Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses

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Summary

1. Theoretical models predict that animals will vary their effort to maximize different currencies such as time and energy when the constraints of reproduction change during breeding, but this has been poorly studied in free-ranging animals.

2. Foraging effort (energy per unit time) was examined by comparing mass changes, foraging costs and activity-specific behaviours of Wandering Albatrosses (*Diomedea exulans* Linnaeus) during the incubation and chick-brooding stages. In 1998, 38 albatrosses (20 during incubation and 18 during brooding) were injected with doubly labelled water and equipped with satellite transmitters and activity data loggers.

3. During incubation, albatrosses travelled 3·7 times farther and were at sea 3·2 times longer, yet foraging costs were significantly lower than trips made during brooding (incubation $4·52 \pm 0·50$ SD W kg^{-1} *vs* brooding $4·98 \pm 0·55$ SD W kg^{-1}).

4. The rate of daily mass gain decreased significantly with time at sea during incubation whereas the rate of daily mass gain increased significantly with time at sea during brooding.

5. Foraging effort was higher during brooding, suggesting that birds were minimizing time at sea to maximize the rate of food delivery to chicks. In contrast, foraging effort was lower during incubation, suggesting that birds were maximizing time at sea and minimizing the energy costs of foraging.

6. Foraging costs were also different between sexes. However, this was related to body size differences and not to differences in foraging effort as suggested in previous studies.

Key-words: Energy expenditure, Wandering Albatrosses

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Introduction

Reproduction is a demanding period for most animals because adults must balance their own energy requirements with those of their offspring, especially when the residual reproductive value of adults is high (Stearns 1992). Thus, parents should regulate the intensity of their effort in response to the changing demands of time and energy during reproduction (Goodman 1974; Drent & Daan 1980; Ydenberg *et al*. 1994). While foraging, adults may increase their effort when provisioning large broods (Daan, Deerenberg & Dijkstra 1996), when adjusting to offspring requirements (Bolton 1995; Bertram, Welham & Ydenberg 1996) or as environmental conditions vary during reproduction (Costa, Croxall & Duck 1989; Boyd *et al*. 1994). In these cases, parents may opt to maximize the rate of energy delivery to offspring at the expense of higher costs to themselves to find food. In contrast, the period leading up to the birth or hatching of offspring is likely to impose very different energy demands on adults because animals are primarily foraging for themselves, to build energy reserves that will be used to grow a fetus and synthesize milk (in mammals), or to fast during incubation (in birds). Time constraints are also implicit in the foraging decisions of adults because time can limit the duration and distance over which parents can forage from a central place (Orians & Pearson 1979; Stephens & Krebs 1986).

As central place foragers, pelagic seabirds (e.g. albatrosses and petrels) rely on patchy, ephemeral prey distributed far from shore, yet they must always return to land to breed (Lack 1968; Ashmole 1971). As a result, reproduction can impose constraints on the durations over which adults can travel from a breeding colony while searching for food. This is especially true of the brooding period when time at sea is reduced so that parents can brood and feed chicks frequently (Ricklefs 1983). Foraging ranges and flight costs also determine the profitability of transporting food loads over a given distance, which in turn can affect the

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quantity of energy that is delivered to chicks (Penny-cuick, Croxall & Prince 1984). Thus, the intensity of foraging effort, defined as the energy expended per unit time, probably varies substantially over the course of a breeding season for most, if not all seabird species (e.g. Chappell *et al*. 1993; Bevan *et al*. 1995, 2002). When considering the reproductive investment that parents make during a breeding season, we might expect foraging effort to increase as the value of off-spring increases. However, the extent that seabird parents adjust their foraging effort when breeding is poorly understood, particularly when parents make the transition from caring for an egg to provisioning a chick. This transition is probably quite dramatic because adults switch from feeding only themselves during incubation to feeding a chick and fulfilling their own energy requirements during chick-rearing (e.g. Chappell *et al*. 1993; Bevan *et al*. 2002). To test this, we measured time at sea, foraging activity, mass gain and energy expenditure of breeding Wandering Alba-trosses (*Diomedea exulans* Linnaeus) to examine how foraging effort varies in relation to the constraints of reproduction during incubation and brooding.

Wandering Albatrosses are sexually dimorphic (Tickell 1968; Shaffer, Weimerskirch & Costa 2001c) and the sexes typically segregate into different foraging locations while at sea (Prince *et al*. 1992; Weimerskirch *et al*. 1993; Weimerskirch 1995). Females forage at greater distances over pelagic waters north of their breeding colonies whereas males most commonly feed in more southerly waters. Despite these differences in foraging behaviour, males and females share breed-ing duties equally (Tickell 1968; Weimerskirch 1995; Weimerskirch & Lys 2000). Foraging effort is therefore likely to be higher in females than in males (Salamolard & Weimerskirch 1993; Arnould *et al*. 1996). However, this difference has yet to be substantiated by measure-ments of energy expenditure and foraging activity. Therefore, a second goal of our study was to examine the foraging effort of male and female Wandering Albatrosses by measuring activity levels, foraging beha-viour and energy expenditure in relation to reproductive stage using factorial analyses (e.g. ANOVA).

Materials and methods

The study was conducted during the austral summer of 1998 on Possession Island, Crozet Archipelago, south-western Indian Ocean (46°S, 52°E). Twenty birds (10 of each sex from different nests) were studied during the incubation stage from February to early March. Another 18 birds (nine of each sex from differ-ent nests) were studied during mid- to late March, when chicks were 3–5 days old. Wandering Albatross chicks are normally brooded by parents for approxi-mately 30 days, after which chicks are large enough (~2–3 kg) to be left unattended on nests (Tickell 1968).

The sex of each adult was determined by plumage characteristics (Weimerskirch, Lequette & Jouventin

1989) and prior reproductive histories (Weimerskirch & Jouventin 1987). Because most Wandering Alba-trosses on Crozet were banded as chicks, it was possi-ble to establish the age of all but two of the study animals. The mean age of adult males was $21·0 ± 8·3$ SD years and the mean age of adult females was $20·7 ± 8·0$ SD years. We were also able to confirm that all but three birds (two unknown age and one known age individual) had prior breeding experience.

AT-SEA METABOLIC RATES AND ENERGY EXPENDITURE

Doubly labelled water (DLW; $^3HH^{18}O$) was used to determine field metabolic rates (FMR) and water influx rates (WIR) of Wandering Albatrosses (Lifson & McClintock 1966; Nagy 1980; Nagy & Costa 1980; Speakman 1997). All birds were captured off the nest just after relief by their partner. A cloth hood was placed over the head, and 3–4 ml of blood was sam-pled from a vein on the tarsus. Albatrosses were given an intraperitoneal injection of 15 ml of sterile water containing 10 atom percentage oxygen-18, 2·15 MBq ml^{-1} of tritiated water and 0·9% NaCl. Total mass of the injected volume ($±0·01$ g) was determined gravimetric-ally by weighing the syringe before and after injection using a portable field balance (CT200, Ohaus Corp., Pine Brook, NJ). Each bird was weighed to the nearest 50 g using a Salter spring balance (Salter Weightronix Ltd, West Bromwich, UK). Birds were then released next to their nests to await equilibration of the iso-topes. Albatrosses attempting to depart were captured and held for the remainder of the equilibration period (~120 min). Shaffer, Costa & Weimerskirch (2001b) determined in a separate study that 100 min was suffi-cient for isotope equilibration in Wandering Albatross adults. Following equilibration, each bird was recap-tured and 4–6 ml of blood was collected from a vessel on the opposite leg from the previous sampling. A sat-ellite transmitter and activity data logger were attached (details described below), and the bird was released near its nest. Upon returning from sea, injected birds were recaptured and a final 4–6 ml blood sample was collected and final body mass measured. In most cases, birds were weighed within 2–3 h of their return to the colony. However, six birds were captured imme-diately upon returning from sea before they resumed nesting duties (three during incubation and three dur-ing brooding stage).

All blood samples were collected with a syringe and 22 gauge needle, transferred to a vacutainer (B-D brand with no additives; Beckton-Dickinson, Franklin Lakes, NJ), and stored at 5–8 °C before centrifugation. Serum was transferred to 2-ml plastic screw cap vials (with silicon O-rings; Sarstedt Inc., Newton, NC) and frozen at −5 °C until analyses were performed in May 1998. Specific activity of tritiated body water was deter-mined in triplicate by scintillation spectrometry (LS 6500, Beckman Coulter Inc., Fullerton, CA) of ~90 µl

of water in 10 ml of Ecolite + scintillation cocktail (ICN Pharmaceuticals, Irvine, CA). Water was obtained by distilling 100-μl aliquots of serum following methods described in Ortiz, Costa & Le Boeuf (1978). Specific activity of oxygen-18 water was determined by mass ratio spectrometry of water distilled from blood serum (Metabolic Solutions, Nashua, NH).

Initial total body water was calculated using the initial dilution space of oxygen-18. Final body water content was calculated as the initial fractional water content times the final body mass. Rates of CO_2 production were determined using equation 2 in Nagy (1980), and water flux was calculated using equations 4 and 6 in Nagy & Costa (1980). These equations assume that an animal's body mass, and therefore body water volume, change linearly through time. Carbon dioxide production was converted to units of energy expenditure in kilojoules using a conversion factor of 1 litre CO_2 = 25·2 kJ (Adams, Brown & Nagy 1986), which was based on the chemical composition of a squid and fish diet consumed by albatrosses (Clarke & Prince 1979; Croxall & Prince 1980; Croxall & Prince 1982). Mass-specific FMR was calculated by dividing absolute FMR (in watts) by adult body mass (in kilograms) because absolute FMR was determined to scale isometrically with body mass for Wandering Albatrosses (log $W = 0.694 + 0.980$ log kg; 95% CI of slope = ± 0·318; $F_{1,52} = 38.2$, $P < 0.001$, $R^2 = 0.424$).

All study nests were visible with the unaided eye from a single vantage point within the colony, so nests were monitored continuously throughout the day. Observations were only conducted during daylight hours because previous research has shown that adults do not return to or depart from the colony at night (Weimerskirch & Lys 2000). Thus, time at sea was determined by a combination of direct observation of departures and returns, or by the analysis of activity logger data and satellite positions. Because DLW measurement intervals included brief periods ashore (birds were either on or near their nest), at-sea energy expenditure (W kg^{-1}) was corrected following methods of Costa & Prince (1987). At-sea metabolic rate (MR) was estimated as

(at-sea MR) = [Measured FMR – (incubation MR × proportion of time ashore)/proportion of time at sea],

where incubation MR was determined to be 2·0 ± 0·2 W kg^{-1} (Shaffer *et al.* 2001b).

Field metabolic rates were determined for 11 out of 20 birds (seven males and four females) injected with DLW during incubation and 14 out of 18 birds (8 males and 6 females) injected with DLW during brooding. During incubation, six birds were at sea for 11 days or longer (maximum 15·80 days) so final oxygen-18 values were too close to background levels to permit accurate measurements of metabolism. However, water influx rate was measured in 28 out of the original 38 birds injected with DLW since tritiated

water levels were sufficiently above background to permit accurate water flux determinations. In addition, 6 of the original 18 brooding birds departed the colony before a postequilibration sample was collected. All 6 birds were recaptured upon returning from sea and a final blood sample was obtained, so FMR was determined by back-calculating the initial isotope enrichment using an initial TBW of 46·8% (mean for 8 brooding birds was 46·8 ± 3·8 SD%). This method is similar to the single sample method described in Speakman (1997). Because FMRs of all 6 birds were within the range measured for the remaining brooding birds (39·8– 65·3 W), and were less than 1·5 standard deviations from the mean, all data were included in the analysis.

AT-SEA FORAGING BEHAVIOUR AND ACTIVITY PATTERNS

Movement patterns of injected birds were studied using satellite platform terminal transmitters (PTT 100, Microwave Telemetry, Columbia, MD). Each bird was equipped with a 20–30 g PTT attached to feathers on the back with white adhesive tape. The PTTs transmitted a signal every 90 s, but generally 6–12 geographical locations from each bird were obtained and processed daily by Service Argos (CLS Argos, Toulouse, France). Analysis of geographical locations was performed with ELSA software (CLS Argos) using standard Argos class designations (class 0–3, A, and B) to evaluate the accuracy of locations. The data were manually filtered by discarding positions that exhibited a maximum velocity of 90 km h^{-1} between consecutive locations, which is slightly higher than the measured maximum flight speed of Wandering Albatrosses (Pennycuick 1982). The discarded data were also of low quality as determined by Argos classification and they represented <10% of locations for all birds combined. After filtering the data, there was a total of 1745 geographical locations in the following proportions: class 3 (1·5%), class 2 (2·6%), class 1 (10·0%), class 0 (42·2%), class A (22·8%) and class B (20·9%). Consequently, we were able to quantify (1) foraging locations, (2) total distance and daily flight distance, (3) maximum range or distance from the colony and (4) maximum and mean rates of travel (i.e. ground speed between Argos positions) for tagged albatrosses.

Foraging activity of injected birds was quantified using 25-g Wet-Dry activity data loggers (Francis Scientific Instruments, Cambridge, UK). Each logger was fixed to the bird's tarsus by taping the logger to a plastic identification band. Loggers were programmed to sample for 1 s every 7·5 or 15 s to detect whether the unit was wet or dry, and these sampling periods were linked to the local hour. Therefore, a change in the wet or dry condition indicated when a bird was in flight (dry) or on the sea surface (wet). The number and frequency of landings (or take-offs) were determined by counting the number of changes in the wet or dry condition, and percentage time in flight per day was determined

Table 1. Comparisons of foraging behaviour and energy expenditure in adult male and female Wandering Albatrosses during the incubation and brooding stages. General linear models (GLM) were used to test for interactions between stage and sex (full model). Probabilities presented for stage and sex separately are those of the reduced model. All data are presented as means ± SD with sample sizes given in parentheses

| Parameter | Sex | Reproductive stages | | Statistical probabilities | | Stage × Sex |
		Incubation	Brooding	Stage	Sex	
Time at sea (day)	Both	8·51 ± 3·67 (19)	2·70 ± 0·62 (17)	<0·001	0·518	0·869
Total distance (km)	Both	3834 ± 2134 (17)	1049 ± 467 (14)	<0·001	0·061	0·498
Daily distance (km day^{-1})	Male	409 ± 100 (9)	324 ± 124 (8)	0·140	0·001	0·595
	Female	537 ± 129 (8)	498 ± 117 (6)			
Mean rate of travel (km h^{-1})	Male	22·4 ± 3·1 (9)	17·1 ± 4·9 (8)	0·035	0·005	0·340
	Female	26·1 ± 5·7 (8)	24·2 ± 5·0 (6)			
Maximum rate of travel (km h^{-1})	Both	78·5 ± 7·2 (17)	60·5 ± 15·0 (14)	<0·001	0·194	0·041
Total mass change (% body mass)	Both	8·0 ± 7·0 (18)	4·4 ± 5·5 (17)	0·078	0·307	0·824
Field metabolic rate (W kg^{-1})	Both	4·52 ± 0·50 (11)	4·98 ± 0·55 (14)	0·046	0·271	0·808

by summing the total amount of time the logger registered a dry condition in a 24-h day. Ten injected birds went to sea with a 30-g SECUP logger (DK-log 120, Pillbox Logger, Driesen + Kern GmbH, Bad Bramstedt, Germany) instead of a Wet-Dry activity data logger. The SECUPs operated by recording changes in temperature associated with air or water at 32-s intervals. Details of loggers and analysis procedures are described in Wilson, Weimerskirch & Lys (1995). Thus, for each trip to sea, the activity loggers allowed us to quantify (1) percentage time in flight and on water, (2) frequency and total number of landings (or take-offs) and (3) diurnal foraging activity of each albatross. Collectively, the activity loggers and satellite PTTs weighed less than 1% of a bird's body mass.

Statistical analyses were performed using SYSTAT 10 (SPSS Inc., Chicago, IL) with a significance level of $P \leq 0.05$ for t-tests, least-squares regressions, ANOVA and ANCOVA. Two-way factorial ANOVAS were used to test for interactions between sex and reproductive stages using the general linear model (GLM). When reporting GLM results, the full model included the interaction term (sex × stage) and the reduced model excluded the interaction term. Statistical analyses of proportional data (e.g. % mass change, % total body water, % time in flight) were performed after the data were arcsine-transformed. All data are presented as means ± 1 standard deviation (SD).

Results

The energy expenditures and foraging activities of the three study animals with no known breeding experience were first compared with the rest of the known-aged study population. In all comparisons, there were no statistical differences between groups ($0.20 \leq P \leq 0.90$) and none of the three study animals fell outside the range of data for the other birds. Therefore, factorial analyses were performed on all birds.

BODY SIZE AND MASS CHANGE

On average, male Wandering Albatrosses were 23% heavier than females (10.92 ± 0.80 kg vs 8.87 ± 0.77 kg, respectively; $t = -8.05$, df = 36, $P < 0.001$). However, there were no intrasexual body mass differences between birds in either reproductive stage. The mean total mass change per foraging trip (% of body mass) was not significantly different between reproductive stages or between sexes (Table 1). However, total mass change (in kg) significantly increased with time at sea during brooding but not during incubation (Fig. 1a, brooding stage; $F_{1,15} = 16.0$, $P = 0.001$, $R^2 = 0.517$). Average daily mass change was not significantly different between reproductive stages or between sexes (combined; 0.12 ± 0.14 kg day^{-1}), but daily mass change was significantly more variable during brooding than during incubation (F-test for equality of variances, $F_{16,17} = 4.05$, $P = 0.003$). In addition, mean daily mass change was significantly greater than zero during both reproductive stages (paired t-test; incubation $t = 5.11$, df = 17, $P < 0.001$ and brooding $t = 2.76$, df = 16, $P = 0.014$). Lastly, the rate of daily mass change (g day^{-1}) significantly increased with time at sea during brooding (Fig. 1b; $F_{1,15} = 12.3$, $P = 0.003$, $R^2 = 0.450$) whereas the rate of daily mass change significantly decreased with time at sea during incubation ($F_{1,15} = 10.1$, $P = 0.006$, $R^2 = 0.401$).

ENERGY EXPENDITURE AND WATER INFLUX

Absolute field metabolic rate (FMR) was 16% higher in males than in females (53.3 ± 7.1 W vs 46.0 ± 7.5 W, respectively; $t = -2.47$, df = 23, $P = 0.022$), and there was no significant interaction with reproductive periods. In contrast, mass-specific FMR of albatrosses was ~10% higher during brooding compared with incubation (Fig. 2). However, there was no significant difference between the sexes (Table 1). Water influx rate was 54% greater ($t = -4.45$, df = 26, $P < 0.001$) after foraging trips during incubation (1232 ± 281 ml day^{-1}) than
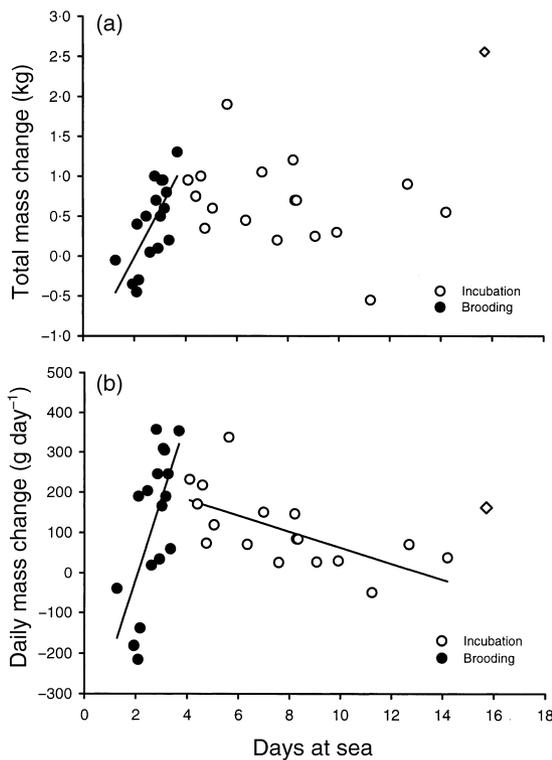
Fig. 1. Changes in adult body mass for individual Wandering Albatrosses following a single trip to sea. (a) The total change in mass as an absolute difference. (b) The same data represented as the rate of mass change per day. In both plots, the diamond represents a bird that was considered a statistical outlier (based on residuals analysis) and was therefore excluded from the analyses. In (a) total mass change significantly increased ($F_{1,15} = 16 \cdot 0$, $P = 0 \cdot 001$, $R^2 = 0 \cdot 517$) with time at sea during the brooding stage only. In (b) daily mass change significantly increased ($F_{1,15} = 12 \cdot 3$, $P = 0 \cdot 003$, $R^2 = 0 \cdot 450$) with time at sea during the brooding stage whereas daily mass change significantly decreased ($F_{1,15} = 10 \cdot 1$, $P = 0 \cdot 006$, $R^2 = 0 \cdot 401$) during the incubation stage.

during brooding (801 ± 229 ml day^{-1}), but there was no significant difference between the sexes. For all birds combined, mean TBW was $47 \cdot 6 \pm 3 \cdot 5\%$ ($N = 28$) of body mass and the percentage of TBW turnover per day was on average $21 \cdot 6\%$ day^{-1} in males and $30 \cdot 4\%$ day^{-1} in females.

FORAGING BEHAVIOUR

On average, adults were at sea $3 \cdot 2$ times longer (Fig. 2) and they travelled total distances that were $3 \cdot 7$ times further during incubation than during brooding (Table 1). The total distance adults travelled while at sea was also significantly positively correlated with time at sea (Fig. 3; $F_{1,29} = 102$, $P < 0 \cdot 001$, $R^2 = 0 \cdot 779$). As a result, maximum foraging ranges from the breeding colony during incubation (843 ± 333 km) were generally over twice as far as those of the brooding stage (329 ± 174 km). Adults primarily concentrated foraging efforts in pelagic waters during incubation, whereas during brooding, birds foraged mainly along the shelf surrounding Crozet. Distances flown per day

were similar between reproductive stages. However, females travelled significantly greater distances per day than males during both reproductive stages (Table 1). Moreover, the mean rate of travel was significantly higher for females than for males, and was significantly higher for both sexes during the incubation stage than during the brooding stage (Table 1). The maximum rate of travel was higher during incubation, but there was a significant interaction between reproductive stage and sex (Table 1). A pairwise multiple comparison with a Bonferroni correction revealed that only maximum travel rates of males during brooding were significantly lower ($P = 0 \cdot 002$) than either sex during incubation. Lastly, mean percentage time in flight ($50 \cdot 9 \pm 13 \cdot 9\%$) and mean landings per day ($15 \cdot 0 \pm 9 \cdot 9$) were not significantly different between reproductive stages or sexes.

Discussion

Our ability to measure mass changes, energy expenditure and foraging activity simultaneously on male and female Wandering Albatrosses allowed us to study how adults vary the intensity of their foraging effort (i.e. energy expenditure per unit time) in relation to the constraints of reproduction. Foraging costs were higher during brooding than during incubation, yet foraging trips were shorter in both duration and distance covered. Concomitantly, the rate of adult body mass gain increased with time at sea during brooding but decreased with time at sea during incubation. These results demonstrate that adults increase their foraging effort during the period when parents are caring for chicks compared with the period when adults are incubating eggs.

CHANGES IN FORAGING EFFORT DURING INCUBATION AND BROODING

The need to provision chicks frequently during brooding appears to limit the duration of time at sea, and this may ultimately constrain adults to forage in areas that are relatively close to the breeding colony (Fig. 3). This major change in foraging behaviour also had a significant effect on patterns of mass gain and foraging effort in adults. For example, birds gained more total mass after long trips to sea during incubation than during short trips to sea during brooding, but the average daily mass gain was similar between both reproductive stages. When considering the rate of mass gained as a function of time at sea (Fig. 1b), adults responded very differently between reproductive stages. During the incubation stage, the rate of daily mass gained decreased with time at sea and foraging costs were lower. Thus, foraging effort of adults was lower during the incubation stage despite the fact that birds remained at sea for longer periods and travelled greater distances to forage. In contrast, adults were able to increase the rate of daily mass gain with time at
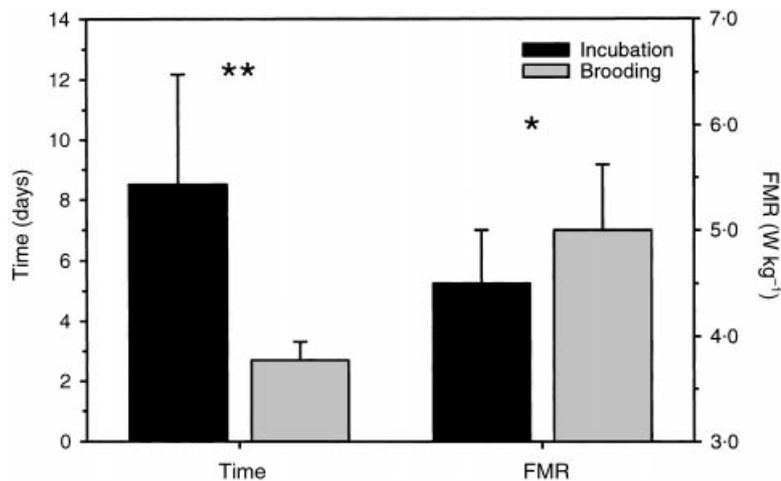
Fig. 2. Comparisons of time at sea and field metabolic rate (FMR) of Wandering Albatrosses breeding in 1998. Means (±1 SD) for each stage are presented for both sexes combined because no significant differences were observed in mass-specific FMR or time at sea (Table 1). Statistical differences are denoted as follows $*P < 0.05$, $**P < 0.001$.
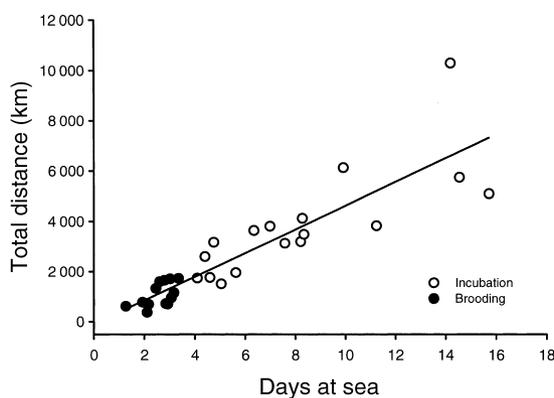

Fig. 3. Total distance flown by Wandering Albatrosses plotted as a function of time at sea in days during the incubation and brooding stages ($F_{1,29} = 102$, $P < 0.001$, $R^2 = 0.779$). ANCOVA was used to test for the effect of an interaction on the regression (stage × time at sea; $F_{1,27} = 0.004$, $P = 0.951$) before data from both periods were combined.

sea during the brooding stage even though foraging trips were shorter and foraging costs were higher, indicating that foraging effort of adults was greater (Fig. 2).

Given that Wandering Albatrosses altered their foraging effort between reproductive stages, it seems highly probable that adults were attempting to maximize different currencies (i.e. reduction in foraging cost per unit time *vs* rate of energy delivery to the chick) during each reproductive stage as described by the model of Ydenberg *et al.* (1994). This model (Fig. 4) predicts that when the rate of food intake is low (energy limited), adults should maximize efficiency (energy gained per energy expended). Conversely, the model predicts that adults should maximize the rate of energy delivery to offspring when time is a constraint (time limited). During the incubation stage, Wandering Albatrosses primarily forage in pelagic

waters far from the breeding colony (Weimerskirch *et al.* 1993; this study). Food is likely to be patchily distributed and ephemeral in nature (Ashmole 1971), so we would expect adults to maximize foraging efficiency (Fig. 4). Furthermore, time away from the nest will be less constraining on adults because the duration of foraging trips is determined primarily by the rate at which adults recover body reserves lost during the previous incubation shift (Weimerskirch 1995). Indeed, our observations are consistent with this prediction because foraging costs were lower during the incubation stage compared with the brooding stage, yet adults gained similar or greater body mass while foraging during the incubation stage. In contrast, the energy requirements of growing chicks will impose time constraints on adults during the brooding stage. Hence, adults decrease time at sea and concentrate their efforts in areas of known productivity such as the Crozet Shelf and surrounding waters (Weimerskirch *et al.* 2002; this study). This change in foraging effort enables adults to maximize the rate of energy delivery to chicks by minimizing time at sea. Again, our results support the prediction of Ydenberg's model (Ydenberg *et al.* 1994) because the foraging costs of adults during brooding were higher than those measured during incubation even though time at sea decreased during brooding. Consequently, foraging effort of adults was higher during the brooding stage than during the incubation stage (Fig. 4).

Although energy expenditure was higher for adults during the brooding stage, it is not clear why this should be the case because birds conducted shorter foraging trips with lower total distance travelled per trip. Nonetheless, it is possible to make several predictions based on the foraging patterns of birds during both periods. Previous studies have shown that the number of landings and take-offs is one of the most important factors affecting foraging costs in Wandering Albatrosses (Weimerskirch *et al.* 2000; Shaffer, Costa & Weimerskirch 2001a). In the present study, both the number of landings per day and percentage of time in flight were similar between reproductive stages, suggesting that albatrosses maintained similar foraging intensities during each stage. However, the rate of travel of birds (mean and maximum) were different between stages (Table 1). The reduction in travel speeds during brooding could have resulted from changes in search behaviour and how birds use wind to travel. Overall, this may influence how albatrosses are able to soar at a low cost. When searching over shelf breaks and submarine plateaux, Wandering Albatrosses are known to exhibit a higher proportion of area-concentrated search behaviour, which includes an increase in the sinuosity of movements over the water (i.e. side to side sweeps), resulting in a lower rate of travel (Weimerskirch, Wilson, & Lys 1997; Weimerskirch *et al.* 2002). These search patterns are more characteristic of foraging trips made during the brooding stage when birds search for food along the
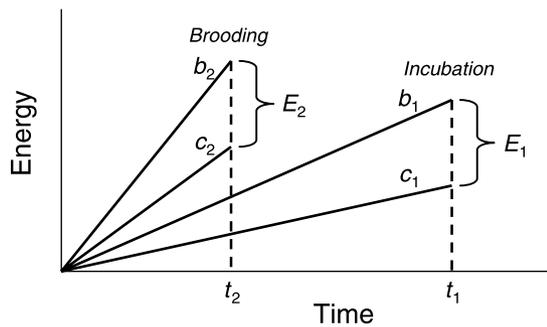
Fig. 4. A model of foraging effort that illustrates the relationship between time (t), energy gain (b) and cost (c) (redrawn from Figure 2 of Ydenberg *et al*. 1994). The net energy gain (E) is equivalent in both cases. However, $c_2 > c_1$ and $t_2 < t_1$, which is similar to the results of the present study. During the incubation stage, foraging adults maximize efficiency by reducing effort (cost per unit time) whereas during brooding, foraging time is minimized by increasing effort.

Crozet Shelf and adjacent waters. Furthermore, the frequent changes in direction and the reduction in flight speeds may require birds to use more flapping flight, which is known to be energetically costly for Wandering Albatrosses (Weimerskirch *et al*. 2000; Shaffer *et al*. 2001a). In contrast, albatrosses foraging in pelagic waters during incubation make large looping patterns in which the birds are able to exploit wind to soar at a low cost (Weimerskirch *et al*. 2000). Thus, when foraging close to the islands, albatrosses may not be able to use wind as effectively for travel as they are able to during pelagic foraging, which could increase foraging costs.

Changes in foraging behaviour throughout reproduction are well documented in a variety of other pelagic seabird species (Blue Petrel, *Halobaena caerula*, Chaurand & Weimerskirch 1994; Short-Tailed Shearwater, *Puffinus tenuirostris*, Weimerskirch & Cherel 1998; Black-Browed Albatross, *Thalassarche melanophrys*, Bevan *et al*. 1995; Sooty Shearwater, *Puffinus griseus*, Weimerskirch 1998; Cory's Shearwater, *Calonectris diomedea*, Granadeiro *et al*. 1998). Most of these species conduct both long and short foraging bouts in an alternating fashion, which is thought to be a consequence of changes in energy requirements of adults and chicks. However, only Bevan *et al*. (1995) measured the cost of foraging in adults during a complete breeding cycle and they determined that energy expenditure did not significantly differ between any of the reproductive stages (i.e. incubation, brooding or chick rearing). It should be noted, however, that their results were pooled over multiple years, so interannual differences could have masked any change in the foraging costs of adults between reproductive stages. Regardless, more studies performed within a single year but over multiple phases of the breeding cycle could provide significant insight into the mechanisms that constrain foraging effort of adult seabirds when breeding.

SEX-SPECIFIC COMPARISONS OF FORAGING EFFORT

Previous studies have suggested that foraging effort is greater in female Wandering Albatrosses than in males because females generally travel further from the colony to search for food, yet time at sea is similar for both sexes (Salamolard & Weimerskirch 1993; Weimerskirch 1995; Arnould *et al*. 1996). With respect to distance and rate of travel, our results support the concept of greater effort by females even though both sexes spent similar periods at sea. However, these differences in behaviour did not result in greater energy expenditure by females (i.e. W kg^{-1}). Two previous studies (Weimerskirch *et al*. 2000; Shaffer *et al*. 2001a) showed that landings and take-offs had a greater influence on foraging cost than distance travelled or flight speed in Wandering Albatrosses. Thus, it is conceivable that the sex-specific differences in foraging behaviour observed in this and the previous studies are related to differences in morphology (Shaffer *et al*. 2001c) rather than to differences in foraging effort *per se*. Although absolute FMR was different between the sexes, we attribute this to body size differences and not foraging effort because FMR in watts scaled isometrically with body mass (see Methods).

EFFECT OF EXPERIMENTAL MANIPULATION

Of the 38 birds that were injected and equipped with satellite transmitters and activity data loggers, only one bird (a female) did not return to the colony. The at-sea movement patterns of this bird were tracked for 20 days before the satellite transmitter ceased operation, but these data were not included in any of the analyses.

During the incubation period, foraging trip durations of birds from 52 nests were monitored daily by following the changeover patterns between partners at each nest. Overall, time away from the nest of unmanipulated birds was not different from that of albatrosses that were injected with isotopes and equipped with transmitters and loggers. Furthermore, mean trip durations and mass gains of the study birds in each period (Table 1) were well within the range of measurements collected on Wandering Albatrosses in previous studies (Weimerskirch *et al*. 1993; Weimerskirch 1995; Weimerskirch & Lys 2000). Lastly, albatrosses from 14 of 20 nests hatched a chick, and overall reproductive success (i.e. percentage of chicks fledged per chicks hatched) of albatrosses in the present study was nearly 90%, which was substantially higher than that determined for the entire breeding population in 1998 (76·6%; Shaffer *et al*. 2001a). Therefore, we believe that the effect of our manipulations was minor and that the behaviour of albatrosses in this study was representative of the normal population breeding of Wandering Albatrosses on Possession Island.

Conclusions

The results of the present study demonstrate that foraging effort in Wandering Albatrosses is variable and that birds appear to modify their effort to accommodate the constraints of time and energy during reproduction (e.g. incubating an egg to rearing a chick). These changes in effort suggest that adults were maximizing efficiency by decreasing foraging effort during the incubation stage when time at sea was less of a constraint, whereas adults increased foraging effort during the chick-brooding stage when time was a constraint. In addition, the foraging effort of males and females was similar despite gender-related differences in daily distance flown and mean rate of travel. It is conceivable that these differences in foraging behaviour could be related to the sexual dimorphism and flight performance of Wandering Albatrosses rather than to differences in energy expenditure and effort.

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