

ARTICLE

Yutaka Watanuki · Akinori Takahashi · Katsufumi Sato
Akiko Kato · Charles A. Bost

Inter-colony and sex differences in the effects of parental body condition and foraging effort on the brood growth of Adélie penguins

Received: March 3, 2003 / Accepted: July 15, 2003 / Published online: September 6, 2003

Abstract Among colonies with different foraging distances, central-place-foraging seabirds may change their foraging and reproductive efforts. We compared the body condition, meal frequency, and diving behavior of male and female Adélie penguins at two locations: Dumont d'Urville, where there was little sea ice and they foraged in open waters far from the colony; and Syowa, where there was heavy, fast sea ice and they foraged in ice cracks close to the colony. The parental mass decrease rate during the chick-rearing period was similar between colonies and between sexes. A large individual variation in meal frequency positively affected the brood growth rate, but daily underwater time did not. A weak but significant positive effect of body condition on brood growth rate was found only in males at Syowa. It was suggested that males work with better body condition than females. We propose the hypothesis that the regional difference in the distance to the feeding sites and the sex difference in body energy reserve might constrain the capacity to regulate reproductive effort.

Key words Food provisioning · Body condition · Seabird · Foraging distance · Diving time

Y. Watanuki¹ (✉)
Laboratory of Animal Ecology, Graduate School of Agriculture,
Hokkaido University, Sapporo 060-8589, Japan

A. Takahashi
Department of Polar Science, Graduate University for Advanced
Studies, Tokyo Japan

K. Sato · A. Kato
National Institute of Polar Research, Tokyo Japan

C.A. Bost
Centre d'Ecologie et de Physiologie Energetiques, CNRS, Strasbourg
France

Present address:

¹Graduate School of Fisheries Sciences, Hokkaido University,
3-1-1 Minatocho, Hakodate 041-8611, Japan
Tel. +81-138-408862; Fax +81-138-408863
e-mail: ywata@fish.hokudai.ac.jp

Introduction

It is a central assumption of the life-history strategy that parents of long-lived animals allocate resources for the production of offspring and their own maintenance (Stearns 1992). Foraging distance is hypothesized to constrain this resource allocation in central-place-foraging birds (Ydenberg 1994; Houston et al. 1996). Seabirds provisioning chicks by commuting between colonies and distant foraging places are good examples. Some change their resource allocation between long and short foraging trips within a breeding season (Weimerskirch et al. 1997; Chaurand and Weimerskirch 1994), between years of different foraging distances (Hamer et al. 1993; Kitaysky et al. 2000), and also between colonies with different food availability (Monaghan et al. 1989). Year-to-year and between-colony differences in foraging distance are known, consequently, to affect chick growth and fledging success (Monaghan et al. 1996; Suryan et al. 2000; Clarke et al. 2002).

The body condition or energy reserve of the individual parent relates to the food-provisioning rates in some seabird species. Parents with a better body condition are known to provision faster by bringing larger meals to chicks more frequently, hence raising faster-growing chicks (Lorentsen 1996; Tverra et al. 1998). This may partly be due to individual variation in the feeding effort or efficiency or in reproductive effort (Barbraud et al. 1999; Wendeln and Becker 1999). Environmental factors also are known to mediate the effects of body condition on resource allocation (Weimerskirch et al. 2001). To understand further how foraging distance constrains the resource allocation pattern, additional studies of colonies with different foraging distances will be useful.

Adélie penguins *Pygoscelis adeliae* feed chicks 0.2–1.0 kg meals comprising krill and fish, after foraging trips lasting 10–60 h and with a 15–110 km range in the sea-ice zone around Antarctica (Croxall et al. 1988; Trivelpiece et al. 1990; Kerry et al. 1995; Clarke et al. 1998). Regional and between-year variations in the distance to foraging sites and prey availability affect foraging-trip duration, meal size,

and chick production (Fraser et al. 1992; Watanuki et al. 1993, 2002; Ainley et al. 1998; Wienecke et al. 2000; Clarke et al. 2002). The penguins' diving behavior can be monitored easily with bird-borne data loggers. Therefore, this species is a suitable subject for an analysis of the effects of foraging distance on the resource-allocation pattern.

Our aim is to determine how individual variations in foraging and reproductive effort affect chick growth rate in colonies with different foraging distances. Adélie penguins forage within 4 km of the colony at Syowa (Japanese Antarctic research station) in a fast sea-ice area (Watanuki et al. 1999; Kato et al. 2003), but they forage in areas 36–37 km away from the colony at Dumont d'Urville (French Antarctic research station) in a mixed sea-ice and open-sea area (Wienecke et al. 2000; Rodary et al. 2000). On average, foraging-trip duration, parental body mass change during the trip, meal size, and chick production are known to vary between these colonies (Watanuki et al. 2002). We compared the body condition, meal frequency, and diving behavior of male and female Adélie penguins from these two colonies to examine the effects of foraging distance on the relationships between body condition, foraging effort, and food provisioning.

Methods

Study area

The study was conducted at Hukuro Cove colony (150–200 pairs; 69.1°S, 39.4°E) 30 km south of Syowa station in the summer of 1995/1996 (Syowa 95) and the summer of 1996/1997 (Syowa 96), and at the Biomar colony (1,800 pairs; 66.7°S, 140.0°E) at Dumont d'Urville station in the summer of 1996/1997 (DDU 96). The study period was between late December, when most chicks had hatched, and late January, when most chicks had entered the crèche. At Syowa 95 and Syowa 96, the >1-m-thick fast sea ice extended more than 100 km from the colony throughout the summer (S. Ushio, personal communication). At DDU 96, the fast sea ice extended more than 50 km from the colony until the end of December and broke out completely after that (Rodary et al. 2000; K. Sato, personal observation).

Monitored birds

Both parents were captured about 5 days after the hatching of their chicks and were measured, weighed, and then banded with colored flipper bands and numbered with hair dye on their chests. These birds were designated as MONITORED birds. Bill depth, bill length, and head length were measured with calipers to 0.1 mm and flipper width was measured to 1 mm (CCAMLR 1991; Kerry et al. 1992). The sexes of parents were determined by their sizes following Kerry et al. (1992). We arbitrarily sampled pairs at Syowa 95 in the period of 23–27 December in 1995 (16 pairs with two chicks and 4 pairs with a single chick), and those brood-

ing two chicks at Syowa 96 in the period of 23–30 December 1996 (17 pairs) and at DDU 96 during 29–31 December 1996 (10 pairs).

Parents departing the colonies were captured in most cases. Birds departing the colony have no stomach contents (Watanuki et al. 2002). Some parents attending chicks for at least 3 h were assumed to have fed their chicks and so were captured. Although parents of penguins with small chicks do not always feed all of the food in their stomachs to the chicks within 3 h (Wilson et al. 1989a), we believe that the errors implicit in this assumption would be minimal because parents bring smaller amounts of food when their chicks are young (<100 g in the case of Adélie penguins, Lishman 1985). Time-depth-recording data loggers (TDRs) were then attached to the center of the lower back of each of the parents using quick-set epoxy glue and cable ties. The birds were recaptured in the period of 16–22 January at Syowa 95, 20–31 January at Syowa 96, and 23–30 January at DDU 96. They were weighed after they fed the chicks, and the TDRs were then removed.

The body mass corrected for body size index is often assumed to indicate the body fat reserve in seabirds (Chastel et al. 1995; Tverra et al. 1998), which has been determined in puffins *Fratercula arctica* (Wernham and Bryant 1998) and Leach's storm petrel *Oceanodroma leucorhoa* (Niizuma et al. 2000). To calculate body size index, we performed a principal component analysis including measurements of head length, bill length, bill depth, and flipper width ($n = 94$ birds all sex-colony data were combined). The first principal component (PC1) accounted for 56% of the variance and was used as our body size index. Body condition was defined as the residuals obtained by regression of the initial body mass on this size index. As the relationship between body mass and body size index is known often to differ between males and females in seabirds (Moe et al. 2002), the male and female body condition were calculated separately (Fig. 1).

Meal frequency

The 3- to 5-day watches began at 10-day intervals. Departure time, arrival time, and chick feeding were recorded for MONITORED pairs. This practice potentially excluded long trips (>3 days) and hence gave systematic biases. Based on the continuous recording of departures and arrivals, no bird made trips longer than 3 days between late December 1999 and late January 2000 at Syowa (Y. Watanuki, unpublished data). We believe that the biases would be small enough for individual variation to be analyzed. Mean trip duration and guarding duration (duration of attendance at nests) were calculated for each MONITORED bird that made more than two trips in the 3- to 5-day watch. Then mean trip duration, mean guarding duration, and the number of colony visits with meals (defined as meal frequency) were averaged across the watch periods, and these mean values were used as representatives of individual birds following CCAMLR (1991). To standardize the breeding stages, we analyzed the data between late December and

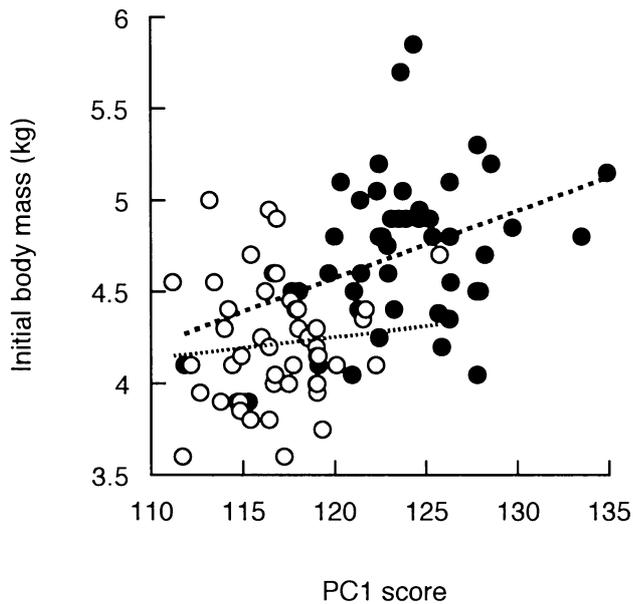


Fig. 1. Relationship between body size index as shown by PC1 score and body mass at the start of chick rearing in females (open circles) and males (closed circles). All colony-year data are combined. Linear regression was significant for males (mass = $0.037 \times \text{PC1} + 0.147$, $r^2 = 0.14$, $n = 47$, $P < 0.05$) but not significant for females (mass = $0.012 \times \text{PC1} + 2.852$, $r^2 = 0.01$, n.s.)

mid-January for Syowa 95 and Syowa 96, and those between early January and late January for DDU 96, as the hatching at DDU 96 started about a week later than that at Syowa 95 and Syowa 96.

Diving behavior

All of the MONITORED birds were fitted with NIPR-type TDRs (14 mm diameter, 85 mm length with a domed top, 27 g, Little Leonardo Co. Ltd., Tokyo) at Syowa 95 and Syowa 96 and UWE-type TDRs (19 mm diameter and 75 mm long with a domed top, 35 g) at DDU 96. TDRs recorded the depth at 3- to 5-s intervals with 1-m accuracy and 0.1-m or 0.5-m resolution over 3 weeks. The data were downloaded with a handheld computer and analyzed with KAISEKI software (MMT Co. Ltd, Tokyo). Activity budgets were estimated from the dive records, with dives of less than 1 m in depth being excluded because this depth was within the error range. Diving-behavior data were collected for 12 females and 13 males at Syowa 95, 14 females and 13 males at Syowa 96, and 8 females and 10 males at DDU 96. Seven birds were not recaptured because they made extraordinarily long trips late in the breeding season. We could not obtain diving data from other birds due to device malfunctions.

We did not examine the effects of the devices on the birds by collecting data from birds without devices in the study period. The trip duration of penguins with devices is generally longer than that of those without devices if the effects are detected (Wilson et al. 1989b; Hull 1997). The trip dura-

tion of Adélie penguins with 40-g devices was longer than that of birds without devices at Davis station (Watanuki et al. 1997). However, trip duration during brooding stage, meal mass, chick growth, and chick survival did not differ between those with and without 80-g TDRs in Adélie penguins in 1989/1990 at Hukuro Cove colony, Syowa (Watanuki et al. 1992). In a thorough study of device effects on Adélie penguins in Ross Sea, Ballard et al. (2001) found no significant effects of 15.7- to 25.4-g devices on trip duration or nesting success. Therefore, we assume that the effects of our TDRs (27–35 g or 0.7–0.9% of 4.0 kg penguins) on MONITORED birds for our analysis of regional and individual variations were negligible in this study.

Chick growth and survival

Chicks of MONITORED birds were marked with numbered tags and were weighed every 5 days with a Pesola spring balance. Repeated weighing did not affect chick survival (Watanuki et al. 1992). Chick growth rate was calculated as a slope of the linear regression of the growth from 27 December to 20 January following Watanuki et al. (1993). The brood growth rate was defined as the sum of the growth rates of *a* (first-hatched) and *b* chicks, if both chicks of the pair survived on 27 December and 20 January. None of the pairs lost chicks during this period at Syowa 95, but each of 4 pairs lost *b* chicks with a mass of 0.3–0.6 kg during this period at Syowa 96. At DDU 96, 3 pairs lost *a* chicks with a mass of 0.1–0.6 kg and 6 pairs lost *b* chicks with a mass of 0.1–0.6 kg. We used the growth rate of a surviving chick as the brood growth rate for these 13 pairs that lost chicks since the chicks were lost when they were small.

Meal size of TRIP birds

To reduce the disturbance of MONITORED birds, stomach contents were collected from the other 8–21 birds carrying TDRs (Watanuki et al. 2002) by the water offloading method (Wilson 1984; CCAMLR 1991). The birds were captured before they fed chicks and were flushed at least three times until the offloading water became clear. The body mass did not decrease after 3–7 flushings, indicating that most of the stomach contents were removed. These birds were designated as TRIP birds and sexed following Kerry et al. (1992). Soon after the flushing, the stomach contents were drained through sieves, weighed to 0.1 g with an electronic balance, and sorted (Watanuki et al. 2002). Prey items were weighed to the nearest 0.1 g. The known mass proportion of these identifiable items was applied to the whole meal mass. The meal energy value was estimated by the reported energy values of each prey (Antarctic krill, 4.35 kJ/g wet; oily Antarctic silver fish, 6.35 kJ/g wet; less oily Notoceniidea fish, 4.00 kJ/g wet, following Watanuki et al. 2002). Body size index and body condition of TRIP birds were calculated with the same equation used for MONITORED birds.

Values are indicated as means \pm SD with sample size in parenthesis. Colony-year and sex differences were examined with two-way analysis of variance (ANOVA) with Scheffe's post hoc test where the mean values for each bird were used. The relationship between the two parameters was examined with linear regression analysis and the significance of the Pearson correlation coefficient was examined by a *t*-test. Different individuals were sampled at Syowa 95 and Syowa 96, hence we treated these as independent data sets.

Results

Colony-year and sex differences

The initial and final body masses did not differ among colony years (Table 1). Body size index did not differ among colony years ($F_{(2,91)} = 0.22$, n.s.; ANOVA). There were no significant colony-year or sex differences in body mass decrease rate (Table 1). Parents made foraging trips that were about twice as long, guarded for a longer duration, and thus visited the colony less frequently with meals in DDU 96 than in Syowa 95 or Syowa 96, and those in the latter two groups did not differ ($P < 0.05$; Table 1). Sex differences were not statistically significant. There were no sex differences in daily underwater time, though the colony-year effects were significant (Table 1). Birds in DDU 96 spent a longer time diving than those in Syowa 95 and Syowa 96 ($P < 0.05$).

Chick survival between 27 December and 20 January was greater in Syowa 95 (100% or 36 of 36 chicks) and Syowa 96 (88% or 30 of 34) than in DDU 96 (55% or 11 of 20, $\chi^2 = 22.21$, $df = 2$, $P < 0.01$). Brood growth rate was greater in Syowa 95 (137.7 ± 46.8 g/day, $n = 20$) and Syowa 96 (133.7 ± 54.1 g/day, $n = 17$) than in DDU 96 (74.3 ± 16.4 g/day, $n = 10$; $F_{(2,44)} = 7.25$, $P < 0.01$) because more pairs lost *a* or *b* chicks in DDU 96. Chick growth rate did not differ among colonies ($F_{(2,73)} = 1.13$, n.s.).

Meal frequency and brood growth

There were positive effects of meal frequency on brood growth for females in all of the colony years and for males in Syowa 96, though the effects were not significant for males in Syowa 95 and DDU 96 (Fig. 2). Pairs that brought meals more frequently (sum of female and male meal frequencies) raised faster-growing broods (Fig. 2). Four pairs reared single-chick broods in Syowa 95, four pairs lost one of two chicks in Syowa 96, and only one pair reared two chicks until the end of the study period in DDU 96. Excluding these pairs, the effects of meal frequency were still significant for males in Syowa 96 ($r^2 = 0.81$, $n = 13$, $P < 0.01$), females in DDU 96 ($r^2 = 0.43$, $n = 9$, $P < 0.05$) and pairs in Syowa 96 ($r^2 = 0.72$, $n = 13$, $P < 0.001$). The effects were marginal in pairs in DDU 96 ($r^2 = 0.32$, $n = 9$, $P = 0.07$). No significant effects were found in females in Syowa 96 ($r^2 = 0.22$, $n = 17$, n.s.), in males in DDU 96 ($r^2 = 0.00$, $n = 9$, n.s.), and in males, females, or pairs in Syowa 95 ($r^2 = 0.00$ – 0.09 , $n = 16$, n.s.); probably because of the small variation in meal frequency in two-chick broods, the effects might not have been detected.

Body condition and brood growth

The effects of parental body condition on brood growth rates varied between sexes and among colonies. Males having a better body condition reared faster-growing broods in Syowa 95 and Syowa 96, but the effects were not significant in DDU 96 (Fig. 3). Excluding single-chick broods, the effects were still significant for males in Syowa 95 ($r^2 = 0.29$, $n = 16$, $P < 0.05$) and Syowa 96 ($r^2 = 0.38$, $n = 13$, $P < 0.05$). Female body condition did not affect the brood growth rate in any of the colony years (Fig. 3). Body condition did not affect meal frequency (both sexes in any of the colony years, $r^2 = 0.00$ – 0.12 , $n = 10$ – 20 , n.s.). Parental mass decrease rate did not correlate with brood growth or meal frequency (both sexes in any of the colony years, $r^2 = 0.00$ – 0.03 , $n = 8$ – 20 , n.s.).

Table 1. Colony-year and sex differences in trip duration, duration of chick guarding, the meal frequency as shown by the number of colony visits, parental body mass, and underwater time in MONITORED birds through brooding and early crèche stages. Means \pm SDs are shown. Colony and sex effects were examined with two-way ANOVA

	Syowa 95		Syowa 96		DDU 96		Significance	
	Females	Males	Females	Males	Females	Males	Colony year	Sex
Number of birds	20	20	17	17	10	10		
Trip duration (h)	22.5 \pm 4.7	21.3 \pm 3.8	23.2 \pm 8.9	18.4 \pm 6.5	41.9 \pm 17.1	40.1 \pm 19.6	<0.001	n.s.
Guard duration (h)	11.3 \pm 4.4	12.5 \pm 4.7	10.4 \pm 4.1	13.6 \pm 5.1	16.2 \pm 4.6	16.5 \pm 2.7	<0.001	n.s.
Meal frequency (n/day)	0.64 \pm 0.22	0.65 \pm 0.14	0.70 \pm 0.23	0.65 \pm 0.28	0.40 \pm 0.11	0.38 \pm 0.13	<0.001	n.s.
Initial body mass (kg)	4.33 \pm 0.32	4.71 \pm 0.36	4.17 \pm 0.34	4.58 \pm 0.39	4.08 \pm 0.32	4.91 \pm 0.55	n.s.	<0.001
Final body mass (kg)	4.05 \pm 0.35	4.31 \pm 0.24	3.80 \pm 0.21	4.29 \pm 0.39	3.99 \pm 0.21	4.54 \pm 0.40	0.06	<0.001
Mass decrease rate (g/day) ^a	11.5 \pm 13.4	17.5 \pm 13.0	13.7 \pm 8.4	13.2 \pm 7.4	5.0 \pm 8.9	14.2 \pm 18.0	n.s.	0.08
Daily underwater time (h) ^b	4.75 \pm 1.15	4.49 \pm 1.21	5.26 \pm 1.75	4.82 \pm 0.95	7.71 \pm 0.98	6.84 \pm 2.02	<0.001	n.s.

^aThe sample sizes were decreased to 19 females at Syowa 95, 15 and 14 females and males, respectively, at Syowa 96, and 8 females at DDU 96, as some birds were not recaptured

^bThe sample sizes were decreased to 12, 13, 14, 13, 8, and 10 for females and males at Syowa 95, Syowa 96, and DDU 96, respectively

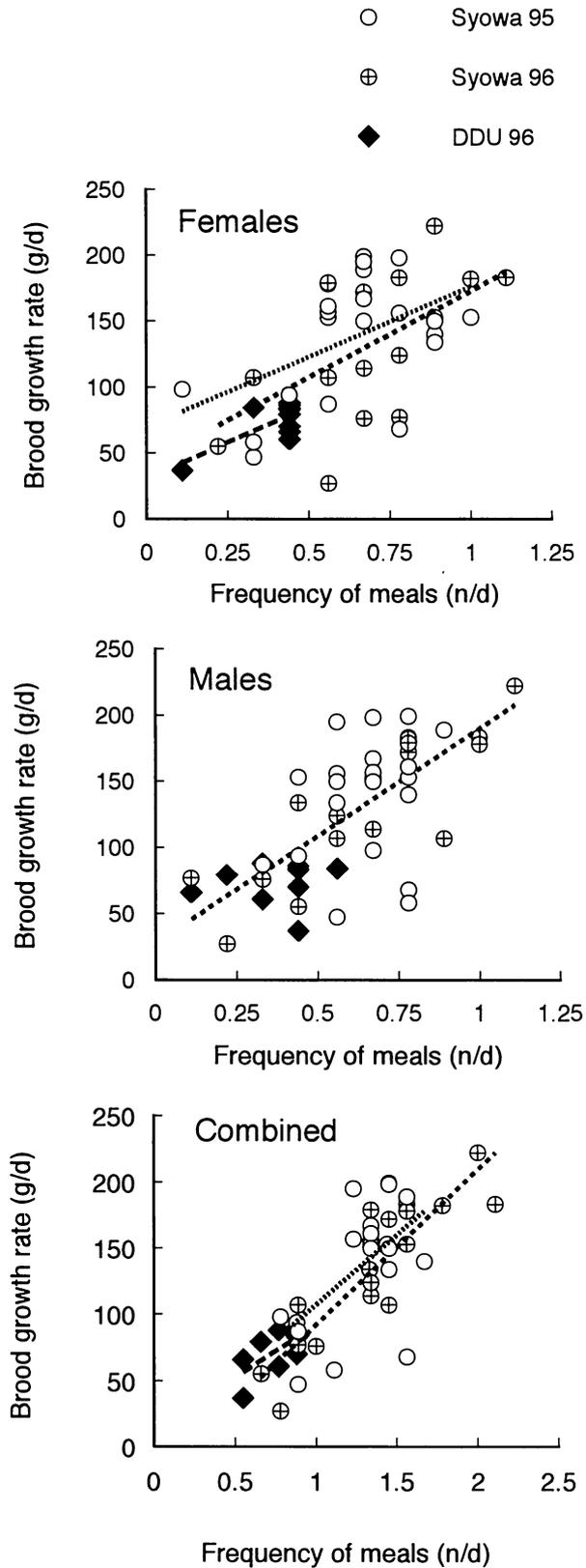


Fig. 2. Effects of meal frequency (number of colony visits per day) by females, by males, and by pairs (male and female frequencies were combined) on brood growth rates where growth rates of *a* and *b* chicks were combined. Statistically significant regressions were found in females at Syowa 95 ($r^2 = 0.21$, $n = 20$, $P < 0.05$), Syowa 96 ($r^2 = 0.26$, $n = 17$, $P < 0.05$), and DDU 96 ($r^2 = 0.45$, $n = 10$, $P < 0.05$), in males at Syowa 96 ($r^2 = 0.69$, $n = 17$, $P < 0.01$), and in pairs (female and male frequencies combined) at Syowa 95 ($r^2 = 0.29$, $n = 20$, $P < 0.01$), Syowa 96 ($r^2 = 0.77$, $n = 17$, $P < 0.01$), and DDU 96 ($r^2 = 0.37$, $n = 10$, $P < 0.05$). No significant effects were found in males at Syowa 95 ($r^2 = 0.01$, $n = 20$, n.s.) and DDU 96 ($r^2 = 0.00$, $n = 10$, n.s.)

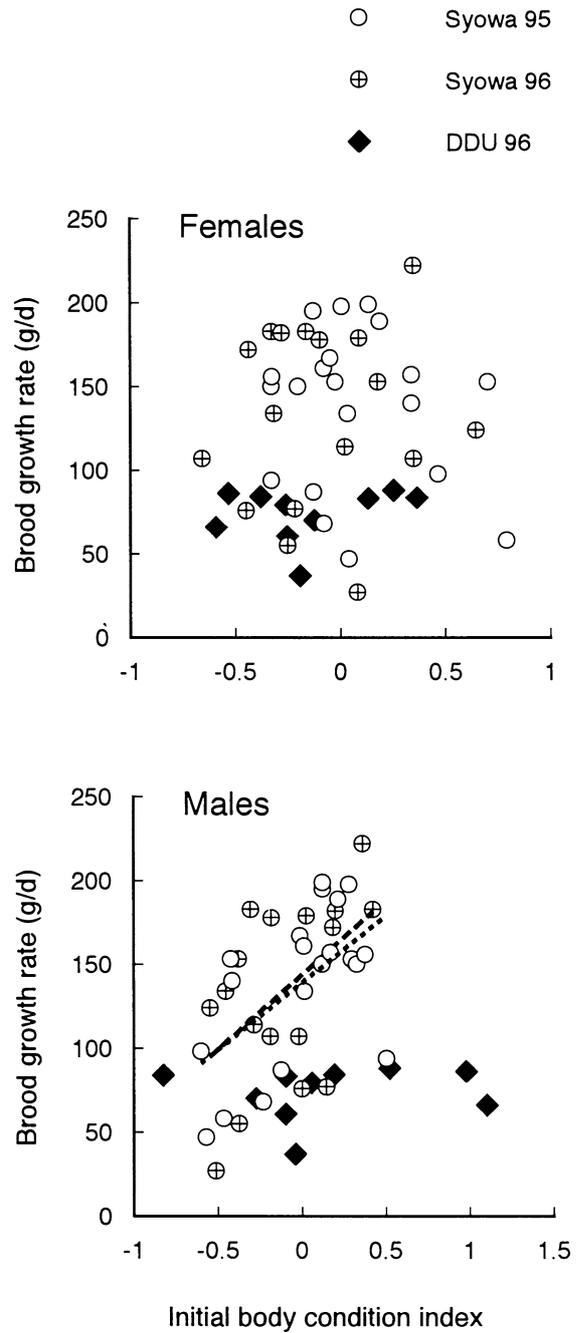


Fig. 3. Effects of initial body condition of parents on their brood growth rate. Effects of females and males are shown separately. Statistically significant regressions were found in males at Syowa 95 ($r^2 = 0.29$, $n = 20$, $P < 0.01$) and Syowa 96 ($r^2 = 0.20$, $n = 17$, $P < 0.05$) but not at DDU 96 ($r^2 = 0.00$, $n = 10$, n.s.). No significant effects were found in females at any of the colony years ($r^2 = 0.00$, n.s.)

Table 2. Colony-year and sex differences in wet mass of meals and energy value of meals based on stomach samples collected from TRIP birds with time-depth-recording data loggers. Means \pm SDs are shown. Colony and sex differences were examined with two-way ANOVA

	Syowa 95		Syowa 96		DDU 96		Significance	
	Females	Males	Females	Males	Females	Males	Colony year	Sex
Number of samples	14	21	10	10	8	20		
Meal size (g wet)	349 \pm 241	373 \pm 195	289 \pm 185	254 \pm 149	476 \pm 198	582 \pm 138	<0.001	n.s.
Energy value (kJ)	1462 \pm 1042	1554 \pm 822	1211 \pm 771	1058 \pm 613	1993 \pm 878	2478 \pm 621	<0.001	n.s.

Underwater time and brood growth

Daily underwater time (sum of underwater time per day) did not affect brood growth rate (both sexes and pairs in any of the colony years; $r^2 = 0.00\text{--}0.13$, $n = 8\text{--}13$, n.s.). The proportion of time at sea and the proportion of underwater time when the birds were out of the colony did not affect the brood growth rate for males or females in any of the colony years ($r^2 = 0.00\text{--}0.23$, $n = 8\text{--}13$, n.s.).

Meal size in TRIP birds

Male and female parents brought meals with similar mass (Table 2). Parents in DDU 96 brought heavier meals with greater energy value than those of parents in Syowa 95 ($P < 0.001$) or Syowa 96 ($P < 0.001$), and the latter two did not differ. No significant effects of body condition or body size index were found on mass or on the energy value of meals (both sexes in any of the colony years; $r^2 = 0.00\text{--}0.12$, $n = 8\text{--}21$, n.s.).

Discussion

Adélie penguin males with a better body condition raised faster-growing broods in Syowa 95 and Syowa 96 but not in DDU 96 (Fig. 3). The result was the same if we used only two-chick broods at Syowa to rule out the possibility that loss of the chicks affected food provisioning. The mechanisms by which the body condition of our male Adélie penguins affects brood growth rate are uncertain. Brood growth rate could be an increasing function of daily food provisioning, that is, meal size \times meal frequency, in seabirds (Huin et al. 2000; Suryan et al. 2002). Parents with a better body condition or larger size bring larger meals more frequently in some species of seabirds (Barbraud et al. 1999; Sæther et al. 1996; Lorentsen 1996; de Leon et al. 1998). We did not detect significant effects of body condition on meal frequency or meal size, though our sample size for each sex at each colony might be too small to make unambiguous conclusions.

Parents with a better body condition may have a high capacity to share more energy with their offspring (Lorentsen 1996) without negative consequences on future reproduction (Wendeln and Becker 1999). We did not find a positive correlation between the initial body condition

and the mass decrease rate, indicating that the energy deficit might not depend on body condition in our study.

There were large individual variations in the daily underwater time (2.4–9.5 h) and in the proportion of underwater time per time out of the colony (14–69%), though these foraging parameters did not significantly affect brood growth rate in either colony. Meal size was independent of underwater time in Adélie penguins breeding at Syowa 95 and 96 and DDU 96, and the estimated food intake per underwater time varied among trips taken by different individuals (Watanuki et al. 2002). These findings imply a large individual variation in the amount of food taken per unit of diving time or in the proportion of energy invested in chicks; hence the effects of foraging time on food provisioning might be ambiguous.

Why was the effect of body condition on brood growth rate observed only at Syowa? The difference in the foraging distance between colonies might be one of the reasons. Parents foraged in small areas of open water in ice cracks along the coast or around icebergs within 1.0–2.1 km of the colony at Syowa 95 because the fast sea ice limited the foraging sites (Watanuki et al. 1999). These birds regularly alternated short trips and short periods of chick guarding, resulting in large meal frequency (Table 1). At DDU, the penguins foraged in the continental shelf or shelf break at a maximum of 36–37 km from the colony by making 25- to 32-h foraging trips during the chick-rearing period in 1994/1995 (Wienecke et al. 2000). The birds may have foraged in waters distant from the colony in the study season (1996/1997) at DDU, as they made longer foraging trips (40–42 h, Table 1). Adélie penguins are known to make longer trips when they forage in more distant places (Clarke et al. 1998).

In areas where Adélie penguins forage in distant places, parents lose greater mass while they are guarding chicks and they have to offset this body mass loss during long foraging trips (Clarke 2001; Watanuki et al. 2002). Thus, parents in DDU 96 may have experienced a large fluctuation of body mass within a foraging cycle. Because of this unpredictability of body condition, individual parents might not invest more in chicks even if they have a better body condition at the start of the chick-rearing period. The mean and variability of prey abundance in foraging areas may also explain these regional differences in the effects of body condition, which should be examined further.

Why was the effect of body condition on brood growth observed only in males? Male Adélie penguins forage in areas closer to the colony than females in the Mawson area and Tera Nova (Clarke et al. 1998). Based on a larger sam-

ple size at various colonies, females seemed to make longer trips than males (Watanuki et al. 2002). However, no clear sex differences in trip duration, meal frequency, and meal energy value were found in this study (Tables 1, 2). Therefore, sex differences in foraging parameters might not be essential factors in this sex difference in the effect of body condition.

Males might have a greater energy reserve than females. At Palmer station in the Antarctic peninsular, where the body masses of chick-rearing male (4.18–4.19 kg) and female (3.70–3.87 kg) Adélie penguins were similar to those in our study, the body masses of males and females at the end of the fast during courtship and incubation were 3.34 kg and 3.49 kg, respectively (Chappell et al. 1993). Male and female Adélie penguins at the end of the fast at Palmer had similar (8–9%, Chappell et al. 1993) lipid contents to that of emperor penguins *Aptenodytes forsteri* (9%) leaving the colony (Groscolas 1990), hence these birds may be at a critical body condition. The body mass of males at the end of our study (Table 1) was 28–36% greater than that at the end of the fast at Palmer, and the body mass of females at the end of our study was only 9–16% greater than that at the end of the fast at Palmer. Therefore, females might have a smaller safety margin, that is, the difference between the working body mass and that at brood desertion, than do males. We propose that in our study areas, males having a better body condition than females have the potential to regulate energy transfer to the chicks depending on their body condition. Similarly, parents of yellow-nosed albatrosses *Diomedea chlororhynchos* can regulate the mass decrease rate that will be transformed into an investment in chicks only in an environment where parents have a greater safety margin (Weimerskirch et al. 2001).

In conclusion, the weak but significant positive correlation between body condition and brood growth found in males at Syowa suggests that the regional difference in the foraging distance and the sex difference in the body energy reserve may limit the capacity to regulate parental investment in Adélie penguins.

Acknowledgments We are grateful to Y. Miyamoto, H. Ichikawa, Y. Niizuma, D. Rodary, and W. Bonreau for field assistance, B. Leroy and S. Ushio for arranging satellite image data of sea-ice distribution, M. Takagi and two anonymous referees for invaluable comments on the manuscript. Logistical and financial support were provided by National Institute of Polar Research, Institut Français pour la Recherche et la Technologie Polaires and Terres Australes et Antarctiques Françaises. We especially thank members of JARE 37 and 38 at Syowa, and those of Missions 46 and 47 at DDU for kind assistance and Prof. Y. Naito for his help in all phases of the research.

References

- Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biol* 20:311–319
- Ballard G, Ainley DG, Ribic C, Barton KR (2001) Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. *Condor* 103:481–490
- Barbraud G, Weimerskirch H, Robertson GG, Jouventin P (1999) Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *J Anim Ecol* 68:1179–1192
- CCAMLR (1991) CCAMLR ecosystem monitoring program: standard methods for monitoring studies. CCAMLR, Hobart, Australia
- Chappell MA, Janes DN, Shoemaker VH, Bucher TL, Maloney SK (1993) Reproductive effort in Adélie penguins. *Behav Ecol Sociobiol* 33:173–182
- Chastel O, Weimerskirch H, Jouventin P (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246
- Chaurand T, Weimerskirch H (1994) The regular alternation of short and long trips in the Blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J Anim Ecol* 63:275–282
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. *Polar Biol* 20:248–258
- Clarke J, Kerry K, Irvine L, Philips B (2002) Chick provisioning and breeding success of Adélie penguins at Bechervaise Island over eight successive seasons. *Polar Biol* 25:21–30
- Clarke JR (2001) Partitioning of foraging effort in Adélie penguins provisioning chicks at Bechervaise Island, Antarctica. *Polar Biol* 24:16–20
- Croxall JP, McCann TS, Prince PA, Rothery P (1988) Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987. In: Sahrhage D (ed) Antarctic ocean and resources variability. Springer, Berlin Heidelberg New York, pp 261–285
- de Leon A, Fargallo JA, Moreno J (1998) Parental body size affects meal size in the chinstrap penguin (*Pygoscelis antarctica*). *Polar Biol* 19:358–360
- Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increase in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol* 11:525–531
- Groscolas R (1990) Metabolic adaptations to fasting in emperor and king penguins. In: Davis LS, Darby JT (eds) Penguin biology. Academic Press, San Diego, Calif., pp 269–296
- Hamer KC, Monaghan P, Uttley JD, Walton P, Burns MD (1993) The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis* 135:255–263
- Houston AI, Thompson WA, Gaston AJ (1996) The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the thick-billed Murre. *Funct Ecol* 10:432–439
- Huin N, Prince PA, Briggs DR (2000) Chick provisioning rates and growth in black-browed albatross *Diomedea melanophrys* and grey-headed albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 142:550–565
- Hull CL (1997) The effect of carrying devices on breeding royal penguins. *Condor* 99:530–534
- Kato A, Watanuki Y, Naito Y (2003) Annual and seasonal changes in foraging site and diving behavior in Adélie penguins. *Polar Biol* 26:389–395
- Kerry KR, Agnew DJ, Clarke JR, Else GD (1992) The use of morphometric parameters for determination of sex of Adélie penguins. *Wildl Res* 19:657–664
- Kerry KR, Clarke JR, Else DG (1995) The foraging range of Adélie penguins at Bechervaise Island, Mac. Robertson Land, Antarctica as determined by satellite telemetry. In: Dann P, Norman I, Reilly P (eds) The penguins, ecology and management. Surrey Beatty, Chipping Norton, Australia, pp 216–243
- Kitaysky AS, Hunt GL Jr, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296
- Lishman G (1985) The food and feeding ecology of Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) at Signy Island, South Orkney Islands. *J Zool (Lond)* 205:245–263
- Lorentsen S-H (1996) Regulation of food provisioning in the Antarctic petrel *Thalassoica antarctica*. *J Anim Ecol* 65:381–388
- Moe B, Langseth I, Fyhn M, Gabrielsen GW, Bech C (2002) Changes in body condition in breeding kittiwakes *Rissa tridactyla*. *J Avian Biol* 33:225–234
- Monaghan P, Uttley JD, Burns MD, Thaine C, Blackwood J (1989) The relationship between food supply, reproductive effort and

- breeding success in Arctic terns *Sterna paradisaea*. *J Anim Ecol* 58:261–274
- Monaghan P, Wright PJ, Bailey MC, Uttley JD, Walton P, Burns MD (1996) The influence of changes in food abundance on diving and surface-feeding seabirds. In: Montevecchi WA (ed) *Studies of high-latitude seabirds 4. Trophic relationships and energetics of endotherms in cold ocean systems*. Can Wildl Serv Occas Pap 91:10–19
- Niizuma Y, Takahashi A, Tokita N, Hayama S (2000) A body condition index based on body mass and external measurements of live leach's storm-petrels. *Jpn J Ornithol* 49:131–137
- Rodary D, Wienecke BC, Bost CA (2000) Diving behaviour of Adélie penguins (*Pygoscelis adeliae*) at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. *Polar Biol* 23:113–120
- Sæther B-E, Lorentsen S-H, Tverra T, Andersen R, Pedersen HC (1996) Size-dependent variation in reproductive success of a long-lived seabird, the Antarctic petrel (*Thalassoica antarctica*). *Auk* 114:333–340
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Suryan RM, Irons DB, Benson J (2000) Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *Condor* 102:374–384
- Suryan RM, Irons DB, Kaufman M, Benson J, Jodice PGR, Roby DD, Brown ED (2002) Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser* 236:273–287
- Trivelpiece WZ, Trivelpiece SG, Geupel GR, Kjelson J, Volkman NJ (1990) Adélie and chinstrap penguins: their potential as monitors of Southern Ocean marine ecosystem. In: Kerry KR, Hempel G (eds) *Antarctic ecosystems: ecological change and conservation*. Springer, Berlin Heidelberg New York, pp 191–202
- Tverra T, Sæther BE, Anes R, Erikstad K (1998) Regulation of food provisioning in the Antarctic petrel: the importance of parental body condition and chick body mass. *J Anim Ecol* 67:699–704
- Watanuki Y, Mori Y, Naito Y (1992) Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. *Polar Biol* 12:539–544
- Watanuki Y, Kato A, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. *J Anim Ecol* 62:634–646
- Watanuki Y, Kato A, Naito Y, Robertson G, Robinson S (1997) Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biol* 17:296–304
- Watanuki Y, Miyamoto Y, Kato A (1999) Dive bouts and feeding sites of Adélie penguins rearing chicks in an area with fast sea ice. *Colon Waterbirds* 22:120–129
- Watanuki Y, Kato A, Sato K, Niizuma Y, Bost CA, Le Maho Y, Naito Y (2002) Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biol* 25:672–681
- Weimerskirch H, Cherel Y, Guenot-Chaillet F, Ridoux V (1997) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78:2051–2063
- Weimerskirch H, Zimmermann L, Prince P (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behav Ecol* 12:22–30
- Wendeln H, Becker PH (1999) Effects of parental quality and effort on the reproduction of common terns. *J Anim Ecol* 68:205–214
- Wernham CV, Bryant DM (1998) An experimental study of reduced parental effort and future reproductive success in the puffin, *Fratercula arctica*. *J Anim Ecol* 67:25–40
- Wienecke BC, Lawless R, Rodary D, Bost C-A, Thomson R, Pauly T, Robertson G, Kerry KR, Le Maho Y (2000) Adélie penguins foraging behaviour and krill abundance along the Wilkes and Adélie land coasts, Antarctica. *Deep-Sea Res II* 47:2573–2587
- Wilson RP (1984) An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–112
- Wilson RP, Ryan PG, Wilson M-P (1989a) Sharing food in the stomachs of seabirds between adults and chicks—a case for delayed gastric emptying. *Comp Biochem Physiol* 94:461–466
- Wilson RP, Coria NR, Spairani HJ, Adelung D, Culik B (1989b) Human-induced behavior in Adélie penguins *Pygoscelis adeliae*. *Polar Biol* 10:77–80
- Ydenberg RC (1994) The behavioral ecology of provisioning in birds. *Ecoscience* 1:1–14