INDIVIDUAL VARIATION OF FORAGING BEHAVIOR AND FOOD PROVISIONING IN ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*) IN A FAST-SEA-ICE AREA

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Abstract.—To understand the effects of foraging behavior on the amount of food provided to chicks (meal mass and frequency), we monitored nest attendance and diving behavior of 20 Adélie Penguin (*Pygoscelis adeliae*) pairs that were rearing chicks. Because ice forms on the sea surface at night, parents foraged through cracks or within leads in the sea ice mainly during 0800–2400 hours. Birds that departed the colony in the afternoon and returned in the evening of the same day fed their chicks more frequently than those that made longer trips (i.e., those that departed in the afternoon and returned the next day or departed in the early morning and returned that evening). When the duration of the longest dive bout during each trip was longer, parents brought back heavier meals that contained larger krill. On average, birds made longer dive bouts when diving to greater depths. Thus, daily foraging pattern and foraging depth affected the provisioning rate, but the proportion of time spent foraging during the potential foraging period, total underwater time per day, and parental body condition were not. We suggest that temporal variability in prey availability and individual differences in foraging behavior affect the provisioning rate and, thus, chick growth. *Received 1 August 2008, accepted 4 November 2009.*

Key words: Adélie Penguin, diving, provisioning, *Pygoscelis adeliae*, sea ice, trip duration.

Variación Individual en el Comportamiento de Forrajeo y la Entrega de Alimento en *Pygoscelis adeliae* en Áreas Marinas con Hielo

Resumen.—Para entender los efectos del comportamiento de forrajeo sobre la cantidad de alimento entregada a los pichones (masa y frecuencia de las meriendas), monitoreamos la atención de los nidos y el comportamiento de buceo de 20 parejas de pingüinos *Pygoscelis adeliae* que estaban criando pichones. Debido a que sobre la superficie del mar se forma hielo en la noche, los padres forrajearon a través de grietas o en áreas de aguas abiertas rodeadas por hielo marino principalmente entre las 0800 y las 2400 horas. Las aves que abandonaron la colonia en la tarde y regresaron en la noche del mismo día alimentaron a sus pichones más frecuentemente que las que hicieron viajes más largos (i.e., aquellas que salieron en la tarde y regresaron al día siguiente, o las que salieron temprano en la mañana y regresaron esa noche). Cuando la duración de la inmersión más larga de cada viaje fue mayor, los padres trajeron meriendas más pesadas que contenían krill de mayor tamaño. En promedio, las aves realizaron inmersiones más prolongadas cuando se sumergían a mayores profundidades. Por lo tanto, el patrón diario de forrajeo y la profundidad de forraejo afectaron la tasa de aprovisionamiento, pero la proporción del tiempo invertido forrajeando durante el período potencial de forrajeo, el tiempo total bajo el agua por día y la condición corporal no la afectaron. Sugerimos que la variación temporal en la disponibilidad de presas y las diferencias individuales en el comportamiento de forrajeo afectan la tasa de aprovisionamiento y, por lo tanto, el crecimiento de los pichones.

Individual variation in foraging effort, foraging efficiency, and energy allocation to offspring contribute greatly to individual differences in reproductive success of seabirds (Pugesek 1983, Reid 1988, Thomas and Coulson 1988, Lewis et al. 2006, Daunt et al. 2007). Individuals often differ in choice of foraging site and foraging time (Irons 1998, Hamer et al. 2001), and these differences presumably cause variation in the dynamics of chick provisioning by individual pairs. The provisioning rate (energy delivered to chicks per day) is a function of meal frequency (number of meals brought per day) and mass of a single meal. Thus, how foraging behavior relates to these two components is a key question.

There are large intercolony, interannual, and individual differences in the frequency and mass of meals fed to chicks in the Adélie Penguin (*Pygoscelis adeliae*; Ainley et al. 1998, Ballard et al. 2001, Salihoglu et al. 2001, Clarke et al. 2002, Watanuki et al. 2002). Individual variation in trip duration may be affected by distance to feeding sites (Clarke et al. 2006), guard duration on land, and body condition (Clarke 2001). In turn, trip duration and foraging time affect meal frequency, meal mass, and parental body-mass gain, sometimes in a nonlinear fashion (Chappell et al. 1993, Ainley et al. 1998, Watanuki et al. 2002). Duration of dive bouts, defined as a series of dives, in the latter part of a trip may also affect meal mass, because parents probably collect food for their chicks during later foraging bouts (Croxall and Davis 1990).

Fast sea ice remains in Lützow-Holm Bay, Antarctica, during summer, and Adélie Penguins walk across the ice to forage in small open cracks (<15 m long) within 4 km of the colony (Watanuki et al. 2003). At night (2400–0800 hours local time), the cracks become closed by new ice (Watanuki et al. 1997). Thus, a limited number of foraging sites in predictable locations are used, and foraging time is not critically affected by searching for feeding sites but is limited by ice formation during the night. Large individual variations exist in foraging sites used, trip duration, dive depth, daily underwater time, and body condition (Takahashi et al. 2003, Watanuki et al. 2003), but how these differences affect nestling provisioning is not known.

We studied how individual variations in foraging behavior and body condition affected the frequency and mass of meals delivered to chicks and, hence, the provisioning rate. We analyzed factors that affected the durations of each foraging trip and dive bout, factors that determined the mean meal frequency delivered by each parent and the mean provisioning rate of each pair, and factors that affected the meal mass returned to chicks.

Methods

Study area and field work.—The study was conducted at Hukuro Cove colony (150–200 pairs; 69.0°S, 39.6°E), 30 km south of Syowa Station, in summer 1999–2000. Fast sea ice (>1 m thick) was present throughout the study period, from 26 December 1999, when the last chicks had hatched, to 10 February, when the first 10 fledglings left the colony. We focused on behavior during the "brood stage" (28 December–11 January), when male and female parents foraged and guarded the chicks alternately. This is the most critical stage for reproductive success in Adélie Penguins (Clarke et al. 2002).

Monitored birds.—Between 26 and 28 December, we captured both parents of 20 pairs with two-chick broods, about 5 days after hatching, and designated them as "monitored" birds. Parents departing the colony, presumably with empty stomachs, were weighed and marked (Watanuki et al. 2002). Bill depth, bill length, bill and head length, flipper width at the carpal joint, and total flipper length (from the tip to the base of the frontal edge) were measured. Sex was determined using the depth and length of the bill and flipper width following Kerry et al. (1992). The first principal component (PC1) in a principal component analysis of these five measures, which explained 62% of the total variation ($n = 40$), was used as the body size index. We used size-corrected body mass as the body condition index (Chastel et al. 1995). Regression of body mass on body size index yielded almost identical results for

females and males, so we pooled female and male data and used the residual mass of each bird as its body condition index.

To measure nest attendance and diving behavior, radio transmitters and data loggers (see below) were attached to the lower back of all monitored birds with Tesa tape (Beiersdorf AG, Hamburg, Germany) and plastic cable ties (Wilson et al. 1997). These were later removed between 25 January and 1 February. Radiotransmitters (diameter: 10 mm; length: 45 mm; mass: 9.5 g, with a 20-cm aerial; ATS, Isanti, Minnesota) operating at 146–148 MHz were used. The nest attendance of birds was recorded with an RX-900 receiver (Televilt, Lindesberg, Sweden) every 4 min (Watanuki et al. 2003), and trip and guard duration were calculated using departure and arrival time. We assumed that the parents fed their chicks upon every colony visit (Y. Watanuki pers. obs.). Feeding locations were determined almost every day by triangulation from two stations once or twice during the evening (Watanuki et al. 2003).

Data loggers (UME 200DT; diameter: 15 mm; length: 50 mm, with a domed top; mass including battery: 14.0 g; Little Leonardo, Tokyo) were programmed to record depth at 3-s intervals with 1-m accuracy over a 4-week period. Dives shallower than 1 m were excluded because these fell within the error range of the instrument. Data were analyzed with IGOR PRO software (Wave Metrics, Lake Oswego, Oregon) to obtain, for each bird, dive depth and duration and time on the surface after the dive. We assumed that all dives were foraging dives (Watanuki et al. 1999). All dives seemed to be V-shaped, a form typically used for foraging under fast ice with no clear bottom (Watanuki et al. 1999). Dive bout duration was obtained by determining the inflection point (186 to 414 s) of the distribution of surface time on a log scale by a nonlinear least-squares analysis (Sibly et al. 1990).

To estimate the provisioning rate (kg brood^{-1} day^{-1}) for each pair, the chicks were marked and weighed every 5 days (Watanuki et al. 2002). Repeated weighing did not affect chick survival (Watanuki et al. 1992). We estimated the daily mass change of the chicks by assuming a linear growth rate. We estimated the mass of food eaten by each chick per day from the daily mass change of the chicks, using a linear formula that explained 77% of the variation in the provisioning rate (Watanuki et al. 1994). This formula was not significantly different from that obtained for Adélie Penguins with different foraging patterns at Magnetic Island, Australian Davis Station (Watanuki et al. 1994). Therefore, we believe that it is applicable for different years at the same colony. We combined the meal mass per day of the *a*-chick (first hatched) and the *b*-chick and used the mean value throughout the brood stage as the provisioning rate.

"Trip" birds.—To examine how trip duration, diving behavior, and prey composition affected meal size, we captured another 35 birds that were brooding 1 or 2 chicks as they departed the colony and designated them as "trip" birds. They were measured, weighed, and fitted with time-depth-swim speed-recording data loggers (mass: 50–60 g, diameter: 20–21 mm, length: 100–115 mm; W380M-PDT, Little Leonardo) programmed to record depth at 1-s intervals with 1-m accuracy. These birds left the colony within 1 h of capture. We then watched them continuously for 3–7 days and recaptured them when they returned and before they fed their chicks.

At recapture, the devices were removed and the stomach contents were collected by the water-offloading technique (Wilson

1984), drained, and weighed with an electronic balance; this measurement was defined as the meal mass (Watanuki et al. 2002). Prey items were sorted into Antarctic Krill (*Euphausia superba*), Crystal Krill (*E. crystallorophias*), amphipods, and fish, and each component was then weighed separately. For krill composition, we used subsamples of ~50 g. We measured the total length (from tip of rostrum to end of tail) of 5 to 50 (average = 40.0) individual Antarctic Krill from each sample. The difference between the parental mass at departure and mass at arrival, excluding stomach contents, was taken as the parental mass accumulation.

Sample birds and analyses.—We sampled 8–17 trips of each of the 40 monitored birds during the brood stage. A single pair lost their *b*-chick during the brood stage, and no dive data were collected for a single male because this bird had not returned by the end of the field-work period. Thus, we sampled 1,741–4,924 dives and 56–162 dive bouts from each of 39 birds. We also sampled 142–842 dives during 8–18 dive bouts from each of the 35 trip birds. Foraging sites were available only during the day. Parents departing in the morning may return within that day or extend their trip until the next day, and those departing in the evening may extend the trips. Thus, we categorized trips according to departure and arrival times by a hierarchical cluster analysis using Ward's method in SPSS, version 14 (SPSS, Chicago, Illinois; see Jansen et al. 1998).

To examine factors that affected the duration of each foraging trip and those that affected the duration of each dive bout, we used a linear mixed-effects model in SPSS with birds as the random factor. We estimated the fit of the model by the restricted maximum-likelihood method and examined the significance of the effects of fixed factors with a Type III test. We examined the significance of the covariance parameter estimates (birds) using a Wald Z test. Proportional data (e.g., proportion of underwater time) were arcsine-transformed before analysis. Dive depth and dive bout duration, but not trip duration, were skewed and, hence, were log transformed before analysis.

We examined the direct and indirect effects of the individual means of trip duration, guard duration, dive depth, and dive bout on the meal frequency of each bird and on the mean provisioning rate of each pair of monitored birds using a path analysis in AMOS, version 6 (Amos Development Corporation 1995–2005). We averaged trip duration over 5-day periods (CCAMLR 1991) and used the grand average across all 5-day periods as the mean value for each bird. Mean guard duration was calculated similarly. The path models initially included *a priori* all potential independent variables and covariates, on the basis of our understanding of the foraging behavior of Adélie Penguins in the study area and the results of previous penguin studies (e.g., Chappell et al. 1993, Ainley et al. 1998, Clarke 2001, Walker and Boersma 2003). Paths and covariates with nonsignificant ($P > 0.1$) coefficients were then removed. Among potential models with every combination of path and covariate, the one with the lowest BCC_0 value (Browne-Cudeck fit function criteria) was assumed to be the best-fit model (Browne and Cudeck 1989).

RESULTS

Daily foraging pattern and trip type.—Foraging trips of monitored birds were clustered into three types: trips that started in the afternoon and ended the next afternoon (overnight), those
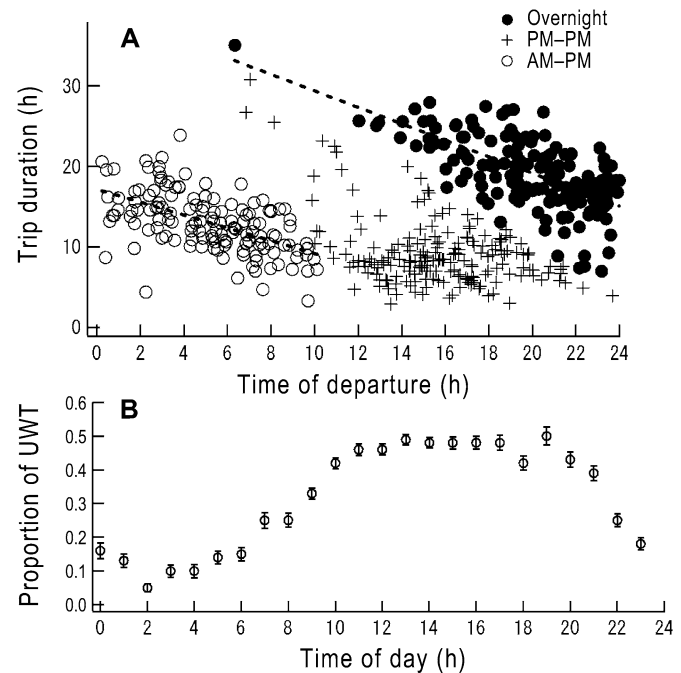

FIG. 1. (A) Trip duration in relation to departure time in monitored Adélie Penguins (see text) breeding at Hukuro Cove colony near Syowa Station, Antarctica, during the brood stage for each trip type. A single overnight trip with an extraordinarily long duration (46.2 h) is not shown. Significant fitted simple linear regression lines are shown for overnight and AM–PM trips (see text). (B) Daily changes in the proportion of underwater time (UWT) during foraging trip in each 1-h period (local time). Means ± 1 SE across individual birds are shown.

that started in the afternoon and ended by midnight (PM–PM), and those that started in the morning and ended that evening (AM–PM) (Fig. 1A). The PM–PM trips were shorter than the overnight and AM–PM trips (Table 1). Males made shorter trips (mean ± SD = 12.0 ± 5.8 h; $n = 248$) than females (15.2 ± 6.0 h; $n = 245$) (Table 1), but the frequency of each type of trip did not differ between the sexes ($\chi^2 = 5.158$, df = 4, nonsignificant).

Between 0800 and 2400 hours, birds spent >20% of the time diving while foraging. They spent less time diving between 2400 and 0800 hours (Fig. 1B), when the sites tended to be covered by ice. Consequently, underwater time per trip was relatively greater during PM–PM trips than during overnight or AM–PM trips (Table 1). Overnight and AM–PM trips, but not PM–PM trips, that started later in the day tended to be shorter (Fig. 1A and Table 1, significant interaction term). Departure time did not affect underwater time (Table 1), nor did pretrip guard duration affect trip duration.

The type of the next trip after an overnight, PM–PM, or AM–PM trip was not random ($\chi^2 = 42.152$, df = 4, $P < 0.001$; Table 2). Cell-by-cell testing showed that birds made PM–PM ($\chi^2 = 10.741$, df = 1, $P < 0.01$) and AM–PM ($\chi^2 = 4.663$, df = 1, $P < 0.05$) trips after trips of the same type more often than would be expected with random combinations of trip types. Birds made PM–PM after overnight trips ($\chi^2 = 9.05$, $P < 0.01$) and AM–PM trips after PM–PM trips ($\chi^2 = 10.460$, df = 1, $P < 0.01$) less often than expected.

Table 1. Trip duration and percentage of time spent underwater (means ± SD) during foraging trips, by trip type (see text for definitions), for Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica. Effects of sex, trip type, trip start time, and guard duration before each trip were examined using a linear mixed-effects model with Type III ANOVA with birds as a random factor. Significance of the covariance parameter (birds) was examined with Wald Z. Sample sizes were 494 trips of 40 monitored birds (see text), except for underwater time, because diving data were not collected for one bird and during some trips.

Trip type	Trip duration (h)	Underwater time (%)
Overnight	19.3 ± 4.3	26.6 ± 9.7
PM–PM	9.2 ± 4.3	41.4 ± 14.4
AM–PM	13.0 ± 3.7	36.3 ± 11.8
Fixed effects		
Sex	$F = 13.8$, df = 1 and 36.3, $P < 0.01$	$F = 1.7$, df = 1 and 38.5, $P = 0.20$
Trip type	$F = 42.2$, df = 2 and 439.0, $P < 0.001$	$F = 17.0$, df = 2 and 399.4, $P < 0.001$
Time of day	$F = 148.6$, df = 1 and 441.3, $P < 0.001$	$F = 2.1$, df = 1 and 392.4, $P = 0.14$
Trip type * time of day	$F = 4.22$, df = 2 and 443.7, $P < 0.05$	$F = 17.0$, df = 2 and 398.7, $P < 0.001$
Guard duration	$F = 1.0$, df = 1 and 440.9, $P = 0.32$	—
Random birds effect	Wald Z = 1.856, P = 0.063	Wald Z = 3.055, $P < 0.01$

Longest dive bout per trip in monitored birds.—Monitored birds tended to make their longest dive bout in the latter part of each trip. We divided the total number of dive bouts in a trip into sequential increments of 10% each and determined the number of trips in which the longest bout occurred in each increment. This number increased along the sequence ($r_s = 1.00$, $P < 0.01$, $n = 10$). In 41% of all trips, the longest bout occurred during the last two increments (20%). The occurrence of the longest bout along the sequence did not differ among types of trips (linear mixed-effects model, $F = 0.5$, df = 2 and 400.9, $P = 0.63$).

Feeding during potential foraging periods.—Birds foraged in the afternoon and stopped diving around midnight during overnight and PM–PM trips. Birds also foraged the next morning during these overnight trips (Fig. 2). On AM–PM trips, birds usually started diving after 0800 hours (Fig. 2). Thus, the four potential foraging periods (time between the first and last dive, excluding surface times longer than 2 h; Watanuki et al. 1999) can be classified as follows: afternoon on an overnight trip, morning on an overnight trip, afternoon on a PM–PM trip, and morning on an AM–PM trip.

The underwater time per potential foraging period did not differ among potential foraging periods (Table 3). By contrast, the duration of the longest dive bout during afternoon foraging on overnight trips was about half that during other potential foraging periods (Table 3). Moreover, the duration of the longest bout became shorter at later times of day only during afternoon foraging periods (significant interaction term).

Table 2. Frequency of each trip type (see text for definitions) that followed immediately after the three possible trip types for Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica.

Trip type	Type of following trip		
	Overnight	PM–PM	AM–PM
Overnight	57	35	50
PM–PM	50	100	27
AM–PM	31	46	48

Meal frequency.—We found large individual variation in mean trip duration (8.4–21.4 h), mean guard duration (7.1–22.3 h), proportion of PM–PM trips (0.00–0.73), and mean meal frequency (0.60–1.13 day^{-1}). Meal frequency did not differ between males (0.85 ± 0.10 day^{-1}; $n = 20$) and females (0.83 ± 0.13 day^{-1}; $n = 20$) ($F = 0.365$, df = 1 and 38, nonsignificant). Mean trip duration was shorter for birds that made more PM–PM trips and foraged at sites closer to the colony, and meal frequency was higher for birds whose mean trip duration and guard duration were shorter (Fig. 3A, B). The path analysis showed that body condition was independent of mean trip duration, mean guard duration, and meal frequency.

Dive depth and dive bout duration in monitored birds.—Dive bout duration increased with the mean dive depth in monitored birds (linear mixed-effects model with the type of bout fixed, birds a random factor, and the mean dive depth of each bout a covariate; $F = 234.7$, df = 1 and 3,923, $P < 0.001$; Fig. 4A), but the effect of dive depth was smaller on the longest bouts (significant interaction term, $F = 35.8$, df = 1 and 3,926.4, $P < 0.001$; Fig. 4A).
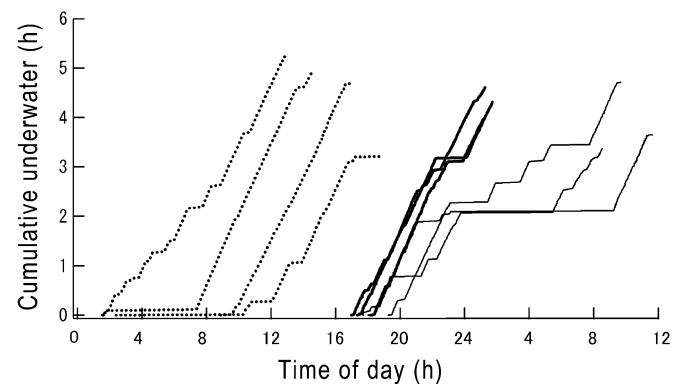

Fig. 2. Typical patterns of cumulative underwater time in relation to trip departure time (0000–2400 hours) for Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica. Data from all 10 trips of a single monitored bird (see text) are shown. Dotted lines = AM–PM trips, bold solid lines = PM–PM trips, and light solid lines = overnight trips (see text for definitions).

TABLE 3. Percentage of time spent underwater and duration of the longest dive bout during potential foraging periods (means ± SD) for Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica. Effects of the potential foraging period and the start time of the potential foraging period were examined using a linear mixed-effects model with a Type III ANOVA with birds as a random factor. Significance of the covariance parameter (birds) was examined with Wald Z. Sample sizes were 545 potential foraging periods of 39 monitored birds.

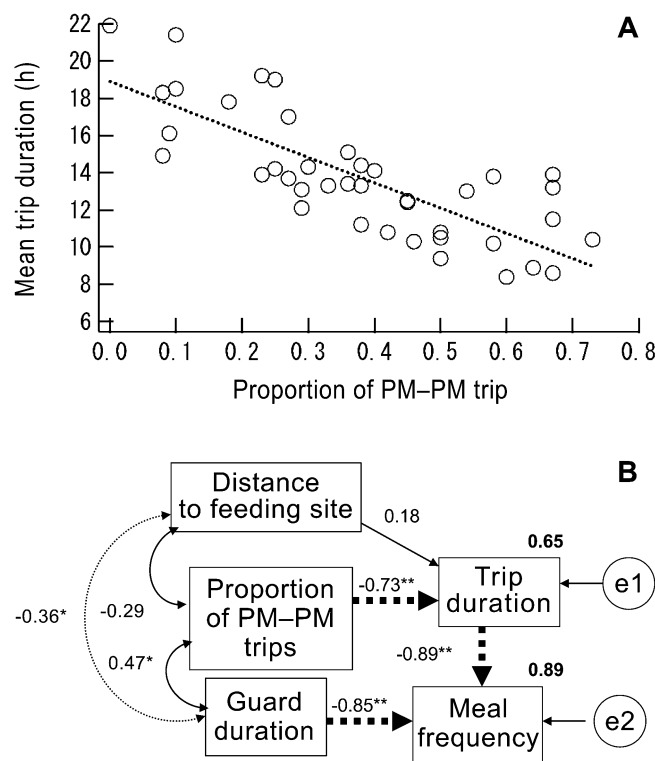| Potential foraging period	Underwater time (%)	Duration of the longest bout (min)
Afternoon on overnight trip	48.3 ± 13.2	71.2 ± 54.5
Morning on overnight trip	47.5 ± 18.8	158.7 ± 100.3
Afternoon on PM–PM trip	52.1 ± 11.3	153.3 ± 85.7
Morning on AM–PM trip	45.9 ± 11.5	176.3 ± 102.6
Fixed effects		
Potential foraging period	$F = 0.9$, df = 3 and 509.4, $P = 0.46$	$F = 2.7$, df = 3 and 511.9, $P = 0.04$
Time of day	$F = 0.9$, df = 1 and 510.6, $P = 0.35$	$F = 3.3$, df = 1 and 513.1, $P = 0.07$
Potential foraging period * time of day	$F = 0.7$, df = 3 and 510.9, $P = 0.56$	$F = 3.0$, df = 3 and 513.3, $P = 0.03$
Random birds effect	Wald Z = 2.531, $P < 0.05$	Wald Z = 2.405, $P < 0.05$

FIG. 3. (A) Mean trip duration in relation to the proportion of PM–PM trips taken by each monitored Adélie Penguin (see text for definitions). Data collected at breeding at Hukuro Cove colony near Syowa Station, Antarctica. The fitted significant linear regression line shows the trend. (B) Path analysis results for mean trip duration and mean meal frequency of individuals. The standard partial regression coefficient (*$P < 0.05$; **$P < 0.01$) and the square of the multiple correlation coefficient are shown on the paths and to the upper right of the dependent-variable boxes, respectively. e1 and e2 are errors. Only paths and covariates of the best-fit model are shown. Paths with a negative partial regression coefficient are shown by thick broken lines. Body condition index had no significant effect or covariance in the model and is not shown.
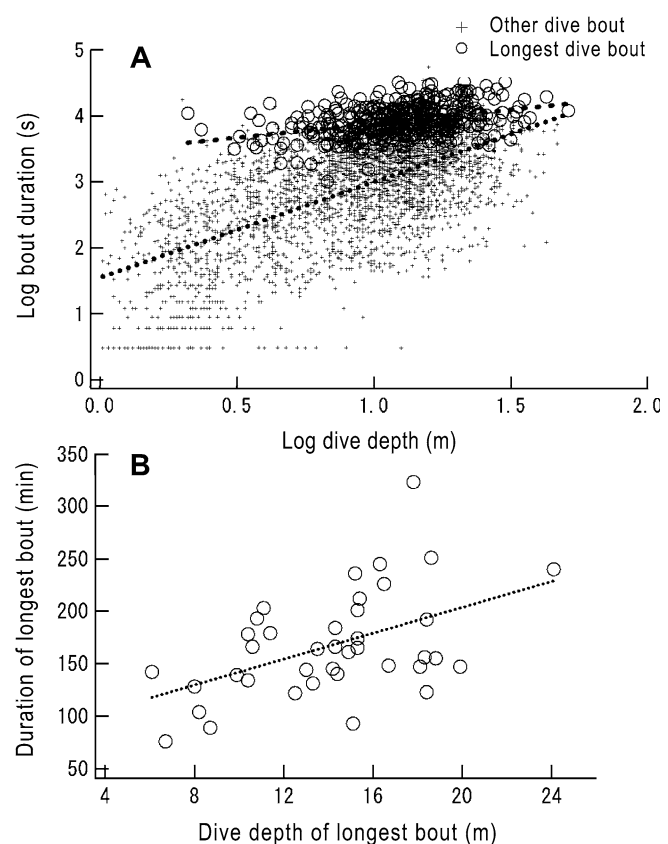

FIG. 4. (A) Dive bout duration in relation to mean dive depth for the longest dive bout per trip and for all other dive bouts in monitored (see text) Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica. (B) Dive bout duration in relation to mean dive depth for individual birds (mean values). Simple significant linear regression line trends are shown.

To examine the effect of the sequence of dives on dive depth, 20 dive bouts of 10 arbitrarily chosen birds were sampled. Dive depth increased during 6 bouts ($r = 0.209$ to 0.589, $P < 0.05$) and decreased during 4 bouts ($r = -0.411$ to -0.174, $P < 0.05$), and no significant trends were found during the other 10 bouts ($r = -0.261$ to 0.131, nonsignificant).

There was large individual variation in dive depth during the longest dive bout per trip (Fig. 4B). The duration of the longest dive bout per trip in individual birds increased with their average dive depth during longest bouts (standard partial regression coefficient, $\beta = 0.24$, $P < 0.001$; square of multiple correlation coefficient, $R^2 = 0.491$; Fig. 4B), whereas the body size index was independent of the mean dive depth (path analysis).

Meal and parental mass in trip birds.—Meal mass varied between 33 and 848 g. Antarctic Krill dominated (78–100% of wet mass), whereas Crystal Krill (0–9%), fish (0–10%), and amphipods (0–1%) were minor prey. We classified each trip by type using the same criteria as for monitored birds. Brood size ($F = 0.062$, df = 1 and 33, $P = 0.805$) and trip type ($F = 0.712$, df = 2 and 32, $P = 0.498$) did not affect meal mass. Birds brought back larger meals that contained larger krill after trips with longer dive bouts per trip (Fig. 5A, B), but trip duration and body mass at departure did not affect meal mass.

Trip duration, body mass at departure, and duration of the longest dive bout did not affect parental mass accumulation during the trip (path analysis). The duration of the longest dive bout did not depend on the mean dive depth of the longest bouts in trip birds, but when all dive bouts were included in the analysis, bout
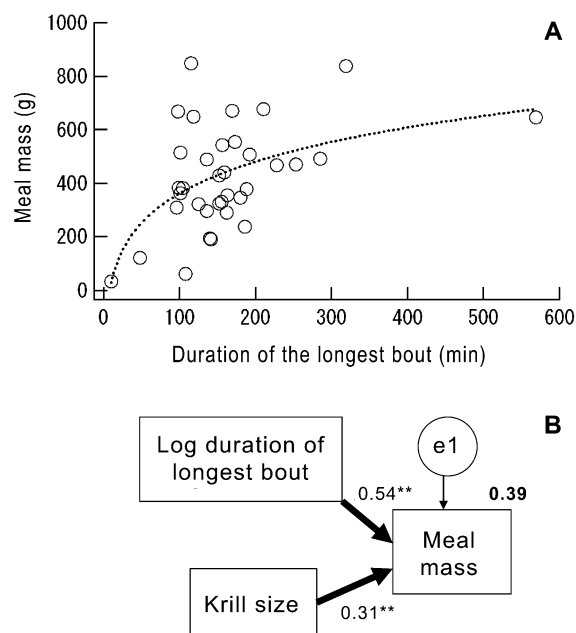
duration increased with mean dive depth ($r = 0.509$, $F = 230.674$, df = 1 and 660, $P < 0.001$) as in monitored birds. Krill size and dive depth were not significantly related.

Provisioning rate.—Excluding the single-chick brood, the mean provisioning rate varied between 0.64 and 1.04 kg day^{-1}, and the brood mass (sum of the masses of the two chicks) at the end of the brood stage varied between 2.65 and 5.00 kg among pairs. Path analyses showed that the provisioning rate increased with the sum of male and female meal frequencies ($\beta = 0.51$, $P < 0.05$; $R^2 = 0.25$) and positively affected brood mass at the end of the brood stage ($\beta = 0.93$, $P < 0.01$; $R^2 = 0.88$). There were no direct effects of underwater time per day or body condition on brood mass.

Meal mass was not measured in monitored birds. Instead, we used the mean duration of the longest dive bout in each trip as a proxy for meal mass in these birds, because in trip birds meal mass increased with the duration of the longest dive bout ($r^2 = 0.47$; Fig. 4). We then obtained meal index as the product of meal frequency and mean duration of the longest dive bout. Pairs with a larger meal index had a higher provisioning rate, which positively affected brood mass (Fig. 6A). Direct effects of underwater time
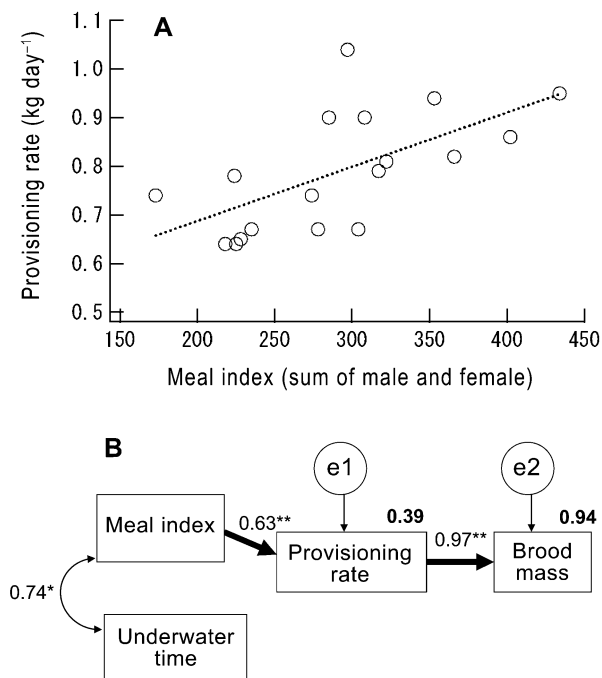

FIG. 6. (A) Provisioning rate in relation to the sum of male and female meal indices (meal frequency × duration of the longest bout per trip) for monitored (see text) pairs of Adélie Penguins breeding at Hukuro Cove colony near Syowa Station, Antarctica. A pair that lost their *b*-chick during the brood stage and another pair for which no male dive data were collected are excluded. The fitted simple linear regression line is shown. (B) Path analysis results for mean meal provisioning rate (kg day^{-1} brood^{-1}) and brood mass (sum of *a*- and *b*-chick masses) at the end of the brood stage. The sum of male and female values (underwater time, meal index, body condition index) were used as independent variables. The mean of the male and female body condition index had no significant effect or covariance in the model and is not shown. For additional explanation, see Figure 3 caption.

FIG. 5. (A) Meal mass in relation to the duration of the longest dive bout during each trip in "trip" Adélie Penguins (see text) breeding at Hukuro Cove colony near Syowa Station, Antarctica. The fitted significant power equation trend line is shown. (B) Path analysis results for meal mass. Initial body mass, trip duration, and mean dive depth of the longest bout had no significant effect and are not shown. For additional explanation, see Figure 3 caption.

per day and body condition were not significant, though underwater time and meal index covaried positively (Fig. 6B). The meal index explained the provisioning rate (39%; Fig. 6B) better than meal frequency alone (25%), which indicates that meal mass also influenced the provisioning rate.

Discussion

Foraging trip and meal frequency.—Penguins (Kooyman et al. 1992, Wilson et al. 1993) and gannets (Garthe et al. 2000) forage mostly during daylight hours, but they sometimes make long overnight trips. Thus, chick-rearing seabird parents must decide whether to return to the colony within a day or extend their foraging until the next day (Lewis et al. 2004). Our study demonstrates the importance of this behavioral decision with regard to meal frequency and, hence, the provisioning rate.

In Adélie Penguins, neither chick growth and survival nor adult foraging-trip duration are adversely affected by the attachment of devices similar in size (2.2–4.9 cm^2 maximum cross section) to that used in this study (1.8–3.5 cm^2) (Watanuki et al. 1992, 2003; Ballard et al. 2001). We believe, therefore, that device effects were small enough to allow individual variation in foraging behavior to be analyzed.

Parents that took shorter trips fed their chicks more frequently (Fig. 3B), and PM–PM trips were the shortest of the three trip types we observed. The duration of the longest dive bout was shorter during afternoon foraging on overnight trips than during PM–PM trips (Table 2). Mori (1998) suggested theoretically that diving birds make longer dive bouts if they encounter a good prey patch. If the parents stop foraging when they obtain a certain amount of prey (Croxall and Davis 1990), then birds encountering good prey patches would return sooner to their offspring, which would result in PM–PM trips. By contrast, birds feeding at poor prey patches—and, hence, making shorter diving bouts—might extend their foraging trip and feed again the next morning to fulfill their own and their chicks' energy demand, which would result in overnight trips (see Ropert-Coudert et al. 2004).

The proportion of PM–PM trips varied among birds, and birds that made relatively more PM–PM trips made shorter trips (Fig. 3A). Moreover, birds tended to make consecutive PM–PM trips, whereas they followed AM–PM or overnight trips with either AM–PM or overnight trips. In fact, the proportion of PM–PM trips was negatively correlated with the proportion of AM–PM trips ($r = -0.739$, $P < 0.001$) or overnight trips ($r = -0.465$, $P < 0.001$) in individual birds, but AM–PM trips were not correlated with overnight trips ($r = -0.260$, nonsignificant). Thus, birds that found good prey patches, as well as those that fed at sites close to the colony (Fig. 3), appeared to make short PM–PM trips repeatedly, thereby increasing meal frequency.

Foraging behavior and meal mass.—Seabird parents may forage and digest food for their own energy expenditure first, and collect extra food and store it for their offspring only toward the end of each foraging trip (Croxall and Davis 1990, Ropert-Coudert et al. 2004). In support of this hypothesis, the meal mass brought back from a trip was greater when the longest dive bout per trip was longer (Fig. 5), and the longest dive bouts most often occurred in the latter part of the trip.

Birds that made deeper dives had longer dive bouts (Fig. 5B), and birds brought back larger meals after trips with longer dive bouts. Birds are expected to make numerous deep dives only when the benefit of obtaining prey of higher quality at depth outweighs the cost of traveling to and from greater depths (Mori 1988). Adélie Penguin parents in this area feed on the larger, and more energy-rich (Clarke 1980), Antarctic Krill, when they dive deeper (≤70 m; Endo et al. 2000), which is consistent with the observation by Ichii (2000) that larger Antarctic Krill occur at deeper depths. However, the trip birds in this study mainly made shallow dives (5–18 m, on average), and the size of the Antarctic Krill in the stomach samples was not related to dive depth. Krill size was larger in heavier meals in our study; therefore, prey patch quality may be a key factor linking dive depth, bout duration, and meal size.

In our study area, individual parents consistently dove to about the same depth during observation periods of 2–5 h in the same small patches of open water and throughout the entire chick-rearing period (~1 month) (Takahashi et al. 2003, 2004). Dive depth also varied between individuals. Thus, different individuals seemed to prefer diving to different depths. This individual difference in dive depth affected meal mass, though the causal mechanism is unclear. Larger seal and penguin species, and larger individuals, have been shown to dive deeper (Kooyman and Kooyman 1995, Kelly and Wartzok 1996, Watanuki and Burger 1999, Walker and Boersma 2003), but we did not find a relationship between body size and dive depth. Individual variation in body-mass-independent basal metabolic rate, as reported in the Black-legged Kittiwake (*Rissa tridactyla*; Bech et al. 1999), may explain the relationship and should be studied.

Body condition.—Parents of Procellariiformes accumulate energy reserves when they make long trips to feed in productive waters distant from the colony (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1997). In colonies of Adélie Penguins that forage far from the colony, those with smaller departure mass make longer trips, during which they accumulate more energy reserves (Clarke 2001, Watanuki et al. 2002).

In trip birds, trip duration, initial body mass, and duration of the longest dive bout were independent of parental mass accumulation during each trip. In monitored birds, the pretrip guard duration did not affect the duration of the subsequent trip, and the initial body condition index did not affect the mean trip duration or the provisioning rate. These results suggest that Adélie Penguins in the year of our study may have been able to maintain their body condition and feed their chicks by repeated short trips to nearby sea-ice cracks when fast sea ice that remained near the colony limited the number of available foraging sites. On the other hand, data collected in other years with variable sea-ice conditions have shown that the decreased rate in the body mass gain of parents during chick rearing affected the brood growth rate (Takahashi et al. 2003). Sea-ice conditions affect prey abundance and availability to Adélie Penguins (Loeb et al. 1997, Ainley et al. 1998). When sea ice or icebergs restrict the size of foraging areas, Adélie Penguins may deplete prey within these areas, which results in competition for food resources (Ainley et al. 2006).

In conclusion, diurnal changes in feeding opportunities among cracks in fast sea ice induced individual variation in the frequency and mass of meals in Adélie Penguins. We suggest that individual variation in the provisioning rate resulted partly from

interactions between temporal and spatial patterns of prey availability and individual differences in foraging behavior.

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