

Reproductive effort in Adélie penguins

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Summary. We estimated reproductive effort (energy expenditures for reproduction, as opposed to maintenance) in Adélie penguins breeding at Palmer Station, Antarctica. Data on body composition changes and metabolic rate were obtained using isotopic methods. Adélie breeding behavior consists of an initial courtship stage (during which both sexes fast), incubation, the ‘guard’ stage (when chicks are 1 to 18–28 days old), and the ‘creche’ stage (from the end of guarding until chicks are 38–45 days old). Both males and females lost considerable mass during the initial stages of the reproductive season, but males fasted longer and lost more mass. Mass losses of both sexes consisted of 66% depot fat and 34% lean tissue. Mass and body composition remained constant once birds resumed feeding. The metabolic expenditure for the foraging necessary to accumulate the mass lost while fasting – one component of reproductive effort – was about 63 MJ in males and 39 MJ in females. Field metabolic rates (FMR) were low during courtship and while incubating, increasing more than 2-fold when birds resumed foraging. Although mean FMR increased between incubation and the creche stage, differences between stages were small and not significant. We used FMR data and an energy balance model to estimate the cost of feeding chicks. Results suggest a maintenance FMR of about $2.7 \times$ basal metabolism (BMR), increasing to $3.4\text{--}3.6 \times$ BMR during the creche stage. The reproductive effort (as metabolic expenditures) associated with feeding chicks is 31 MJ (males) to 36 MJ (females). Cumulative reproductive effort is 94 MJ in males and 75 MJ in females, or 5.3–6.2% of the annual energy budget. The reproductive effort devoted to chick care does not appear to be constrained by physiological or time limitations. Instead, selection to reduce the risk of predation may prevent the evolution of increased parental care.

Introduction

Since Williams (1966) outlined the concept of tradeoffs between present and future reproduction as a fundamental aspect of life history, the allocation of resources to breeding – termed ‘reproductive effort’ – has attracted considerable theoretical and empirical attention. Much current research is focused on parental care (Clutton-Brock 1991), especially in species where it is a major part of parental investment (*sensu* Trivers 1972). Factors that affect the magnitude of parental care, such as predation or physiological or time limits to parental foraging effort, are of particular interest.

Many studies have explored reproductive effort and parental care, but these efforts are frequently compromised by problems of technique and interpretation (Clutton-Brock 1985). Investments in reproduction have been described in terms of, for instance, parental time budgets or mass changes, relative or absolute clutch size, prey capture rates, feeding visit or lactation frequency, offspring size or growth rates. Use of such a variety of ‘units’ complicates comparative analyses and makes it difficult to place reproductive effort within the context of an animal’s physiological capabilities. For these purposes reproductive effort is most usefully quantified in terms of energetics, such as metabolic expenditures for reproductive behavior and the energy equivalence of body composition changes necessary for the production of offspring – especially when these expenditures are referenced to maintenance costs.

In this paper we analyze the energy equivalence of reproductive effort in Adélie penguins, *Pygoscelis adeliae*. Adélies are good subjects for investigations of parental care in monogamous, long-lived species. They are abundant and colonial, nest in accessible terrain, are easy to individually mark and observe, and are amenable to experimental manipulation because of their flightlessness and tameness. Moreover, many aspects of Adélie energetics, ecology, life history, and behavior have been described (e.g., Spurr 1975; Ainley and DeMaster 1980; Ainley et al. 1983; Trivelpiece et al. 1987; Trivelpiece and

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Trivelpiece 1990; Chappell et al. 1989, 1990, 1993a, 1993b; Nagy and Obst 1992; Culik and Wilson 1992). Adélie reproductive effort is particularly interesting because the species' breeding cycle contains two distinct phases of metabolic intensity. In the initial phase the birds fast for several weeks at low metabolic rates, depleting body stores of fat and protein while establishing territories, courting, and building nests. Females resume foraging after laying two eggs; males do so after completing the first incubation shift. The second phase, with considerably higher average metabolic rates, begins after the birds resume feeding and continues through the period of provisioning chicks.

Our study combines time budget data with measurements of energy expenditures to estimate the magnitude of Adélie reproductive effort throughout the breeding season. We compare the components and cumulative total of reproductive effort in males and females. To explore the possibility that reproductive effort is limited by physiological constraints (e.g., Drent and Daan 1980; Peterson et al. 1990), we compare the birds' metabolic rates during breeding with the intensity of physiological effort during other parts of the annual cycle. Finally we discuss other aspects of Adélie ecology and behavior that may influence reproductive effort.

Methods

Study area and animals. The study site was 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 approximately 20 discrete colonies. There were 2700–2800 nests in the seven colonies from which we selected study birds during the 1990–1991 and 1991–1992 breeding seasons.

Adult Adélies return to Torgersen Island in mid-October after spending the winter in the pack ice. Establishment of territories and courtship occur in late October and early November and eggs are laid between 7 and 28 November. Incubation lasts 32–36 days and hatching takes place between 10 and 30 December. Chick rearing consists of the 'guard' stage, when at least one parent continually attends small chicks, and the subsequent 'creche' stage, when large chicks are left unattended. The guard stage lasts from hatching until chicks are 18–28 days old and the creche stage lasts until chicks are abandoned at 35–45 days. Fledging (departure of chicks to sea) begins in late January and is completed by the end of February.

We tagged adult penguins with numbered aluminum flipper bands. Sex was determined initially from within-pair size differences (males average 5–10% heavier than females) and confirmed by observing mating behavior. Each year we marked both adults in 140–170 pairs during the period of courtship and territoriality. These nests were checked daily, except when weather or sea ice conditions precluded access to Torgersen Island. Checks were continued until late in the creche stage, and we compiled extensive records of nest attendance by adults (daily presence or absence) and the status of eggs or chicks. While parents were being handled, we artificially warmed eggs and small chicks within our clothing to prevent hypothermia and predation by skuas (*Catharacta macrorhynchos* and *C. lonnbergi*).

Body composition. We determined body composition (amounts of depot fat and lean tissue) from body mass and total body water content (TBW) measured by isotope dilution. To avoid aberrant readings caused by stomach contents (which can compose >20% of body mass), we restricted measurements to birds with no palpable food in the stomach. Most birds (except during the creche stage)

were known to have fasted >24 h before measurements. Penguins were weighed (± 25 g) on an Ohaus electronic platform balance, and injected in the pectoralis muscle with water containing either deuterium (D; ^2H) or both D and ^{18}O (doubly labeled water, or DLW). Isotope loadings were 0.11–0.15 g D and 0.20–0.27 g ^{18}O per kilogram body mass. At 2–3 h after injection we collected a blood sample (2–5 ml) from an interdigital vein in the foot. Isotope concentrations were determined with mass spectroscopy (K.A. Nagy, University of California, Los Angeles, California, USA; Metabolic Solutions Inc., Acton, Massachusetts, USA). We obtained background (pre-injection) ^{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), so we used mean background values of 2000.4 ppm ^{18}O and 151.2 ppm D for calculations. Several individuals were used for more than one TBW determination. In these cases we sampled blood prior to the second injection to account for residual isotope.

TBW was computed using the equations in Nagy (1983). We calculated the mass of depot fat (m_{depot}) and lean tissue (m_{lean}) by the method described in Ortiz et al. (1978). From dissection and freeze-drying of tissues from four freshly dead penguins we determined that free water constitutes $9.5 \pm 0.5\%$ of the mass of depot fat and $70 \pm 1\%$ of the mass of lean tissues (including bone, blood, and integument). Since $\text{TBW} = 0.095 m_{\text{depot}} + 0.7 m_{\text{lean}}$ and $M_b = m_{\text{depot}} + m_{\text{lean}}$, then:

$$m_{\text{depot}} = 1.157 \times M_b - 1.653 \times \text{TBW} \quad (1)$$

and

$$m_{\text{lean}} = M_b - m_{\text{depot}}$$

We measured body composition at six times: (1) arrival (within 24 h of a bird's return to the colony in October); (2) courtship (both sexes but no eggs present at a nest site); (3) the end of the fasting period (immediately prior to egg laying and less than 4 days before the first foraging trip for females, less than 4 days before the end of the first incubation spell for males); (4) incubation subsequent to the first foraging trip; (5) guard stage; and (6) creche stage. The energy equivalences of changes in fat and protein stores were computed using values of 39.4 kJ/g lipid and 17.8 kJ/g protein (Nagy 1983).

Our calculations assume that water and energy contents of depot fat and lean tissue remained relatively constant over time, even though absolute quantities and proportions changed substantially. Changes in the water content of depot fat during fasting can lead to inaccuracies (Reilly and Fedak 1990). Small samples of adipose tissue from lean Adélies had water contents of 12–15%. Thus our calculations probably underestimate m_{depot} in lean penguins by 5–7%. Because m_{depot} is a small fraction of M_b in lean penguins, the error in estimates of m_{lean} is <2%. For energetic calculations we assumed that dry matter lost in lean tissue was primarily protein. A recent study of fasting great-winged petrels (*Pterodroma macroptera*; Groscolas et al. 1991) confirmed this assumption and validated the accuracy of TBW-based determinations of body composition.

Time budgets and foraging behavior. To study behavior at sea, we deployed electronic time-depth recorders (TDRs) on 48 penguins during the incubation, guard, and creche stages. TDRs were attached to the feathers of the lower back with epoxy glue and plastic cable ties (Chappell et al. 1993a). After the birds returned from foraging trips we removed the TDRs and downloaded dive records to computers for analysis. Details of analysis protocols and Adélie diving behavior are presented elsewhere (Chappell et al. 1993a). At Palmer Station, Adélie diets are almost exclusively Antarctic krill (*Euphausia superba*), which has a metabolizable energy content of 3.5 kJ/g wet mass (Nagy and Obst 1992).

Energy utilization. We measured energy metabolism with doubly labeled water (Lifson and McClintock 1966). Field procedures and isotope loadings were as described for TBW studies, except that a second blood sample was obtained 2–8 days after the initial sample.

Residual isotope levels from final samples exceeded backgrounds by at least 10 times the standard deviation of backgrounds (all final D levels and most final ^{18}O levels exceeded backgrounds by >20 background SDs). Field metabolic rate (FMR) as CO_2 production was calculated using the equations in Nagy (1983). We computed the energy equivalence of CO_2 production using factors of $27.7 \text{ kJ l}^{-1}\text{CO}_2$ for fasting birds metabolizing fat and $25.8 \text{ kJ l}^{-1}\text{CO}_2$ for birds metabolizing krill (Nagy 1983; Nagy and Obst 1992). Field metabolic rates were also expressed as multiples of basal metabolic rate (BMR; $313 \text{ kJ kg}^{-1}\text{d}^{-1}$; Chappell and Souza 1988). For several birds we calculated FMR from the fraction of time spent swimming:

$$\text{FMR (in multiples of BMR)} = 1.30 + 6.89 \cdot (\text{fraction of time swimming}) \quad (2)$$

$$r^2 = 0.81$$

The estimated cost of swimming is therefore $2.56 \text{ MJ kg}^{-1}\text{d}^{-1}$, and the cost of terrestrial activity is $0.407 \text{ MJ kg}^{-1}\text{d}^{-1}$. This equation was derived from 34 DLW measurements of FMR with simultaneous measurements of swimming time obtained from TDRs (Chappell et al. 1993b).

Statistics. Data were analyzed with least-squares regression, *t*-tests, and (when testing for combined effects of nesting stage and sex) multivariate ANOVA. Comparisons among ANOVA groups were made with Scheffé tests. The significance level was $P < 0.05$. Results are expressed as $\bar{x} \pm \text{SD}$.

Results

Effects of handling

Our procedures appeared to cause little short-term disturbance and very few long-term effects on breeding behavior. Birds immediately resumed courtship, incubation, chick feeding, or guard behavior in 347 of 352 post-handling releases. Four other individuals did so within 1 h, and only 1 bird (a female during early courtship) abandoned its nest. Most of our study pairs successfully reared chicks. Fledging success (number of fledglings per nest) in study colonies was identical to that in undisturbed colonies (1.0 chicks/nest in 1990–1991; 1.3 chicks/nest in 1991–1992).

Nest attendance

We obtained complete records of incubation attendance for 154 pairs. Adélie pairs averaged 5.6 ± 1.7 exchanges of incubation duties; thus each parent averaged 2.8 foraging trips during the incubation stage. Cumulative time incubating was considerably larger in males (19.6 ± 2.3 days) than in females (15.3 ± 2.3 days; $P < 0.0001$, *t*-test for correlated samples).

In 176 pairs that raised at least one chick, males spent 15% more time at the nest (14.0 ± 3.5 days) than females (12.2 ± 2.9 days) during the guard and creche stages. The difference, though small, was significant ($P < 0.0001$, *t*-test for paired samples). The sum of male and female attendance is less than the duration of chick care (37–45 d) because chicks were usually unattended during the creche stage except for brief feeding visits.

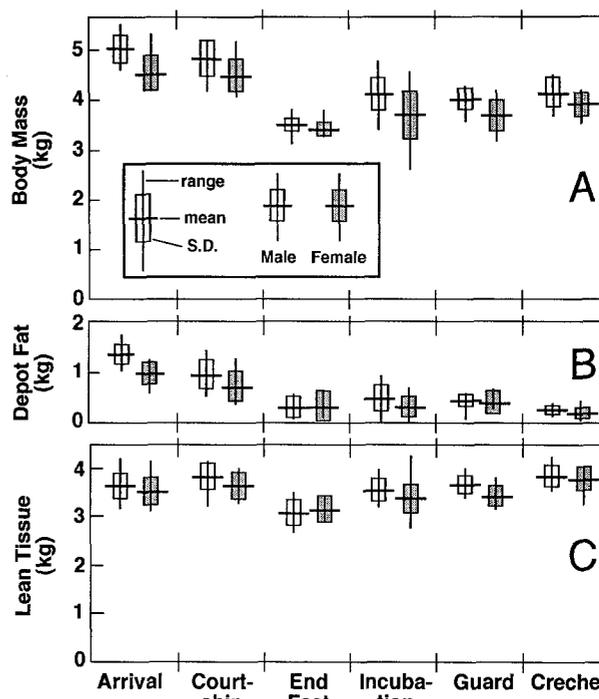


Fig. 1A–C. Changes in A body mass B depot fat and C lean tissue during the reproductive season. Data are shown separately for males and females

Body composition changes

Males averaged heavier than females ($P = 0.008$; Fig. 1a; $n = 55$ males and 57 females), and sex significantly affected the relationship between mass and nesting stage ($P = 0.019$). Both sexes lost considerable mass during the initial fast ($P < 0.0001$), but males lost more than females. Mass increased following the end of the fast in males ($P < 0.0001$) but not in females, and there was no change in mass during the final three stages (incubation, guard, and creche) in either sex.

Depot fat comprised most of the mass loss of both sexes (Fig. 1b), declining sharply after arrival ($P < 0.001$). Males lost more fat than females ($P = 0.0014$). There were no significant changes in depot fat from the end of the fast through the creche stage in either sex.

In males, the mass of lean tissue decreased significantly between arrival and the end of the initial fast ($P = 0.0003$; Fig. 1c). Some lean tissue was recovered after the end of the fast ($P = 0.001$), but there were no significant differences among the incubation, guard, and creche stages. The lean tissue mass of females at the end of the fast was significantly lower than during the arrival and courtship stages ($P = 0.025$). However, there was no difference between the end of the fast and the final three stages.

To summarize, shifts in body composition occurred primarily between arrival and the end of the initial fast (Fig. 1, Table 1). On average, males lost 1.77 kg of mass, composed of 1.17 kg of depot fat and 0.60 kg of lean tissue. Females lost 1.04 kg of mass, composed of 0.68 kg of depot fat and 0.36 kg of lean tissue. Once they

Table 1. Body composition changes in male and female Adélie penguins during the breeding season

Sex	Nesting stage	<i>n</i>	Body mass (kg)	Depot fat (kg)	Depot fat (% mass)	Lean tissue (kg)	Lean tissue (% mass)
Male	Arrival	10	5.10 ± 0.27	1.43 ± 0.18	28.1 ± 3.3	3.67 ± 0.26	71.9 ± 3.3
	End fast	7	3.34 ± 0.14	0.26 ± 0.21	7.8 ± 6.3	3.08 ± 0.25	92.2 ± 6.3
	IGC	30	4.06 ± 0.27	0.43 ± 0.23	10.5 ± 5.3	3.63 ± 0.21	89.5 ± 5.2
Female	Arrival	10	4.53 ± 0.35	1.00 ± 0.19	22.0 ± 3.7	3.53 ± 0.29	78.0 ± 3.7
	End fast	3	3.49 ± 0.12	0.32 ± 0.30	9.1 ± 8.4	3.17 ± 0.28	90.9 ± 8.4
	IGC	37	3.77 ± 0.38	0.29 ± 0.21	7.5 ± 5.3	3.47 ± 0.29	93.2 ± 4.9

Body composition was determined from mass and total body water (see text). The nesting stages are: *arrival* (within 24 h of returning to the colony in October); *end fast* (within 4 days of the initial foraging trip following egg laying for females, and within 4 days of

the end of the first incubation spell for males); *IGC* (the mean of the incubation, guard, and creche stages). Note: data from the courtship period (between arrival and the end of the fast) are not included here. Values are mean ± SD

Table 2. Field metabolic rates (FMR) of Adélie penguins at different stages of the reproductive season

Sex	Nesting stage	<i>n</i>	Body mass (kg)	FMR kJ/day	FMR/BMR
Male	Courtship	5	4.68 ± 0.28	1594 ± 625	1.22 ± 0.35
	Incubation (land only)	9	4.18 ± 0.24	1481 ± 520	1.12 ± 0.35
	Incubation (land and sea)	4	4.08 ± 0.23	3089 ± 348	2.42 ± 0.35
	Guard	12	4.18 ± 0.21	3833 ± 601	2.93 ± 0.55
	Creche	7	4.19 ± 0.29	4184 ± 1070	3.19 ± 0.91
Female	Courtship	9	4.43 ± 0.49	1766 ± 399	1.48 ± 0.44
	Incubation (land only)	9	3.95 ± 0.29	1422 ± 267	1.16 ± 0.25
	Incubation (land and sea)	4	3.68 ± 0.29	3523 ± 869	3.05 ± 0.65
	Guard	12	3.70 ± 0.32	3740 ± 943	3.23 ± 0.92
	Creche	9	3.87 ± 0.21	4070 ± 1356	3.36 ± 1.14

FMRs are expressed as kJ/day and as multiples of basal metabolic rate (FMR/BMR). Basal metabolic rate was computed as body mass in kg × 313 kJ kg⁻¹ · d⁻¹; to avoid the confounding effects of high body fat content during courtship we calculated courtship BMR from the mean mass during the rest of the breeding season (3.81 kg for females, 4.17 kg for males). Two values for the incubation stage are shown: one for birds incubating eggs (land only), and a combined value for incubation and foraging at sea. Values are mean ± SD

resumed feeding, males quickly regained much of the lean tissue lost while fasting, but neither sex accumulated depot fat during the remainder of the breeding season.

We obtained measurements from the same individual at both arrival and the end of the fast for 6 males and 2 females. The males lost 1.92 kg of mass, composed of 1.30 kg of depot fat and 0.62 kg of lean tissue, in 37 days of fasting (range 35–42 days; the females lost 1.27 kg of mass, composed of 0.82 kg of depot fat and 0.45 kg of lean tissue, during 21 days of fasting (range 18–24 days). Thus fasting males lost an average of 52 g/day, composed of 35 g of depot fat and 17 g of lean tissue. Females lost 60 g/day composed of 39 g of depot fat and 21 g of lean tissue.

Approximately 94% of the energy used by fasting Adélie was derived from lipids and 6% from protein (there were no significant differences between males and females). This is similar to lipid:protein utilization ratios in other fasting seabirds (reviewed in Groscolas et al. 1991), which range from 83% lipid:17% protein in Wilson's storm petrels (*Oceanites oceanicus*) to 96% lip-

id:4% protein in emperor penguins (*Aptenodytes forsteri*).

Field metabolic rates

We obtained DLW measurements from 30 foraging Adélie (Chappell et al. 1993b) and derived FMR from time budgets for an additional 19 birds (3 during incubation, 13 during the guard stage, and 3 during the creche stage). Addition of the time budget estimates to the DLW data changed predicted FMR by <1% for each nesting stage. We also measured the FMR of 31 birds during terrestrial activity (Table 2). Absolute FMR (kJ/day) changed dramatically with nesting stage ($P < 0.0001$). Although the FMR of females was slightly higher than that of males, the difference was not significant ($P = 0.50$) and there was no interaction between sex and stage ($P = 0.94$). Results were similar when FMR was expressed as a multiple of BMR: large changes with stage ($P < 0.0001$) but no effect of sex ($P = 0.09$) and no interaction ($P = 0.87$).

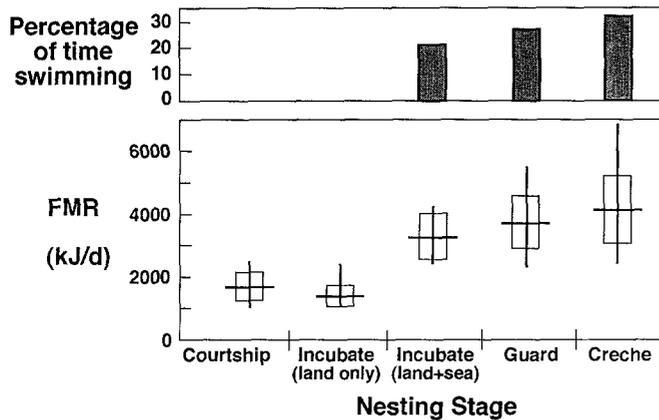


Fig. 2. Field metabolic rates (FMR) and the percentage of time birds spent swimming at different nesting stages. Data are pooled means for males and females (there were no significant differences between the sexes). Symbols as in Fig. 1

Most of the change in FMR was associated with the occurrence of foraging during the incubation, guard, and creche stages and the lack of it during courtship (Fig. 2). The mean FMR of foragers (3818 kJ/day) was 2.4 times higher than that of non-foragers (1562 kJ/day). Although mean FMR (males and females combined) increased between the incubation and guard stages and between the guard and creche stages, the differences were not significant. Our data on FMR during foraging is similar to allometric estimates for breeding birds (e.g., Daan et al. 1990), and to results of two other recent DLW studies of Adélie energetics during chick care (3500 kJ/day, Culik and Wilson 1992; 3900 kJ/day, Nagy and Obst 1992). Unfortunately, neither of the latter studies contains TDR data on foraging behavior.

We used the mean FMR of 2.73 times BMR during the incubation stage (the average of periods on land and at sea) as a measure of average maintenance metabolism, since at this time the adults were caring only for themselves and body composition was relatively stable (Fig. 1).

Discussion

We focus our discussion of Adélie reproductive effort on five questions: (1) How is reproductive effort divided between the initial fasting period and the period of chick care? (2) How large is reproductive effort compared to maintenance costs, both during the breeding season and in terms of annual energy budgets? (3) How similar are male and female reproductive effort in this monogamous species? (4) Is reproductive effort limited by constraints of time or physiological performance? (5) What other ecological or behavioral factors may limit reproductive effort?

Reproductive effort associated with fasting

Long fasts are an obligatory part of Adélie breeding behavior. What fraction of the fat and protein stores lost during these fasts is used for reproduction? The most obvious component is egg production. In addition to the mass loss we measured between arrival and the end of the fast (Fig. 1; Table 1), females lay two eggs, each containing 13 g of fat and 10 g of protein (dry mass; unpublished data). Eggs account for 4% of the fat, 16% of the protein, and 6% of the energy lost by females. In males, sperm production has an unknown but probably very small cost. Other possible contributions to reproductive effort during this period are any metabolic costs of courtship and incubation. However, FMRs of fasting birds (Table 2, Fig. 2) were only slightly higher than BMR (by 22–48% during courtship and 12–16% while incubating). Thermoregulatory costs (equal to about 17% of BMR during courtship and 14% of BMR during incubation; Chappell et al. 1990) account for much or all of the increase above BMR. We conclude that metabolic costs of courtship behavior are low and that incubation has little or no metabolic cost. Hence, most of the mass lost by fasting adults (especially males) does not contribute directly to reproductive activities or offspring.

Nevertheless, fasting does have a substantial cost that is part of reproductive effort: the cost of the foraging needed to acquire the body stores used during the fast. Without this expenditure the birds could not fast, and therefore could not breed. Mass losses totaled 1.05 kg lipid and 0.18 kg protein in males, and 0.61 kg lipid and 0.11 kg protein in females. Females invested another 26 g lipid and 20 g protein in eggs. The best estimate of the energy cost of fat and protein deposition (including the energy content of the deposited materials) is 53 kJ/g for both substances (Pullar and Webster 1977), although other studies give slightly lower values (van Es 1989). Therefore the pre-breeding mass gain required accumulation of 65 MJ by males and 40.6 MJ by females, equivalent to the metabolizable energy in 18.6 and 11.6 kg of krill, respectively.

Calculating the cost of acquiring that food requires knowledge of foraging efficiency (metabolizable kJ captured/kJ expended) and time budgeting. The proportion of swim time spent hunting is constant during the breeding season (Chappell et al. 1993b), but this may not be the case when birds do not have to commute between hunting areas and nests. Assuming that food availability is the same as during the breeding season, foraging efficiency associated with pre-breeding mass gain could be as low as 1.55 (if food intake is proportional to total swim time) or as high as 3.09 (if travel time is constant and food intake is proportional to hunting time only; both values from Chappell et al. 1993b). We calculated costs accordingly (Appendix 1; Table 3). Actual efficiency is probably intermediate, so we used averaged estimates of 62.7 MJ (males) and 39.4 MJ (females) for the metabolic cost of the pre-breeding mass gain. These costs, equal to 12–18 days of maintenance metabolism, are a major part of reproductive effort even though they occur outside the breeding season *per se*.

Table 3. The metabolic cost of the pre-breeding mass gain in Adélie penguins

Sex	Required gain (MJ)	Efficiency	Additional swim cost (MJ)	Additional swim time (h)	Reduced land cost (MJ)	Net cost (MJ)
Male	65	1.55	118	268	18.8	99
		3.09	31	70.7	4.9	26
Female	40.6	1.55	73.8	180	11.5	62
		3.09	19.4	47.4	3.0	16

The required gain is the metabolizable energy necessary for deposition of the fat and protein lost during fasting (53 kJ/g dry mass of fat or protein). Net cost is the cost of additional swimming minus the cost of an identical period of on-land activity. Swim costs were calculated according to Appendix 1 as: swim cost = (net gain)/(efficiency-1). Estimates are based on two foraging models:

(1) food intake is directly proportional to total swim time (hunting+travel) and efficiency=1.55; (2) food intake is directly proportional to hunting time only and efficiency=3.09. Efficiency values are from Chappell et al. (1993b). Activity costs for 4.15-kg males and 3.8-kg females are: swimming, 0.44 MJ/h (males), 0.14 MJ/h (females); terrestrial, 0.070 MJ/h (males), 0.064 MJ/h (females)

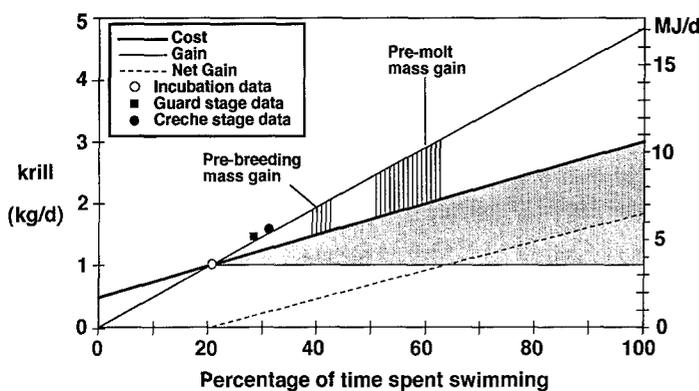


Fig. 3. A model of time and energy budgets of a 4.15-kg male Adélie penguin based on measured values of foraging efficiency and energy expenditures on land and at sea. Energy is shown in terms of krill consumption (assuming a metabolizable energy content of 3.5 kJ/g krill), megajoules per day (MJ/d), and as the factorial increase of field metabolic rate (FMR) above basal metabolism (BMR). The shaded area indicates metabolic rates above the maintenance value of 3550 MJ/d, and the distance between the gain and cost curves indicates the excess (or deficit) of energy intake vs. energy expended. Approximate values for the mass gain rates prior to breeding (assuming a period of 40 d) and molting are indicated, along with measured values of krill consumption for the incubation, guard, and creche stages

Reproductive effort during chick provisioning

The cost of additional foraging to obtain food for chicks is the other large component of Adélie reproductive effort. In many birds, particularly small passerines, the frequency of feeding visits is impressive and chick provisioning is often viewed as requiring large increases in foraging time and energy costs. Parent penguins feed chicks relatively infrequently (e.g., Costa 1991), but costs may still be considerable. For example, in the final stage of chick care, little penguins (*Eudyptula minor*) rearing one or two chicks expend twice as much energy as required for maintenance (Gales and Green 1990). Do Adélies, which also rear one or two chicks, experience similarly high costs?

Ideally, one would calculate chick provisioning costs by comparing FMR obtained simultaneously from breeders and nonbreeders. We were unable to do this because nonbreeders are difficult to identify and recapture. Instead, we compared mean FMR during the incubation stage (when birds catch food only for themselves; 3306 kJ/d) to FMR during chick care (3787 and 4120 kJ/d during the guard and creche stages, respectively). Assuming that prey availability and the ratio of hunting time to travel time were constant between nesting stages (Chappell et al. 1993b), the cost of chick provisioning was small: 481 kJ/d during the guard stage and 814 kJ/d during the creche stage.

That estimate is tenuous, since FMR was highly variable and differences between stages were not statistically significant (Fig. 2). Accordingly, we made additional cost estimates based on a model of the interaction between swim time, energy balance, and prey capture. The model used metabolic rates during swimming ($2.56 \text{ MJ kg}^{-1} \text{ d}^{-1}$) and on land ($0.407 \text{ MJ kg}^{-1} \text{ d}^{-1}$) derived from equation 2. During the breeding season, food intake was a linear function of swim time and foraging efficiency during swimming was 1.55 (Chappell et al. 1993b). If f_{swim} is the fraction of a day spent swimming, then:

$$\text{energy intake} = f_{\text{swim}} \times 3.98 \text{ MJ kg}^{-1} \text{ d}^{-1} \quad (3)$$

and

$$\text{energy expenditures} = f_{\text{swim}} \times 2.56 \text{ MJ kg}^{-1} \text{ d}^{-1} + (1 - f_{\text{swim}}) \times 0.407 \text{ MJ kg}^{-1} \text{ d}^{-1} \quad (4)$$

We ran the model for 4.15-kg males (Fig. 3) and 3.80-kg females; results were similar for both sexes. When solved for observed values of f_{swim} during the incubation, guard, and creche stages (20.9%, 28.3%, and 31.6% respectively; Chappell et al. 1993), the model predicted provisioning costs of 595 kJ/d during the guard stage and 880 kJ/d during the creche stage. When solved for the quantities of krill brought to chicks (207 g/d and 307 g/d in the guard and creche stages, respectively; Chappell et al. 1993), the estimates were 870 kJ/d during the guard stage and 1290 kJ/d during the creche stage.

For calculations of reproductive effort we used mean values from all three estimates: 650 kJ/d during the guard stage and 995 kJ/d during the creche stage. During chick-rearing, females spent 15% more time away from the nest than males; a difference of about 8% was reported for Adélie at Cape Crozier (Ainley et al. 1983). Accordingly, we assumed that female foraging time was 15% higher than male foraging time and adjusted estimates of reproductive effort to 695 kJ/day (guard) and 1065 kJ/day (creche) for females and 605 kJ/day (guard) and 925 kJ/day (creche) for males. This is equivalent to a creche-stage FMR of about 3.4 times BMR in males and 3.6 times BMR in females, and is consistent with slightly higher measured FMR values in females (Table 2). Birds spend about 21 days in the guard stage and 20 days in the creche stage, so the total reproductive effort devoted to feeding chicks is 36 MJ in females and 31 MJ in males.

The cumulative cost of provisioning chicks is equivalent to 9 days (males) to 11 days (females) of maintenance metabolism. Nevertheless, the concept of large increases in energy expenditures during chick rearing does not apply to Adélie penguins. Our estimate of the energy devoted to chick provisioning during the creche stage (when chick food requirements are highest) is a 27–33% increase in FMR above that of a nonbreeder. Moreover, creche-stage adults spend only a third of their time foraging (i.e., swimming); the other two-thirds is largely spent resting. Adélie conform to the suggestion of Weathers and Sullivan (1989) that chick care does not require a large increase in parental work loads in many bird species.

Physiological limits to chick care

Even though parent Adélie spend relatively little time foraging and their reproductive effort is small, is it possible that they are operating at a physiological upper limit? Several authors (e.g., Drent and Daan 1980; Peterson et al. 1990; Daan et al. 1990) have suggested that during the reproductive season many species operate at or near maximum sustainable metabolic rates. If this is true for Adélie, parents would be unable to sustain a higher reproductive effort even if selection favored such an increase.

Examination of energetics and prey capture rates during the period of pre-molt fat accumulation suggests this is unlikely. During the 4–5 weeks after they stop feeding chicks, adult Adélie gain 2.5 kg or more of mass (Penney 1967; Adams and Brown 1990). Molting penguins must mobilize large quantities of protein during feather growth. Therefore the ratio of lean tissue loss to fat loss during molt is probably higher than during the courtship fast (66% fat and 34% lean tissue). We assumed that the pre-molt mass gain is 50% lean tissue and 50% fat, or approximately 1.25 kg of depot fat (1.13 kg lipid) and 1.25 kg of lean tissue (0.375 kg protein). Since deposition of 1 g of lipid or protein requires 53 kJ, the birds need to acquire 80 MJ. This is equal to the metabolizable energy in 22.5 kg of krill in 28–35 days, or 650–820 g krill per day – considerably larger than the rate of krill deliv-

ery to chicks. Our foraging model (Fig. 3) predicts that to achieve this net gain, Adélie need to catch 1.3–1.6 kg krill/day in addition to the ~1 kg krill/day needed for maintenance. By comparison, creche phase adults catch 500–600 g of krill/day in addition to maintenance requirements. The necessary increase in swim time – from 21% of total time for maintenance to 50–60% of total time during the pre-molt period – generates an FMR 85–100% above maintenance FMR. That is more than twice the increments in FMR and swim time that occur during the creche stage. Even if most of the increase in swimming during the pre-molt period is devoted to hunting (i.e., foraging efficiency ~3), the estimated energy cost is higher than the highest cost associated with chick provisioning.

We conclude that breeding Adélie operate below their maximum capabilities of utilizing time and energy. Similar results have been reported for kestrels (*Falco tinnunculus*; Masman et al. 1988, 1989) and yellow-eyed juncos (*Junco phaeonotus*; Weathers and Sullivan 1989).

Annual energy budgets

Resource allocation on an annual basis is often used in discussions of reproductive effort. Our data provide a fairly complete picture of Adélie energetics during the reproductive season, but for more than half the year adults are away from breeding colonies. There are no data on wintertime energy expenditures so we assumed that winter FMR is similar to mean FMR during incubation (at both times, birds forage only for themselves). This probably underestimates winter FMR, since wind and low temperatures can increase thermoregulatory costs (Chappell et al. 1989, 1990) and food may be scarce in winter, but it provides a useful comparative baseline. We calculated pre-molt FMR as described above; for the 21-day molt period we used a metabolic rate of $1.75 \times \text{BMR}$ (Croxall 1982; Adams and Brown 1990). Since the rate of mass accumulation prior to the breeding season is unknown, we arbitrarily assumed a period of 40 days (the length of this period makes little difference to estimates of annual energy budgets).

Annual energy budgets are about 1500 MJ for breeding males and 1400 MJ for breeding females (Fig. 4). Cumulative reproductive effort is approximately 94 MJ in males and 75 MJ in females (6.2% and 5.3% of annual expenditures, respectively). Due to uncertainties in the efficiency and cost of the pre-breeding mass gain, the latter estimates may contain substantial errors (20–30 MJ). Annual food intake is about 440 kg for males and 410 kg for females. Of these totals, males use 37.4 kg (8.5%) and females use 33.4 kg (8.1%) for reproduction, either delivered directly to offspring or metabolized to support reproductive activities.

Reproductive investment is often computed as the quantity of food delivered to offspring (e.g., Costa 1991), but from the perspective of the parent the cumulative expenditure of energy and materials for reproduction is probably more important. In this respect, Adélie reproductive effort is low compared to that of several other

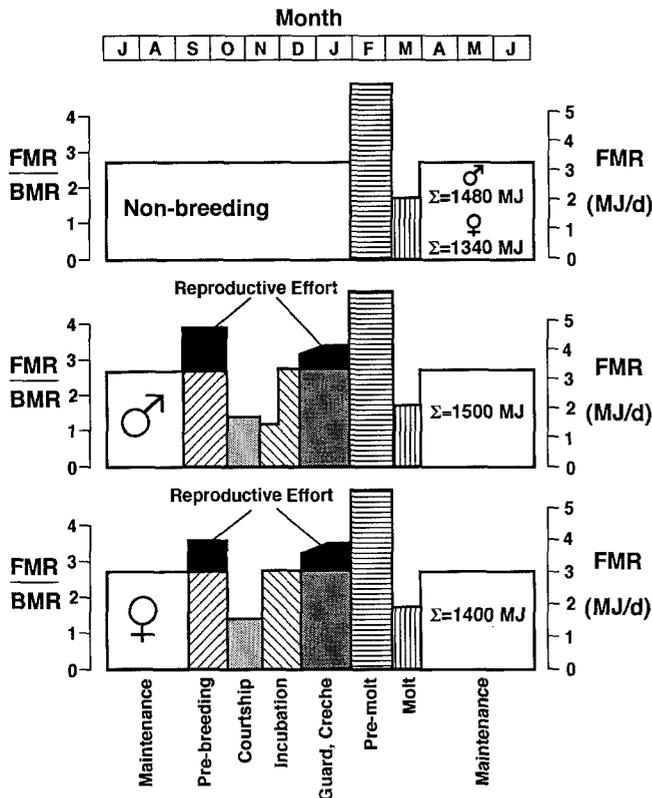


Fig. 4. Annual energy expenditures for breeding males, breeding females, and nonbreeding adult Adélie penguins. Expenditures are shown according to time and nesting stage; black areas indicate reproductive effort (the portion of energy expenditure devoted to reproduction)

endotherms. Little penguins devote 12% of annual energy metabolism and 22% of annual food intake to reproduction (Gales and Green 1990). The wandering albatross (*Diomedea exulans*), a species with an extremely long chick growth period and very low FMR, delivers 15% of annual food intake to offspring and an additional unmeasured fraction is metabolized to support reproductive activities (Adams et al. 1986). The fraction of annual energy metabolism spent on reproduction by female golden-mantled ground squirrels (6%) is about the same as for Adélie. However, reproduction accounts for a much higher proportion (24%) of this squirrels' annual food intake (Kenagy 1987).

A traditional approach for estimating reproductive effort is to compare energy budgets of breeding and nonbreeding individuals. In Adélie, this leads to a somewhat surprising observation: the estimated annual energy expenditures of nonbreeders are only slightly less than those of breeders (Fig. 4). This is because nonbreeders do not need to undertake a courtship and incubation fast. The energy breeders save during fasts (when FMR is 40–55% of maintenance FMR) is equal to a large fraction of their total reproductive effort.

Differences between males and females

In monogamous species with extensive biparental care, investment in offspring by males and females is expected

to be roughly equivalent (Trivers 1972). Adélie generally conform to this model, although there are substantial differences in the investment patterns of the two sexes. Because they assume the first incubation shift, males fast considerably longer and lose more mass than females (Fig. 1, Table 1). However, during the period of chick care females spend slightly more time foraging than males (as reported for macaroni penguins, *Eudyptes chrysolophus*, by Davis et al. 1989). Approximately 33% of male reproductive effort goes to feeding chicks and 67% to preparing for the courtship fast. In females, 48% of reproductive effort goes to feeding chicks and 52% to preparing for the courtship fast. The energy content of eggs (included in fast preparation costs) is only 2% of female reproductive effort.

Males have higher total reproductive effort than females, both absolutely and as a fraction of the annual energy budget. Most of the difference arises because males fast longer than females, and therefore spend more energy acquiring a greater quantity of pre-breeding body stores. Males are better able to perform the first incubation shift because (1) they are slightly larger than females and hence are better able to withstand long fasts, and (2) females invest some of their body stores in eggs and therefore have a reduced capacity for additional fasting.

Other factors affecting reproductive effort

Since Adélie are able to sustain considerably more hunting effort than occurs during chick care, it is unclear why selection has not led to increased reproductive effort during the guard and creche stages, or even to increased clutch size. The tendency of Adélie parents to abandon chicks 1–2 weeks prior to fledging is also puzzling. Many chicks starve before fledging (Spurr 1975), many fledglings are too small to survive (unpublished data; W.Z. Trivelpiece and W.R. Fraser, personal communications), and it is reasonable to assume that chicks would benefit if parents provided additional care. What factors might limit chick care in Adélie?

Most life history theories assume that for iteroparous species each episode of breeding has an associated cost of reproduction (Williams 1966; Bell 1980), such as reduced parental survival, growth, or condition or other factors that decrease the number of future offspring. It is usually assumed that reproductive effort and the cost of reproduction are correlated (e.g., Nur 1984), but the relationship (if any) is usually difficult to quantify (Clutton-Brock 1985, 1988; Reznick 1985, 1992). For Adélie, two aspects of breeding behavior are obvious possibilities for costs of reproduction: (1) depletion of energy reserves, and (2) increased predation risk.

It is uncertain if the change in body composition during the breeding season directly influences overwinter survival or subsequent reproductive success. Immediately after breeding, Adélie are able to recover condition very rapidly in preparation for the molt. Birds that finish breeding in poor condition may be less likely to successfully complete the molt, or may finish molting with low energy stores for use during the winter. However, there

is no evidence that additional foraging for chicks would have a negative effect on overall condition at the end of the breeding season. Also, it seems unlikely that delaying molt by ~10 days of additional chick feeding would cause difficulties for parents, particularly since sympatric chinstrap and gentoo penguins successfully molt several weeks later than Adélie.

Predation risk during breeding can strongly influence reproductive effort (Lima 1987). The Adélie's major predator is the leopard seal *Hydrurga leptonyx*. These seals congregate at penguin breeding colonies, intercepting birds near the shore as they depart and return from foraging trips (Penney and Lowry 1967; personal observations). The survival of Adélie breeders is lower than that of nonbreeders, and the most likely cause is leopard seal predation (Ainley and DeMaster 1980; Ainley et al. 1983). Presumably, breeding penguins suffer increased risks because they are more vulnerable clustered near colonies than when dispersed at sea. At Palmer Station, leopard seal predation accounted for 51 of 53 adult Adélie we found freshly dead or saw being killed (the other 2 deaths were from unknown causes). No adult mortality occurred during terrestrial activities. We estimated death rates during the 1990–1991 season by counting banded adults that disappeared before their chicks were 33 days old and did not reappear the following year (chicks are typically >38 days old when abandoned). Birds that lost broods to flooding or skua predation were excluded from calculations. Of 296 birds, 35 disappeared (12 during incubation and 23 during chick care). Some of the 'missing' penguins may have lost bands instead of dying; we assumed a band loss rate of 5%. The estimated mortality rate was therefore 11%. Since adults make about 30 foraging trips during a breeding season, the probability of death was 0.4% per trip.

Another way of evaluating the risk of breeding is to compare annual mortality rate with that during the 100-day breeding season. Annual survival of banded adults in the Antarctic Peninsula is highly variable, with a mean of 65–70% (Trivelpiece and Trivelpiece 1990). Therefore the daily mortality rate when birds are not breeding is about 0.08–0.1%, compared to 0.12% during the breeding season.

These are rough approximations of death rate, but they indicate that breeding behavior entails substantial risks for Adélie. For example, continuing parental care until chicks fledged (instead of abandoning them 10 days before fledging) would probably increase the fitness of chicks – but would also reduce the survival of parents. Another 10 days of additional feeding (7–8 foraging trips), has an associated risk of dying of 2.5–3%. The risk for parents that do not provide additional food is unknown, but because they disperse from the colony they are probably much more difficult for seals to locate. Accordingly, we suggest that the fitness loss due to increased predation risk is greater than the fitness benefit from continuing chick care until fledging. A similar argument would apply to increasing the number of foraging trips during the guard and creche stages.

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Appendix 1. To calculate the metabolic costs (C) of the foraging necessary to obtain a net gain of G_{net} units of energy at a foraging efficiency (= Joules captured/Joules expended) of E , we used the following formula:

$$\text{Since } G_{\text{net}} + C = C \cdot E, \text{ then } G_{\text{net}} = C \cdot (E - 1)$$

$$\text{and } C = G_{\text{net}} / (E - 1)$$

Increasing the time spent foraging requires an equivalent reduction in time spent on land, so the actual cost is less than C by a quantity equal to the terrestrial metabolic rate times the duration of additional foraging

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