

# Plasticity in foraging strategies of inshore birds: how Little Penguins maintain body reserves while feeding offspring

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**Abstract.** Breeding animals face important time and energy constraints when caring for themselves and their offspring. For long-lived species, life-history theory predicts that parents should favor survival over current reproductive attempts, thus investing more into their own maintenance than the provisioning of their young. In seabirds, provisioning strategies may additionally be influenced by the distance between breeding sites and foraging areas, and offshore and inshore species should thus exhibit different strategies. Here, we examine the provisioning strategies of an inshore seabird using a long-term data set on more than 200 Little Penguins, *Eudyptula minor*. They alternated between two consecutive long and several short foraging trips all along chick rearing, a strategy almost never observed for inshore animals. Short trips allowed for regular provisioning of the chicks (high feeding frequency and larger meals), whereas long trips were performed when parent body mass was low and enabled them to rebuild their reserves, suggesting that adult body condition may be a key factor in initiating long trips. Inshore seabirds do use dual strategies of alternating short and long trips, but from our data, on a simpler and less flexible way than for offshore birds.

**Key words:** bimodal trips; body condition; chick rearing; *Eudyptula minor*; foraging strategies; Little Penguin; parental investment; Phillip Island, Victoria, Australia; trip duration.

## INTRODUCTION

When breeding, animals face important time and energy trade-offs between caring for themselves and for their young (Trivers 1974), and the outcomes of this parent–offspring conflict largely influence overall reproductive success (Nur 1988). Life-history theory predicts that to maximize its lifetime reproductive success, an individual will invest a specific amount in reproduction resulting from the trade-off between the benefits and costs associated with raising chicks (Stearns 1989). In this context, long-lived birds are expected to favor their survival at the expense of the current breeding attempt (Stearns 1989, Mauck and Grubb 1995, and see the “prudent parent” in Drent and Daan 1980), and should minimize risks when investing in their offspring (Goodman 1974). Parental investment, defined as “any investment by the parent in an individual offspring that increases the offspring chances of surviving at the cost of the parent ability to invest in other offspring” (Trivers 1972), includes features in birds such as nest building, egg incubation, chick rearing, nest defense, and foraging. Yet, for many bird species, the chick-provisioning

phase is the critical period of investment due to high energetic costs (Drent and Daan 1980), as during chick rearing, parents must decide whether and how to allocate the energy they gather between themselves and their offspring. However, nutritional and energetic requirements often differ between adults and their offspring (Murphy 1996) and food may come from different patches when parents are self-catering or caring for their young (Markman et al. 2004). Central-place foragers, such as seabirds, are faced with the additional constraint of returning to a central breeding site on land (or ice) to feed their offspring (Costa 1991), which limits the range of suitable foraging areas. Decisions regarding foraging grounds and hunted prey are then to be considered in the light of such trade-offs.

For seabirds to compromise between offspring provisioning and body maintenance, it has been suggested that parents may alternate between short coastal trips to provision their offspring, and long trips to more remote feeding grounds to restore and maintain their body condition (Weimerskirch et al. 1994, 1997a, Weimerskirch 1998). However, factors triggering a parent’s choice to undertake a long or short foraging trip may differ between species. For instance, if Sooty Shearwaters, *Puffinus griseus*, seem to respond to a threshold in their body condition below which they will always initiate a long foraging trip (Weimerskirch 1998),

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other species seem able to alter the length of foraging trips in response to the body condition of the chicks (Weimerskirch et al. 2000). Although trips of bimodal durations have been widely reported in procellariiforms (Chaurand and Weimerskirch 1994, Weimerskirch et al. 1994, 1997a, 1998, Granadeiro et al. 1998, Booth et al. 2000, Congdon et al. 2005), the indication of dual feeding is very limited outside this taxon, with a few alcids as exceptions, such as Thick-billed Murres, *Uria lomvia* (note that both short and long trips have been reported for that species, but not for the same individuals; Benvenuti et al. 1998) and Little Auks, *Alle alle* (Welcker et al. 2009). Aside from Little Auks, all these species are offshore birds, foraging at great distances from their colonies. Yet, the provisioning strategy of seabirds often depends on the distance birds have to travel to reach their foraging grounds, and provisioning strategies are thus expected to be drastically different between offshore and inshore species.

Inshore species such as the Black-browed Albatross, *Diomedea melanophris*, the Shy Albatross, *Thalassarche cauta*, or the Gentoo Penguin, *Pygoscelis papua*, perform short-lasting trips both during incubation and chick rearing (Weimerskirch et al. 1986, Williams and Rothery 1990, Hedd 1998). As these birds do not rely on distant food resources, their foraging trips are much shorter (ranging from six hours to a couple of days, depending on the species) and far more frequent than offshore species (Weimerskirch et al. 1997b). However, to support the annual requirements of an inshore species, food must be adequately predictable and abundant in inshore areas (Hedd 1998). Variable food and environmental conditions across breeding seasons would entail different energetic costs for parents. Yet, when food supply changes within the foraging range, virtually nothing is known on whether and how inshore seabirds adapt their foraging strategies to continue provisioning food both for themselves and their offspring. A recent study on breeding Adélie Penguins, *Pygoscelis Adeliae*, showed that changes in environmental conditions (such as ice cover or presence of icebergs) affected their foraging behavior, with less food brought back to the chicks, longer foraging trips, and higher body mass loss for the parents along the season (Ballard et al. 2010). However, no concomitant change in the foraging strategy was observed (Ballard et al. 2010), and Adélie Penguins seemed unable to respond to these changes.

Here we examined the provisioning strategies of an inshore seabird species, the Little Penguin, *Eudyptula minor*. Little Penguins are visual hunters that only feed at sea during the daytime (Cannell and Cullen 1998, Collins et al. 1999, Ropert-Coudert et al. 2006) and return ashore to nest only after sunset (Klomp and Wooller 1991, Chiaradia and Nisbet 2006). They have one of the shortest foraging ranges among seabirds (<20 km; Collins et al. 1999), and therefore they can be good models of inshore species, which constitute the majority

of seabirds. Little Penguins have also occasionally been observed to make longer (several days) trips during chick rearing (Collins et al. 1999, Weavers 1992), and previous studies have reported their use of bimodal-trip strategies during incubation to optimize both reproduction and survival, potentially using longer trips to target more profitable distant prey patches (Kato et al. 2008). Such characteristics thus make Little Penguins ideal models to examine a possible plasticity in foraging strategies of inshore seabirds. Here, using data collected over eight years of continuous monitoring of more than 200 birds, we investigated whether changes in foraging strategies may be used by these inshore foragers to improve chick provisioning, and which parameters (e.g., sex, year, and so on) may be key determinants underlying provisioning decisions. As one-day trips are the rule during chick guard (Chiaradia and Kerry 1999), we investigated provisioning strategies only during post-guard, a period when parents are not dependent on the attendance of their partner (Daniel et al. 2007), and when chicks are left unattended in the colony. We also addressed the question of whether the length of foraging trips was a response to depleted adult body mass in years of variable food supply.

## METHODS

### *Monitoring and field protocols*

Our study was conducted on Little Penguins at the Summerland Peninsula on the western end of Phillip Island, Victoria, Australia (38°15' S, 143°30' E), where ~14 000 breeding pairs of Little Penguins nest (Cullen et al. 2009). This study was conducted during eight breeding seasons from 2001 to 2008, where 2001 refers to the breeding season in the austral summer of 2001–2002. The study site used for these analyses (see details in Chiaradia and Kerry 1999) is a part of a colony containing 100 artificial burrows (wooden nest boxes), of which 48–76 were occupied in each year. All nesting adults were tagged mostly as chicks (or as adults in few cases) using passive transponder tags (Allflex, Capalaba, Australia), which were then implanted subcutaneously between the scapulae. Birds were later sexed by bill measurements (Arnould et al. 2004), when first found in the colony as adults in subsequent years.

All nests were checked three times a week using a custom-built portable transponder reader. This allowed us to determine the number of chicks fledged and the exact phenology of breeding events: laying, hatching, and fledging dates, as well as the end of the guard stage for each pair. Post-guard (i.e., the period from the first date on which neither adult was present in the nest, to fledging of the last chick) success was defined as the number of chicks fledged (i.e., chicks which were fully adult feathered and of age >40 days when last encountered, were considered fledged) per chicks reaching post-guard.

Chicks were weighed three times a week to the nearest gram during post-guard. Fledging body mass was thus

considered as the mass recorded at the last encounter prior to fledging (see details in Chiaradia and Nisbet 2006).

#### *Foraging trips*

Foraging trips were recorded using an Automatic Penguin Monitoring System (APMS) designed by the Australian Antarctic Division (Kerry et al. 1993). The APMS was located on the main colony entrance between the beach and the colony and consisted of a weighing platform to determine the body mass of the penguins, a transponder reader to record the identity of the individual and two infra-red beams to detect the direction of movement of the birds (Kerry et al. 1993). The system automatically recorded the transponder number, date and time, and direction of each arriving and departing penguin (see details in Robinson et al. 2005). Foraging-trip durations were analyzed through the recorded detections. As Little Penguins depart to sea before sunrise and return after sunset, duration in hours can be dependent on the year period (Chiaradia and Kerry 1999). To avoid this bias, we looked at foraging duration at one-day intervals and duration of every foraging trip was rounded in days. Foraging trips were separated into two categories of short ( $\leq 2$  days) and long trips ( $\geq 3$  days) according to the distribution of trip duration (see Appendix: Fig. A1). Short trips lasted  $1.2 \pm 0.0$  days (mean  $\pm$  SE), while long ones lasted  $4.3 \pm 0.1$  days.

#### *Adult body masses and meal size*

We focused our analyses of body masses on the first 40 days of post-guard (the average duration of post-guard was 43 days) since the number of records dropped thereafter by almost 50%, as the birds progressively reduced their returning rate to the colony. Furthermore, raw data from the APMS were adjusted to account for tare drift and error of the system as described in Robinson et al. (2005). Meal size is defined hereafter as the amount of food (in grams) given by an adult to its chicks. During post-guard, as parents stayed for only a few hours at a time in the colony to feed the chicks (Daniel et al. 2007), we used the difference in body mass between a bird entering and then leaving the colony to estimate meal size. Meal sizes found in this study (mean  $258 \pm 1$  g) were consistent with previous findings measured by directly weighing chicks before and after meals (see Fig. 4 in Chiaradia and Nisbet 2006). Three different adult body masses were examined in the following for a given foraging trip: the “departure mass,” which is the mass of the bird leaving the colony at sunrise, the “return mass,” which is the mass of the bird returning to the colony at sunset, and finally, the “post-feeding mass,” which is the mass of the bird going out to sea once more after having fed the chicks. The “return mass” thus equals “post-feeding mass” plus meal size.

#### *Statistics*

All statistics were computed using R 2.8.0 statistical program (R Development Core Team 2008). Data were longitudinal as individual penguins performed several trips in a single post-guard stage and were, moreover, recorded over multiple breeding seasons. Data were modeled using a maximum likelihood mixed-model approach (lme4 package; Bates and Maechler 2009). Mixed models were computed with the individual (bird) as a random effect, enabling us to account for repeated measures. Fitted models were usually generalized linear ones with Poisson distribution for foraging-trip duration or meal size. However, when looking at body masses, a normal distribution was fitted, as the numbers were high enough to assimilate a Poisson distribution to a normal one. Linear models were also computed to compare annual means. Variables were considered significant for  $P < 0.05$ . Results are given as means  $\pm$  standard error (SE).

#### RESULTS

##### *Foraging trips*

Over the eight years that were analyzed, we recorded a total of 14 116 foraging trips ( $n$ ) for 212 different individuals ( $N$ ). Little Penguins mostly performed short daily foraging trips, but were also observed to undertake longer trips lasting several days (mean  $\pm$  SE =  $1.4 \pm 0.0$  days, range = 1–16 days, 74% of one-day trips; Appendix: Fig. A1). Gender did not influence foraging-trip duration ( $1.4 \pm 0.0$  days for both sexes; generalized linear mixed model [GLMM];  $P = 0.59$ ,  $n = 14\ 116$ ,  $N = 212$  birds).

##### *Succession of foraging trips*

Looking over all years together, birds almost exclusively began the post-guard period by undertaking long foraging trips (i.e., in 91% of the cases, 416 out of 459). The proportion of first trips undertaken as long trips was not influenced by the individuals' age (GLMM;  $P = 0.66$ ,  $n = 454$ ,  $N = 189$ ). However, we found that females began the post-guard period by undertaking long foraging trips more often than did males ( $94\% \pm 2\%$  vs.  $87\% \pm 2\%$ ; GLMM;  $P = 0.02$ ,  $n = 459$  [226/233],  $N = 192$  [102/90]). The percentage of post-guard events starting with a long trip varied in between years from 78% in 2001 to 100% in 2002, 2003, and 2005. In years during which the guard period lasted longer, the proportion of birds undertaking long foraging trips at the onset of post-guard was higher (linear model [LM];  $t_7 = 2.99$ ,  $P = 0.02$ ,  $R^2 = 0.60$ ).

In general, birds alternated between long and short foraging trips in a similar pattern. They usually performed two long trips followed by several short ones (overall mean of  $10.0 \pm 0.4$  short trips), resuming two long trips afterwards, and continued this pattern until their chicks fledged (Fig. 1). This pattern of alternation between long and short trips was present regardless of

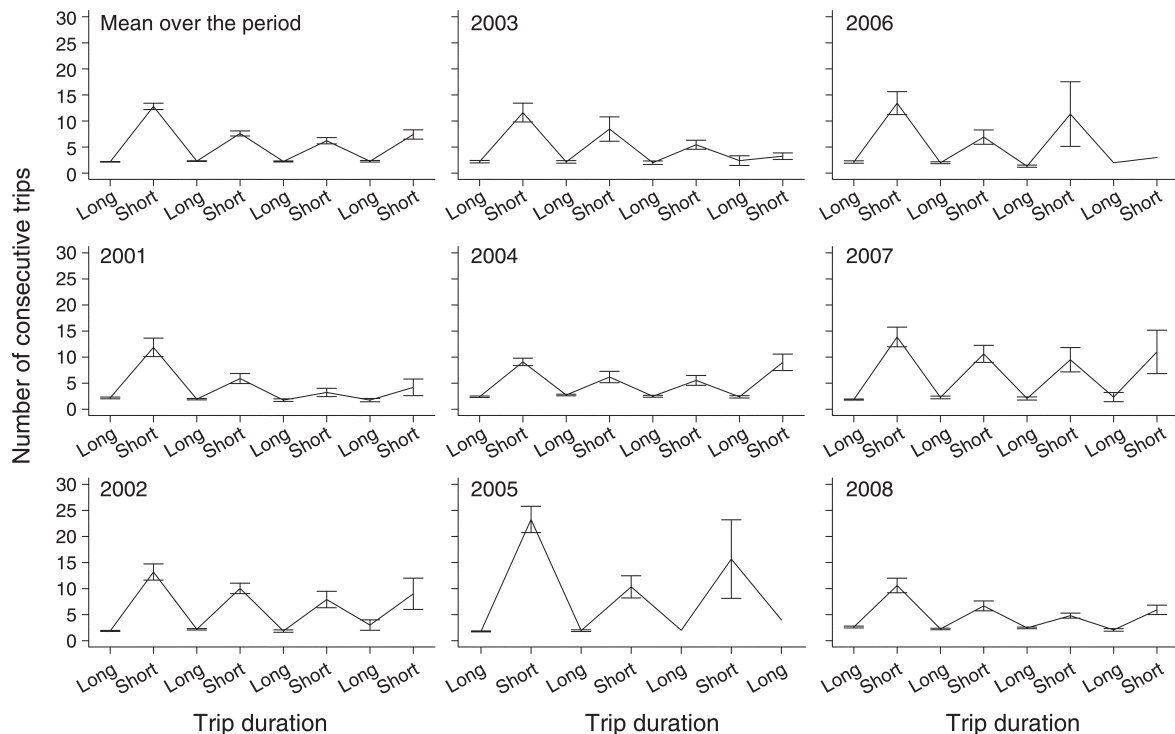


FIG. 1. Pattern of alternation between long and short trips during the post-guard period in Little Penguins, *Eudyptula minor*. Means  $\pm$  SE are given over the whole study period (i.e., eight years) and for each year separately.

sex, age, or year (Fig. 1); however, we observed differences in the frequency of this pattern. While the number of consecutive long trips was constant (independent of the rank of the event, i.e., whether it is the first, second, or  $n$ th time they perform long trips, the sex and the year GLMMs;  $P=0.20$ ,  $P=0.45$ , and  $P=0.054$ , respectively;  $n = 944$ ,  $N = 188$ ), the number of consecutive short trips decreased with the rank of the event and varied between years from 7.5 in 2004 to 20.3 in 2005 on average (GLMMs;  $P < 0.001$ ,  $n = 875$ ,  $N = 185$ ; Fig. 1).

#### Body mass and foraging-trip duration

Importantly, the body masses of birds departing to sea for long trips were significantly smaller than the body masses of birds departing for short trips ( $1050 \pm 5$  g vs.  $1073 \pm 1$  g; linear mixed model [LMM];  $P < 10^{-3}$ ,  $n = 8213$ ,  $N = 164$ ; Fig. 2A). When returning from their foraging trips, birds had put on mass, and their mass gain (return mass-departure mass) was significantly higher after short trips than after long ones ( $265 \pm 2$  g for a short trip vs.  $232 \pm 6$  g for a long one; GLMM;  $P < 10^{-3}$ ,  $n = 4366$ ,  $N = 153$ ). When returning from short trips, birds delivered more food to the chicks than when returning from long trips, as indicated by their body mass loss during the few hours they spent in the colony feeding the chicks ( $267 \pm 2$  g vs.  $220 \pm 5$  g; GLMM;  $P < 10^{-3}$ ,  $n = 4366$ ,  $N = 153$ ; Fig. 2B). When considering parents' body masses after having fed the chicks, birds

had not gained mass when they returned from a short trip (average of  $2 \pm 1$  g lost, but not significantly different from 0; GLMM;  $P = 0.8$ ,  $n = 4014$ ,  $N = 149$ ; Fig. 3A), whereas, on the contrary, birds returning from a long trip had gained  $12 \pm 4$  g on average (GLMM;  $P = 0.02$ ,  $n = 352$ ,  $N = 121$ ; Fig. 2A). This pattern was further confirmed by analyses of body mass after a set of consecutive trips. At the end of a set of long trips, a bird gained  $19.9 \pm 10.9$  g, while at the end of a set of short trips, a bird had lost  $22.6 \pm 8.4$  g (GLMM;  $P < 0.001$ ,  $n = 1171$ ,  $N = 84$ ).

#### Impact on chick rearing

The percentage of long trips did not affect the length of the post-guard stage (GLMM;  $P=0.57$ ,  $n = 318$ ,  $N = 160$ ). However, it significantly influenced chick development both through post-guard success (i.e., chick survival; GLMM;  $P < 0.001$ ,  $n = 426$ ,  $N = 176$ ) and chick mass at fledging (GLMM;  $P = 0.01$ ,  $n = 315$ ,  $N = 154$ ). Indeed, an increase of 1% in the percentage of the long trip lead to an almost 10% decrease in post-guard success (LM on annual means; slope =  $-9.4$ ,  $t_7 = -5.24$ ,  $P = 0.002$ ; Fig. 3), and resulted in a drop of  $33 \pm 12$  g in chick mass at fledging (LM on annual means; slope =  $-3300$ ,  $t_7 = -2.567$ ,  $P = 0.042$ ; Fig. 3).

#### DISCUSSION

Little Penguins alternated long and short foraging trips during late chick rearing, a strategy well known in

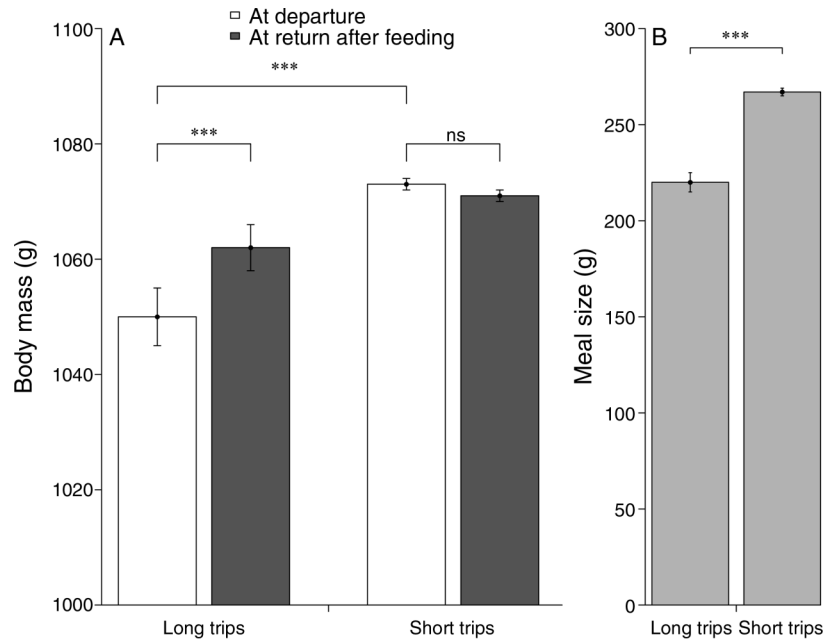


FIG. 2. (A) Changes in parents' body mass (means  $\pm$  SE) before and after short vs. long foraging trips. Post-feeding body mass (dark gray) corresponds to parents' body mass after feeding the chicks. (B) Meal size (mean  $\pm$  SE) given to the chicks after short vs. long trips.

\*\*\*  $P < 0.001$ ; ns, nonsignificant.

offshore seabirds, but virtually never observed in inshore species. Inshore seabirds do not rely on distant food resources and usually perform short foraging trips to coastal areas close to their breeding sites, as, for instance, in Black-browed and Shy Albatrosses, or Adélie Penguins (Weimerskirch et al. 1986, Hedd 1998, Ballard et al. 2010). Some inshore species also exhibit a dual pattern of short and long trips either in duration or distance (see murrens in Benvenuti et al. 1998 and Gentoo Penguins in Lescroël and Bost 2005). However, this dual

pattern resulted from a mutually exclusive behavior, i.e., some birds conducted short trips, while others conducted long ones (depending on sex, breeding site location, and so on). Here, it is important to note that alternations of short and long trips were observed on the same individuals, refuting the hypothesis of specialization of inshore birds to rigid travelling mode. In Little Penguins, individuals typically conducted a majority of short trips. However, parents appeared to exhibit plasticity in behavioral foraging strategies, as they

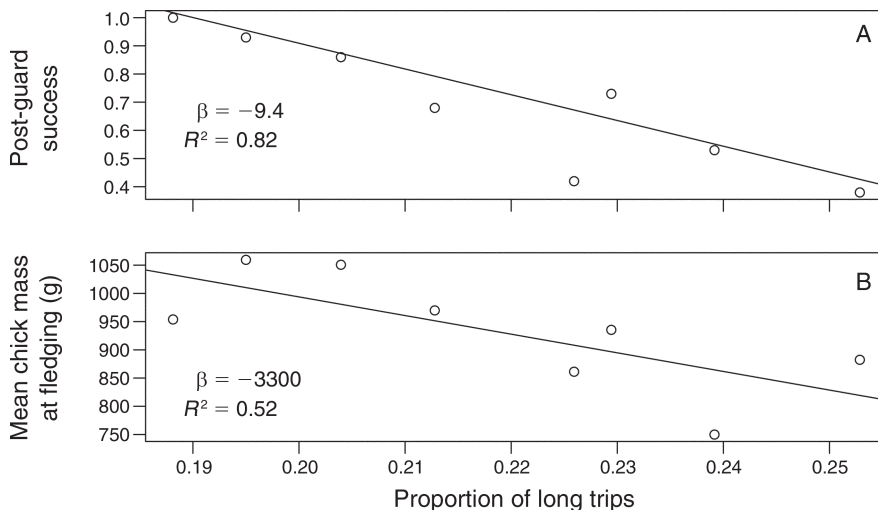


FIG. 3. Impact of foraging-trip duration on (A) post-guard success and (B) fledging body mass. Regression lines and statistics ( $R^2$  and regression coefficients) are indicated.

regularly alternated short trips with longer foraging bouts to compromise between providing both for their chicks' needs and their own. At first glance, the pattern exhibited by foraging parents (subsequently alternating between several short trips and two long trips) may seem relatively constant. This result may suggest that foraging strategies are not as diverse in Little Penguins as that observed in offshore seabirds, and thus, lack flexibility to environmental conditions. However, while it is true that there is only small variation in the number of long trips performed in a row (i.e., adults always leave for two long foraging trips in a row), there is much greater variation in the number of short trips achieved in between long trips (Fig. 1). Such plasticity in trip frequency could be an adaptation to respond to fluctuating resources availability.

Short trips are used to provide food regularly to the chicks, whereas long trips seem to meet parent needs. Short trips were indeed associated with no reserve gains for the adults, but significantly bigger meals for the chicks, and thus, a guarantee of more frequent food supply for growing offspring. This is especially important in inshore species, whose chicks cannot sustain long periods of starvation (Chiaradia and Nisbet 2006), unlike offshore birds (Cherel and Le Maho 1985, Schultz and Klomp 2000). Short trips thus appeared at least as beneficial for Little Penguin chicks as they are reported to be for the chicks of offshore species (Weimerskirch 1998). This was further confirmed by our findings of a negative impact of increased proportion of long trips on chick survival and fledgling masses. However, after a number of successive (chick-provisioning) short trips, adults faced depleted reserves, and ultimately jeopardized their survival. Thus, when the breeding parent reached a low threshold in its body mass, it typically seemed to shift to long trips to improve its body condition. Therefore, we suggest that adult body condition triggers the choice between short and long trips in Little Penguins, as in the Blue Petrel, where it has been suggested that adults may regulate their foraging strategies so that their body mass does not go below a certain mass threshold (Chaurand and Weimerskirch 1994). According to life-history theory (Stearns 1989, Mauck and Grubb 1995) and the resulting prudent parent hypothesis (Drent and Daan 1980), long-lived animals such as Little Penguins should mostly focus on maintaining their own condition, rather than that of their offspring. Accordingly, in our study, parents appeared to invest into chick provisioning (performing short foraging trips) for as long as they were able to maintain a certain body condition. When body condition dropped, long trips became mandatory. This was confirmed by the fact that after the guard phase (a phase constituted of short trips solely), almost all birds shifted to long trips, the only exceptions being when a shorter than usual guard period enabled parents to maintain a sufficient body condition, for them to perform some extra short trips.

Long trips are usually associated with foraging in more distant areas. In colonial species, various studies have shown that prey availability is generally lower close to the colonies than further away, resulting either from intraspecific competition or prey depletion (Lewis et al. 2001, Ainley et al. 2003, 2004). Distant trips may then reduce competition (Birkhead and Furness 1985), as when adults depart from a single location, the density of birds will decrease with increasing distance from that location. This was, for instance, suggested for the Blue Petrel (Chaurand and Weimerskirch 1994). In Little Penguins, trip duration and distance traveled are highly correlated, at least for trips lasting <10 days (see Fig. 3 in Collins et al. 1999), which represent the vast majority of the trips. Long journeys during chick rearing could thus be explained by the targeting of more distant and profitable prey patches, as previously suggested by Kato et al. (2008) during incubation. However, we found that the total mass gain (i.e., the mass of prey foraged) was higher after short foraging trips than after long ones. One may then find this in contradiction with the hypothesis that birds target greater prey patches further away from the colony. Yet, this may be explained by the fact that food may be entirely processed when parents return from long trips, whereas it may be only partially digested in the birds' stomach when they return from short trips (Wilson et al. 1989). Additionally, differences in strategies when foraging for themselves or for the chicks may result from different nutritional requirements, such as higher levels of proteins needed for chick growth (Partridge and Green 1985). For instance, in King Penguins, the winter diet of the chicks appears to rely mostly upon cephalopods caught over the continental shelf, whereas parents hunting for themselves do so much further away from the island on a combination of cephalopods and high-protein myctophids (Cherel et al. 1993). Parents may thus target different locations to forage on different prey depending on whether food is to be allocated to the chicks or themselves. Stable-isotope analysis, a method used to determine diet segregation, showed that the diet of adults and chicks exhibited different  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in Little Penguins, suggesting that they do not rely on the same resources and that their foraging zones are different (Chiaradia et al. 2010). Finally, long trips could also result from longer time spent foraging, but in the same areas as the ones used for short trips, as suggested by Ropert-Coudert et al. 2004. Spending longer in the same foraging areas, birds may be less opportunistic and encounter higher quality items (classic central place foraging, *sensu* Orians and Pearson 1979).

Thus, it seems that inshore seabirds (such as Little Penguins) may exhibit some plasticity in their foraging strategies, though for those species, strategies appear less flexible than those of offshore seabirds. It is interesting to note that this plasticity was not observed in another inshore penguin, the Adélie Penguin (Ballard et al. 2010), perhaps due to the smaller and inflexible time

window to breed at the Antarctic continent. Explanations for bimodal strategies in inshore species thus warrant further investigations, and using data-loggers to investigate potential differences in foraging areas and/or diving behavior between short and long trips, should provide valuable insight on behavioral adaptations to a fluctuating environment.

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## 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 William 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.
- Arnould, J. P. Y., P. Dann, and J. M. Cullen. 2004. Determining the sex of little penguins (*Eudyptula minor*) in northern Bass Strait using morphometric measurements. *Emu* 104:261–265.
- Ballard, G., K. Dugger, N. Nur, and D. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405:287–302.
- Bates, D., and M. Maechler. 2009. lme4: linear mixed-effects models using Eigen and S4 classes. R package version 0.999375-31. R Foundation for Statistical Computing, Vienna, Austria. (<http://CRAN.R-project.org/package=lme4>)
- Benvenuti, S., F. Bonadonna, L. Dall'Antonia, and G. A. Gudmundsson. 1998. Foraging flight of breeding thick-billed murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115:57–66.
- Birkhead, T. R., and R. W. Furness. 1985. Regulation of seabird populations. Pages 147–167 in R. M. Sibly and R. H. Smith, editors. *Behavioural ecology, ecological consequences of adaptive behaviour*. Blackwell, London, UK.
- Booth, A. M., E. O. Minot, R. A. Fordham, and M. J. Imber. 2000. Co-ordinated food provisioning in the little shearwater *Puffinus assimilis haurakiensis*: a previously undescribed foraging strategy in the Procellariidae. *Ibis* 142:144–146.
- Cannell, B. L., and J. M. Cullen. 1998. The foraging behaviour of little penguins *Eudyptula minor* at different light levels. *Ibis* 140:467–471.
- Chaurand, T., and H. Weimerskirch. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63:275–282.
- Cherel, Y., and Y. Le Maho. 1985. Five months of fasting in king penguin chicks: body mass loss and fuel metabolism. *American Journal of Physiology* 249:R387–R392.
- Cherel, Y., C. Verdon, and V. Ridoux. 1993. Seasonal importance of oceanic myctophids in king penguin diet at Crozet Islands. *Polar Biology* 13:355–357.
- Chiaradia, A., M. G. Forero, K. A. Hobson, and J. M. Cullen. 2010. Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science*. (<http://icesjms.oxfordjournals.org/content/early/2010/06/29/icesjms.fsq067>)
- Chiaradia, A., and K. R. Kerry. 1999. Nest attendance and breeding success in the Little Penguins *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology* 27:13–20.
- Chiaradia, A., and I. C. T. Nisbet. 2006. Plasticity in parental provisioning and chick growth in Little Penguins *Eudyptula minor* in years of high and low breeding success. *Ardea* 94:257–270.
- Collins, M., J. M. Cullen, and P. Dann. 1999. Seasonal and annual foraging movements of Little Penguins from Phillip Island, Victoria. *Wildlife Research* 26:705–721.
- Congdon, B. C., A. K. Krockenberger, and B. V. Smithers. 2005. Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the wedge-tailed shearwater. *Marine Ecology Progress Series* 301:293–301.
- Costa, D. P. 1991. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *American Zoologist* 31:111–130.
- Cullen, J. M., L. E. Chambers, P. Dann, and P. C. Coutin. 2009. Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Marine Ecology Progress Series* 378:269–278.
- Daniel, T. A., A. Chiaradia, M. Logan, G. Quinn, and R. Reina. 2007. Synchronized group association in little penguins, *Eudyptula minor*. *Animal Behaviour* 74:1241–1248.
- Drent, R. H., and S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68:225–252.
- Goodman, D. 1974. Natural selection and cost of ceiling on reproductive effort. *American Naturalist* 108:247–268.
- Granadeiro, J. P., M. Nunes, M. Silva, and R. W. Furness. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chickrearing period. *Animal Behaviour* 56:1169–1176.
- Hedd, A. 1998. Foraging ecology of Shy Albatrosses *Thalasarche cauta* breeding in Australia: Implications for interactions with longline fisheries. Dissertation. University of Tasmania, Hobart, Australia.
- Kato, A., Y. Ropert-Coudert, and A. Chiaradia. 2008. Regulation of trip duration in an inshore forager, the little penguin (*Eudyptula minor*), during incubation. *Auk* 125:588–593.
- 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 NIPR Symp. Polar Biology, Tokyo, Japan.
- Klomp, N. I., and R. D. Wooller. 1991. Patterns of arrival and departure by breeding little penguins at Penguin Island, Western Australia. *Emu* 91:32–35.
- Lescroël, A., and C.-A. Bost. 2005. Foraging under contrasting oceanographic conditions; the gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series* 302:245–261.
- Lewis, S., T. N. Sheratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819.
- Markman, S., B. Pinshow, J. Wright, and B. P. Kotler. 2004. Food patch use by parent birds: to gather food for themselves or for their chicks? *Journal of Animal Ecology* 73:747–755.
- Mauck, R. A., and T. C. Grubb. 1995. Petrel parents shunt all experimentally increased reproductive costs to their offspring. *Animal Behaviour* 49:999–1008.

- Murphy, M. E. 1996. Nutrition and metabolism. Pages 31–60 in C. Carey, editor. *Avian energetics and nutritional ecology*. Chapman and Hall, New York, New York, USA.
- Nur, N. 1988. The cost of reproduction in birds: an examination of the evidence. *Ardea* 76:155–168.
- Orians, G. H., and N. E. Pearson. 1979. On the theory of central place foraging. Pages 154–177D in J. Horn, R. D. Mitchell, and G. R. Stairs, editors. *Analysis of ecological systems*. Ohio State University Press, Columbus, Ohio, USA.
- Partridge, L., and P. Green. 1985. Intraspecific feeding specializations and population dynamics. Pages 207–226 in R. M. Sibly and R. H. Smith, editors. *Behavioural ecology, ecological consequences of adaptive behaviour*. Blackwell, London, UK.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.r-project.org>)
- 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., 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.
- Schultz, M. A., and N. I. Klomp. 2000. Does the foraging strategy of adult short-tailed shearwaters cause obesity in their chicks? *Journal of Avian Biology* 31:287–294.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, editor. *Sexual selection and the descent of man 1871–1971*. Aldine Press, Chicago, Illinois, USA.
- 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. 1998. How can a pelagic seabird provision its chick when relying on a distant resource? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *Journal of Animal Ecology* 67:99–109.
- Weimerskirch, H., C. Barbraud, and P. Lys. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology* 81:309–318.
- Weimerskirch, H., O. Chastel, T. Chaurand, L. Ackerman, X. Hindermeier, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parent. *Animal Behaviour* 47:472–476.
- Weimerskirch, H., Y. Chastel, F. Cuenot-Chaillet, and V. Ridoux. 1997a. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* 78:2051–2063.
- Weimerskirch, H., P. Jouventin, and J. C. Stahl. 1986. Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128:195–213.
- Weimerskirch, H., T. Mougey, and X. Hindermeier. 1997b. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635–643.
- Welcker, J., A. M. A. Harding, N. J. Karnovsky, H. Steen, H. Strøm, and G. W. Gabrielsen. 2009. Flexibility in the bimodal strategy of a high Arctic alcid, the little auk *Alle Alle*. *Journal of Avian Biology* 40:388–399.
- Williams, T. D., and P. Rothery. 1990. Factors affecting variation in foraging and activity patterns of gentoo penguins (*Pygoscelis papua*) during the breeding season at Bird Island, South Georgia. *Journal of Applied Ecology* 27:1042–1054.
- Wilson, R. P., P. G. Ryan, and M. P. Wilson. 1989. Sharing food in the stomachs of seabirds between adults and chicks - a case for delayed gastric emptying. *Comparative Biochemistry and Physiology* 94(A):461–466.

#### APPENDIX

Histogram of foraging-trip duration in chick-rearing Little Penguins (*Ecological Archives* E092-163-A1).