**ORIGINAL PAPER**

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# Geographical variation in morphometry of black-browed and grey-headed albatrosses from four sites

**Abstract** Differences in morphometry between five populations of black-browed albatrosses (*Diomedea melanophrys*) and four populations of grey-headed albatrosses (*D. chrysostoma*) are examined. Two clear groups of black-browed albatrosses are evident, with birds from the subspecies *Diomedea melanophrys impavida* showing significant differences in several variables from those from the subspecies *Diomedea melanophrys melanophrys*. For groups from the latter subspecies, birds from South Georgia had larger measures than those from Kerguelen. A similar pattern to that of *Diomedea melanophrys melanophrys* was found between the groups of grey-headed albatrosses. Analysis of foraging distances relative to adult body-size index and the duration of chick-rearing periods suggests that differences in chick-provisioning rates between populations of conspecifics could account for at least some of the observed differences in adult morphometry.

## Introduction

Environmental explanations for geographic variation in phenotypes are increasingly recognised (Martin and Bellot 1990; Rhymer 1992; Krogstad et al. 1996). For bird populations, body size in adults has been linked to early development and environmental influences (James 1983; Boag 1987; Rhymer 1992; Burns 1993). Chick-growth rates, peak masses and fledging masses all vary in response to food availability during the chick-rearing period for many species (Ricklefs and Peters 1981; Barrett et al. 1987). For example, both inter-population and inter-annual variation at the same colonies have been noted for puffins (*Fratercula arctica*) (Nettleship 1972; Harris 1978, 1980, 1985; Brown and Nettleship 1984; Barrett et al. 1987). Not only do morphological traits vary among populations, but also life-history traits (Stearns 1992). For example, food supply has been linked to variations, both in the timing of breeding and the size of clutches (Blondel et al. 1991; Martin 1995; Krogstad et al. 1996). Thus where chick-provisioning rates vary among populations, differences in adult body size and in aspects of the breeding cycle may arise.

A first step in understanding how phenotypes vary among populations is to document inter-population differences. Albatrosses are highly philopatric, with individuals commonly nesting within metres of their natal sites, with the result that immigration between breeding colonies is rare, and between islands rarer still (Warham 1990). Although they have long-ranging foraging strategies (Weimerskirch et al. 1993; Prince et al. 1998; Weimerskirch 1998) breeding sites are distant from one another and few overlaps at sea exist between breeding populations. With such slight inter-population interchange, environmental influences on phenotype could be expected to develop readily in albatrosses.

In this paper we examine the between-site differences in morphometry for five populations of black-browed albatrosses (*Diomedea melanophrys*) and four populations of grey-headed albatrosses (*D. chrysostoma*). The study used a standardised set of measures taken from birds from several sites by a single team. Information on the duration of the chick-rearing period is also reviewed. Using multi-variate statistics, we test whether birds from different sites can be correctly classified to their site of origin using this simple set of morphological measures. In addition, the phenotypic differences in morphometric measures and chick-rearing periods are related to the foraging distances travelled by adults during chick rearing, with the aim of examining how provisioning rates may influence adult body size.

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## Materials and methods

### Study species and sites

Black-browed albatross and grey-headed albatross breed sympatrically throughout the Southern Ocean. Our work was carried out at four sub-Antarctic sites: South Georgia (SG), Kerguelen (KE), Iles Crozet (CR) and Campbell Island (CA). Comparison of morphometric characters between sites necessitated new data gathering to ensure homogeneity in the data set.

In a recent taxonomic review, major groupings within the genus *Diomedea* were examined (Nunn et al. 1996). This resulted in a reinstatement of the genus *Thalassache*, encompassing the two study species and the smaller albatrosses known as mollymawks. Between-site differences within currently accepted species were not examined and, therefore, we conservatively use existing naming. Morphological differences are apparent for black-browed albatrosses with the subspecies *Diomedea melanophrys impavida* endemic to Campbell Island (Westerskov 1960; Marchant and Higgins 1990). At Campbell Island, both *Diomedea melanophrys impavida* and the more widespread *Diomedea melanophrys melanophrys* are found breeding, often in mixed pairs (Moore et al. 1997). In our analysis, these five groups of black-browed albatross are treated separately, while four groups of grey-headed albatross are discussed, one from each site.

Information about the duration of the chick-rearing period has been reviewed, and is used as an indication of chick-growth rates. Foraging for both these species is strongly linked to the Polar Front (Weimerskirch et al. 1997; Prince et al. 1998; Waugh et al. 1999). The distance between this feature and the breeding sites is used as an index of provisioning rate, with birds travelling further assumed to provision chicks at a lower rate. Distances to the Polar Front were estimated using average position in summer of the sea-surface temperature isotherms of 3–5°C (Botkinov 1963).

### Field methods

Each species population is hereafter referred to as "groups" with the population indicated by two initials taken from the site name (CA Campbell, CR Crozet, KE Kerguelen, SG South Georgia). The subspecies *Diomedea melanophrys impavida* from Campbell Island is referred to as IM to separate this group from birds of the nominate subspecies measured at Campbell Island. Measurements of birds were made at four sites (the handlers are in parentheses): CA (S. Waugh, P. Prince), KE (H. Weimerskirch), CR (H. Weimerskirch) and SG (P. Prince). Measurements were taken for the following variables: exposed culmen length (culmen), tarsus length (measured with the leg bent at the joints with the foot and femur – tarsus) and flat wing chord (wing). Birds were weighed using a spring balance accurate to 1% during the chick-rearing period, just after they had delivered a meal to chicks, and this sample of birds was different from those measured at most sites.

### Analysis

We tested for heterogeneity between data sets collected in different years and by different handlers at the same site for the same species, using paired Student's *t*-tests with separate variances for each variable. These showed no significant differences ($t < |1.7|$, n.s.). Lilliefor's test showed that for each variable from at least one site, data deviated from normality. All variables were normalised using a $log_{10}$ transformation before inter-group differences were tested.

Statistical analysis was performed using Systat 6.0 (Wilkinson 1996) and between-group differences in culmen, tarsus and wing were used in the comparisons. One-way ANOVA was used to test for between-group differences in each variable.

To test for correct classification of individual birds to their group of origin, jack-knifed classification matrices were generated using a discriminant analysis. To describe "distances" between each pair of groups, an *F*-matrix was generated using Mahalanobis D2 statistics, along with *F*-to-remove statistics, which allow the determination of the variables that are most important in differentiating between the groups. To visualise the inter-group differences, canonical variates analyses were conducted, using group as the discriminating factor. This analysis generates two or more orthogonal axes (Canonical Variates 1 and 2, hereafter CV1 and CV2), which constitute the linear combination of measurement variables that best discriminate between the groups.

## Results

### Black-browed albatrosses

Black-browed albatrosses showed significant between-group differences in each measurement variable (Table 1). The discriminant analysis indicated that the IM group was most distinct from other groups, being correctly classified in 76% of cases. Other groups were not clearly discriminated, being classified correctly in

**Table 1** Mean morphometric measures (mm) of breeding black-browed and grey-headed albatross and mass (g) $\pm$ standard deviation (*n.d.* no data)

| | *n* | Culmen | Tarsus | Wing | Mass |
|---|---|---|---|---|---|
| **Black-browed albatross** | | | | | |
| CA | 11 | 118.6 ± 3.5 | 87.1 ± 2.3 | 530 ± 11.1 | n.d. |
| CR | 35 | 117.7 ± 3.2 | 87.2 ± 2.6 | 518 ± 15.4 | n.d. |
| IM | 86 | 112.5 ± 2.9 | 85.9 ± 3.1 | 522 ± 12.7 | 2750 ± 161 {10} |
| KE | 64 | 118.1 ± 3.9 | 84.6 ± 4.2 | 519 ± 11.4 | 3655 ± 353 {65} |
| SG | 25 | 119.0 ± 2.4 | 88.3 ± 2.6 | 537 ± 10.5 | 3560 ± 396 {35} |
| ANOVA ($log_{10} x$) | | $F_4 = 43.4$ | $F_4 = 8.6$ | $F_4 = 11.3$ | $F_{2,107} = 28.2$ |
| | | $P < 0.0001$ | $P < 0.001$ | $P < 0.001$ | $P < 0.001$ |
| **Grey-headed albatross** | | | | | |
| CA | 47 | 112.0 ± 3.9 | 85.6 ± 3.4 | 516 ± 15.8 | 3355 ± 355 {5} |
| CR | 65 | 112.4 ± 3.0 | 86.2 ± 3.7 | 520 ± 15.7 | 3565 ± 318 {6} |
| KE | 70 | 111.5 ± 3.2 | 82.2 ± 4.4 | 514 ± 10.2 | n.d. |
| SG | 26 | 114.8 ± 3.8 | 88.5 ± 3.2 | 526 ± 14.4 | 3361 ± 299 {48} |
| ANOVA ($log_{10} x$) | | $F_3 = 6.0$ | $F_3 = 22.12$ | $F_3 = 4.6$ | $F_{2,56} = 1.2$ |
| | | $P < 0.001$ | $P < 0.001$ | $P < 0.001$ | n.s. |

less than 52% of cases for each (Table 2). The between-groups $F$-matrix confirmed this separation of the IM group from others, and especially the SG group (Table 3). Culmen was the most important variable discriminating the groups ($F$-to-remove = 49.1), followed by wing ($F$-to-remove = 11.7).

CV1 explained 74.4% of the variation among groups and was most highly correlated with culmen (Table 4). CV2 explained a further 18.6% of the variation, and was most highly correlated with wing, followed by tarsus (Table 4). CV scores plotted for all individuals in each group show considerable overlap in morphometry among the populations (Fig. 1a). Mean CV scores for each group indicate the centroid of each group and the positions of these relative to one another along the first two canonical variate axes (Fig. 1b). CV1 is more negative with smaller culmen length, while the CV2 score is inversely related to the tarsus and wing measures, putting SG and KE groups at opposite extremes of this axes, with CA and CR birds falling intermediate (Fig. 1b).

Mass showed significant differences between the three groups studied, with the IM group having an average mass 23% smaller than the nearest group, SG (Table 1). SG and KE birds were not significantly different from one another in mass ($t_{63.1} = -1.19$, n.s.).

Grey-headed albatrosses

Each measurement variable showed significant inter-group differences (Table 1). The jack-knifed classification indicated that SG and KE groups best differentiated from others, being classified correctly in 65% and 63% of cases, respectively, while for the other groups only a minority of individuals were correctly classified (Table 2). The between-groups $F$-matrix showed that the SG and KE groups are most different from one another, having the greatest between-group score (Table 3). Tarsus was the most important variable discriminating the groups ($F$-to-remove = 16.04) with wing and culmen having relatively similar and low values ($F$-to-remove = 0.87 and 1.74, respectively).

CV1, explaining 89% of the between-group variation, was most highly correlated with tarsus (Table 4). CV2, explaining 10% of the variation, was relatively evenly correlated with all three measures, as all standardised discriminant functions had similar absolute values (Table 4). Canonical variates scores plotted for all individuals in each group showed considerable overlap in morphometry between groups (Fig. 2a). Mean CV scores show the central placement of CA and CR groups relative to KE and SG birds (Fig. 2b). Here CV1 increases with increasing tarsus length, and CV2 is an index combining all three measurement variables with relatively even weighting.

Grey-headed albatrosses weighed during chick rearing showed no between-group differences in mass (Table 1).

Chick-rearing period

The average time taken to raise chicks at the different sub-Antarctic sites has been noted in more general studies of breeding biology (Table 5). Grey-headed albatrosses take longer than black-browed albatrosses across all sites, and birds of either species from Campbell Island have longer chick-rearing periods than those from South Georgia. KE black-browed albatrosses fell intermediate between these two groups.

Foraging distances, morphometry and chick-rearing periods

The relationship of CV1, used as an index of adult body size for each group, and the distances to major foraging grounds was examined (Fig. 3). No relationship was evident for grey-headed albatrosses (Spearman's rank correlation = 0.2, n.s.), but for black-browed albatrosses a

**Table 2** Results of jack-knifed classification of birds from each group, percentages correctly classified to their group of origin (*n.a.* not applicable)

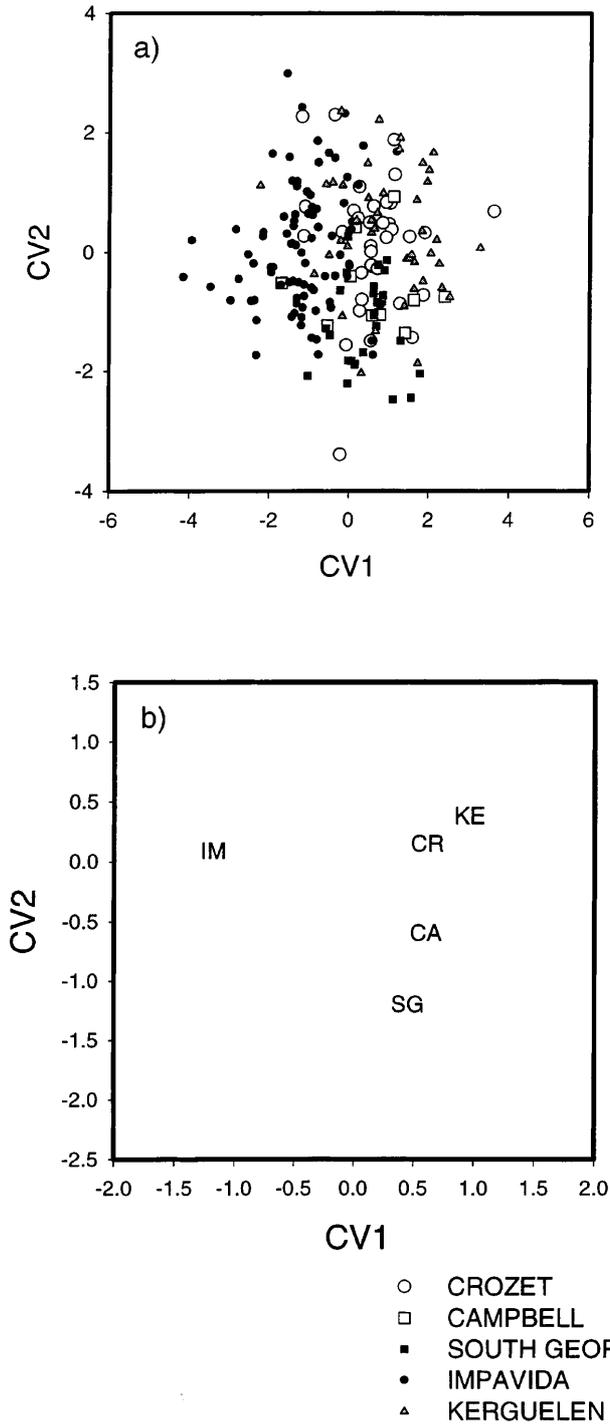| Group | Black-browed albatross (%) | Grey-headed albatross (%) |
|---|---|---|
| CA | 0 | 21 |
| CR | 46 | 22 |
| IM | 76 | n.a. |
| KE | 52 | 63 |
| SG | 48 | 65 |

**Table 3** $F$-matrix results from discriminant analysis for each group of black-browed and grey-headed albatrosses. Higher values indicate greatest inter-group distances

| Group | CA | CR | KE | SG |
|---|---|---|---|---|
| Black-browed albatross | | | | |
| CA | 0.0 | | | |
| CR | 2.74 | 0.0 | | |
| KE | 3.53 | 7.36 | 0.0 | |
| SG | 0.97 | 11.47 | 16.39 | 0.0 |
| IM | 11.72 | 30.15 | 27.58 | 57.32 |
| Grey-headed albatross | | | | |
| CA | 0.0 | | | |
| CR | 0.81 | 0.0 | | |
| KE | 7.91 | 12.43 | 0.0 | |
| SG | 5.80 | 4.09 | 18.21 | 0.0 |

**Table 4** Canonical discriminant functions for each measurement variable (CV1 and CV2) for the two species of albatross. Higher absolute values indicate stronger correlations

| Variable | CV1 | CV2 |
|---|---|---|
| Black-browed albatross | | |
| Culmen | 1.144 | 0.068 |
| Tarsus | −0.247 | −0.426 |
| Wing | −0.353 | −0.812 |
| Grey-headed albatross | | |
| Culmen | 0.094 | 0.850 |
| Tarsus | 0.927 | −0.547 |
| Wing | 0.107 | 0.422 |

significant correlation was found, with those groups foraging at greatest distance having a smaller body-size index (Spearman's rank correlation $= -1.00$, $P < 0.01$). Further, the relationship between foraging distances and the duration of the chick-rearing period, when corrected for adult body mass, was examined (Fig. 4). These data suggest that greater foraging distances are related to longer chick-rearing periods.

## Discussion

Inter-population differences in morphometry

For both species, individuals were correctly classified to their sites of origin in the minority of cases for most groups, suggesting that there is considerable overlap
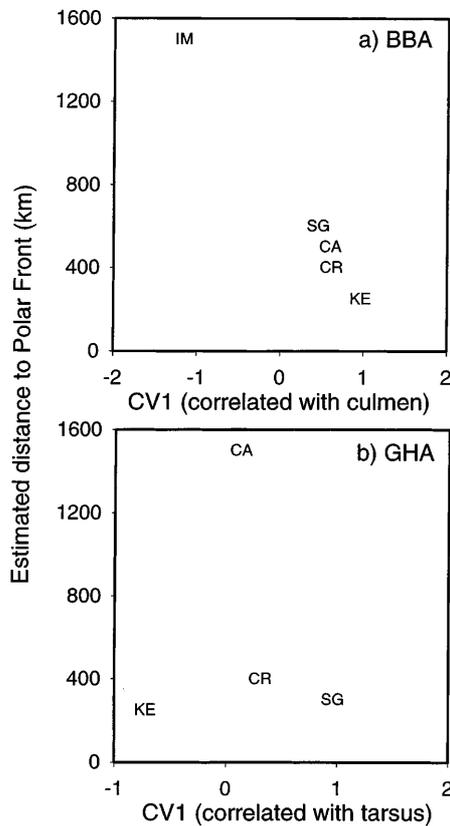


○ CROZET
□ CAMPBELL
■ SOUTH GEORGIA
● IMPAVIDA
▲ KERGUELEN

**Fig. 1 a** Canonical variate scores for individuals from each of five groups of black-browed albatrosses. **b** Canonical variate means for each group

□ CAMPBELL
○ CROZET
■ SOUTH GEORGIA
▲ KERGUELEN
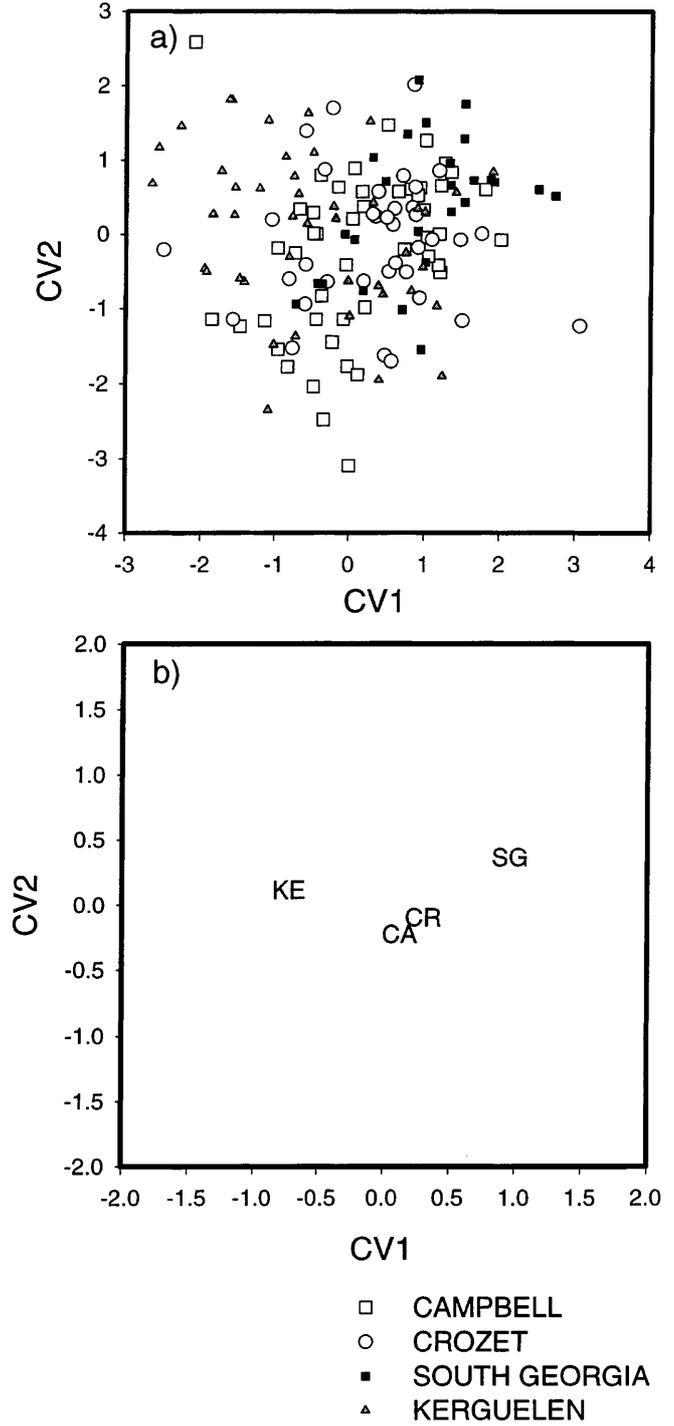
**Fig. 2 a** Canonical variate scores for individuals from each of four groups of grey-headed albatrosses. **b** Canonical variate means for each group

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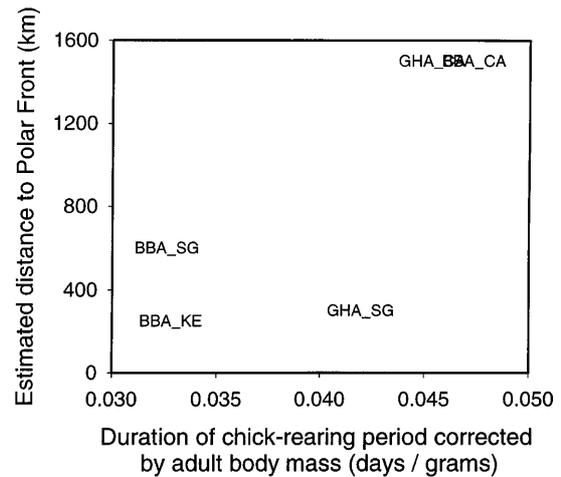**Table 5** The mean duration of chick-rearing periods for the two species of albatross

| Group | Duration of chick-rearing period (days) | Reference |
|---|---|---|
| Black-browed albatross | | |
| IM | 130 | Moore and Moffat (1990) |
| KE | 120 | Weimerskirch et al. (1997) |
| SG | 116 | Tickell and Pinder (1975) |
| Grey-headed albatross | | |
| CA | 152 | Moore and Moffat (1990) |
| SG | 141 | Tickell and Pinder (1975) |



**Fig. 4** Foraging distance in relation to the duration of the chick-rearing period for black-browed albatrosses (BBA) from three groups (CA, SG, KE) and grey-headed albatrosses (GHA) from two groups (CA, SG)

between the species groups in morphometry. Sexual dimorphism in both species may have contributed to this overlap (Marchant and Higgins 1990), but as data were not available from all sites on the sex of the birds measured, this factor could not be taken into account in the between-site analysis.

For black-browed albatrosses, the IM birds could be seen as a clear outgroup from the others, being correctly classified in 76% of cases, and having large *F*-matrix values in comparison to other groups. This differentiation was principally due to the significantly shorter culmen of the IM group. The significant difference in mass is another characteristic separating this group from the others. Among the remaining groups of black-



**Fig. 3** Foraging distance in relation to body-size index for **a** black-browed and **b** grey-headed albatrosses

browed albatrosses, differentiation was along a gradient related to wing and tarsus length, as indicated by CV2, and placed the KE and SG groups at extremes of the range, with the CR and CA groups falling intermediate.

For grey-headed albatrosses, the KE and SG groups were classified correctly in 63% and 65% of cases respectively, indicating that these groups are most distinct from others. The groups were distinguished mainly on the tarsus measure, with KE birds having smallest and SG birds largest mean tarsi measures.

These results suggest that black-browed albatrosses show greatest inter-group differentiation, dividing into two groups in accord with the existing segregation of subspecies, while grey-headed albatrosses show between-group differences but no clear outgroup is evident. Black-browed albatrosses from the subspecies *Diomedea melanophrys melanophrys*, and grey-headed albatrosses both show a gradient of body size, noticeable in measurement variables, but not in mass. Interestingly, for the two species, KE and SG groups are most distinct from one another, while CA and CR groups are intermediate.

Contributing factors

The similarities or differences in body size appear not to be related to distances between sites, as the groups that had closest morphometric properties as indicated by *F*-matrix results were not those geographically closest. However, the tendencies for decreasing body-size index (CV1) to be related to both increasing foraging distances and increased duration of chick-rearing period suggest that inter-group differences in chick-provisioning rates may play a role in determining adult body size. Adults foraging furthest from the breeding sites (IM black-browed albatrosses and CA grey-headed albatrosses, Waugh et al. 1999) could be expected to provision chicks at a lower rate than birds from other sites, due to the

costs incurred by commuting to more distant zones (Houston 1993, 1995). This assertion is supported by provisioning-rate data for black-browed and grey-headed albatrosses from South Georgia (P. Prince unpublished data), Kerguelen (Weimerskirch et al. 1997) and Campbell Island (S. Waugh and H. Weimerskirch unpublished data), with Campbell Island birds of both species delivering food to chicks at a lower rate than at other sites. Lower feeding rates may result in either slower growth of chicks, and/or in chicks that are smaller at fledging (Ricklefs and Peters 1981; Barrett et al. 1987). These may consequently be smaller as adults since these birds do not grow further after fledging, increasing in mass only after leaving the nest. For snow petrels (*Pagodroma nivea*) from the Antarctic continent, a similar pattern has been observed, with birds of smaller body size found breeding farthest from open waters, and hence travelling further to forage (Barbraud et al., in press).

Geographical differences in morphometry may be the result of a combination of factors for pelagic seabirds. Inter-site differences in foraging environment should be considered of prime importance among the causal factors. Studies including a greater number of populations and species whose ecology and morphometry are well documented are necessary to address these hypotheses further.

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