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# ENERGETICS OF FORAGING IN BREEDING ADÉLIE PENGUINS[1]

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*Abstract.* We studied foraging energetics in Adélie Penguins (*Pygoscelis adeliae*) using doubly labeled water (DLW) and time–depth recorders (TDR). Measurements were made during three nesting stages: late incubation, the guard stage (when small chicks were continuously guarded by at least one parent), and the subsequent creche stage (when large chicks were left unattended). Nest relief cycle times decreased from 229 h during incubation to 33.3 h during the creche stage, and the fraction of time birds spent swimming increased from 20.8% during incubation to 31.6% during the creche stage. The fraction of swim time spent in hunting dives and bottom time did not change significantly at different nesting stages. Field metabolic rates (FMR) were 2.73 × basal metabolic rate (BMR) during incubation, 3.03 × BMR during the guard stage, and 3.29 × BMR during the creche stage; due to high variance these values did not differ significantly. Estimated metabolic rate during swimming was 8.2 × BMR. Rates of prey capture (grams of krill per hour of swimming, per hour of hunting dives, and per hour of bottom time) did not change at different stages. Food provided to chicks was 20.9% (guard stage) to 23.3% (creche stage) of the food metabolized by adults. Our data suggest that (1) prey capture by Adélies is limited primarily by their ability to find krill swarms and not by limitations in harvest rates or energy efficiency after prey have been located, and (2) reproductive effort in Adélies does not require a large increase in either energy expenditures or foraging time.

*Key words: Antarctica; chick provisioning; energy cost of reproduction; field metabolic rates; foraging efficiency;* Pygoscelis adeliae; *seabird; spheniscid; swimming energetics; time budgets.*

## INTRODUCTION

The energetics of foraging in animals providing parental care are of considerable interest (Clutton-Brock 1991). In such species a parent's ability to forage effectively is a key factor in its ability to rear offspring—the fundamental basis of reproductive success. Foraging energetics are important from an ecological perspective as well, since food requirements are central to trophic relationships. Penguins are excellent subjects for investigations of monogamous, long-lived species with extensive parental care because of their coloniality, flightlessness, and tameness. For these reasons, and because penguins are important components of many marine ecosystems, there have been several studies of penguin energetics during the reproductive season. Most of these were based on isotopic turnover techniques (Kooyman et al. 1982, Nagy et al. 1984, Costa et al. 1986, Green et al. 1988, Davis et al. 1989, Nagy and Obst 1992).

By themselves, isotopic studies allow calculation of food intake but provide little additional data on penguin foraging biology, since hunting occurs at sea where it is impossible to observe by conventional methods. The recent development of microprocessor-based recorders, which allow dive-by-dive examination of foraging trips, has yielded remarkable insights into at-sea behavior and the physiology of diving (Kooyman and Croll 1987, Croxall et al. 1988, Kooyman 1989). Simultaneous energetic and behavioral measurements provide detailed insights into time and energy budgets during foraging trips, food intake and prey capture rates per dive or per unit time during hunting, and foraging efficiency. To date only two species have been studied with a combination of the two techniques: Gentoo Penguins (*Pygoscelis papua*; Williams et al. 1992) and King Penguins (*Aptenodytes patagonicus*; Kooyman et al. 1992).

Here we describe the energetics of foraging of Adélie Penguins (*Pygoscelis adeliae*). This species is one of the most abundant penguins, with a population of 2–3 × $10^6$ breeding pairs distributed around the Antarctic continent and neighboring islands (Croxall and Lishman 1987). We have previously reported results from time–depth recorder (TDR) studies of Adélie diving behavior and physiology (Chappell et al. 1993*b*). In the present study we combined TDR data with doubly

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labeled water measurements of energy expenditures. We obtained data at different stages of chick growth to look for changes in energy budgets and foraging behavior as chick food requirements increased. Comparisons to the incubation period (when adults were foraging only for themselves) allowed us to estimate the time and energy costs of obtaining food for chicks.

## Methods

### *Study area*

We worked on Torgersen Island, near Palmer Station (64°46′ S, 64°05′ W) on Anvers Island off the west coast of the Antarctic Peninsula. About 8000 pairs of Adélies nest on Torgersen in ≈20 discrete colonies. There were 2700–2800 nests in the seven colonies from which we selected study birds. We studied foraging during the 1990–1991 and 1991–1992 breeding seasons in the months of December, January, and February.

### *Study animals*

We marked adults with numbered aluminum flipper bands; sex was determined from within-pair size differences (males average 5–10% heavier than females) and by observing mating and incubation behavior (Ainley et al. 1983). By checking nests daily (weather and sea ice conditions permitting), we compiled records of nest attendance (daily presence or absence) and the status of eggs or chicks from the time of pair formation through the end of parental care. We studied energetics during incubation (1–17 d prior to hatching), the "guard" stage, when at least one parent continually attends small chicks (hatching to age 18–28 d), and the subsequent "creche" stage, when large chicks are left unattended. The creche stage lasts until chicks are abandoned at 37–45 d.

### *Doubly labeled water studies*

We measured energy metabolism, total body water content (TBW), and water flux using the doubly labeled water technique (DLW; Lifson and McClintock 1966). We selected individuals for DLW studies after inspecting nest attendance records and determining that prospective test birds were behaving normally. Birds attending chicks were not captured unless they had finished delivering food to offspring and we were satisfied that they had little or no food in the stomach. Penguins were hand-captured at their nests, weighed to ±25 g (range in body mass: 3.4–4.6 kg) on an Ohaus electronic platform balance, and injected with DLW in the pectoralis muscle. During incubation, when birds spent 2–5 d at sea, isotope loadings were ≈0.27 g $^{18}O$ and 0.15 g deuterium (D; $^{2}H$) per kilogram of body mass. During the guard and creche stages, when at-sea periods were 1–2 d, we decreased loadings to 0.20 g $^{18}O$ and 0.11 g D/kg. After injections, penguins were released at their nests. Following a 2–3 h equilibration period the birds were temporarily recaptured while an initial blood sample (4–5 mL) was collected from an interdigital vein into a heparinized Vacutainer tube. Labeled birds departed to sea within 42–104 h of the initial sample during incubation, and within 1–40 h during the guard and creche stages. Returning foragers were weighed and final 4–5 mL blood samples were collected. By watching nests continually we were able to weigh and sample 20 returning foragers before they fed chicks.

Disturbance due to handling was minimal; in 95 of 98 releases the birds immediately resumed incubation, chick feeding, or guard behavior, and the other three individuals did so within 1 h. We warmed eggs and small chicks while parents were being handled, and no chicks or eggs were lost as a result of our manipulations.

Isotope concentrations in blood samples were determined with mass spectroscopy (K. A. Nagy, University of California, Los Angeles, California, USA; Metabolic Solutions Inc., Acton, Massachusetts, USA). We initially obtained background $^{18}O$ and D levels from 16 penguins. Variance in backgrounds was small (coefficients of variation were 0.13% for $^{18}O$ and 1.5% for D), particularly when compared to enrichment levels for initial and final samples. Therefore we used mean background values (2000.4 mg/kg for $^{18}O$ and 151.2 mg/kg for D) for all subsequent calculations. Carbon dioxide production, TBW, and water flux were computed according to Nagy (1983). We converted $CO_2$ production into heat production using values of 27.7 kJ/L of $CO_2$ for fasting birds and 25.8 kJ/L of $CO_2$ for foraging birds eating a mixed diet of fat and protein (Nagy 1983, Nagy and Obst 1992). Field metabolic rates (FMR) were expressed as kilojoules per day or as multiples of basal metabolic rate (BMR; 313 $kJ \cdot kg^{-1} \cdot d^{-1}$; Chappell and Souza 1988). The latter estimate helped to account for mass differences among individuals.

### *Dive recorders*

All penguins labeled with DLW, along with 17 additional birds, carried time–depth recorders (Mark 4.5, Wildlife Computers, Woodinville, Washington, USA). These 45 g units stored 1.5–7.5 d of diving data (at sample intervals of 1 and 5 s, respectively) with a depth resolution of ±1 m and clock accuracy of ±5 s/d. They also had an immersion sensor that indicated when birds were in the water.

Details of TDR analysis protocols and Adélie diving behavior are presented in Chappell et al. (1993*b*). To briefly summarize: We attached TDRs to a patch of rapid-hardening epoxy glue on the center of the lower back and secured them with plastic cable ties threaded through the feathers between the skin and the glue patch. When penguins were recaptured we removed the TDRs and downloaded dive records to IBM-compatible computers. Hunting dives consisted of a rapid descent to depth, a period termed "bottom time" spent at relatively constant depth or with slow, irregular depth

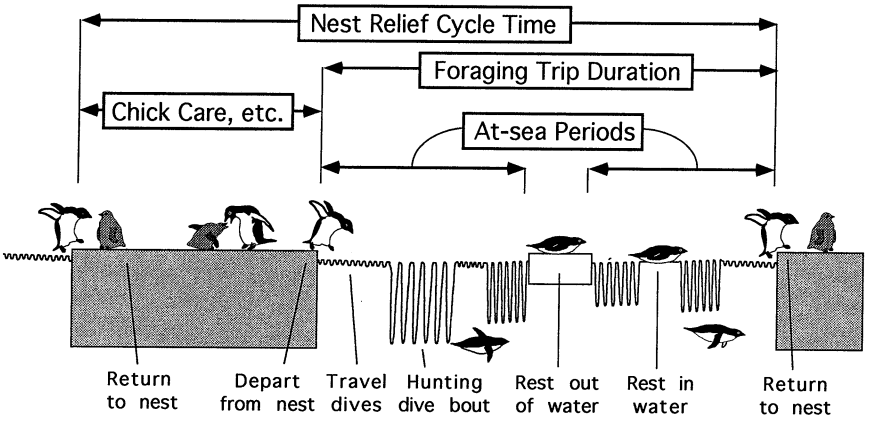


FIG. 1. Schematic diagram of the behavior of adult Adélie Penguins during the breeding season.

changes, and a rapid ascent to the surface. We assumed that prey capture occurred only during bottom time. The depth, duration, and bottom time for each dive were calculated with software from Wildlife Computers and "stripchart" plots of dive records produced with custom software.

### *Statistics*

Data were analyzed with least-squares regression and multivariate analysis of variance and ANCOVA; the significance level was $P < .05$. Post hoc comparisons among ANOVA groups were made with Scheffé tests. Results are shown as mean ± 1 SD.

## RESULTS

### *Time budgets*

The activity of breeding Adélies is cyclical, with one nest relief cycle being defined as the time between returning to the colony from a foraging trip to incubate eggs or care for chicks, and returning from the next foraging trip (Fig. 1). Nest relief cycle times during incubation (Table 1) were determined from nest attendance records because time–depth recorders (TDRs) were deployed in the middle of the birds' incubation bouts (which lasted several days). Thus the TDR records were substantially shorter than nest relief cycles and contained disproportionate amounts of swim time. During the guard and creche stages, measurement intervals included one or more complete cycles, and cycle times were determined from TDR records. In all cases, TDR records were analyzed to determine the amount of time spent swimming, performing hunting dives, and feeding (= bottom time). These times were divided by cycle time to estimate the fraction of total time spent in various activities. We obtained usable time budgets from 24 foraging penguins in each of the two breeding seasons (Table 1).

TABLE 1. Time budgets of foraging Adélie penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons. Time budgets were obtained from time–depth recorder (TDR) records and nest observations.* Values are shown as mean ± 1 SD.

| | Nesting cycle stage† | | |
|---|---|---|---|
| | Incubation | Guard stage | Creche stage |
| *N* | 8 | 24 | 16 |
| Nest relief cycle time (h) | 229 ± 69 | 40.2 ± 8.6 | 33.3 ± 9.9 |
| % of time swimming | 20.8 ± 8.7 | 28.3 ± 10.0 | 31.6 ± 12.1 |
| Swim time per foraging trip (h) | 44.5 ± 13.8 | 11.4 ± 5.1 | 10.5 ± 3.5 |
| Hunting dive time as % of swim time | 35.2 ± 10.9 | 30.6 ± 13.6 | 31.6 ± 14.6 |
| Hunting dive time per foraging trip (h) | 14.9 ± 4.0 | 3.49 ± 2.00 | 3.92 ± 1.38 |
| Hunting dive time per day (min) | 98.4 ± 32.8 | 131 ± 84 | 164 ± 137 |
| Bottom time as % of swim time | 15.4 ± 4.4 | 15.1 ± 4.5 | 16.1 ± 5.2 |
| Bottom time per foraging trip (h) | 6.69 ± 2.22 | 1.72 ± 0.90 | 1.66 ± 0.83 |
| Bottom time as % of cycle time | 3.08 ± 1.25 | 3.96 ± 1.98 | 5.10 ± 2.47 |
| Bottom time per day (min) | 44.4 ± 18.1 | 57.9 ± 29.3 | 73.4 ± 35.6 |

* Nest relief cycle time is the duration of a complete cycle of foraging and nest attendance (i.e., the time between departing on one foraging trip, returning to the nest, and departing on the next foraging trip; Fig. 1). Bottom time is the portion of a dive spent at relatively constant depth; we presume that it is the time when prey are pursued and captured.

† Incubation extends 1–17 d prior to hatching; guard stage is when at least one parent continually attends small chicks (hatching to 18–28 d); creche stage is when large chicks are left unattended (until chicks are abandoned, at 37–45 d).

A typical foraging trip contained 1–6 periods of sustained swimming ("at-sea periods"; Fig. 1) lasting 20 min to 26 h (mean 6.45 ± 4.7 h; $N = 127$). At-sea periods were separated by "rest periods" of 1–20 h when birds were out of the water. Foraging trips lasted longer, and the cumulative time spent swimming between departing from and returning to the nest was larger during incubation than during the guard and creche stages (swim time = 44.5 ± 13.8 h, $N = 8$; 11.4 ± 5.1 h, $N = 24$; 10.5 ± 3.5 h, $N = 16$; respectively; $F = 51.8$, df = 2, 46, $P < .0001$). However, the fraction of the daily time budget spent swimming did not differ significantly at different stages of the breeding cycle ($P = .43$), averaging 28.2 ± 10.2%, or ≈7 h/d.

Adélies spent relatively little time pursuing prey. The proportion of total swimming time spent in hunting dives averaged 31.7 ± 14.8% and did not differ significantly between incubation, guard, and creche stages ($P = .4$). Hunting dives require a surface recovery period lasting about 50% of dive duration (Chappell et al. 1993*b*), so about 48% of swim time was spent in hunting-related activity. Bottom time accounted for a relatively constant fraction (15.4 ± 4.7%) of swimming time; this fraction did not differ significantly between nesting stages ($P = .8$). The mean duration of bottom time was 4.2 ± 2.2% of the daily time budget, or about 60 min/d.

Surface travel (porpoising or shallow, short-duration dives with minimal surface intervals) occupied most of the 52% of swim time not spent hunting. However, most TDR records also contained short rest periods (10–40 min) during which the birds were in the water but apparently not swimming. Travel time between the colony and foraging sites varied from <10 min to 5 h, with means of 70 min (outbound) to 75 min (inbound; Chappell et al. 1993*b*). Assuming that the birds travel in straight lines, these times correspond to distances of about 9 km at 2 m/s (the preferred swim speed; Culik and Wilson 1991) or about 16 km if all travel is by porpoising at 3.7 m/s (Hui 1987). The maximum distance of continuous travel, assuming 100% porpoising, was 67 km. We have no data on direction or distance of travel within and between bouts of hunting dives.

### *Body composition*

The water content of adult Adélies was 61.9 ± 2.2% during incubation, 63.9 ± 3.1% during the guard stage, and 66.5 ± 1.5% during the creche stage. These values differ significantly ($P < .0001$). Assuming that depot fat (adipose tissue used primarily for energy storage) contains 10% water and lean tissue contains 70% water (Ortiz et al. 1978, Chappell et al. 1993*a*), lean tissue mass remained relatively constant but depot fat content declined from 10% of body mass during incubation to 4% during the creche phase. That is equivalent to a loss of ≈290 g of depot fat over 50 d, or ≈5.8 g/d (lipid loss: 5.2 g/d).

### *Field metabolic rates and swimming energetics*

We obtained 30 doubly labeled water (DLW) measurements from foraging penguins, plus 4 from TDR-carrying birds that did not go to sea. For the latter, field metabolic rate (FMR) was 2022 ± 439 kJ/d (1.74 ± 0.25 × basal metabolic rate [BMR]). The FMR of foragers ranged from 2412 to 6915 kJ/d (1.83 to 6.24 × BMR). Most of this variance was apparently due to differences in the amount of swimming time. There was a strong correlation (Fig. 2A) between FMR and the fraction of the measurement interval the birds spent swimming:

$$\text{FMR} = 1796 + 7310 \cdot (\text{fraction of time spent swimming}), \text{ where FMR is in kilojoules per day.}$$
$$r^2 = 0.79,\ F = 123,\ \text{df} = 1, 32,\ P < .0001. \quad (1)$$

Slightly more variance is explained if factorial FMR (= FMR/BMR) is substituted for absolute FMR (Fig. 2B):

$$\text{factorial FMR} = 1.30 + 6.89 \cdot (\text{fraction of time spent swimming})$$
$$r^2 = 0.81,\ F = 137,\ \text{df} = 1, 32,\ P < .0001. \quad (2)$$

The FMR of birds resting on land is predicted to be 1.3 × BMR, and the predicted metabolic rate during swimming is 8.2 × BMR.

Because fractional swim time is a good predictor of FMR, we supplemented DLW measurements with FMR for other individuals predicted with Eq. 2 from TDR records (3 birds during incubation, 13 during the guard stage, and 3 during the creche stage). Addition of FMR derived from TDR time budgets did not significantly change the mean FMR for any nesting stage (<1% difference between combined and DLW only estimates) . Since DLW and TDR sample intervals during incubation ($N = 5$) were less than the lengths of nest relief intervals, we corrected these measurements to reflect actual nest relief cycles using the value of 1.3 × BMR for the fraction of the cycle spent out of the water and not included in the measurement interval.

The combined data (Table 2) yield FMR/BMR ratios of 2.73 ± 0.60 during incubation, 3.04 ± 0.80 during the guard stage, and 3.29 ± 1.01 during the creche stage. There were no significant differences between males and females or between stages. The mean FMR was 3.09 × BMR, or ≈4010 kJ/d for a 4.15-kg male and 3675 kJ/d for a 3.80-kg female.

### *Food intake rates and foraging efficiency*

Estimates of food intake and foraging efficiency require data on food energy content and metabolizable

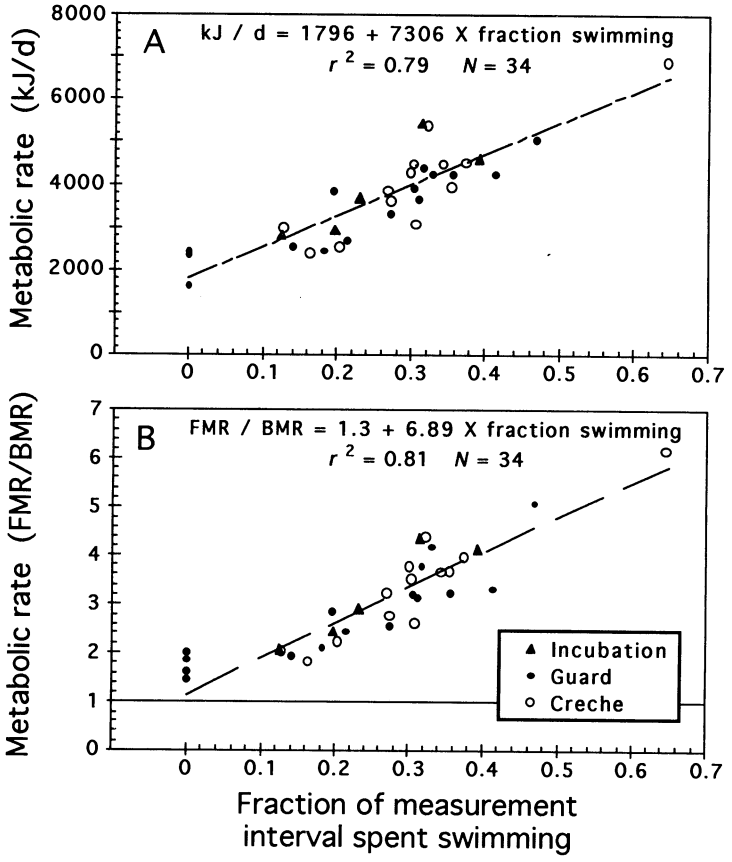


FIG. 2. Results from simultaneous doubly labeled water and time–depth recorder studies of the relationship between the fraction of time spent swimming and field metabolic rate (FMR) for adult Adélie Penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons. Metabolic data are expressed in units of kJ/d in (A) or as the factorial increase of FMR above basal metabolic rate (BMR) in (B).

energy efficiency, rates of energy expenditure, and overall energy balance. Near the Antarctic Peninsula, Antarctic krill (*Euphausia superba*) comprise 95–99% of Adélie diets (Volkman et al. 1980, Lishman 1985); all the diet samples we obtained at Palmer were >95% krill. We calculated food intake using the following assumptions: (1) penguins replaced all the energy they expended during a cycle, minus 204 kJ/d (equal to the energy content of the average lipid loss of 5.2 g/d); (2) the energy content of krill fresh mass was 4.99 kJ/g (Nagy and Obst 1992); and (3) metabolizable energy efficiency was 0.72 (Russell P. Herwig, *unpublished data*). Thus for every kilojoule of energy expended penguins had to eat 0.278 g of krill. We assumed that any mass change (in addition to the 5.2 g/d of fat loss) during a foraging trip was comprised of undigested food (if birds gained mass) or excreta (if birds lost mass).

Food intake as a function of hunting effort is shown

TABLE 2. Field metabolic rates (FMR) of Adélie penguins near Palmer Station, Antarctica, at different stages of the breeding season. All data are for birds that foraged during the measurement period. Data were obtained with doubly labeled water (DLW) and time–depth recorder (TDR)-derived time budgets during the 1990–1991 and 1991–1992 breeding seasons (see *Results: Time budgets* and *Field metabolic rates and swimming energetics*). Differences between DLW only and combined DLW–TDR estimates are <1%.

| Nesting stage* | Sex | *N* | Mass (kg) | FMR (kJ/d) | FMR/BMR |
|---|---|---|---|---|---|
| Incubation | Male | 4 | 4.08 ± 0.23 | 3077 ± 348 | 2.41 ± 0.35 |
| | Female | 4 | 3.84 ± 0.29 | 3630 ± 252 | 3.02 ± 0.65 |
| Guard | Male | 12 | 4.18 ± 0.21 | 3833 ± 601 | 2.93 ± 0.55 |
| | Female | 12 | 3.70 ± 0.32 | 3740 ± 943 | 3.23 ± 0.92 |
| Creche | Male | 7 | 4.19 ± 0.29 | 4184 ± 1070 | 3.19 ± 0.91 |
| | Female | 9 | 3.87 ± 0.21 | 4070 ± 1356 | 3.36 ± 1.14 |

* For definitions and durations of stages see Table 1: footnote †.

TABLE 3. Prey capture rates by Adélie penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons. Mass change data during the guard and creche stages were obtained only from returning birds captured before they fed chicks.

| | Nesting cycle stage* | | |
|---|---|---|---|
| | Incubation | Guard stage | Creche stage |
| Krill yield of swimming time (g/h) | 167 ± 35.2 | 163 ± 27.4 | 176 ± 32.8 |
| Krill yield of hunting dive time (g/h) | 513 ± 182 | 482 ± 189 | 534 ± 361 |
| Krill yield of bottom time (g/h) | 1168 ± 438 | 1030 ± 375 | 1138 ± 523 |
| Krill yield per hunting dive (g) | 11.3 ± 3.73 | 9.38 ± 3.74 | 10.4 ± 5.02 |
| Krill yield per foraging trip (kg) | 7.23 ± 2.07 | 2.02 ± 0.70 | 2.25 ± 0.66 |
| Mass change during foraging trip (g) | 128 ± 196 | 298 ± 259 | 397 ± 259 |
| *N* | 8 | 9 | 11 |

* For definitions and durations of stages see Table 1: footnote †.

in Table 3 for 8 penguins during incubation and 20 penguins caring for chicks (the latter adults were weighed prior to feeding chicks). Food intake was significantly correlated with the number of hunting dives, total time spent swimming, total time spent in hunting dives, and total bottom time (Fig. 3; $r^2 = 0.68$, 0.92, 0.67, and 0.74, respectively; $P < .0001$ in all cases). There were no significant differences between males and females or between stages for any of these parameters. Penguins captured 10.3 ± 4.2 g of prey during each hunting dive, and 18.5 ± 7.38 g of prey per minute of bottom time.

We calculated foraging efficiency as the ratio of metabolizable energy captured to energy expended swimming, assuming the metabolic rate during swimming was 8.2 × BMR, or 107 $kJ \cdot kg^{-1} \cdot h^{-1}$. There were no significant effects of sex or nesting stage on efficiency (Table 4). Mean foraging efficiency was 1.55 ± 0.30 averaged over total swim time, 4.63 ± 2.45 averaged over total hunting dive time, and 10.0 ± 3.91 averaged over total bottom time.

Mass gains during foraging trips (an index of the food available for delivery to chicks) averaged 298 g during the guard stage and 397 g during the creche stage; the two values did not differ significantly ($P = .33$). Mass changes were highly variable; two birds lost mass during foraging trips, while three others gained >600 g. If birds that did not gain mass are excluded from calculations, mass gains averaged 347 g during the guard stage and 426 g during the creche stage. There was no significant relationship between mass change and total hunt dive time or total bottom time ($P = .53$ and $P = .45$, respectively), or to the duration of the last at-sea period prior to recapture (Fig. 4A; $P = .51$). However, there was a weak correlation between total swim time and mass gain (Fig. 4B; $r^2 = 0.23$, $P = .035$). Foragers gained 128 g during incubation, but actual gains were

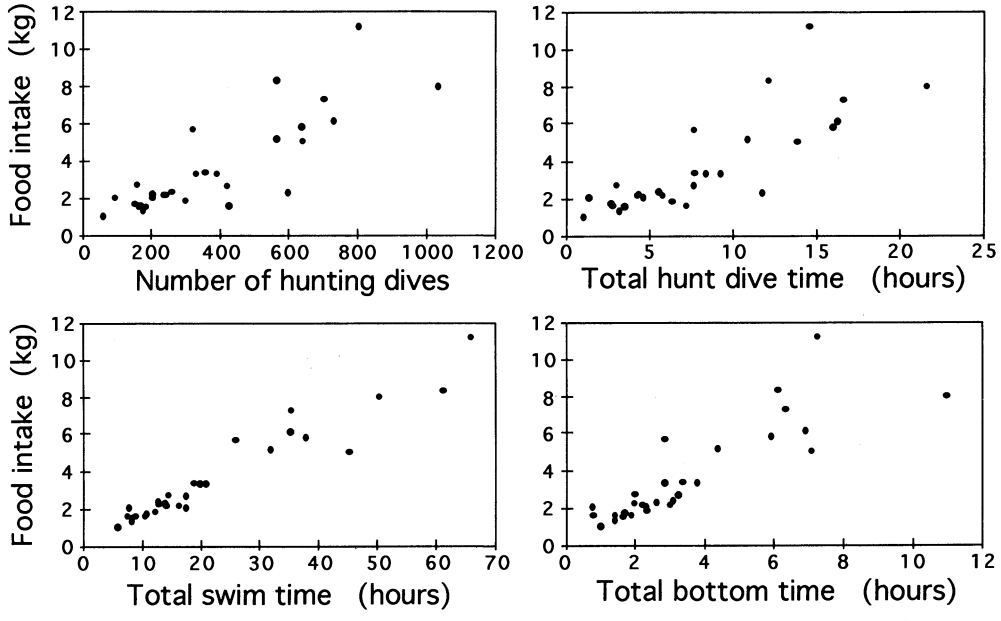


FIG. 3. Relationships between food intake during foraging trips and several aspects of foraging behavior for adult Adélie Penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons.

TABLE 4. Energy efficiency of foraging by Adélie penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons. Efficiency was calculated as the ratio of (metabolizable energy in captured prey) to (energy expended swimming) for several components of the time budget. Total hunt time is hunting dive time plus surface intervals, using the assumption that surface intervals = 50% of hunting dive duration (Chappell et al. 1993*b*).

| Budget component | Nesting cycle stage* | | |
|---|---|---|---|
| | Incubation | Guard stage | Creche stage |
| Swimming | 1.54 ± 0.27 | 1.45 ± 0.27 | 1.58 ± 0.28 |
| Hunting dives | 4.68 ± 1.31 | 4.29 ± 1.84 | 4.88 ± 3.47 |
| Total hunt time | 3.12 ± 0.87 | 2.86 ± 1.23 | 3.25 ± 2.31 |
| Bottom time | 10.6 ± 3.08 | 9.09 ± 2.94 | 10.3 ± 5.16 |
| *N* | 8 | 9 | 11 |

* For definitions and durations of stages see Table 1: footnote †.

probably somewhat higher because these birds were not recaptured until 1–12 h after returning to their nests. Excluding individuals whose body mass did not increase, mass gains averaged 1.8 ± 1.9%, 17.2 ± 7.3%, and 18.9 ± 11.7% of total food intake during the incubation, guard, and creche stages, respectively. The value for incubation was significantly less than for the guard and creche stages ($P = .016$), but the latter two did not differ from each other ($P = .56$). Mass gains represented 20.7% and 23.3% of food metabolized by parents during the guard and creche stages, respectively.

### *Water flux*

Within nesting stages, isotopic measurements of water influx and efflux did not differ significantly, and there was no difference between the guard and creche stages (means = 264 ± 86 $mL \cdot kg^{-1} \cdot d^{-1}$ influx and 293 ± 110 $mL \cdot kg^{-1} \cdot d^{-1}$ efflux). Water exchange was significantly lower during incubation (131 ± 57 $mL \cdot kg^{-1} \cdot d^{-1}$ influx and 129 $mL \cdot kg^{-1} \cdot d^{-1}$ efflux; $P = .041$ and .030, respectively). We also estimated influx of free water and metabolizable energy from food utilization, assuming the free water and energy contents of krill wet mass to be 0.77 g/g and 3.59 kJ/g, and assuming that 0.024 g of metabolic water was produced per kilojoule of energy metabolized (Nagy 1983, Nagy and Obst 1992). Water influx from food did not differ between stages (176 ± 34, 246 ± 116, and 248 ± 73 $mL \cdot kg^{-1} \cdot d^{-1}$ during incubation, guard, and creche stages, respectively), averaging 230 ± 88 $mL \cdot kg^{-1} \cdot d^{-1}$.

## DISCUSSION

### *Energy metabolism and costs of swimming*

Our measurements of Adélie field metabolic rates are not unusual for breeding birds. The mean field metabolic rate (FMR) for incubation, guard, and creche stages (3.09 × basal metabolic rate [BMR], or ≈3860 kJ/d for a 4-kg adult) is 40% higher than expected for a 4-kg seabird (2750 kJ/d; Nagy 1987), but is within the range of FMR of breeding birds in general (1.3–6.7 × BMR, mean 3.37; Peterson et al. 1990). Adélie FMR is also within the range of FMRs reported for other breeding penguins: slightly higher than the FMR of African Penguins (*Spheniscus demerus*; 2.6 × BMR; Nagy et al 1984) and Gentoo Penguins (*Pygoscelis papua*; 2.5–3 × BMR; Davis et al. 1989), but lower than the FMR of King Penguins (*Aptenodytes patagonicus*; 4.6 × BMR; Kooyman et al. 1992), Little Penguins (*Eudyptula minor*; 5.9 × BMR; Gales and Green 1990), and Macaroni Penguins (*Eudyptes chrysolophus*; 3.8–4.3 × BMR; Davis et al. 1989). A recent study of guard-stage Adélies at Torgersen Island (Nagy and Obst 1992) produced an FMR of 3900 kJ/d for a 3.81-kg adult, quite similar to our findings at the same location (Nagy and Obst's estimate of 3.8 × BMR is based on a lower value of BMR—269 $kJ \cdot kg^{-1} \cdot d^{-1}$—than our value of 313 $kJ \cdot kg^{-1} \cdot d^{-1}$).

The regression of metabolic rate measured by DLW (doubly labeled water) against fraction of measurement interval spent swimming (Fig. 2) extrapolates to a swimming cost of 8.2 × BMR. That is considerably higher than estimates for several other species of penguins, particularly for calculations of aerobic dive limits (Kooyman 1989). It is also higher than oxygen consumption rates of Adélies in a swim canal, which average 4 × BMR at the preferred underwater speed of 2 m/s (Culik and Wilson 1991). Several factors could account for the difference. (1) Culik and Wilson measured the cost of underwater swimming, but our data also include the costs of considerable porpoising (cycles of high-speed underwater swimming, usually at depths of 1–5 m, interspersed with leaps through the surface), which Adélies use for travel between breeding colonies and foraging sites (Trivelpiece et al. 1986, Hui 1987, M. A. Chappell, V. H. Shoemaker, D. N. Janes, S. K. Maloney, and T. L. Bucher, *personal observations*). Porpoising at high speed may have a higher energy cost per unit time than underwater swimming at lower speed (Hui 1988), although it provides a similar or possibly lower cost of transport. The mean duration of travel for Palmer Adélies, during which the birds were porpoising at least part of the time, was estimated from time–depth recorder (TDR) data as 2.4–3.6 h/d (30–45% of total swim time). (2) The DLW data include specific dynamic action (SDA), or the energy cost of utilizing foodstuffs, in addition to expenditures for exercise, thermoregulation, etc. The fraction of assimi-

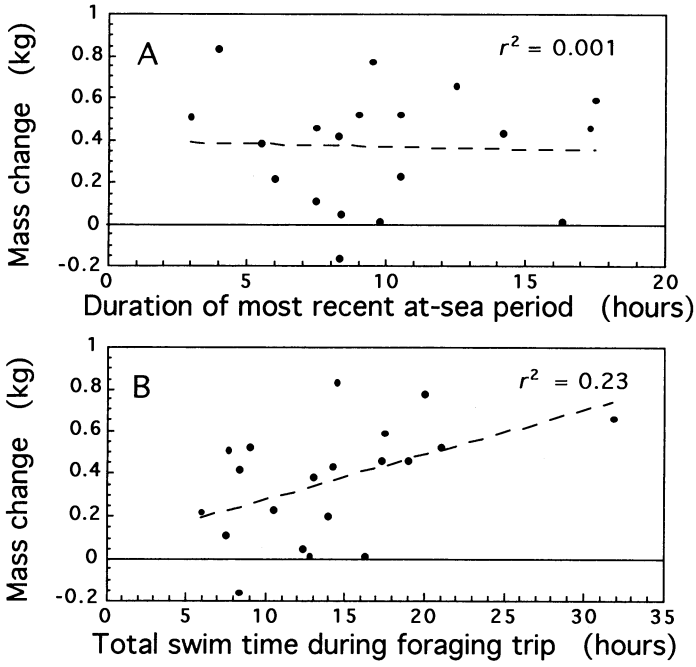


FIG. 4. Mass change during foraging trips (an index of the quantity of food available for delivery to chicks) as a function of (A) the duration of the most recent at-sea period, and (B) the total time spent swimming during the foraging trip, for adult Adélie Penguins near Palmer Station, Antarctica, during the 1990–1991 and 1991–1992 breeding seasons.

lated energy consumed in SDA is 30% for protein, 13% for fat, and 5% for carbohydrate (Harper 1979). Since the krill diet of Adélies contains roughly 80% protein and 20% lipid (dry mass fractions), ≈25% of assimilated energy is lost to SDA. This reduces our estimate of the metabolic cost of swimming to about 6 × BMR. (3) TDRs increased frontal cross-sectional areas of penguins by 1.5–2%, which presumably increased drag. Estimates of the cost of carrying instruments vary (Wilson et al. 1986, Culik and Wilson 1991, Croll et al. 1992), and it is likely that TDR attachment increased the cost of swimming to some extent. However, it is worth noting that our FMR data are quite similar to Nagy and Obst's (1992) FMR measurements on Adélies that did not carry attached instruments. (4) Anaerobiosis during hunting dives engenders an energy penalty to pay the cost of recycling lactate. This may increase the average metabolic rate above the actual cost of swimming (Chappell et al. 1993*b*).

Results from three other studies also suggest that at-sea metabolic rates in penguins average higher than 4 × BMR. Nagy et al. (1984) used a combination of DLW and time budgeting to calculate an at-sea metabolic rate of 8–9 × BMR in African Penguins. A similar approach was used by Davis et al. (1989) to produce estimates of 5.9–7.7 × BMR for at-sea metabolism in Gentoo and Macaroni Penguins. King Penguins have a swimming metabolic rate of 4.3–4.6 × BMR (estimated from both swim tunnel and DLW data; Kooyman et al. 1992).

Given the oxygen stores of Adélies (≈52 mL/kg), the metabolic rate during diving could be no larger than 2.9 × BMR if most (>90%) hunting dives are entirely aerobic (Chappell et al. 1993*b*). That value is considerably smaller than the metabolic rate of 4–6 × BMR indicated by our DLW data, so many or most hunting dives must have an anaerobic component. As for King and Emperor Penguins (Kooyman et al. 1992), Adélie diving behavior does not seem to be consistent with the concept that most voluntary diving in marine mammals and birds is aerobic (Kooyman 1989).

### *Water balance*

Body water content increased slightly but significantly during the breeding season, indicating a decline in fat content. That observation suggests that Adélies did not maintain condition during chick care despite being able to feed frequently. However, the rate of fat loss during chick care (5.2 g/d) was much less than that of fasting birds during the period of courtship and (for males) the initial incubation bout (40–50 g/d; Chappell et al. 1993*a*).

Estimates of water influx based on deuterium dilution were similar to estimates based on food consumption, suggesting that water intake from drinking was minimal. Similar results were obtained for Adélies by Nagy and Obst (1992) and for several other penguin species by Gales and Green (1990). The water economy index (WEI) is the ratio of water influx to energy use. The WEI for Palmer Adélies was 0.241 ± 0.055 mL/kJ, considerably higher than expected for carnivores (0.08–0.14; Nagy and Peterson 1988) and also higher than that of African

Penguins eating fish (0.15; Nagy et al. 1984). The difference is largely due to the high water content of krill. Assuming Adélies do not drink, the measured WEI is equal to the value of 0.24 mL/kJ predicted for a krill diet (1 g of krill contains 0.77-mL preformed water and yields 0.086 mL of water from the oxidation of 3.59 kJ of metabolizable energy; Nagy and Obst 1992).

*Cycle times and time spent foraging*

Adélie cycle times show considerable geographic variation. At King George Island, cycles lasted ≈48 h during the guard phase, with half that time spent at the nest; creche phase cycles averaged 24 h and only ≈2 h/d was spent in the vicinity of the nest (Trivelpiece et al. 1987). Lishman (1985) reported cycles at Signy Island of 42–55 h during the guard stage and 38–44 h in the creche stage. Compared to data from King George and Signy, cycles at Torgersen Island were somewhat shorter during the guard stage (40.2 h) and intermediate during the creche stage (33.3 h). Based on cycle times and the duration of feeding visits, Trivelpiece et al. (1987) assumed that Adélies at King George Island could spend >20 h/d swimming during the creche stage. However, our TDR data indicate that the proportion of time spent swimming was much less for Torgersen birds (≈7.6 h/d). During both guard and creche stages, Torgersen Adélies spent two thirds of their time out of the water, although they were usually away from the colony during the creche stage.

Assuming that surface intervals lasting 50% of dive duration are necessary after hunting dives (Chappell et al. 1993*b*), about half of total swim time is spent in hunting-related activities. This is similar to estimates of 51–52% of foraging trip duration spent hunting in Gentoo Penguins (Williams et al. 1992). Nevertheless, hunting dives and prey pursuit comprise a small fraction of an Adélie's daily time budget, even during the creche stage when chick food requirements are highest (Table 1). If our assumption that prey are only captured during bottom time is correct (see below), Adélies are able to satisfy their energy requirements and those of their chicks in only 44 min/d (incubation) to 73 min/d (creche stage) of actual prey pursuit.

Williams et al. (1992) suggest that Gentoo Penguins capture some prey during the descent and ascent phases of deep dives. However, they provide little supporting evidence. In Adélies most hunting dives are characterized by smooth, rapid, and constant descent and ascent rates, contrasting with slow irregular depth changes during bottom time (Chappell et al. 1993*b*). We feel these characteristics are inconsistent with prey pursuit during descent and ascent.

*Foraging range*

The distances penguins travel on foraging trips is unclear. Trivelpiece et al. (1987) calculated the maximum foraging range of three pygoscelid penguins at King George Island from traveling speed and the time spent away from nests, using the simple assumption that range = speed × swim time divided by two. Their Adélies had a potential foraging range of 50 km. Wilson et al. (1989) attached speed meters to penguins near Palmer Station and determined that guard-stage Adélies swam mean distances of 28 km during foraging trips, for a maximum range of 14 km. However, the distance figure includes vertical movement during dives and does not incorporate bearing changes that reduce range, so the actual foraging radius was <14 km.

Our data on mean travel time to and from the colony (between departing the colony and the first hunting dive and between the last hunting dive and returning to the colony) suggest a mean foraging range of 7–9 km. That value is based on a mean swim speed of 2 m/s; but within sight of the colony, departing and returning Adélies always porpoised. If the entire travel time was spent porpoising (3.8 m/s), the mean foraging range was 12–16 km. We consider 7–16 km to be minimal estimates of foraging range since episodes of traveling at the beginning and end of a foraging trip comprised only 15% (incubation) to 60% (creche stage) of total travel time. Initial and final travel times during trips were not larger during incubation (when total swim time was 44.5 h per trip) than during the guard and creche stages (when total swim time was 11.4 and 10.5 h per trip). However, we also emphasize that Adélies often foraged within 1 km of the colony (we occasionally observed them feeding within 200 m of shore).

*Prey capture rates*

Rates of prey capture were remarkably consistent during different nesting stages (Table 3). Palmer Adélies caught ≈10.3 g of krill per hunting dive, or ≈8.5 g/min of hunting dive time and 18.5 g/min of bottom time. Croxall and Davis (1990) estimated prey capture rates for Chinstrap (*Pygoscelis antarctica*), Gentoo, and Macaroni Penguins foraging on krill near South Georgia, the South Orkney Islands, and the South Shetland Islands. Using their data, we calculate capture rates ranging from 15.3 to 44.3 (mean 24.4) g per hunting dive, and 7.2 to 20.8 (mean 13.9) g/min of hunting dive time. These estimates are higher than our data for Adélies; several factors may be responsible for the difference. (1) Interspecific differences in diving behavior may influence foraging time budgets and time use efficiency. Croxall and Davis (1990) used values of hunting dive duration from 90 s (Macaroni Penguins) to 128 s (Gentoo Penguins), while the mean duration of hunting dives for Palmer Adélies is 72 s (Chappell et al. 1993*b*). Although Croxall and Davis (1990) do not present data on bottom time, it is likely that longer dive duration would increase bottom time per dive, especially if dive depths were similar. (2) Prey availability may have been lower near Palmer than in the other areas. (3) The number of hunting dives may have been underestimated in the studies compiled by Croxall and Davis (1990). None of these studies used re-

corders that provide detailed records of each dive. A more recent TDR study of Gentoo Penguins (Williams et al. 1992) produced an estimate of 18 g of krill per hunting dive.

Calculating the number of krill captured per unit of time requires knowledge of prey size. Adélies feed on a fairly wide size range of krill. In the South Orkney Islands most of their prey (by mass) is in the 30–60 mm length category (Lishman 1985). In the South Shetland Islands, krill eaten by Adélies average 42 mm (Volkman et al. 1980). Krill in these length classes range from ≈0.25 to 1.1 g (Siegel 1987). Assuming that Palmer Adélies catch krill within this mass range and that prey are caught only during bottom time, capture and handling times per krill range from 0.8 s for 0.25 g krill (1.25 krill/s) to 3.6 s for 1.1 g krill (0.28 krill/s). Croxall and Davis (1990) and Williams et al. (1992) computed capture rates for Chinstraps, Gentoos, and Macaronis in terms of hunting dive time instead of bottom time and obtained values from 0.08 to 1 krill/s. Comparable rates for Palmer Adélies are similar: 0.13 to 0.57 krill/s.

It is interesting to compare the overall foraging biology of Adélies to that of two other species for which detailed TDR data are available: the congeneric Gentoo Penguin (5–6 kg) and the much larger King Penguin (12–14 kg). Palmer Adélies feeding on large krill (1 g) catch about 10 krill per dive; this number rises to 40 per dive for small krill (0.25 g). The mean dive duration for Adélies was 1.2 min. Gentoos at South Georgia feed primarily on large krill (>1 g); they catch ≈13 krill per dive with a mean dive duration of 2.8 min (Williams et al. 1992). Kooyman et al. (1992) report that King Penguins at South Georgia and Possession Islands feed primarily on small fish (1–7 g) and catch 9–16 fish per dive. Dive duration in King Penguins varies from 2.5 min (shallow nocturnal dives) to 5–7 min (deep diurnal dives). Each of the three species catch about the same number of prey per dive, despite large differences in body mass, prey type, and dive duration.

### *Foraging efficiency*

The gross energy efficiency of foraging (the ratio of metabolizable energy intake to energy expended) calculated for an entire foraging trip was modest: 1.5–1.6 J gained for each J expended by the bird. Efficiency increased markedly after prey had been located. Assuming that swimming metabolic rate remained constant during different parts of the hunting dive cycle (descent, bottom time, ascent, and surface interval), efficiency was 4.6:1 during hunting dives and 3.09:1 during hunting activity (dives + surface intervals). During the actual pursuit of prey (bottom time) it increased to 10:1. These high values, along with the rather small fraction of total swim time devoted to hunting dive time and bottom time, suggest that prey capture by Adélies is limited primarily by their ability to find krill swarms (search time), and not by limitations in harvest rates (pursuit and handling time) or energy efficiency after prey have been located.

Weathers and Sullivan (1991) examined the foraging of Yellow-eyed Juncos (*Junco phaeonotus*) on the basis of net efficiency (energy intake/[energy cost of foraging − resting energy expenditure]). Since Yellow-eyed Junco foraging involves very little travel time, the appropriate comparison would be to Adélie hunting activity. Assuming the cost of swimming in Adélies is 8.2 × BMR and the resting expenditure is 1.3 × BMR, net efficiency is 18.8% higher than gross efficiency. Juncos attain considerably higher net efficiencies (15:1 to 25:1) than Adélies (3.7:1), presumably because (1) the primarily terrestrial hunting behavior of juncos has a much lower energy cost than Adélie swimming, and (2) resting rates of energy expenditure are proportionally higher in juncos than in Adélies.

### *Chick provisioning*

During the breeding season adult Adélies need to catch enough food to feed their chicks as well as to fuel their own metabolic expenditures. The food requirements of young chicks are low, and their consumption rate is probably limited by their own digestive capacity. However, as chicks grow their food requirements increase rapidly. By the time chicks are 2–3 wk old they can rapidly consume a parent's entire stomach contents, and consumption rates are limited by parental food delivery rates. Food loads of creche-stage Adélie foragers at King George Island, measured as stomach content mass, averaged ≈600 g (Trivelpiece et al. 1987). At Signy Island, meal sizes for single creched chicks (= food loads) were 270–390 g (Lishman 1985). Our estimate of stomach content mass for Palmer Adélies was 347 g during the guard stage and 426 g for birds feeding creched chicks, which is consistent with the King George and Signy Island data.

Again, Kooyman et al.'s (1992) study of King Penguins provides an interesting comparison to Adélies. King Penguins return to their colonies with food loads averaging 1.85–2.0 kg, or 310–322 g/d gained during foraging trips. That food load is a slightly larger fraction of empty body mass (14%) than the average mass gains of Palmer Adélies (8.7 and 10.7% during the guard and creche stages, respectively). However, the rate of mass gain of a 4-kg Adélie feeding creched chicks is 307 g/d—nearly the same as for a 13-kg King Penguin. Assuming that Adélies rear an average of 1–1.3 chicks from two eggs (King Penguins have a single chick), absolute rates of food delivery per unit time are only slightly lower for the small Adélie chick than for the large King Penguin chick. This calculation is consistent with the much faster maturation rate of Adélie chicks (50 d to fledging compared to King Penguin chicks: >300 d to fledging). Per unit of body mass, Adélie Penguins accumulate food for chicks at a rate of 77 $g \cdot kg^{-1} \cdot d^{-1}$, three times faster than King Penguins (25 $g \cdot kg^{-1} \cdot d^{-1}$).

Adélies use 75–80% of captured food to fuel their own metabolism, compared to 85% in King Penguins. These differences are probably related to the much longer trip durations and foraging ranges of King Penguins, which spend most of their time at sea where energy expenditures are high. These high costs require King Penguins to metabolize a higher proportion of captured prey than Adélies.

We expected that the quantity of food brought to chicks would be correlated to hunting effort by the parents. Penguins usually had more than one at-sea period per foraging trip; we assumed that food caught early in a trip is likely to be digested for use by the parent, and therefore most or all of the food available for chicks is captured primarily during the last at-sea period before returning to the colony. To our surprise, there was no relationship between the mass gain and the duration of the last at-sea period (Fig. 4A); instead, mass gain was significantly correlated to the total time spent swimming on a foraging trip (Fig. 4B). This observation suggests that, contrary to our initial hypothesis, some of the food caught in the early stages of a foraging trip is available to chicks.

The prey capture rates of Adélies are substantial: each creche-stage adult catches 1.4–1.6 kg of krill per day. However, the portion of captured food that was actually available to chicks was only 20.7% (guard stage) to 23.3% (creche stage) of the food used by adults to fuel their own metabolism. The relatively small increase in total foraging needed to support chicks was reflected in the minor increase in mean FMR between incubation (when parents are catching food only for themselves; 2.73 × BMR) and the guard (3.04 × BMR) and creche (3.29 × BMR) stages. Taken together, these data indicate that reproductive effort in Adélies does not require a large increase in either energy expenditures or foraging time.

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## Literature Cited

Ainley, D. G., R. E. LeResche, and W. J. L. Sladen. 1983. Breeding biology of the Adélie Penguin. University of California Press, Los Angeles, California, USA.

Chappell, M. A., D. N. Janes, V. H. Shoemaker, T. L. Bucher, and S. K. Maloney. 1993*a*. Reproductive effort in Adélie Penguins. Behavioral Ecology and Sociobiology, *in press*.

Chappell, M. A., V. H. Shoemaker, D. N. Janes, T. L. Bucher, and S. K. Maloney. 1993*b*. Diving behavior during foraging in breeding Adélie Penguins. Ecology **74**:1204–1215.

Chappell, M. A., and S. L. Souza. 1988. Thermoregulation, gas exchange, and ventilation in Adélie Penguins (*Pygoscelis adeliae*). Journal of Comparative Physiology B **157**: 783–790.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey, USA.

Costa, D. P., P. Dann, and W. Disher. 1986. Energy requirements of free-ranging Little Penguins, *Eudyptula minor*. Comparative Biochemistry and Physiology A **85**:135–138.

Croll, D. A., S. D. Osmek, and J. L. Bengtson. 1992. An effect of instrument attachment on foraging trip duration in Chinstrap Penguins. Condor **93**:777–779.

Croxall, J. P., and R. W. Davis. 1990. Metabolic rate and foraging behavior of *Pygoscelis* and *Eudyptes* penguins at sea. Pages 207–228 *in* L. S. Davis and J. T. Darby, editors. Penguin biology. Academic Press, San Diego, California, USA.

Croxall, J. P., R. W. Davis, and M. J. O'Connell. 1988. Diving patterns in relation to diet of Gentoo and Macaroni Penguins at South Georgia. Condor **90**:157–167.

Croxall, J. P., and G. S. Lishman. 1987. The food and feeding ecology of penguins. Pages 101–133 *in* J. P. Croxall, editor. Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, England.

Culik, B. M., and R. P. Wilson. 1991. Energetics of underwater swimming in Adélie Penguins (*Pygoscelis adeliae*). Journal of Comparative Physiology **161**:285–291.

Davis, R. W., J. P. Croxall, and M. M. O'Connell. 1989. The reproductive energetics of Gentoo (*Pygoscelis papua*) and Macaroni (*Eudyptes chrysolophus*) Penguins at South Georgia. Journal of Animal Ecology **58**:59–74.

Gales, R., and B. Green. 1990. The annual energetics cycle of Little Penguins (*Eudyptula minor*). Ecology **71**:2297–2312.

Green B., N. Brothers, and R. Gales. 1988. Water, sodium, and energy turnover in free-living Little Penguins, *Eudyptula minor*. Australian Journal of Zoology **36**:429–440.

Harper, H. A. 1979. Calorimetry: elements of nutrition. Pages 596–612 *in* H. A. Harper, V. W. Rodwell, and P. A. Mayes, editors. Review of physiological chemistry. Lange Medical Publications, Los Altos, California, USA.

Hui, C. A. 1987. The porpoising of penguins: an energy-conserving behavior for respiratory ventilation? Canadian Journal of Zoology **61**:333–343.

———. 1988. Penguin swimming. II. Energetics and behavior. Physiological Zoology **61**:344–350.

Kooyman, G. L. 1989. Diverse divers. Springer-Verlag, Berlin, Germany.

Kooyman, G. L., Y. Cherel, Y. Le Maho, J. P. Croxall, P. H. Thorson, V. Ridoux, and C. A. Kooyman. 1992. Diving behavior and energetics during foraging cycles in King Penguins. Ecological Monographs **62**:143–163.

Kooyman, G. L., and D. A. Croll. 1987. Feeding patterns of Emperor Penguins. Antarctic Journal of the United States **22**:221.

Kooyman, G. L., R. W. Davis, J. P. Croxall, and D. P. Costa. 1982. Diving depths and energy requirements of King Penguins. Science **217**:726–727.

Kooyman, G. L., S. E. Eckert, C. A. Kooyman, and M. Horning. 1990. Natural history of Emperor Penguins at Cape Washington. Antarctic Journal **25**:219–220.

Lifson, N., and R. McClintock. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology **12**:46–74.

Lishman, G. S. 1985. The food and feeding ecology of Adélie Penguins (*Pygoscelis adeliae*) and Chinstrap Penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of Zoology, London **205**:245–263.

Nagy, K. A. 1983. The doubly labeled water ($^3HH^{18}O$) method: a guide to its use. UCLA Publication Number 12-1417. University of California–Los Angeles, Los Angeles, California, USA.

———. 1987. Field metabolic rate and food requirement scaling in birds and mammals. Ecological Monographs **57**: 111–128.

Nagy, K. A., and B. S. Obst. 1992. Food and energy requirements of Adélie Penguins (*Pygoscelis adeliae*) on the Antarctic Peninsula. Physiological Zoology **65**:1271–1284.

Nagy, K. A., and C. C. Peterson. 1988. Scaling of water flux rate in animals. University of California Press, Berkeley, California, USA.

Nagy, K. A., W. R. Siegfried, and R. P. Wilson. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demerus*. Ecology **165**:1648–1655.

Ortiz, C. L., D. Costa, and B. J. Le Boeuf. 1978. Water and energy flux in elephant seal pups fasting under natural conditions. Physiological Zoology **51**:166–178.

Peterson, C. C., K. A. Nagy, and J. Diamond. 1990. Sustained metabolic scope. Proceedings of the National Academy of Sciences (USA) **87**:2324–2328.

Siegel, V. 1987. Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. Marine Biology **96**: 483–495.

Trivelpiece, W. Z., J. L. Bengtson, S. G. Trivelpiece, and N. J. Volkman. 1986. Foraging behavior of Gentoo and Chinstrap Penguins as determined by new radiotelemetry techniques. Auk **103**:777–781.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adélie, Gentoo, and Chinstrap penguins at King George Island, Antarctica. Ecology **68**:351–361.

Volkman, N. J., P. Presler, and W. Z. Trivelpiece. 1980. Diets of pygoscelid penguins at King George Island, Antarctica. Condor **82**:373–378.

Weathers, W. W., and K. A. Sullivan. 1991. Foraging efficiency of parent juncos and their young. Condor **93**:346–353.

Williams, T. D., D. R. Briggs, J. P. Croxall, Y. Naito, and A. Kato. 1992. Diving patterns and performance in relation to foraging ecology in the Gentoo Penguin, *Pygoscelis papua*. Journal of Zoology, London **227**:211–230.

Wilson, R. P., W. S. Grant, and D. C. Duffy. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology **67**:1091–1093.

Wilson, R. P., K. A. Nagy, and B. S. Obst. 1989. Foraging ranges of penguins. Polar Record **25**:303–307.