate in Table 1. The LMM estimates indicate that the final average mass observed at an age of ~280 days was more similar between islands than maximal mass (Fig. 4), but more frequent measurement of the Macquarie Island chicks would have been required for the alternative hypothesis of a different final mass to be detected with adequate power (Candy & van den Hoff 2010). The almost 1 kg greater average maximum mass for Bird Island is likely due to the continued increase in the chicks' mass between days ~180 to ~230 old, whereas, at Macquarie Island, birds did not consistently increase their mass (Figs. 4 & 5).

Such differences suggest adult birds raising chicks at Macquarie Island experienced poorer quality foraging conditions than adults raising chicks at Bird Island. The productivity of the Southern Ocean marine ecosystem is known to be highly variable, both spatially and temporally, and such variability affects all ecosystem levels, especially top-predators (Croxall 1992) such as albatrosses. While nothing is known of the foraging areas for adults raising chicks at Macquarie Island, other studies have shown separation between foraging grounds for adults raising chicks at other breeding locations. Chick-rearing Wandering Albatrosses from South Georgia foraged in the south-west Atlantic Ocean along the edge of the Patagonian shelf, around the Falkland Islands or over pelagic waters north and west of South Georgia (Prince *et al.* 1998), while at Marion and Crozet Islands they foraged in southern Indian

Ocean areas (Nel *et al.* 2002, Weimerskirch 1998) several thousand kilometres apart. It could be assumed that adults raising chicks at Macquarie Island might also forage in ocean areas separated from areas used by other breeding populations, and those areas might differ in forage quality; however, such a statement requires validation. A collaborative comparative study could determine whether chick growth parameters indeed differ between populations in the same year. Furthermore, telemetry studies overlapping in time could determine whether there are differences or similarities in foraging grounds.

### Model comparison

In comparing the RE-LMM and the NLMM, Figure 5 shows that the predicted trajectory of average mass for Bird Island was very similar between models, and each fitted the age-specific average mass data very well. The comparison for Macquarie Island (graph not shown) was similar, although the age-specific average mass trend was much noisier, as expected owing to the small number of repeat observations. The RE-LMM fitted these average masses near their maximum slightly better at Bird Island and considerably better for ages less than 20 days. The dip in average mass around age 150–180 days (August–September) was illustrated by the cubic spline RE-LMM predictions but smoothed over by the reverse Gompertz model (Fig. 5). The question is whether this “dip” is of biological significance in general, rather than simply an artefact of the particular sample of chicks or the year of sampling. There was also a “dip” in average mass between ages 200–250 days for the Macquarie Island chicks (Fig. 4), but, unlike the for the Bird Island chicks, this occurred nearer the age of maximum mass. Such a dip in mass gain across the chicks measured certainly suggests a break in parental care for a sustained period, perhaps due to winter lows in productivity that imposed difficulties on the parents' ability to allocate sufficient resources to both the chick and themselves.

### CONCLUSIONS

The distinctive period of mass loss endured by chicks between maximum mass and mass at the time of fledging is unusual among birds, but typical of many Procellariiforme species, including Wandering Albatross (Warham 1990). Thus, specific models that can be used to estimate a maximum mass in the absence of an asymptote are required to construct growth curves (Huin & Prince 2000). Selected model coefficients can be used to identify when the chicks are most at risk of low body mass; e.g., poor winter forage quantity or quality or both may be a key to low fledging weights. Chick rearing takes about a year for Wandering Albatross (Warham 1990), and, therefore, indices of foraging success such as chick growth are likely to integrate a signal from the whole marine ecosystem over seasonal and annual periods.

While fisheries bycatch is an important factor in albatross mortality (Croxall & Gales 1998), it is not the only factor that can influence their population levels. Variation in parental investment, measured as chick mass, is highly likely to affect fledging survival, especially in the first year of life when the chicks are naïve foragers. Measuring “natural” baseline variation in chick growth is now almost impossible, even in isolated parts of the world such as Antarctica, because the effects of humans have spread worldwide. Historical data, such as those presented here, remain the only source of such information.

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