

CONTRASTING STRATEGIES OF PROVISIONING AND CHICK GROWTH IN TWO SYMPATRICALLY BREEDING ALBATROSSES AT CAMPBELL ISLAND, NEW ZEALAND¹

SUSAN M. WAUGH

NIWA, P.O. Box 8602, Christchurch, New Zealand, and CEBC, CNRS, Beauvoir-sur-Niort, 79360 France

HENRI WEIMERSKIRCH AND YYES CHEREL

CEBC, CNRS, Beauvoir-sur-Niort, 79360 France

PETER A. PRINCE²

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

Abstract. The provisioning strategies of two closely related species of albatross breeding sympatrically were studied at Campbell Island, New Zealand. Black-browed Albatrosses (*Diomedea melanophrys*) had a higher provisioning rate of chicks than Grey-headed Albatrosses (*D. chrysostoma*) as a result of a higher feeding frequency. Provisioning and satellite-tracking data suggest that Black-browed Albatrosses forage over neritic waters in trips of up to 5 days, in combination with longer trips over oceanic waters. In contrast, it was not possible to separate clearly short and long trips in Grey-headed Albatrosses, but they probably forage mostly over oceanic waters, combined with rafting or feeding near the colony during stays of short duration at sea. No inter-annual differences in foraging trip duration were apparent between years for either species. Chicks were fed larger meals at older ages and when in poorer condition, probably due to a limitation on the rate of assimilation of food. For both species, chick condition after feeding did not influence the duration of foraging trips. Black-browed Albatrosses from Campbell Island feed locally in neritic waters and up to 2,000 km from the colony, in contrast to conspecifics from other sites which feed principally over neritic waters. Grey-headed Albatrosses were largely dependent on oceanic resources as for conspecifics studied elsewhere. This study shows that foraging and provisioning strategies are flexible within species, allowing them to exploit more or less distant resources.

Key words: Black-browed Albatross, chick growth, *Diomedea chrysostoma*, *Diomedea melanophrys*, foraging strategy, Grey-headed Albatross, provisioning.

INTRODUCTION

The performance of seabirds in finding and delivering food to their young can be measured through their provisioning rate, the net energy delivered during any given period (Schoener 1971, 1987). Although many aspects of a species' ecology may influence this rate, it is, nevertheless, a sensitive indicator of performance, and may vary between species (Lack 1968), seasons, and individuals (Weimerskirch et al. 1995, 1997a, 1997b). Ultimately, the provisioning rate affects clutch size (Lack 1968), chick growth rate (Ricklefs 1968), survival of young, and therefore parental fitness (Clutton-Brock 1991). In Procellariiformes, clutch size is one, and thus variation in provisioning performance can be

measured directly by the food intake of a single chick. Even in closely related species of similar size, significant differences occur in the growth rate and chick-rearing period. For example, differences between Black-browed (*Diomedea melanophrys*) and Grey-headed Albatrosses (*D. chrysostoma*) in provisioning rate (Tickell and Pinder 1975) and diet quality (Prince 1980) result in a longer chick rearing period and biennial breeding for Grey-headed Albatrosses (Prince et al. 1994). Satellite telemetry studies have shown that these species have species-specific foraging strategies. Black-browed Albatrosses at the Kerguelen Islands feed exclusively on shelf areas (Cherel and Weimerskirch 1995, Weimerskirch et al. 1997a), and move between two shelf areas at South Georgia (Prince et al. 1997). Foraging also is linked to the Polar Frontal Zone (PFZ). In comparison, Grey-headed Albatrosses are seldom found over shelf areas around the Crozet

¹ Received 28 July 1998. Accepted 6 July 2000.

² Deceased.

and Kerguelen Islands (Weimerskirch et al. 1988), and forage mainly over oceanic waters at South Georgia, but also concentrate on part of the PFZ (Prince et al. 1997).

Whether provisioning rate in seabirds is regulated by chick needs or limited by adult energy regimes is unclear (Ricklefs 1992, Ricklefs and Shew 1994, Hamer and Hill 1997). For some species, there appears to be little relationship between chick condition and adult foraging performance, as meal sizes are independent of trip duration, chick condition, or meal mass (Hamer and Hill 1993, Hamer 1994). However, for other species, the condition of chicks has some influence on adult foraging strategies (Ricklefs et al. 1985). For example, British Storm-Petrel (*Hydrobates pelagicus*) adults return more quickly to feed chicks in poorer condition (Bolton 1995). Recently, differing modes of regulation have been linked to a species' foraging strategy, with neritic-only feeders having less ability to respond to chick needs than those species which divide their time between oceanic and neritic feeding (Weimerskirch 1998).

Black-browed Albatrosses at Campbell Island are on average 25% lighter than conspecifics from other sites (Waugh et al. 1999a), and belong to another sub-species (*D. m. impavida*). The fledging period takes longer at Campbell Island than at other sites (Tickell and Pinder 1975, Weimerskirch et al. 1997b). Grey-headed Albatrosses have similar morphometry across sites, but at Campbell Island the fledging period is longer than at South Georgia (Tickell and Pinder 1975, Moore and Moffat 1990). These variations suggest that between-site intra-specific differences in foraging behavior may be considerable. The aims of this study are to examine whether (1) the provisioning and foraging strategies differ between Black-browed and Grey-headed Albatrosses at Campbell Island, (2) the two species differ from birds at other sites as a result of exploiting different environments, (3) chick growth differs between species and years, and (4) the performance of individual adults is related to chick food requirements.

METHODS

Foraging of Grey-headed and Black-browed Albatrosses was studied at Campbell Island (52°S, 169°E), New Zealand during the 1995–1996 and 1996–1997 breeding seasons (hereafter 1996 and 1997, respectively). Approximately 26,000

pairs of Black-browed Albatrosses and 6,000 pairs of Grey-headed Albatrosses nest at the site annually (P. Moore, unpubl. data). The study colony at Bull Rock South contains annually approximately 8,000 and 300 breeding pairs of each species, respectively. Several species of petrel also breed at the site, but numbers have been greatly diminished by the presence of rats (*Rattus norvegicus*) and cats (*Felis domesticus*) (Bailey and Sorensen 1962).

The study area contained birds of both species and these were observed continuously during daylight hours to estimate foraging and provisioning parameters. One adult from each nest was marked with a 5–10 cm band of picric acid on the breast during incubation, and during the study period the identity of each visiting adult was noted, and its behavior observed continuously while it was at the colony, along with its times of arrival and departure. Chicks were weighed to the nearest 50 g using a 10-kg Salter spring balance every day at 04:00, 19:00 (Universal Time + 12 hr), and just after each feed, giving information about the meal mass and the growth rate of chicks. All chicks studied survived the study period.

The study was undertaken in three periods: 9–23 January 1996, 9–23 January 1997, and 6–20 February 1997. During the January 1996 and February 1997 periods, provisioning and foraging strategies and chick growth were examined, whereas in January 1997, only chick growth was measured. Samples of 35, 40, and 32 Black-browed Albatross chicks were used in January 1996, January 1997, and February 1997, respectively, along with 24, 15, and 35 Grey-headed Albatross chicks, respectively, for the same periods.

Chicks were aged during the 1997 season from their hatching dates. Chicks from the two species were between 24–37 days old at the start of the January study period in 1997. During the 1996 season, hatching data were not available, but we considered chicks to be of equivalent age between seasons, as three seasons of hatching data showed maximum variation in the mean hatching date of only 4 days in Black-browed Albatrosses and 3 days in Grey-headed Albatrosses at Campbell Island (S. Waugh and P. Moore, unpubl. data). During the study periods, chicks were in the rapid phase of growth (Ricklefs 1973) and had not yet attained peak weights. For these species, chicks aged between 30–80

days are in the t_{10-90} phase of growth (Tickell and Pinder 1975), which is the period required for growth from 10 to 90% of asymptotic weight (Ricklefs 1973). During this phase, growth curves fitted to different equations can most readily be compared (Ricklefs 1973), hence we considered that comparison between the linear regressions of growth curves across groups to be valid.

Albatrosses feed their chicks by regurgitation, thus whole food items cannot be counted, and estimation of meal masses relies on weighing chicks to determine mass differences before and after feeding. It is necessary to take account of the mass chicks lose through respiration and defecation between feedings to estimate meal masses (Ricklefs et al. 1985). We estimated average rates of mass-loss for chicks of each species by calculating the proportion of body weight lost per hour during the first 6 hr, 6–12 hr, 12–24 hr, and 24 hr or more, after a feed. The estimated weight lost before each chicks' feeding event was subtracted from its last pre-feed weight, and the difference between this value and the post-feed weight gave the estimated meal mass. Daily provisioning rate was estimated using the average meal mass delivered daily for each individual adult.

We estimated breeding success by weekly inspections of nests from the beginning of incubation until 1 February in 1996 and 1997, except for 10 November to 4 January in the 1996 season, when no visits were made.

Satellite telemetry was carried out on seven adult Black-browed and five adult Grey-headed Albatrosses feeding chicks (see Waugh et al. 1999b). They were fitted with Toyocom 2038 (55 g) and Microwave 100 (30 g) satellite transmitters following the methods of Weimerskirch et al. (1997b). Ten and five foraging trips were followed, respectively. Satellite-tracking data were analyzed using GIS ARC-INFO, integrated with bathymetric data. Bathymetry was interpolated from 500-m depth grids that were generated by ARC-INFO, from contour data sourced from the General Bathymetric Chart of the Oceans (GEBCO) (British Oceanographic Data Centre 1994). Five Black-browed and four Grey-headed Albatrosses were fitted with 20-g temperature-recorders at the tarsus. These devices log the bird's activity (Wilson et al. 1995) and measure the sea-surface temperature (SST), thereby indicating in which water-mass birds

were foraging (Weimerskirch et al. 1995). We estimated minimum foraging ranges from these records by calculating the closest distance between Campbell Island and the lowest (or highest) temperatures recorded based on SST accessed through the Integrated Global Ocean Services System (IGOSS) (Reynolds and Smith 1992).

STATISTICAL ANALYSES

We tested for differences between breeding success, the number of birds undertaking only neritic trips, between years or species using χ^2 tests. Chick growth was examined using the regression of chick-mass upon date for each chick, with the slope of the equation indicating the growth rate. Growth data from the beginning and the last 14 days of each study period gave initial masses and growth rates, respectively, and were compared using students *t*-tests.

Pre-feed chick condition was calculated for each individual at each feeding-event by taking the residuals of the linear regression on the chicks weight at that time. After-feed condition estimates are the residuals from the regression of post-feed weights on time. Meal mass and chick condition before and after feeding were examined in relation to the duration of foraging trips and the time since the chicks' previous meal using Pearson's correlation. Data for meal mass and the interval since the previous meal were normalized with square root transformations, and foraging trip duration by a log transformation (Zar 1984).

Between species, year, and species \times year interactions for the foraging parameters were tested using ANOVA with year and species as factors. Means and standard deviations are used throughout, and for all statistical tests, the level of significance was 0.05.

RESULTS

BREEDING SUCCESS

There were significant inter-annual differences for Black-browed (breeding success 68%, $n = 101$, and 87%, $n = 100$, respectively; $\chi^2_1 = 10.1$, $P < 0.01$), but not for Grey-headed Albatrosses (68%, $n = 93$, and 74%, $n = 81$, respectively; $\chi^2_1 = 0.8$). The differences in breeding success between the species were significant in 1997 ($\chi^2_1 = 4.9$, $P = 0.02$), but not 1996 ($\chi^2_1 = 0.1$). Hatching success details were not available for 1996, but in 1997, fledging success (number of

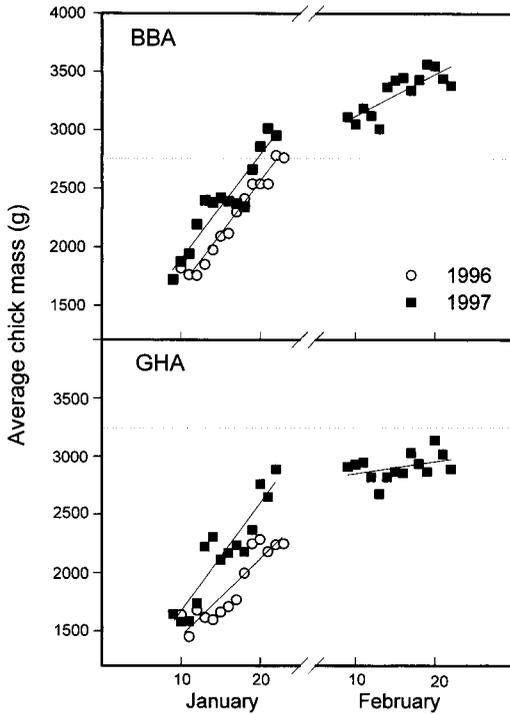


FIGURE 1. Growth of Black-browed (BBA) and Grey-headed Albatross (GHA) chicks at Campbell Island, studied during January 1996 and 1997, and February 1997. Linear regression lines are shown for each group of chicks for Black-browed Albatrosses (January 1996: $y = 86.3x + 806$; January 1997: $y = 87.3x + 1,039$; February 1997: $y = 35.5x + 1,733$) and for Grey-headed Albatrosses (January 1996: $y = 66.0x + 789$; January 1997: $y = 91.3x + 751$; February 1997: $y = 10.3x + 2,450$). Dotted lines indicate average adult mass during the chick-rearing period.

hatched chicks surviving to 1 February) was 93% for Black-browed Albatrosses and 90% for Grey-headed Albatrosses.

CHICK GROWTH

Growth rates were positive, and differed significantly from zero for all groups of chicks except Grey-headed Albatrosses in February 1997 (Fig. 1). Chick growth in the January periods showed no significant inter-annual differences for Black-browed Albatross, but Grey-headed Albatross chicks grew faster in the second year ($t_{34.8} = -3.0, P = 0.01$, t -tests with separate variances throughout this section), but did not have different initial weights ($t_{52.8} = -0.2$). Between the two species, the masses of chicks at the beginning of the study periods varied in January 1996 ($t_{55.1} = 3.0, P = 0.01$) and January 1997 ($t_{70.4} = 3.1, P = 0.01$), but not in February 1997 ($t_{51.1} = 0.7$), with Black-browed Albatross chicks being heavier at the beginning of the periods. There were no significant differences in growth rate between species in any period.

NUMBER AND DURATION OF VISITS PER DAY

The average number of visits to nests per day varied between species but not between years, with Black-browed Albatrosses visiting more frequently (Table 1). The duration of visits to the colony showed species, year, and species \times year effects. Black-browed Albatrosses stayed for shorter times at the colony than Grey-headed Albatrosses during both years, and for both spe-

TABLE 1. Foraging parameters ($\bar{x} \pm SD [n]$) of Grey-headed (GHA) and Black-browed Albatrosses (BBA). $df = 1, 1$ for all tests.

Parameter	Species	January 1996	February 1997	Effect	F	P
No. visits per nest per day	BBA	1.14 \pm 0.28 (35)	0.99 \pm 0.22 (32)	species	32.7	0.001
	GHA	0.78 \pm 0.23 (24)	0.78 \pm 0.23 (15)	year	2.0	ns
				species \times year	2.5	ns
Duration of stay at the colony (hr)	BBA	0.19 \pm 0.09 (69)	0.13 \pm 0.04 (63)	species	7.9	0.01
	GHA	0.49 \pm 0.78 (46)	0.15 \pm 0.07 (28)	year	13.9	0.001
				species \times year	5.7	0.02
Duration of foraging trip (days)	BBA	1.64 \pm 1.00 (68)	1.64 \pm 0.71 (63)	species	10.2	0.01
	GHA	2.16 \pm 1.26 (45)	2.10 \pm 1.27 (28)	year	0.1	ns
				species \times year	0.0	ns
Meal mass (g)	BBA	393 \pm 78 (35)	474 \pm 67 (32)	species	11.6	0.001
	GHA	456 \pm 130 (24)	542 \pm 104 (15)	year	19.0	0.001
				species \times year	0.0	ns
Proportion of visits without chick being fed	BBA	0.06 \pm 0.07 (35)	0.02 \pm 0.05 (32)	species	0.0	ns
	GHA	0.03 \pm 0.06 (22)	0.07 \pm 0.09 (24)	year	0.4	ns
				species \times year	11.4	0.001

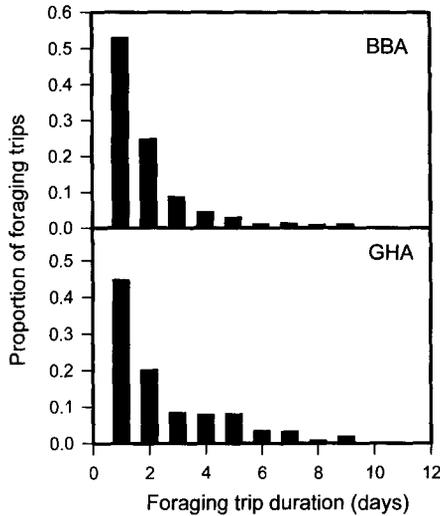


FIGURE 2. The distribution of foraging trip durations for Black-browed (BBA) and Grey-headed Albatrosses (GHA), averaged over two seasons.

cies, the duration of stays were shorter in 1997 than 1996 (Table 1).

FORAGING TRIP DURATIONS

The distributions of the duration of foraging trips were positively skewed for both species, with an abundance of short trips (Fig. 2). Mean trip duration showed significant differences between species only (Table 1). Black-browed Albatrosses were undertaking shorter trips on average than Grey-headed Albatrosses. The distribution of maximum foraging ranges from the colony of birds fitted with satellite-trackers or temperature-loggers indicates that for Black-browed Albatrosses ($n = 12$ birds), trips of less than 5 days duration came from birds travelling to less than 600 km at maximum range from the colony (Fig. 3). For these trips, the water depths at the maximum ranges were less than 1,000 m, indicating that birds were foraging exclusively over the Campbell Plateau during these short trips. Longer trips were over deep waters (2–7 km depth). Based on these findings, for subsequent analyses we divided foraging trips by Black-browed Albatrosses into neritic trips of 0–5 days duration and oceanic trips of greater than 5 days. For Grey-headed Albatrosses, the division between neritic and oceanic trips was unclear ($n = 9$ birds, Fig. 3). Satellite-tracked Grey-headed Albatrosses foraged over deep waters during 3-day trips. Additionally, for this

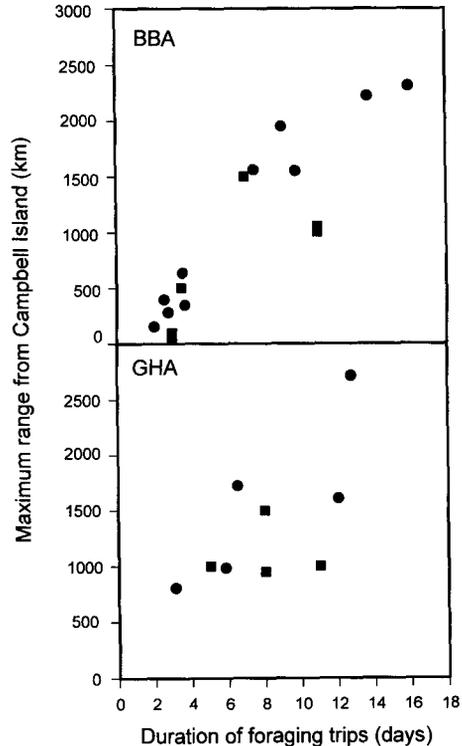


FIGURE 3. Relationship between the maximum range and duration of individual foraging trips for Black-browed (BBA) and Grey-headed Albatrosses (GHA). Circles = satellite tracked birds, squares = birds with temperature-recorders.

species, a high number of short foraging trips (Fig. 2) was recorded from the provisioning-rate study; we were unable to discern whether these were foraging trips on the Campbell Plateau or simply birds resting at sea near the colony between attempts to feed chicks.

NERITIC AND OCEANIC TRIPS

For Black-browed Albatrosses, neritic trips were predominant in the foraging strategy, with 86% ($n = 69$) and 85% ($n = 63$) of visits to the chick following these trips in 1996 and 1997, respectively. The proportion of birds which undertook only neritic trips (1996: 49%, 1997: 34%) did not differ significantly between years ($\chi^2_1 = 2.2$, $P > 0.1$). The maximum numbers of successive neritic trips for Black-browed Albatrosses were 16 and 9 in 1996 and 1997, respectively. Mean durations of neritic foraging trips (1996: $x \pm SD = 1.3 \pm 0.4$ days, $n = 90$; 1997: 1.3 ± 0.6 days, $n = 63$) and oceanic trips (1996: 7.1 ± 1.3 days,

$n = 35$; 1997: 7.2 ± 1.1 days, $n = 21$) showed no significant differences between years for Black-browed Albatrosses ($-0.4 < t < 0.6$). Black-browed Albatrosses delivered $14 \pm 22\%$ ($n = 69$) of meals after long trips in 1996 and $15 \pm 17\%$ ($n = 63$) in 1997. The proportion of time birds spent in long trips was $33 \pm 36\%$ ($n = 69$) in 1996 and $40 \pm 31\%$ ($n = 63$) in 1997. There were no significant inter-annual differences in either of these parameters.

For Grey-headed Albatrosses, trips were not divided into oceanic and neritic trips for analysis. However, some birds performed successive trips of less than 3 days duration in 1996 (2%) and 1997 (3%). The maximum number of successive trips of this length was 10 and 8, respectively, for the same years.

MEAL MASS

Meal masses differed between years and species, with Grey-headed Albatross chicks receiving larger meals than Black-browed Albatross chicks in both years, and meals delivered in February 1997 being larger than those from January 1996 in both species (Table 1). The occurrence of chicks receiving no meal during an adult's visit showed no differences between years and species (Table 1). However, there was a significant species \times year effect, due to a decrease in the proportions between years for Black-browed Albatrosses, and an increase for Grey-headed Albatrosses. Meal mass increased with date for Grey-headed Albatrosses in both 1996 ($r = 0.30$, $n = 167$, $P < 0.001$) and 1997 ($r = 0.23$, $n = 120$, $P = 0.01$), but not for Black-browed Albatrosses (1996: $r = -0.01$, $n = 385$; 1997: $r = 0.06$, $n = 369$).

INFLUENCE OF CHICK CONDITION ON ADULT PROVISIONING

The mass of meals delivered was inversely related to chick condition before feeding for Black-browed and Grey-headed Albatrosses in 1996 ($r = -0.44$, $n = 385$, $P < 0.001$; $r = -0.40$, $n = 167$, $P < 0.001$, respectively) and 1997 ($r = -0.46$, $n = 369$, $P < 0.001$; $r = -0.44$, $n = 120$; $P < 0.001$, respectively). In accord with this, meal mass increased with the time since chicks were last fed in the two species in 1996 (Black-browed Albatrosses, $n = 385$, $r = 0.22$, $P < 0.001$; Grey-headed Albatrosses, $n = 167$, $r = 0.28$, $P < 0.001$) and 1997 (Black-browed Albatrosses, $n = 369$, $r = 0.30$, $P <$

0.001 ; Grey-headed Albatrosses, $n = 120$, $r = 0.32$, $P = 0.001$).

The mass of the meal increased with the duration of foraging trips for Grey-headed Albatrosses in 1996 ($r = 0.18$, $n = 141$, $P = 0.04$) and 1997 ($r = 0.25$, $n = 108$, $P < 0.01$). For Black-browed Albatrosses, meal mass did not show a strong relationship with trip duration in either year (1996: $r = -0.10$, $n = 359$, $P = 0.05$; 1997: $r = 0.04$, $n = 340$). The condition of the chicks of both species after feeding had no influence on the duration of the subsequent trip in 1996 (four tests, $0.03 < r < 0.16$).

DAILY PROVISIONING BY ADULTS

For Black-browed Albatrosses, the daily provisioning rate by adults was 141 ± 73 g day⁻¹ ($n = 70$) in 1996 and 183 ± 74 g day⁻¹ ($n = 63$) in 1997. For Grey-headed Albatrosses, the average rate was 108 ± 58 g day⁻¹ in 1996 ($n = 46$) and 157 ± 62 g day⁻¹ ($n = 28$) in 1997. Provisioning rates were significantly higher in the second year of study ($F_{1,105} = 19.4$, $P < 0.001$) and higher for Black-browed than Grey-headed Albatrosses ($F_{1,105} = 8.7$, $P < 0.01$), but there was no interaction effect ($F_{1,105} = 0.2$).

DISCUSSION

FORAGING AND PROVISIONING STRATEGIES AT CAMPBELL ISLAND

Black-browed and Grey-headed Albatross foraging strategies at Indian and Atlantic Ocean sub-Antarctic sites have been characterized as neritic and oceanic, respectively (Weimerskirch et al. 1986, 1988, 1997b, Cherel and Weimerskirch 1995, Prince et al. 1997). The more diverse foraging strategies found in Black-browed Albatrosses from Campbell Island, however, show this species is capable of adapting greatly to the environmental characteristics surrounding its breeding sites.

Satellite tracking of Black-browed Albatrosses from Campbell Island suggests that they divided their time between the extensive Campbell Plateau and oceanic foraging trips up to 2,000 km from their breeding site, mainly to the PFZ or to the east of the Campbell Plateau (Waugh et al. 1999b). Birds were evidently undertaking two types of foraging trips: trips of less than 5 days duration that are exclusively over shelf waters (neritic trips), and longer foraging trips over oceanic waters. Most individuals followed in this study carried out both long and short for-

aging trips, thus were exploiting both foraging environments. Such a combination of strategies has been well established for several other Procellariiform species, and is thought to allow pelagic seabirds to rely on distant resources to fledge their chicks (Weimerskirch et al. 1993, 1995, 1997b, Weimerskirch 1998). Use of two contrasting foraging strategies by Black-browed Albatrosses has not been demonstrated before. It also is a novel finding that a seabird species uses either exclusively neritic, or a mixture of neritic and oceanic foraging strategies depending on the site of origin.

In contrast, Grey-headed Albatrosses occur rarely over shelf waters at other sites and are thought to feed mainly over deeper waters (Weimerskirch et al. 1986, 1988, Prince et al. 1997). Consistent with this, satellite-tracked birds from Campbell Island traveled to oceanic water even when undertaking relatively short trips (3 days, Waugh et al. 1999b). However, birds followed in the provisioning study commonly undertook short trips (less than 2 days). Average daily distances of travel for satellite-tracked Grey-headed Albatrosses suggest that these trips would be within 400–500 km range of Campbell Island over the Campbell Plateau, suggesting that Grey-headed Albatrosses could spend a significant proportion of their time feeding over shelf waters. Some birds performed up to 10 trips of less than 3 days duration successively, suggesting that foraging relatively close to the colony may be important for some individuals.

These different foraging strategies are reflected in the differing chick-provisioning strategies of the two species at Campbell Island. Grey-headed Albatrosses delivered larger meals less often than Black-browed Albatrosses, although the result was a lower provisioning rate than for Black-browed Albatrosses.

DIFFERENCES BETWEEN YEARS AT CAMPBELL ISLAND

The two years represented favorable breeding seasons at Campbell Island, with breeding success above the median recorded for six previous years of study (Waugh et al. 1999c). Slight inter-specific differences in breeding success were apparent, with Black-browed Albatrosses having higher overall breeding success in 1996 than 1997, and having significantly higher breeding success than Grey-headed Albatrosses in 1997. Thus, it would appear in the slightly poorer year

(1997), Grey-headed Albatrosses had relatively greater difficulty in raising chicks than Black-browed Albatrosses. Some inter-annual differences in foraging and provisioning strategies could be accounted for by the fact that chicks were about 28 days older in the second year of study.

For Black-browed Albatrosses, the older chicks of the second year were provisioned at a higher rate with larger meal masses, presumably due to greater energy needs of older compared to younger chicks. In addition, for older chicks, a lower proportion was not fed during visits, and colony-visits were shorter. These factors suggest a limitation in the ability of small chicks to receive meals and is consistent with the findings of other studies which showed that in storm petrels (Ricklefs 1992) and Black-browed Albatross (Weimerskirch et al. 1997b), meal sizes could be influenced by the chick's ability to assimilate food. Despite the age difference in chicks, the foraging strategies of Black-browed Albatrosses did not differ between years, with birds undertaking similar proportions of neritic and oceanic trips, and trips were of similar average duration. These results indicate that at least for neritic foraging trips, which form the majority of trips for this species, birds may be exploiting a food source which does not vary in location between years, as for conspecifics at Kerguelen Island (Weimerskirch et al. 1997b). The lack of increase in meal sizes during each two-week study period for this species further indicates a limitation on foraging, perhaps because birds have fixed commuting times, and thus return to the colony with whatever they find during the hours available for foraging. Chick growth in January was similar between years for Black-browed Albatrosses. This may result from an intrinsic growth rate (Prince and Ricketts 1981) and/or similar feeding conditions between years.

Similar inter-annual patterns in foraging and chick provisioning were evident for Grey-headed Albatrosses, with no detectable differences in the mean duration of foraging trips between years. Older chicks were provisioned at a higher rate as meals were larger, and the durations of stay at the colony by adults were longer for younger chicks. Chick growth showed more inter-annual variation in this species, not differing significantly from zero in the second year. A reliance on different and more distant food sources

could explain these differences compared to Black-browed Albatrosses. Meal sizes increased during each two-week period, again suggesting differences in food availability compared to Black-browed Albatrosses.

REGULATION VERSUS LIMITATION

A variety of provisioning responses by adult Procellariiformes has been described (Ricklefs et al. 1985, Bolton 1995, Weimerskirch et al. 1997a, 1997b). In some studies, adults provisioned independently of chick needs, suggesting an intrinsic rhythm in adult visitation (Ricklefs 1992, Hamer and Hill 1993, Ricklefs and Shew 1994). The long inter-feed interval by individual adults produces a high probability of a visit by the bird's partner between successive feeds. Therefore, chick condition after a meal conveys relatively little information about what the chick's needs will be when the adult returns after its subsequent foraging trip (Ricklefs 1992). In other studies, adults adjusted their provisioning rates, returning more quickly to feed chicks in poorer condition, although they were unable to deliver larger meals (Bolton 1995, Weimerskirch et al. 1995). For Black-browed Albatrosses at the Kerguelen Islands, birds responded to experimental overfeeding of chicks by the lengthening of foraging trips, thus provisioning at lower rates when chicks were in good condition (Weimerskirch et al. 1997b). However, the converse did not apply—underfed chicks received only slightly larger meals at the same rate as chicks at control nests. The ability of adults of different species to regulate their provisioning appears linked to their species-specific foraging strategies. Species with oceanic foraging habits are able to increase their provisioning rates by increasing the proportion of foraging trips in near-shore areas (Weimerskirch et al. 1995). For species which use a single strategy of short, frequent trips, as is typical for Black-browed Albatrosses at sites other than Campbell Island and for other neritic feeders, the ability to increase the frequency of feeds is limited and birds may regulate provisioning of chicks in a limited way by the size of meals rather than the duration of trips (Weimerskirch et al. 1997b).

We investigated the relationships between chick condition, meal size, and foraging trip duration to test whether the study species were influenced by chick needs in the same ways. Both Black-browed and Grey-headed Albatrosses de-

livered larger meals to chicks in poorer condition, and to chicks that had fasted longer since their last meal, indicating that they could respond to the nutritional status of their chick by giving more food. The ability of chicks to consume larger meals when they are in poorer condition is likely to be the mechanism explaining these results, as recently fed chicks did not take large meals from their parents. In both species, adults did not respond to the condition of chicks after a feed, as there was no relationship between this factor and the duration of the subsequent foraging trip. Here, Black-browed and Grey-headed Albatrosses show similar responses to other petrel (Ricklefs 1992, Hamer and Hill 1994) and albatross species (Weimerskirch et al. 1997a).

Provisioning strategies of the two species differed both in duration of foraging trips and the meal-mass delivered. For Black-browed Albatrosses, the size of the meal brought to chicks showed no relationship to the duration of the foraging trip in either year, indicating that meal size is determined by the adult's foraging success. In some species, adults return to feed their chick after attaining a threshold quantity of food (Bolton 1995), whereas in other species, they return regardless of the amount of food obtained (Weimerskirch et al. 1997a). At Campbell Island, a significant proportion of meals is delivered after neritic trips by Black-browed Albatrosses. For Grey-headed Albatrosses, the size of meals delivered was proportional to the duration of the previous foraging trip. By relying on more distant resources, meals were delivered less frequently, and therefore, chicks were more often less replete, and so able to receive bigger meals.

COMPARISON AMONG SITES

The length of the chick rearing period of the two species differs among sites. It is longest at Campbell Island, 130 days and 152 days for Black-browed and Grey-headed Albatrosses, respectively (Moore and Moffat 1990), and is shortest at South Georgia, 116 days and 141 days for the two species, respectively (Tickell and Pinder 1975). At the Kerguelen Islands, Black-browed Albatross chicks fledge in 120 days (Weimerskirch et al. 1997b). The long fledging period for Black-browed Albatrosses at Campbell Island is paradoxical, as adults are smaller at this site (Waugh et al. 1999a).

The plasticity in foraging behavior of Black-

browed Albatrosses between sites indicates that the marine environment adjacent to sites has an important influence on the ecology of this species. The physical oceanographic environments differ greatly between the sites. Black-browed Albatrosses at the Kerguelen and Crozet Islands mainly use the shelf areas adjacent to the islands, and rarely forage over deep waters (Weimerskirch et al. 1986, 1997b, Cherel and Weimerskirch 1995). At South Georgia, this species exploits rich, but seasonally-variable krill stocks, feeding over shelves close to South Georgia and the South Orkney Islands (Prince et al. 1997). The PFZ passes relatively close to South Georgia (Peterson and Whitworth 1994) and is located at the Kerguelen Islands (Park et al. 1993). At Campbell Island, there is a more extensive shelf area than at other sites, and likely associated fish-stocks. Despite this, Campbell Island birds undertaking long foraging trips travel up to 2,000 km to the PFZ and other deep water areas, and thus are travelling farther than conspecifics, which undertake only neritic feeding trips. Therefore, at Campbell Island, Black-browed Albatrosses behave more like an oceanic feeding species, with the lengthened chick-rearing period a probable result. Grey-headed Albatrosses appear to follow similar foraging strategies to conspecifics at other sites, and rely mainly on oceanic resources.

This study has shown a clear division of foraging strategies into neritic and oceanic foraging trips for Black-browed Albatrosses breeding at Campbell Island. It highlights the flexibility of foraging and provisioning strategies within the same species foraging in different environmental conditions. For Grey-headed Albatrosses, the foraging strategy is principally oceanic. It is unclear whether this species also relies on resources from the Campbell Plateau. Further satellite-tracking and provisioning studies are needed to examine this question.

ACKNOWLEDGMENTS

The project was funded by the Department of Conservation, including the Conservation Services Levy paid by the New Zealand Commercial Fishing Industry, National Institute of Water and Atmosphere, Centre National de la Recherche Scientifique, and the French Foreign Ministry. For assistance in the field, we thank G. Hedley, S. Kalish, B. Thompson, T. Troup, P. Carnaby, A. Relling, and E. Abraham. We are grateful to the Department of Conservation staff at Southland Conservancy for logistical support, and S. Ude, P. Sa-

gar, and British Antarctic Survey for assistance with the satellite tracking program. We thank A. Weathers, D. Anderson, G. Robertson, K. Hamer, I. West, and two anonymous referees for comments on the manuscript.

LITERATURE CITED

- BAILEY, A. M., AND J. H. SORENSEN. 1962. Subantarctic Campbell Island. Proc. Denver Mus. Nat. Hist. 10: 1-301.
- BOLTON, M. 1995. Food delivery to nestling storm petrels: limitation or regulation? *Funct. Ecol.* 9:161-170.
- BRITISH OCEANOGRAPHIC DATA CENTRE. 1994. General bathymetric chart of the oceans. British Oceanographic Data Centre, Birkenhead, UK.
- CHEREL, Y., AND H. WEIMERSKIRCH. 1995. Seabirds as indicators of marine resources: Black-browed Albatrosses feeding on ommastrephid squids in Kerguelen waters. *Mar. Ecol. Prog. Ser.* 129:295-300.
- CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, NJ.
- HAMER, K. C. 1994. Variability and stochasticity of meal size and feeding frequency in the Little Shearwater *Puffinus assimilis*. *Ibis* 136:271-278.
- HAMER, K. C., AND J. K. HILL. 1993. Variation and regulation of meal size and feeding frequency in Cory's Shearwater *Calonectris diomedea*. *J. Anim. Ecol.* 62:441-450.
- HAMER, K. C., AND J. K. HILL. 1994. The regulation of food delivery to nestling Cory's Shearwater *Calonectris diomedea*; the roles of parent and offspring. *J. Avian Biol.* 25:198-204.
- HAMER, K. C., AND J. K. HILL. 1997. Nestling obesity and variability of food delivery in Manx Shearwaters, *Puffinus puffinus*. *Funct. Ecol.* 11:489-497.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- MOORE, P. J., AND R. D. MOFFAT. 1990. Mollymawks on Campbell Island. Science and Research Internal Report 59. Dept. Conserv., Wellington, New Zealand.
- PARK, Y. H., L. GAMBERONI, AND E. CHARRIAUD. 1993. Frontal structure, water masses and circulation in the Crozet Basin. *J. Geophys. Res.* 98:12361-12385.
- PETERSON, R. G., AND T. WHITWORTH. 1989. The subantarctic and polar fronts in relation to deep water masses through the southwest Atlantic. *J. Geophys. Res.* 94:10817-10838.
- PRINCE, P. A. 1980. The food and feeding ecology of the Grey-headed Albatross *Diomedea chrysostoma* and Black-browed Albatross *D. melanophris*. *Ibis* 122:476-488.
- PRINCE, P. A., J. P. CROXALL, AND A. G. WOOD. 1997. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries, p. 137-167. In G. Robertson [ED.], Albatross ecology and conservation. Surrey Beatty and Sons, Chipping Norton, Australia.
- PRINCE, P. A., AND C. RICKETTS. 1981. Relationships between food supply and growth in albatrosses:

- an interspecies cross-fostering experiment. *Ornis Scand.* 12:207–210.
- PRINCE, P. A., ROTHERY, P., J. P. CROXALL, AND A. G. WOOD. 1994. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136:50–71.
- REYNOLDS, R. W., AND T. M. SMITH. 1992. Improved global sea-surface temperature analyses. *J. Climate* 7:929–948.
- RICKLEFS, R. E. 1968. Patterns of growth in birds. *Ibis* 110:419–451.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201.
- RICKLEFS, R. E. 1992. The roles of parent and chick in determining feeding rates in Leach's storm-petrel. *Anim. Behav.* 43:895–906.
- RICKLEFS, R. E., C. H. DAY, D. E. HUNTINGTON, AND J. B. WILLIAMS. 1985. Variability in the feeding rate and meal size of Leach's storm petrel at Kent Island, New Brunswick. *J. Anim. Ecol.* 54:883–898.
- RICKLEFS, R. E., AND W. A. SHEW. 1994. Foraging stochasticity and lipid accumulation by nestling petrels. *Funct. Ecol.* 8:159–170.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369–404.
- SCHOENER, T. W. 1987. A brief history of optimal foraging theory, p. 5–99. *In* A. C. Kamil, J. Krebs, and H. R. Pulliam [EDS.], *Foraging behavior*. Plenum Press, New York.
- TICKELL, W. L. N. 1970. Biennial breeding in albatrosses, p. 549–557. *In* M. W. Holdgate [ED.], *Antarctic ecology*. Vol. 1. Academic Press, London.
- TICKELL, W. L. N., AND R. PINDER. 1975. Breeding biology of the Black-browed Albatross *Diomedea melanophrys* and Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 117:432–451.
- WAUGH, S. M., P. A. PRINCE, AND H. WEIMERSKIRCH. 1999a. Geographical variation in morphometry of Black-browed and Grey-headed Albatrosses at four sites. *Polar Biol.* 22:189–194.
- WAUGH, S. M., H. WEIMERSKIRCH, Y. CHEREL, U. SHANKAR, P. A. PRINCE, AND P. M. SAGAR. 1999b. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar. Ecol. Progr. Ser.* 177:243–254.
- WAUGH, S. M., H. WEIMERSKIRCH, P. J. MOORE, AND P. M. SAGAR. 1999c. The population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Campbell Island 1942–1996. *Ibis* 141:216–225.
- WEIMERSKIRCH, H. 1998. How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *J. Anim. Ecol.* 66:99–109.
- WEIMERSKIRCH, H., J. A. BARTLE, P. JOUVENTIN, AND J. C. STAHL. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* 90:214–219.
- WEIMERSKIRCH, H., O. CHASTEL, AND L. ACKERMAN. 1995. Adjustment of parental effort to manipulated foraging ability in pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav. Ecol. Sociobiol.* 36:11–16.
- WEIMERSKIRCH, H., O. CHASTEL, T. CHAURAND, L. ACKERMAN, X. HINDERMEYER, AND J. JUDAS. 1994. Alternative long and short foraging trips in pelagic seabird parent. *Anim. Behav.* 47:472–476.
- WEIMERSKIRCH, H., Y. CHEREL, F. CUENOT-CHAILLET, AND V. RIDOUX. 1997a. Alternative foraging strategies and resource allocation by male and female albatrosses. *Ecology* 78:2051–2063.
- WEIMERSKIRCH, H., P. JOUVENTIN, AND J. C. STAHL. 1986. Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128:195–213.
- WEIMERSKIRCH, H., T. MOUGEY, AND X. HINDERMEYER. 1997b. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behav. Ecol.* 8:635–643.
- WEIMERSKIRCH, H., M. SALAMOLARD, F. SARRAZIN, AND P. JOUVENTIN. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110:325–342.
- WILSON, R. P., H. WEIMERSKIRCH, AND P. LYS. 1995. A device for measuring seabird activity at sea. *J. Avian Biol.* 26:172–176.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, London.