REGULATION OF TRIP DURATION BY AN INSHORE FORAGER, THE LITTLE PENGUIN (*EUDYPTULA MINOR*), DURING INCUBATION

Akiko Kato,[1,4] Yan Ropert-Coudert,[1,2] and Andre Chiaradia[3]

[1]*National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173-8515, Japan;* [2]*Institut Pluridisciplinaire Hubert Curien, Departement d'Ecologie, Physiologie et Ethologie, 23 rue Becquerel, 67087 Strasbourg Cedex 02, France; and* [3]*Phillip Island Nature Park, P.O. Box 97, Cowes, Victoria 3922, Australia*

Abstract.—Both sexes of central-place-foraging seabirds usually share the task of incubation and alternate fasting bouts on the egg with foraging trips at sea. Because foraging strategies during incubation are poorly known, compared with strategies during chick rearing, we examined the foraging behavior of incubating Little Penguins (*Eudyptula minor*), together with nest-attendance behavior. The duration of foraging trips varied greatly (1–9 days). Birds with lower initial body condition made longer foraging trips, and the increase in body condition after multi-day trips was higher than that after single-day trips. During trips of >1 day, females dove more times each day but total underwater time did not differ between the sexes. By contrast, during one-day trips, foraging males made as many dives as females and spent more time underwater. Birds making longer trips spent more time diving on the second day than on the first day. The proportion of dives in which prey was encountered was lower during single-day than multi-day trips; during the latter, the proportion was lower on the first day than on the second and subsequent days. Body condition of Little Penguins seems to be an important factor influencing trip duration during incubation. Little Penguins apparently undergo long trips to target more profitable, distant prey patches. Incubating Little Penguins benefit from combining short and long trips at sea to optimize both reproduction and survival. *Received 26 December 2006, accepted 17 November 2007.*

Key words: body condition, *Eudyptula minor*, Little Penguin, prey-encounter rate, trip duration.

Régulation de la durée des excursions de quête alimentaire chez un oiseau côtier, *Eudyptula minor,* au cours de la couvaison

Résumé.—Les deux sexes d'oiseaux marins s'alimentant à partir d'un point central se partagent habituellement la tâche de la couvaison et alternent les périodes de jeûne au nid et les excursions de quête alimentaire en mer. Puisque les stratégies de quête alimentaire au cours de la couvaison sont peu connues comparativement à celles prévalant au cours de l'élevage des jeunes, nous avons examiné le comportement de quête alimentaire d'*Eudyptula minor* au cours de la couvaison, de même que le comportement de présence au nid. La durée des excursions de quête alimentaire a grandement varié (1–9 jours). Les oiseaux ayant initialement une moins bonne condition corporelle ont fait de plus longues excursions de quête alimentaire; l'amélioration de la condition corporelle après des excursions de plusieurs jours était plus importante que pour les excursions d'un jour. Au cours des excursions de >1 jour, les femelles ont plongé plus de fois quotidiennement que les mâles mais le temps total passé sous l'eau n'a pas différé entre les sexes. Par contraste, au cours des excursions d'un jour, les mâles en quête alimentaire ont effectué autant de plongées que les femelles et ont passé plus de temps sous l'eau. Les oiseaux effectuant des excursions plus longues ont passé plus de temps à plonger le second jour que le premier. La proportion de plongées lors desquelles des proies ont été rencontrées était plus faible au cours des excursions d'un jour que pour celles de plusieurs jours. Pour ces dernières, la proportion était plus faible le premier jour que les jours suivants. La condition corporelle chez *E. minor* semble être un facteur important influençant la durée des excursions au cours de la couvaison. Cette espèce effectue apparemment de longues excursions afin de cibler les nuages de proies plus profitables, bien que lointains. *E. minor* prend avantage à combiner les excursions de courte et de longue durée en mer au cours de la couvaison de manière à optimiser la reproduction et la survie.

Breeding parents face tradeoffs between spending time or energy caring for themselves and caring for their young (Trivers 1974), the outcomes of which influence overall reproductive success (King 1974, Nur 1987). Seabirds are interesting models for behavioral ecological work because they are central-place foragers and the sexes share the reproductive effort. During the chick-rearing period, several species of pelagic- and offshore-foraging seabirds optimize their allocation of time and energy between chick provisioning

[4]E-mail: akiko.k.r@gmail.com

and self feeding by alternating long and short foraging trips (e.g., Weimerskirch et al. 1994). The decision to conduct a long or a short trip seems to be related to changes in the bird's body reserves (Weimerskirch 1995, 1998; Bolton 1996; Weimerskirch et al. 1997; Clarke 2001). It is not known whether inshore birds use the same strategy.

In most penguins, the sexes share incubation and alternate fasting bouts on the nest with foraging trips at sea. During incubation, when parents have only their own energy needs to meet, one might expect them to stay longer at sea to improve their body condition. However, a longer trip would result in depletion of the body reserves of the partner attending the egg. This would increase the probability of the partner then making a longer trip, forcing the returned bird to fast longer during its next incubation shift. An extremely long fast could reduce the bird's body mass to such a point that it might decide to abort breeding in order not to compromise its survival and, consequently, its future reproduction (e.g., Chaurand and Weimerskirch 1994, Weimerskirch 1995). It has been shown that when birds reach an apparent physiological limit they usually desert the nest (Numata et al. 2000, Gauthier-Clerc et al. 2001). Thus, we hypothesized that, ecologically, the situation during incubation is relatively similar to that observed during the chick-rearing stage: incubating birds must balance the need to improve their body condition with the need to minimize trip duration so that their partner does not reach a critical body-mass threshold because of prolonged fasting. In this regard, incubating parents should be expected to regulate the duration of their foraging trips in relation to their body condition so as to balance fasting and feeding periods.

Little Penguins (*Eudyptula minor*), the smallest of all Spheniscidae (with a body mass of ~1 kg), have a mean incubation period of 35.5 days, and males and females share the incubation shift equally (Chiaradia and Kerry 1999). During the austral spring of 2004, we examined the incubation shifts and foraging variables of Little Penguins during the incubation phase using an automated penguin-monitoring system (APMS; Kerry et al. 1993, Chiaradia and Kerry 1999) and miniature accelerometers to derive time–activity budgets and the rate of prey encounter (Ropert-Coudert et al. 2006). Recent technological advances in the field of bio-logging have enabled researchers to monitor various aspects of the foraging behavior of marine animals, even those as small as Little Penguins (Ropert-Coudert and Wilson 2005). We investigated factors that could influence the duration of foraging trips at sea by incubating Little Penguins and the consequences of variability in trip duration to test the hypotheses that (1) inshore-feeding and incubating Little Penguins alternate short and long foraging trips and (2) incubating parents regulate trip duration in relation to their own body condition.

Methods

The study was conducted in a colony of Little Penguins breeding at the Penguin Parade, Phillip Island (38°31′S, 145°09′E), Victoria, Australia, in October–November 2004. Nests (artificial wooden nest-boxes) were checked every second day to establish the laying and hatching dates. We selected 10 pairs of Little Penguins and marked each individual with electronic transponders (TI-RIS; Texas Instruments, Dallas, Texas) that could be identified by the APMS. The APMS provided information on the arrival and departure times from the colony, which were used to determine the durations of the incubation shifts and foraging trips of males and females from the 10 monitored nests. Placed on the natural path used by most of the birds to travel between the beach and their nests, the APMS was located <5 m from the high-tide mark and 5–60 m from the nests in the study site. After crossing the APMS, the birds tended to waddle straight toward their nests, making one or two short stops (<1 min) before they reached them.

In addition, we monitored the foraging behavior during a single trip at sea of five males and five females that were randomly selected from the 10 marked incubating pairs. Foraging activity was monitored using cylindrically shaped four-channel data loggers with domed heads (M190-D2GT; Little Leonardo, Tokyo) that weighed 17 g (15 × 53 mm) and had a flash memory of 128 Mbit in which data were stored at 12-bit resolution. Depth was measured every second by a piezoresistive pressure sensor (FPBS-82A; Fujikura, Tokyo) to ≤190 m with an accuracy of ±1 m and a resolution of 0.05 m. Acceleration was measured along the longitudinal body axis by a capacitive accelerometer (ADXL202E; Analog Devices, Norwood, Massachusetts) between 0 and ±30 m s^{-2} at 16 Hz. This sensor measures both dynamic acceleration (i.e., vibration) and static acceleration (i.e., gravity). Values recorded by loggers were converted into acceleration using linear regression equations. To obtain these calibration equations, values recorded by each logger set at 90°, 0°, and −90° from the horizon were regressed against the corresponding acceleration (9.8 m s^{-2}, 0 m s^{-2}, and −9.8 m s^{-2}, respectively).

Penguins were caught in their nests. Data loggers were deployed using two strips of waterproof Tesa tape (Tesa AG, Hamburg, Germany) rolled around several feathers on the lower back to minimize drag (Bannasch et al. 1994). The use of Tesa tape allowed us to attach the device quickly, which minimized handling stress, and also to recover the loggers without damaging the feathers (Wilson et al. 1997). Attachment of the logger was completed in <5 min, and the birds were released at the entrances of their nests. All equipped birds were recaptured after one foraging trip and the data loggers retrieved. After we removed the loggers, all birds continued to incubate, and all chicks hatched later in the season. The data were downloaded from the loggers onto a computer and analyzed using custom-written programs in IGOR Pro, version 5.03J (Wavemetrics, Portland, Oregon). Given the accuracy of the depth sensors, only dives >1 m were considered for analysis. Dive depth, dive duration, and bottom-phase duration were calculated for each dive. Start and end of bottom phases were defined as the first and last time the depth-change rate became <0.25 m s^{-1} during a dive. Acceleration data were separated into acceleration owing to gravity (low-frequency component) and that resulting from body movements (high-frequency component). High-frequency components were examined using a power spectral density (PSD) analysis to find the main stroke frequency, given that Little Penguins do not change their stroke frequency with depth (Kato et al. 2006). From the results of the PSD analysis, we identified two peaks of stroke frequency. The first peak, at 3.27 ± 0.17 Hz (range: 3.0–3.5 Hz), corresponded to the dominant stroke frequency. Note that the second peak, around 6–7 Hz (i.e., ~2× the dominant frequency), was an artifact of the recording, because both the up- and down-strokes of the flippers were detected by the logger. This second peak was, therefore,
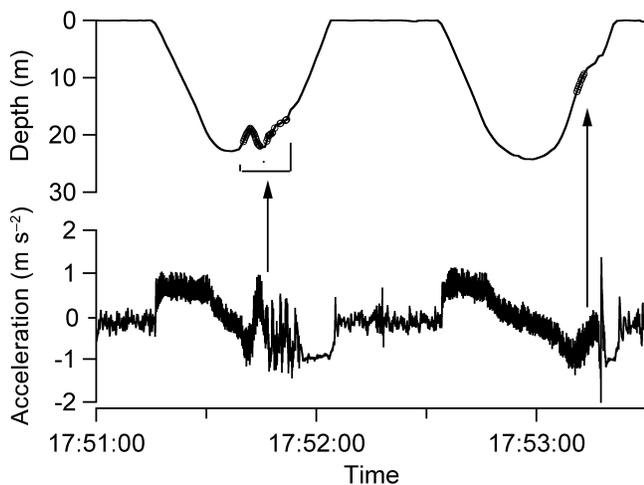
FIG. 1. Typical traces of depth and acceleration of a Little Penguin. Arrows indicate the parts of the dive where high-frequency (>4 Hz) stroke events occurred.

FIG. 2. Foraging-trip duration of male (gray, $n = 53$) and female (black, $n = 48$) Little Penguins during the incubation stage.

not considered in the analysis. From the PSD analysis, birds appeared to use a constant stroke frequency throughout their dives. However, a transient increase in stroke frequency was occasionally observed, these increasing phases occurring in discrete groups (Fig. 1). Following Ropert-Coudert et al. (2006), we assumed that high stroke frequency between 4 and 6 Hz reflected prey pursuit. The proportion of dives that were pursuit dives (i.e., dives where prey pursuit was identified) was calculated for each day of each bird and used as an index of rate of prey encounter.

Birds were weighed before and after the foraging trip, except for one male and one female whose post-trip body mass could not be determined. "Flipper length" was the length of the bent left flipper from the wrist to the tip, measured to the nearest 1 mm using calipers. A long-term dietary study at Phillip Island revealed that Little Penguins return to the colony with empty stomachs during the incubation phase (A. Chiaradia unpubl. data). This allowed us to define a body-condition index (BCI) by dividing body mass by flipper length (Robinson et al. 2005), because this ratio has been shown to be a reliable estimator of the energy reserves of Little Penguins (Hocken 2000, Robinson et al. 2005). The status of the birds was checked throughout the breeding season.

Statistical tests were conducted using STATVIEW, version 5.0J (SAS Institute, Cary, North Carolina). Summary statistics of variables were computed using each individual bird as a sampling unit. Student's t-tests or paired t-tests were used to compare the variables between males and females. Spearman rank correlation test was used to test the relationship between variables. Values are presented as means ± SD. The statistical threshold was 0.05%.

RESULTS

Throughout the incubation phase ($35.1 ± 1.0$ days; $n = 10$ nests), APMS data showed that both males and females made 3–8 foraging trips (Table 1). Foraging-trip duration varied between 1 and 9 days, and both males and females had three peaks of distribution, at 1, 4, and 6 days and at 1, 3, and 7 days, respectively (Fig. 2). Mean trip duration was longer in the middle of the incubation stage (Fig. 3), and
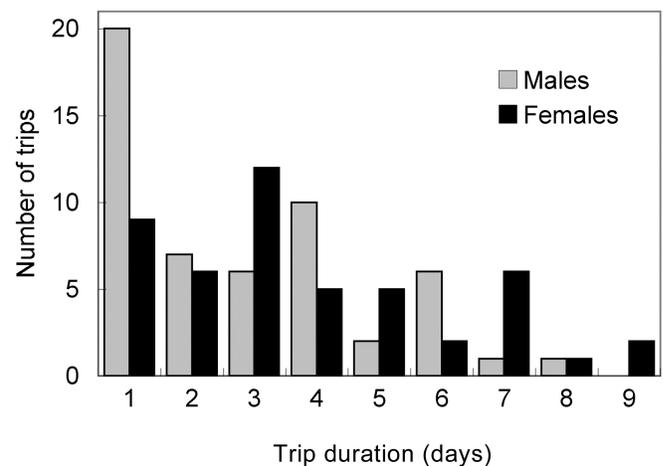
there was no clear alternating pattern of short and long trips. Trip duration was positively correlated with the duration of the previous incubation shift (= trip duration of the partner) for females ($ρ = 0.40$, $P = 0.02$, $n = 37$) but not for males ($ρ = 0.27$, $P = 0.1$, $n = 37$). Trip duration was not correlated with the duration of the individual's previous trip for either males ($ρ = −0.06$, $P = 0.7$, $n = 42$) or females ($ρ = 0.07$, $P = 0.7$, $n = 37$). The mean duration of a foraging trip was longer for females than for males, and the sum of trip duration during the incubation phase was shorter for males than for females (Table 1).

Among birds wearing data loggers, females made longer foraging trips (range: 6–7 days; $n = 5$) than males (range: 1–4 days; $n = 5$); three of these males made single-day trips. Although the body-condition index (BCI) before the trip was higher for males than for females, there was no significant difference in the final
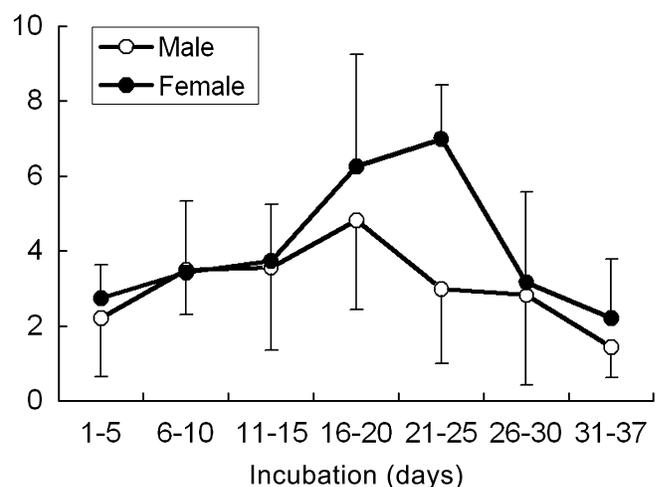
FIG. 3. Change of trip duration in relation to timing of departure within the incubation stage (days since laying grouped into five-day periods) of male and female Little Penguins. Vertical bars indicate standard deviation (SD).

TABLE 1. Foraging-trip, body-condition-index (BCI), and diving variables of male and female Little Penguins. Means ± SD are shown, with sample sizes in parentheses. Differences between males and females were tested by a *t*-test or paired *t*-test.

Variable	Male	Female	t	P
Number of foraging trips	5.3 ± 1.3 (10)	4.8 ± 1.5 (10)	1.2	NS
Trip duration (days)	3.0 ± 0.7 (10)	4.1 ± 1.2 (10)	2.9	0.005
Total trip duration (days)	15.3 ± 2.2 (10)	18.2 ± 1.5 (10)	3.6	0.006
Initial BCI (g mm^{-1})	17.4 ± 1.1 (5)	15.2 ± 0.7 (5)	3.8	0.005
Final BCI (g mm^{-1})	18.2 ± 1.8 (4)	18.0 ± 1.2 (4)	0.2	NS
Dive depth (m)	14.8 ± 2.9 (5)	11.3 ± 2.4 (5)	2.1	NS
Dive duration (s)	35.6 ± 5.2 (5)	26.0 ± 4.1 (5)	3.2	0.01
Dives per day	585 ± 99 (5)	775 ± 139 (5)	2.5	0.04
Daily underwater time (h)	5.67 ± 0.87 (5)	5.46 ± 0.68 (5)	0.4	NS

BCI between males and females (Table 1). Except for one male, body condition improved during a trip for both sexes. The initial BCI was not correlated with the duration of the previous foraging trip ($\rho = 0.46$, $P = 0.17$, $n = 10$), the duration of the last incubation shift ($\rho = -0.04$, $P = 0.9$, $n = 10$), or the incubation stage (number of days after laying; $\rho = 0.32$, $P = 0.34$, $n = 10$). Although birds with lower initial BCI made longer foraging trips ($\rho = -0.75$, $P = 0.02$, $n = 10$; Fig. 4A), neither the final BCI ($\rho = 0.18$, $P = 0.63$, $n = 8$) nor the changes in BCI during a trip ($\rho = 0.60$, $P = 0.11$, $n = 8$; Fig. 4B) were correlated with trip duration. However, the increase in BCI after multi-day trips (2.4 ± 1.0 g mm^{-1}; $n = 6$) was higher than that after single-day trips (0.2 ± 1.4 g mm^{-1}; $t = 2.5$, $P = 0.048$, $n = 2$). Multi-day trips always corresponded to a positive change in BCI, whereas one of the two birds that conducted a single-day trip decreased its BCI (Fig. 4B).

Depth and acceleration data were recorded during all the single-day trips and on the first three or four days of the multi-day trips. A total of 19,577 dives was recorded over the course of all the single- and multi-day trips. Although mean dive depth did not differ significantly between males and females, mean dive duration was longer for males than for females (Table 1). Females dived slightly more often per day than males, and daily time underwater did not differ between males and females (Table 1). Both the initial BCI and the trip duration showed no correlation with the average dive depth ($z = 0.2$, $P = 0.84$, $n = 10$ and $z = -0.99$, $P = 0.32$, $n = 10$), the number of dives per day ($z = -1.0$, $P = 0.32$, $n = 10$ and $z = 0.93$, $P = 0.35$, $n = 10$), or daily time underwater ($z = 0.75$, $P = 0.46$, $n = 10$ and $z = -1.8$, $P = 0.07$, $n = 10$).

When males were at sea for more than one day, they dived less during the first day, and the daily number of dives increased during the second and third days (Fig. 5A). By contrast, males on single-day foraging trips performed as many dives per day as the females. Males on one-day trips spent a relatively large proportion of their time underwater. Birds of either sex that undertook trips of several days' duration (except one female) increased the daily time underwater from the first to the second day (Fig. 5B). On the first and second days, dive depth was deeper and dive duration longer for males than for females. This difference disappeared in the subsequent days as the dive duration and dive depths of females increased (Fig. 5C, D).

The proportion of dives that were pursuit dives was lower during single-day trips than during multi-day trips (single-day

trip: $27.6 \pm 4.8\%$, $n = 3$; multi-day trip: $44.3 \pm 6.2\%$, $n = 7$; $t = 4.1$, $P = 0.03$). The proportion of pursuit dives was lower during the first day than during the second and third days of multi-day trips (first day: $34.9 \pm 10.5\%$, $n = 7$; second day: $46.8 \pm 4.1\%$, $n = 7$; third day: $47.3 \pm 9.5\%$, $n = 7$; analysis of variance and *post-hoc* test, $F = 4.8$, $P = 0.02$; Fig. 5E).
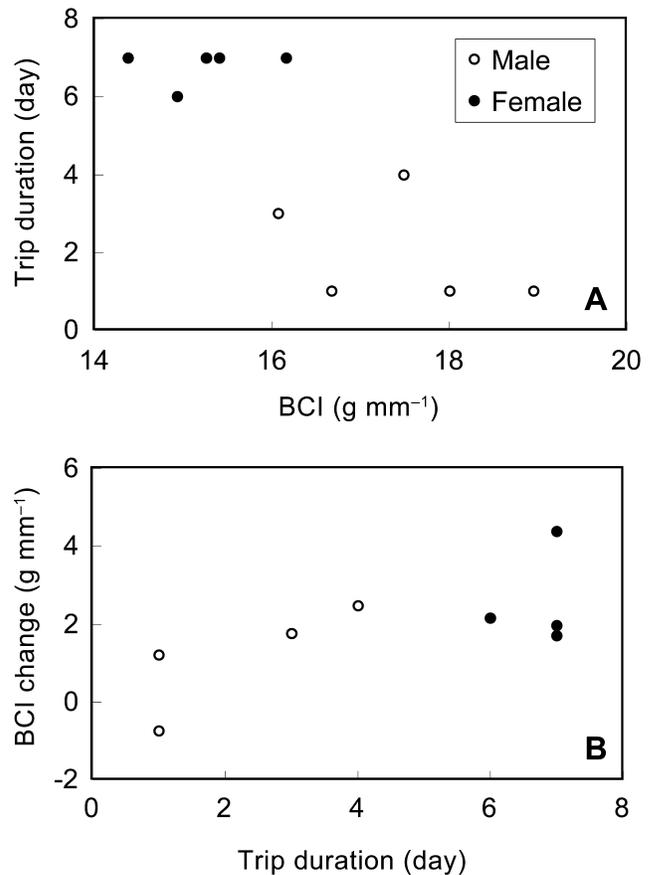
FIG. 4. Relationships (A) between initial body condition and foraging-trip duration and (B) between trip duration and body-condition change of male (open circle) and female (filled circle) Little Penguins.
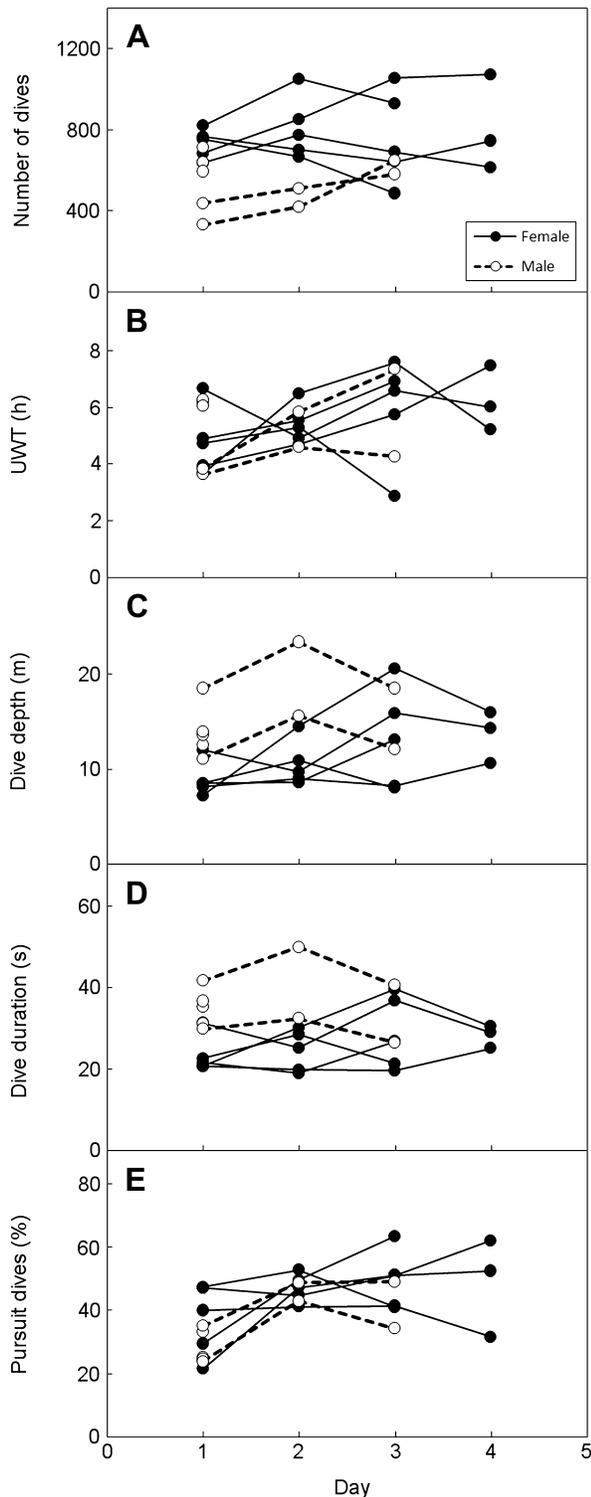
Fig. 5. (A) Number of dives per day, (B) daily time underwater (UWT), (C) average dive depth, (D) dive duration, and (E) proportion of pursuit dives in relation to the day in the trip of male (open circle) and female (filled circle) Little Penguins.

Discussion

In the present study, the variability in duration of foraging trips within and between birds was considerable. Although significantly different, the overall mean trip duration of females was only one day longer than that of males. On the other hand, females equipped with data loggers went to sea in poorer body condition and made much longer trips than males. Chiaradia and Kerry (1999) and Robinson et al. (2005) found no sex difference in the duration of incubation shift or in body condition. This suggests that trip duration was primarily a function of body condition rather than a result of sex-related differences. Similarly, Weavers (1992) and Numata et al. (2000) reported that the trip duration of Little Penguins was short and constant during the first half of incubation and longer and variable in the second half of incubation. On the other hand, lower body condition and longer trip duration of females could be explained by the fact that females need to replace the energy invested in eggs. However, in support of the "body-condition" hypothesis, egg desertion was observed more frequently in a colony where birds made longer trips with lower body condition (Numata et al. 2000). In addition, incubation shifts of successful parents are shorter than those of failed breeders (Chiaradia and Kerry 1999). Finally, Robinson et al. (2005) also reported that breeding success was correlated with body condition during incubation. In light of our results and those of the aforementioned studies, body condition appears to be an important factor that influences trip length during incubation and, accordingly, breeding success in Little Penguins.

Body condition of parents before a foraging trip results from both the energy gained during their previous trip at sea and that consumed during the incubation shift (i.e., fasting period). These two factors determine the duration of the next foraging trip. For instance, European Storm-Petrels (*Hydrobates pelagicus*) decrease and increase their body mass linearly with the lengths of the incubation shifts and those of the foraging trips, respectively (Bolton 1996). In the present study, the duration of the previous foraging trip was not correlated with the duration of the next trip, and body condition was not necessarily higher after longer trips. However, the duration of the previous incubation shift (i.e., foraging-trip duration of the partner) was positively correlated with trip duration in females but not in males. These results suggest that the variability of the trip duration of birds depended on the body condition and, in the case of females, the foraging strategy of their partner.

Several recent studies have shown that prey availability was lower near the colonies than farther away, as a result of interference competition, prey depletion, or both (e.g., Lewis et al. 2001; Ainley et al. 2003, 2004). Because of this, a number of seabird species make foraging trips of bimodal lengths, alternating long and short foraging trips during chick rearing (see Ropert-Coudert et al. 2004). Similarly, in the present study, when body condition was low, Little Penguins tended to make multi-day trips and, as a result, their body condition improved following the trip. The prey-encounter rate (proportion of pursuit dives) in our data suggested that Little Penguins would make long journeys to target more distant and profitable prey patches.

Long trip duration did not necessarily result in higher net energy gain for Little Penguins. Although body condition improved

during a trip, body-condition changes were not correlated with trip length. This is not surprising, given that net gains would depend mostly on prey-encounter rate and foraging success during the trip. In the present study, the diving pattern on the first day differed between birds on single-day trips and those on multi-day trips. Thus, we suggest that Little Penguins have already decided the duration of their trip by the time they went to sea, a decision probably made on the basis of their body condition. Interestingly, S. Robinson et al. (unpubl. data) showed that long foraging trips were not beneficial for post-guarding Little Penguins breeding at the same colony in different years. The strategy of alternating long and short trips may not always be adaptive when conditions change.

Acknowledgments

Literature Cited

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince Willam Sound. Ecology 84:709–723.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: Overlap in colony-specific foraging areas. Ecological Monographs 74:159–178.

Bannasch, R., R. P. Wilson, and B. Culik. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. Journal of Experimental Biology 194:83–96.

Bolton, M. 1996. Energy expenditure, body-weight and foraging performance of storm petrels Hydrobates pelagicus breeding in artificial nesting chambers. Ibis 138:405–409.

Chaurand, T., and H. Weimerskirch. 1994. Incubation routine, body mass regulation and egg neglect in the Blue Petrel Halobaena caerulea. Ibis 136:285–290.

Chiaradia, A. F., and K. R. Kerry. 1999. Daily nest attendance and breeding performance in the Little Penguin Eudyptula minor at Phillip Island, Australia. Marine Ornithology 27:13–20.

Clarke, J. R. 2001. Partitioning of foraging effort in Adélie Penguins provisioning chicks at Béchervaise Island, Antarctica. Polar Biology 24:16–20.

Gauthier-Clerc, M., Y. Le Maho, J.-P. Gendner, J. Durant, and Y. Handrich. 2001. State-dependent decisions in long-term fasting King Penguins, Aptenodytes patagonicus, during courtship and incubation. Animal Behaviour 62:661–669.

Hocken, A. G. 2000. Internal organ weights of the Blue Penguin Eudyptula minor. New Zealand Journal of Zoology 27:299–304.

Kato, A., Y. Ropert-Coudert, D. Grémillet, and B. Cannell. 2006. Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. Marine Ecology Progress Series 308:293–301.

Kerry, K., J. Clarke, and G. Else. 1993. The use of an automated weighing and recording system for the study of the biology of Adélie Penguins (Pygoscelis adeliae). Proceedings of the NIPR Symposium on Polar Biology 6:62–75.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pages 4–85 in Avian Energetics, vol. 4 (R. A. Paynter, Jr., Ed.). Nuttall Ornithological Club, Cambridge, Massachusetts.

Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816–819.

Numata, M., L. S. Davis, and M. Renner. 2000. Prolonged foraging trips and egg desertion in Little Penguins (Eudyptula minor). New Zealand Journal of Zoology 27:277–289.

Nur, N. 1987. Parents, nestlings and feeding frequency: A model of optimal parental investment and implications for avian reproductive strategies. Pages 457–476 in Foraging Behavior (A. C. Kamil, J. R. Krebs, and H. R. Pulliam, Eds.). Plenum Press, New York.

Robinson, S., A. Chiaradia, and M. A. Hindell. 2005. The effect of body condition on the timing and success of breeding in Little Penguins Eudyptula minor. Ibis 147:483–489.

Ropert-Coudert, Y., A. Kato, R. P. Wilson, and B. Cannell. 2006. Foraging strategies and prey encounter rate of free-ranging Little Penguins. Marine Biology 149:139–148.

Ropert-Coudert, Y., and R. P. Wilson. 2005. Trends and perspectives in animal-attached remote sensing. Frontiers in Ecology and the Environment 3:437–444.

Ropert-Coudert, Y., R. P. Wilson, F. Daunt, and A. Kato. 2004. Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. Behavioral Ecology 15:824–830.

Trivers, R. L. 1974. Parent–offspring conflict. American Zoologist 14:249–264.

Weavers, B. W. 1992. Seasonal foraging ranges and travels at sea of Little Penguins Eudyptula minor, determined by radiotracking. Emu 91:302–317.

Weimerskirch, H. 1995. Regulation of foraging trips and incubation routine in male and female Wandering Albatrosses. Oecologia 102:37–43.

Weimerskirch, H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. Journal of Animal Ecology 67:99–109.

Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. Animal Behaviour 47:472–476.

Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet, and V. Ridoux. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. Ecology 78:2051–2063.

Wilson, R. P., K. Pütz, G. Peters, B. Culik, J. A. Scolaro, J.-B. Charrassin, and Y. Ropert-Coudert. 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Society Bulletin 25:101–106.

Associate Editor: J. F. Piatt