Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*

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Summary

1. The investigation covered whether sexual dimorphism could affect flight performance in a manner that is consistent with differences in at-sea distribution of male and female Wandering Albatrosses, *Diomedea exulans* Linnaeus. Adult morphology was also compared to near-fledged chicks to assess whether morphological differences are consistent with different at-sea distributions of adults and fledglings.

2. Body girth, mass, wing span and area were measured on 24 females (16 adults and 8 chicks) and 32 males (20 adults and 12 chicks) breeding in the Crozet Archipelago.

3. On average, adult males had longer wings (4%, 311 ± 4 cm) with 6·8% more area (6260 ± 270 cm^2), but were also 20·4% heavier ($9·44 \pm 0·59$ kg) than adult females. As a result, wing loading in adult males was 12·1% greater than adult females.

4. When compared with adults, total wing area of chicks was lower resulting in higher wing loading because of the incomplete growth of chicks at the time measurements were collected. However, projected chick growth to fledging indicates that wing loading would be lower in fledglings than adults.

5. Because wing loading determines flight speed, it is conceivable that windier regions of the sub-Antarctic/Antarctic are more optimal for male albatrosses because they have higher wing loading. Conversely, wing loading is lower in adult females and fledglings, which could make them better adapted to exploit lighter winds of the subtropical and tropical regions. Thus, size dimorphism may have a functional role in flight performance that influences the at-sea distribution of adult and fledgling Wandering Albatrosses.

Key-words: Crozet, flight performance, morphometrics, sex differences in foraging

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Introduction

Sexual dimorphism in birds may reduce intersexual food competition by the evolution of different phenotypes (e.g. beak shape or body size) that facilitate the separation of feeding niches between sexes (Selander 1966). Although sex differences in beak morphology have been studied (Kilham 1970; Selander 1972; Jönsson & Alerstam 1990), sex differences in body and wing morphology, particularly in relation to flight performance, have received less attention (Harrington, Schreiber & Woolfenden 1972; Andersson & Norberg 1981; Møller 1991). This is surprising given that body size and mass affect wing form and function, and thus flight performance (Warham 1977; Pennycuick 1987; Webb, Speakman & Racey 1992). Consequently, sexual size dimorphism may have a functional influence on flight in birds.

Procellariiformes (albatrosses and petrels) are a diverse order of pelagic seabirds that exhibit a wide range

in body mass and some degree of sexual dimorphism, especially in the large albatrosses and petrels (Warham 1990; Fairbairn & Shine 1993). Feeding niches are also quite variable within this order; however, one characteristic shared by all Procellariiformes is their reliance on wind to fly over the open sea (Warham 1996). Therefore, in species that are highly dimorphic between the sexes, we might expect evolution to shape dimorphic features that optimize flight performance (Møller 1991); especially when foraging location or behaviour differs between the sexes.

Sexual size dimorphism is quite evident in Wandering Albatrosses (*Diomedea exulans* Linnaeus; Tickell 1968). Moreover, recent studies demonstrate that foraging behaviour also differs between males and females, and that sexes segregate into different foraging zones when at sea (Weimerskirch & Jouventin 1987; Prince *et al.* 1992; Salamolard & Weimerskirch 1993; Weimerskirch *et al.* 1993). Female Wandering Albatrosses typically forage in subtropical and tropical waters north of the Crozet Archipelago, whereas males forage closer to

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the colony in sub-Antarctic and Antarctic zones to the south (Weimerskirch *et al.* 1993). In addition, fledglings forage even further north than adults of both sexes (Weimerskirch & Jouventin 1987). Hence, there appears to be a distributional gradient between adult males and females, and between adults and fledglings. Given that Wandering Albatrosses rely on wind to travel over the open sea, and that wind conditions vary significantly between the subtropical and sub-Antarctic regions (Weimerskirch *et al.* 2000b), there is reason to believe that morphological differences between adults of both sexes and between adults and fledglings have a functional role in flight performance. To investigate this, we measured the degree of sexual dimorphism in the body and wings of adult Wandering Albatrosses then examined whether these differences could have a significant affect on flight performance using computer models of Pennycuick (1998). We also compared the morphology of adults and near-fledged chicks in order to assess whether morphological differences are consistent with at-sea distributions of adults and fledgling Wandering Albatrosses.

Materials and methods

The study was conducted on Possession Island, Crozet Archipelago, south-western Indian Ocean (46° S, 52° E) from 30 December 1998 to 31 January 1999 (adults) and 9–10 November 1999 (chicks). In an effort to minimize disturbance to breeding individuals, measurements were collected from 33 non-breeding and 3 breeding adults (20 males and 16 females). Feather plumage was used as an index of maturity and as a determinant of sex (Weimerskirch, Lequette & Jouventin 1989). In addition, a composite index using bill and tarsus measurements was used to differentiate male and female adult Wandering Albatrosses. This method has proven to be very effective in accurately predicting the sex of this species (Berrow *et al.* 1999). Prior reproductive history was also available for all but two adults since these two birds were unbanded at the time of capture (Weimerskirch & Jouventin 1997). The body size of the non-breeding birds used in this study were representative of breeding adults because the range of body masses for the study birds spanned those of breeding adults (Weimerskirch 1992); and 34 out of 36 birds were known to be of adult age. The mean age of adult females in the present study was $15·1 \pm 5·7$ years and for adult males was $16·7 \pm 8·8$ years which is considerably greater than age of first reproduction in Wandering Albatrosses (females $9·6 \pm 1·9$ years and males $10·4 \pm 2·4$ years; Weimerskirch 1992).

The morphometrics of 20 near-fledged chicks (12 males and 8 females) were measured between the ages of 230–240 days as estimated from hatching dates (mean fledging age is $\approx$260 days; Weimerskirch, Barbraud & Lys 2000a). As part of another study, chicks were sexed at $\approx$8–10 weeks of age by modifying molecular techniques described in Fridolfsson & Ellegren

(1999). This method was validated on adult Wandering Albatrosses that were sexed based on prior reproductive histories (J. Lallemand and H. Weimerskirch, unpublished data). However, an earlier study also showed that 260-day-old Wandering Albatross chicks could be sexed with 95% accuracy using a composite index of bill and tarsus measurements (Berrow *et al.* 1999).

GROSS MORPHOLOGICAL MEASUREMENTS

Although three people were required to handle the birds, uniformity in measurement was maintained by having a single individual (S.A.S.) collect all measurements. Albatrosses were weighed to the nearest 50 g with a Salter spring balance (Salter Weigh-tronix Ltd, West Bromwich, UK). Because adults were measured during the early incubation period, and that most birds were non-breeders, it was fairly certain that albatrosses were not storing food in their crops. Thus, adult body mass was considered to reflect the true mass without any payload. The length of the tarsus, culmen, and maximum and minimum bill height were measured with vernier callipers ($\pm 0·5$ mm). Maximum body girth, wing span and wing area were measured following methods in Pennycuick (1999). Wing span was measured as the tip-to-tip distance of both fully outstretched wings and shoulder width was measured as the distance between shoulder joints. A single wing from each bird was traced onto a sheet of white parcel paper by placing the bird's fully outstretched wing onto a flat board. For consistency, all wing traces and tarsus measurements were made on the right side of the body.

ANALYTICAL MEASUREMENTS

Even though body mass is often used for comparing size differences between the sexes, it varies with changes associated in body condition, breeding activity and moulting (Freeman & Jackson 1990; Croxall 1995). Therefore, principal components analysis was used to create a composite body size index for adults and chicks of each sex (Rising & Somers 1989). Single factor scores of body size were derived by incorporating standardized measures (i.e. weighted equally) of maximum girth, shoulder width, wing span, culmen and tarsus. The differences between mean body size scores for each sex were compared using *t*-tests. Collectively, the first principal component (PC1) explained 71% of the variance in body size of adults and 61% of the variance in body size of chicks. Body mass was also regressed against composite body size to determine the general body condition of adults and chicks. It should be noted that body mass and not body size was used in calculations and comparisons involving wing morphology (described below).

Analytical measurements and calculations of body and wing morphology (except wing area, see below) pertinent to bird flight performance were made according to methods of Pennycuick (1989, 1999; see Table 1

Table 1. Symbol legends, formulae, and descriptions of morphological parameters from Pennycuick (1989, 1999) and Tennekes (1996). N – Newton (mass 9.81 m s^{-1})

Variable	Formula	Description
C	–	Maximum body circumference – circumference measured at widest point on body.
S_b	$S_b = C^2/4\pi$	Maximum body frontal area – cross-sectional area of bird at widest point.
–	–	Root chord – the width of the wing measured at the junction with the body.
b	–	Wing span – tip to tip distance between both outstretched wings.
S	–	Wing area – total area of both wings including the region of the body between wings.
c	$c = S/b$	Wing chord – mean wing width.
W	$W = N/S$	Wing loading – an index of force per unit wing area. Greater wing loads require faster flight speeds for gliding flight.
A	$A = b^2/S$	Aspect ratio – a relative index of wing shape, which determines the aerodynamic efficiency of the wing. The higher the aspect ratio, the greater the efficiency (i.e. high lift/drag ratio).

for details). Assuming body girth is circular, maximum body frontal area (S_b) was determined as the cross-sectional area of the bird at its widest point. Total wing area (S) of each bird was calculated by doubling the surface area of a single wing and adding the area between the wings (i.e. interwing area). Wing surface area was determined by copying each trace onto a new sheet of parcel paper. The copy was then cut out and weighed on a balance (±0.1 mg). The mass of each trace was converted to surface area using a standard curve (surface area = $13.7913 + 130.1$ (grams of paper); $P < 0.001$, $r^2 = 0.999$) derived by measuring the area of 20 rectangular sheets of the same paper weighed on the same balance. Interwing area was calculated from the dimensions of shoulder width and root chord, which was measured from the wing trace. Once wing area was calculated, wing loading and aspect ratio were determined.

To evaluate the role of morphometry on flight performance of each sex, program 2 (version 2.1) of Pennycuick (1998) was used to obtain best glide speeds (V_{bg}) and minimum stall speeds. The mean body mass, wing span and area, and maximum frontal area (Table 2) for each sex were used in the flight performance program. Because the program requires physical measurements of the environment, appropriate parameters were measured in the field during the study period.

Daily weather conditions were continuously recorded at 15 min intervals using a Weather Monitor II weather station (Davis Instruments, Hayward, CA) that was located in the nesting colony, 55 m above sea level. Mean ± standard deviation (SD) temperature and barometric pressure during the study period were $9.6 ± 4.2$ °C and $1013.1 ± 8.3$ millibars (air density, $\rho = 1.25$ kg m^{-3}). Average wind speed was $9.6 ± 8.1$ km h^{-1} (max. 117 km h^{-1}) and modal wind direction was predominantly from the west-south-west (WSW, magnetic).

All statistical analyses were performed with Systat 9.0 (Wilkinson 1996) using a significance level of $P \leq 0.05$ for t-tests (two tailed) and general linear models (GLM). All GLM comparisons involving linear and volumetric dimensions (e.g. wing area and body mass) were performed on log$_{10}$-transformed data. Unless stated otherwise, all data are presented as means ±1 SD.

Results

Sexual dimorphism in Wandering Albatross adults and chicks was apparent for almost all parameters measured (Table 2). However, given some overlap in body masses and color phases of feather plumage between sexes, it was useful to determine other parameters that could differentiate males from females. Discriminant function analysis showed that minimum bill height correctly sexed adults in 97% of the cases and measurements of the tarsus correctly assigned sex in 89% of the cases. When combined, both parameters correctly assigned the sex of adults in 94% of the cases as described by the regression: 0.559 minimum bill height +0.159 tarsus −41.785. Likewise, measurements of culmen length of chicks correctly assigned sex in 95% of the cases and 100% of chicks were correctly sexed from a combination of culmen length and maximum bill height measurements as described by the regression: 0.242 culmen + 0.720 maximum bill height −69.037. For both adults and chicks, a negative result indicated female and a positive result indicated male. In addition, univariate comparisons of tarsus and culmen length, and maximum and minimum bill height were all significantly different between males and females in both adults and chicks ($P < 0.001$ for each of the four measurements; Table 2).

DIFFERENCES IN BODY MASS AND SIZE

On average, adult males were 20.4% heavier and 7.3% larger in girth than adult females. Although differences in girth were less than half that of mass, the impact on maximum body frontal area (S_b) was considerable when comparing the frontal area for each sex. Adult males had a significantly larger frontal area (≈ 80 cm^2) than adult females (14.8%; Table 2). When comparing composite body size of adults, males were significantly larger than females ($t = -9.43$, df = 34, $P < 0.001$) and no intrasexual differences in body size were apparent between adults and chicks (Table 2). This result should be interpreted with caution because when body size was scaled to mass, only 26.5% of the variation in body mass could be explained by body

Table 2. Inter- and intrasexual comparisons of morphology of Wandering Albatross adults and near-fledged chicks. Intrasexual comparisons between adults and chicks are denoted by significance levels of $P \leq 0.05$ (*); $P \leq 0.001$ (**). All values are means ±SD and sample sizes are given in parentheses

Parameter	Male	Female	Test	P
Tarsus (mm)				
Adults	128·3 ± 3·1 (20)	121·1 ± 3·2 (16)	$t = -6.85$	<0·001
Chicks	129·2 ± 3·2 (12)	120·5 ± 1·7 (8)	$t = -7.03$	<0·001
Culmen (mm)				
Adults	169·6 ± 3·4 (20)	164·2 ± 4·1 (16)*	$t = -4.35$	<0·001
Chicks	169·4 ± 3·3 (12)	159·4 ± 2·1 (8)*	$t = -7.57$	<0·001
Mass (kg)				
Adults	9·44 ± 0·59 (20)**	7·84 ± 0·62 (16)**	$t = -7.92$	<0·001
Chicks	12·48 ± 0·99 (12)**	10·68 ± 0·76 (8)**	$t = -4.33$	<0·001
Shoulder width (cm)				
Adults	26·6 ± 1·4 (20)*	24·1 ± 1·0 (16)	$t = -6.02$	<0·001
Chicks	25·4 ± 0·8 (12)*	24·1 ± 1·1 (8)	$t = -2.98$	0·008
Maximum girth (cm)				
Adults	88·0 ± 3·1 (20)*	82·0 ± 2·1 (16)	$t = -6.55$	<0·001
Chicks	85·3 ± 1·9 (12)*	83·3 ± 2·6 (8)	$t = -2.01$	0·060
Maximum frontal area (cm²)				
Adults	620 ± 4 (20)*	540 ± 3 (16)	$t = -6.41$	<0·001
Chicks	580 ± 3 (12)*	550 ± 3 (8)	$t = -1.99$	0·062
Body size index (PC1)†				
Adults	1·41 ± 1·06 (20)	− 1·77 ± 0·93 (16)	$t = -9.43$	<0·001
Chicks	1·28 ± 0·91 (12)	− 1·92 ± 0·70 (8)	$t = -8.41$	<0·001
Wing span (cm)				
Adults	311 ± 4 (20)	299 ± 5 (15)	$t = -7.68$	<0·001
Chicks	313 ± 6 (12)	300 ± 3 (8)	$t = -5.39$	<0·001
Wing area (cm²)				
Adults	6260 ± 270 (20)*	5860 ± 230 (15)*	$t = -4.70$	<0·001
Chicks	5960 ± 280 (12)*	5520 ± 250 (8)*	$t = -3.57$	0·002
Mean wing chord (cm)				
Adults	20·1 ± 0·8 (20)**	19·6 ± 0·7 (15)*	$t = -2.18$	0·037
Chicks	19·0 ± 0·8 (12)**	18·4 ± 0·9 (8)*	$t = -1.54$	0·141
Wing loading (N m⁻²)				
Adults	148 ± 10 (20)**	132 ± 11 (15)**	$t = -4.60$	<0·001
Chicks	206 ± 20 (12)**	190 ± 14 (8)**	$t = -1.97$	0·065
Aspect ratio				
Adults	15·5 ± 0·6 (20)**	15·3 ± 0·6 (15)*	$t = -0.73$	0·470
Chicks	16·5 ± 0·8 (12)**	16·3 ± 0·9 (8)*	$t = -0.42$	0·683

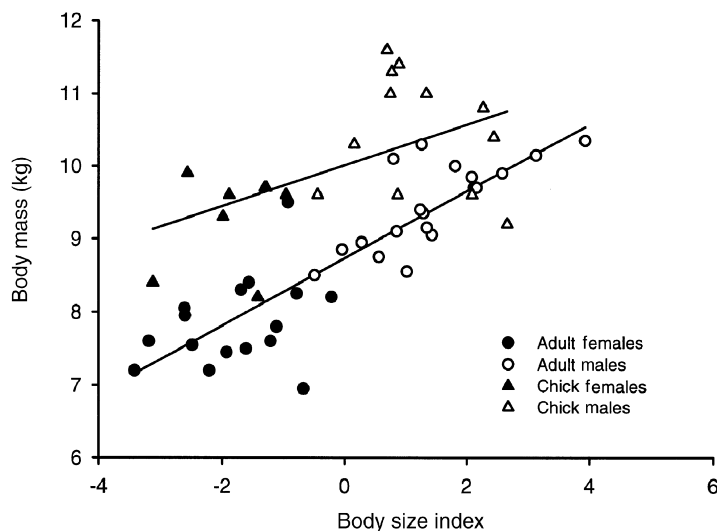†Composite body size index based on the first principal component with no rotation.

Fig. 1. Body mass as a function of body size index for male and female Wandering Albatross adults ($P < 0.001$, $r^2 = 0.751$) and near-fledged chicks ($P = 0.020$, $r^2 = 0.265$). Body size index was calculated using the first factor of a principal components analysis, which incorporated measurements of maximum girth, shoulder width, wing span, culmen and tarsus. Collectively, these five measurements explained 71% of the variance in adult body size and 61% of the variance in fledgling body size.

size in chicks (Fig. 1, $F_{1,18} = 6.50$, $P = 0.020$, $r^2 = 0.265$). In contrast, body size accounted for 75·1% of the variation in adult body mass (Fig. 1, $F_{1,34} = 103$, $P < 0.001$, $r^2 = 0.751$).

DIFFERENCES IN WING SIZE AND SHPAE

Relative to body mass, differences in wing size between sexes of adults and between adults and chicks were subtler, yet still significant. The wings of adult males were 4·0% longer, and had 6·8% more surface area than adult females (Table 2). In addition, the differences in wing span and area were highly correlated with body mass for all adults combined (wing span, $F_{1,33} = 58.7$, $P < 0.001$, $r^2 = 0.640$ and wing area, $F_{1,33} = 19.0$, $P < 0.001$, $r^2 = 0.366$). In contrast, chick wing span and area were highly variable and not significantly correlated with body mass. Although wing span did not differ between adults and chicks, adults had significantly more wing area than chicks (Table 2).

Mean wing chord in adult males was 2·6% greater than adult females; however, because males also had a

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Fig. 2. Aspect ratio as a function of wing area in adult Wandering Albatross. The slopes of each line were not statistically different from each other, however, the intercepts were ANCOVA; $F_{1,32} = 23 \cdot 9$, $P < 0 \cdot 001$. The linear regressions for each sex were statistically significant (males, $F_{1,18} = 26 \cdot 6$, $P < 0 \cdot 001$, $r^2 = 0 \cdot 596$ and females, $F_{1,13} = 13 \cdot 5$, $P = 0 \cdot 003$, $r^2 = 0 \cdot 510$).
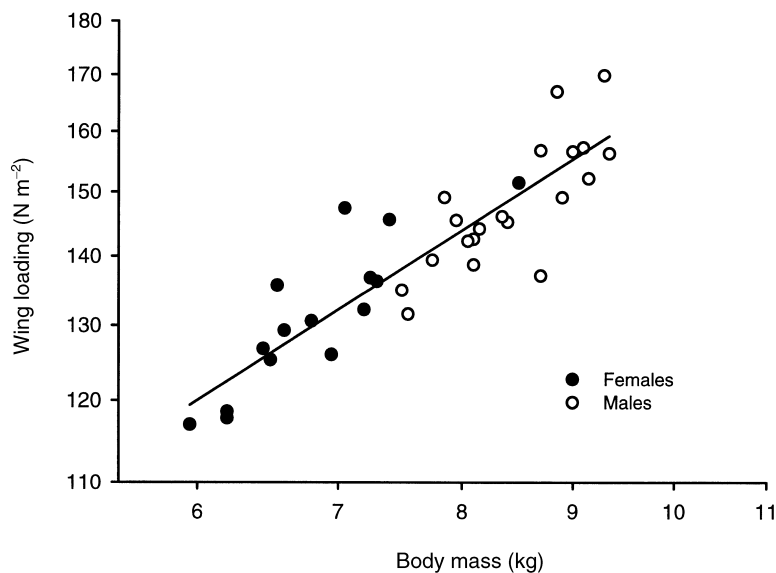
Fig. 3. Allometry of wing loading in Wandering Albatross adults ($P < 0 \cdot 001$, $r^2 = 0 \cdot 797$) plotted on log–log axes.

greater wing span than adult females, aspect ratio did not differ between the sexes in absolute terms (Table 2). Conversely, adult males had a significantly narrower wing per given wing area than adult females (Fig. 2). Chicks of both sexes had wing chords that were ≈6% lower than adults of the same sex (Table 2).

Given that body mass and wing morphology differed between the sexes in adults and between adults and chicks, we would expect wing loading to vary concordantly. Overall, wing loading in adult males was 12·1% greater than adult females ($t = -4 \cdot 60$, df = 33, $P < 0 \cdot 001$) and was highly correlated with adult body mass for both sexes combined (Fig. 3, $F_{1,33} = 130$, $P < 0 \cdot 001$, $r^2 = 0 \cdot 797$). Comparing adults and chicks, both male

and female chicks had significantly ($P < 0 \cdot 001$) higher wing loading (39–44%) than adults of the same sex (Table 2). Lastly, chick wing loading did not correlate with body mass, unlike that which was found for adults.

Discussion

The results of the present study clearly demonstrate that sexual size dimorphism occurs in Wandering Albatrosses. In 11 out of 12 characters measured, males were significantly larger than females and these differences were not all due to isometric scaling. Given that wing morphology of Procellariiformes does not conform to the rule of geometric similitude (Warham 1977), we would expect male Wandering Albatrosses to have higher wing loads than females because wing loading increases more steeply with increasing body mass (Pennycuick 1987).

Although wing loading varies between the sexes of Wandering Albatrosses, it can also vary within individuals as well. For instance, a bird heading to sea after a prolonged shift on the nest will experience a progressive increase in wing loading as body reserves are restored. Similarly, wing loading will change as a function of food loads that are acquired to provision a chick (Weimerskirch & Lys 2000). These examples can be illustrated by modelling the changes in wing loading as a function of mass gained at sea for each sex (Fig. 4a). Comparing a male and female with equal wing loads of 160 N m^{-2}, the difference in mass change between birds is about 0·9 kg or 55% greater in females, which is equivalent to an average chick meal for Wandering Albatrosses (Weimerskirch *et al.* 1997). If the change in mass is a result of food intake, the male would only be at ≈26% of capacity if total payload capacity is 2·8 kg (maximum meal size; Weimerskirch *et al.* 1997). In contrast, the female would be close to 75% of capacity assuming a total payload capacity of 2·2 kg. Alternatively, a change in mass of 1·0 kg effectively shows that wing loading in males would be 16·1 N m^{-2} or 12·2% higher than females. Thus, sex-specific differences in body size can have substantial effects on wing loading, which impacts flight performance.

Glide ratio is the ratio of lift to drag (Pennycuick 1989; Tennekes 1996), and associated with the glide ratio is a flight speed (V_{bg}) that is the most efficient gliding speed per unit distance flown (Pennycuick 1989; Norberg 1990). Since glide ratio is influenced by body mass, it is possible to use the same analogy presented above to model the changes in V_{bg} for male and female Wandering Albatrosses. For example, assuming both sexes experience a mass change of 1·0 kg, an absolute difference of 0·6 m s^{-1} is observed; or that V_{bg} is 3·9% faster in males. Although the difference in best glide speeds appears deceptively small, it is important to recognize that the impact of the potential effects on performance can be substantial because minor changes in speed have a considerable influence on power and drag (Pennycuick 1989; Tennekes 1996). Thus, male
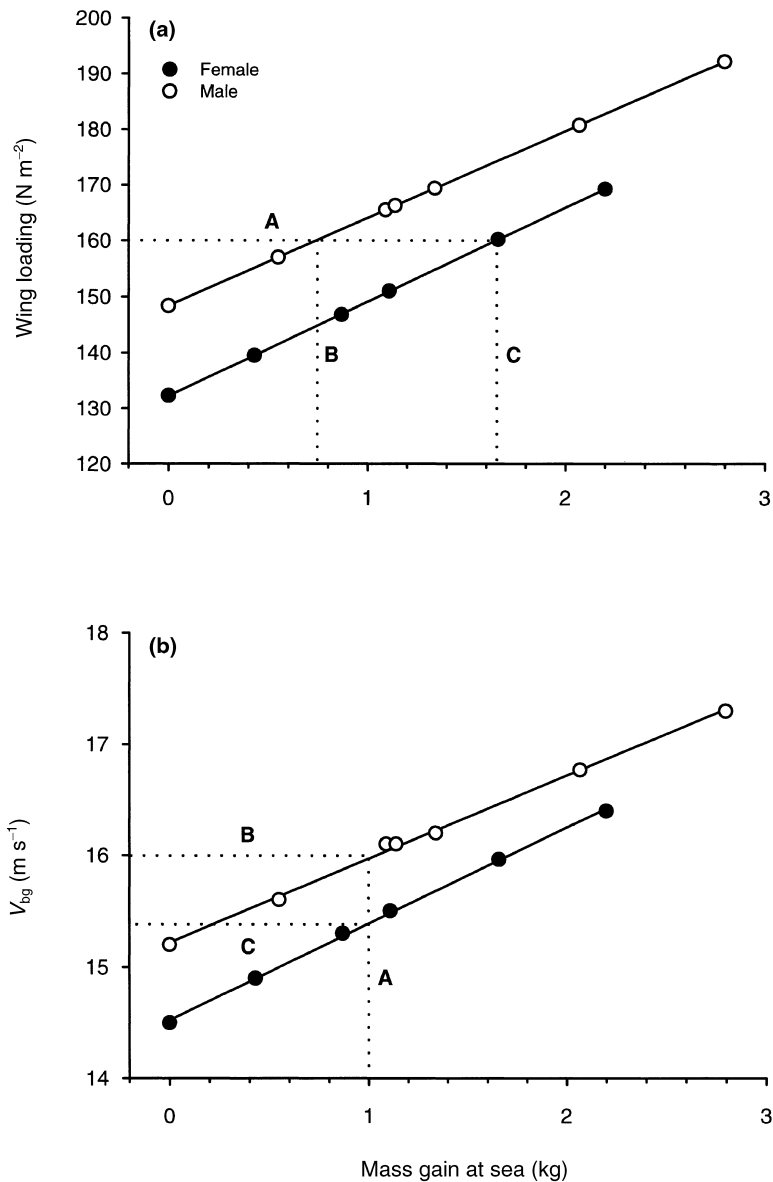
Fig. 4. Models of changing wing loading and best glide speed (V_{bg}) as a function of mass gain at sea (i.e. food gain). (a) The dotted lines represent the difference in mass change of a male (B) and female (C) albatross with equivalent wing loads; dotted line A. In (b), the dotted line A marks an identical change in mass of 1·0 kg for each sex and dotted lines B and C denote corresponding glide speeds. The changes in mass were derived from real data collected on chick meal sizes of Wandering Albatrosses (H. Weimerskirch, unpublished data). Initial wing loads (i.e. mass gain of 0 kg), were determined from 20 adult male and 16 adult female Wandering Albatross. Best glide speed was determined using Program 2 of Pennycuick (1998) from morphological measurements collected in the present study.

exploited by male Wandering Albatrosses, both at Crozet (Weimerskirch *et al.* 1993; Weimerskirch 1995) and at South Georgia (Prince *et al.* 1992). Thus, male Wandering Albatrosses travelling southward would experience strong winds blowing from the west-south-west, which would facilitate the fast airspeeds and increased lift required by their higher wing loading. In contrast, the smaller body size and lower wing loading of females would allow them to exploit subtropical and tropical waters in the north where winds are lighter, thus reducing intersexual competition. This pattern of sexual segregation combined with sex differences in body and wing morphology is consistent with observations of another seabird, the Magnificent Frigatebird (*Fregata magnificens*). Harrington *et al.* (1972) determined that wing loading was significantly higher in female frigatebirds (≈13% greater than males), and that subtle differences in wind conditions possibly affect the at-sea distribution of both sexes, particularly females. Thus, it appears that small differences in wing loading of Wandering Albatrosses and Magnificent Frigatebirds plays a significant role in determining the distributions of each sex.

Sexual size dimorphism in Wandering Albatrosses also has a functional influence on the relationship between chick-provisioning ability and adult body size. Since male Wandering Albatrosses are structurally larger in absolute terms, the size of the crop and proventriculus combined should vary congruently, allowing for the transport of larger food loads compared to females. This is consistent with empirical evidence, which demonstrates that male Wandering Albatrosses transport larger meals to chicks (Weimerskirch *et al.* 1997). Overall, average food loads are ≈11% of adult mass for both sexes; however, comparing absolute meal sizes, males transport 225 g or 26% more than females. Maximum food loads differ similarly such that the maximum meal size delivered by a male was 2·8 kg compared with 2·2 kg for a female (Weimerskirch *et al.* 1997). Thus, male Wandering Albatrosses should be able to store and transport ≈27% more food than females as a direct result of larger body size. Combining larger food loads with a greater frequency in nest visits; it is perhaps not surprising that males assume 61% of chick-provisioning duties (Weimerskirch *et al.* 1997). Similar patterns of chick provisioning are apparent in other seabirds that display sexual size dimorphism. For example, parental roles differ according to size dimorphism in western gulls, *Larus occidentalis* (Pierotti 1981). Male gulls are 25% larger than females (1·14 and 0·88 kg, respectively), and consequently males deliver meals that are ≈34% heavier and consist of larger prey items than females. Thus, it would appear that sexual size dimorphism has a significant ecological role in the provisioning strategy of adult seabirds.

Considering that chicks were measured about a month before fledging, it is likely that tissue growth and feather development of the wings were incomplete. Furthermore, body mass was well above that of normal

Wandering Albatrosses would need to achieve faster flight speeds in order to obtain the best glide speed. Likewise, males have higher stall speeds than females (males = 12·2–13·9 *vs* females = 11·5–13·0 m s⁻¹), suggesting that gliding would be more difficult for males in lighter wind conditions.

Weimerskirch *et al.* (2000b) modelled wind patterns of the Southern Ocean and determined that the region between 40 and ≈55°S exhibits the strongest and most consistent winds compared to subtropical regions in the north. This southerly region is also most commonly

Table 3. Morphological parameters of 230–240-day-old Wandering Albatross chicks projected out to size at fledging and to adult body mass. Wing span was increased by 3% per wing for males and 4% per wing for females (Berrow *et al.* 1999 and Weimerskirch *et al.* 2000a). Wing area was determined by solving the equation, area = (wing span^2/aspect ratio). Wing chord was determined by area/wing span, and wing loading was obtained by [weight/(area/10 000)]. Mean fledging mass was determined in Weimerskirch *et al.* (2000a), and mean adult mass in was determined in the present study. Mass was converted to weight in newtons and aspect ratio was obtained from adult Wandering Albatrosses in the present study (Table 2)

Sex	Mass (kg)	Weight (N)	Wing span (cm)	Wing area (cm^2)	Wing chord (cm)	Aspect ratio	Wing loading (N m^{-2})
At 33 weeks (prefledging)							
Males	12·48	122	313	5960	19·0	16·5	206
Females	10·68	105	300	5520	18·4	16·3	190
At 37 weeks (fledging)							
Males	10·48	103	332	7110	21·4	15·5	145
Females	9·29	91	324	6860	21·2	15·3	133
At 41 weeks (1 month postfledging)							
Males	9·44	93	332	7110	21·4	15·5	130
Females	7·84	77	324	6860	21·2	15·3	112

mass at fledging (10·5 kg in males and 9·3 kg in females; Weimerskirch *et al.* 2000a), thus we would expect wing loading to be higher in chicks than adults (Table 2). If we reduce chick mass to the observed mass at fledging, wing loading decreases by 13–16%. In addition, previous studies also indicate that fledglings depart the colony with larger wings than adults (Berrow *et al.* 1999; Weimerskirch *et al.* 2000a). Therefore, we modelled the changes in wing and body size of chicks to project the size at fledging (Table 3). The results of the model indicate that fledglings would depart to sea with roughly the same wing loading as adults, but at higher body masses. The 'extra' body mass is likely to be an important energy reserve that is consumed while fledglings learn to forage at sea for the first time (Weimerskirch *et al.* 2000a). Assuming all or part of this energy reserve is consumed, fledgling body mass and wing loading would decrease concomitantly. As a conservative estimate, a decline in body mass to that of the average adult would decrease wing loading by 12% (130 N m^{-2}) for male fledglings and 19% (112 N m^{-2}) in female fledglings (Table 3). A lower wing loading would be beneficial for fledglings that exploit regions with lighter wind conditions, such as the subtropics and tropics. As a previous study showed, Wandering Albatross fledglings are observed foraging exclusively in subtropical and tropical latitudes north of the range for adults (Weimerskirch & Jouventin 1987). Moreover, a lower wing loading would also make it easier for fledglings to take off and land on the water; an activity that is energetically expensive for Wandering Albatrosses (Shaffer 2000; Weimerskirch *et al.* 2000b).

Conclusions

The results of the present study indicate that sexual size dimorphism may have a functional significance in adult Wandering Albatrosses. The morphological differences between the sexes and its relationship to flight performance are consistent with the different at-sea foraging distributions of male and female Wandering Albatrosses. Hence, the windier regions of the sub-Antarctic may provide better conditions for males to travel at faster flight speeds required by their larger body size and heavier wing loading compared to females. Conversely, smaller females may be better adapted to exploiting areas with lighter wind conditions to the north. Thus, the evolution of such morphological differences in Wandering Albatrosses could have resulted from the selection of a mechanism to reduce intersexual food competition, or possibly as a way for Wandering Albatrosses to expand the range over which they can forage. The other major result of this study indicates that after accounting for chick growth to fledging size, young birds probably have a wing loading that is lower than adults, which could be viewed as an adaptation that allows younger birds to develop their foraging skills in calmer conditions.

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