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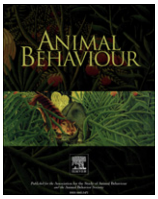

Chick-provisioning strategies used by king penguins to adapt to a multiseasonal breeding cycle

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Parental provisioning strategies are central to life history theory, as one of the main components that adults can adjust to maximize their fitness. In altricial species, newly born young rely entirely on parents for food. Provisioning strategies are thus crucial for offspring survival and growth, but they may also have major consequences for parental lifetime reproductive success, especially in long-lived species. We investigated provisioning strategies in an offshore seabird, the king penguin, *Aptenodytes patagonicus*, through the number of times parents return to the colony to feed their chick, using a pluriannual database on more than 800 microtagged penguins. King penguin chick rearing can be divided into three periods: (1) from thermal emancipation to the onset of winter, (2) winter and (3) from the end of winter to fledging. Overall, we found that the number of feeding visits was larger for males, as well as for older and larger individuals. The timing of the winter low-provisioning period (15 May–1 September; shorter than previously described) did not vary according to sex, age or breeding timing. We found four different parental strategies during the winter period, from complete absence to regular foraging trips, which led to different breeding success rates. These four strategies were observed in the 6 study years, and in both sexes, although in different proportions. They were not explained by individuals' age, and individuals were not consistent across years, the decision to follow a strategy probably reflecting the trade-off between the bird's current condition and its environment.

Life history theory predicts that individuals should maximize their lifetime reproductive success (LRS) by investing a specific amount of time and energy in any reproductive attempt, as the result of a trade-off between benefits and costs associated with current and future reproduction (Williams 1966; Stearns 1989). One of the major resulting questions is then: how do individuals adjust their reproductive effort and parental investment to maximize fitness (Stearns 1992)? If parental investment (see definition in Trivers 1972) includes a variety of activities, such as territory defence or breeding site preparation, offspring provisioning is often considered as the central component of parental care (Clutton-Brock 1991). During this period, parents have to decide whether and how to allocate the energy they gather between themselves and their offspring (Drent & Daan 1980). Provisioning strategies thus represent the core of the trade-off between current reproduction and maintenance, and are consequently of great importance to understand. This is even more relevant for seabirds, which have to travel off their breeding site to find food, incurring the added constraints of central-place foragers (Orians & Pearson 1979). In offshore species, breeding birds go far out to sea before returning to the colony (e.g. up to 15 000 km round-trip in incubating wandering albatrosses, *Diomedea exulans*; Jouventin & Weimerskirch 1990), conducting longer trips than inshore species. To avoid jeopardizing chick survival and to ensure chicks grow optimally, returns have to be timely, and foraging and provisioning strategies need to be efficiently adjusted. Most seabirds are long-lived species, and parents are thus expected to favour their own survival at the expense of the current reproductive event (the 'prudent parent' hypothesis: Drent & Daan 1980; Stearns 1989; Mauck & Grubb 1995), an additional constraint that might shape foraging strategies in these species.

In central-place foragers, time and energy expended during a foraging trip are primary factors limiting a parent's ability to provision chicks (Orians & Pearson 1979). Provisioning rates should thus be affected by physiological capabilities of the parents that may depend on several factors such as age, sex or current physiological state (e.g. body condition: Chaurand & Weimerskirch 1994; Weimerskirch 1998). The widespread increase in reproductive performance with age (Newton 1989) has been suggested to result partly from an increase in foraging efficiency (Martin 1995; Daunt

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et al. 2007); and age-related changes in foraging behaviour and performance have indeed been recorded in some bird species (e.g. Greig et al. 1983; Desrochers 1992; Zimmer et al. 2011). Differences in offspring provisioning between the sexes have also been recorded in numerous species, both monomorphic (Lewis et al. 2002; Quillfeldt et al. 2004; Hamer et al. 2006) and sexually size-dimorphic species (Aho et al. 1997; Weimerskirch et al. 2000; Velando & Alonso-Alvarez 2003; Lewis et al. 2005). These differences are usually attributed to the influence of parents' body size on foraging efficiency and competitive ability (Andersson 1994; Markman et al. 2004). Finally, provisioning and foraging strategies are not solely the results of parental quality but rather the interaction between individual characteristics and extrinsic factors such as environmental conditions. Indeed, prey abundance and distribution affect the time spent foraging and the quantity of food acquired by parents (Pyke 1984).

In this study, we investigated chick-provisioning and foraging strategies in king penguins, *Aptenodytes patagonicus*, breeding in the Crozet Archipelago. The unusual breeding cycle of the king penguins has mainly been described by monitoring a few banded individuals (Stonehouse 1960; Barrat 1976; Weimerskirch et al. 1992; but see Descamps et al. 2002). Instead, we used an automatic monitoring system enabling us to explore parents' return to the colony to care for their chicks over a large number of individuals ($N = 801$) and across several years (2003–2009). As chick rearing lasts for almost a year in this species, provisioning strategies may be adapted to the various conditions endured throughout the year and could well differ according to season. We examined the number of feeding visits by parents, its trend along the whole chick-rearing period and its interannual variability. We previously reported the negative effect of sea surface temperature (SST) increases on breeding success in king penguins (Le Bohec et al. 2008), suggesting that it may be mediated through prey availability and its effect on foraging efficiency. Indeed, changes in SST have repercussions on the primary production and the food chain (Gregg et al. 2003; Behrenfeld et al. 2006), and consequently SST has been frequently used as a local proxy of abundance and distribution of prey for king penguins (Cotté et al. 2007; Le Bohec et al. 2008; Saraux et al. 2011a, b). We therefore explored the potential effect of SST on the number of feeding visits. Finally, we investigated some biotic parameters (sex, age, structural size) that might affect parental effort, since king penguins exhibit a slight sexual size dimorphism (Stonehouse 1960; Barrat 1976).

METHODS

Penguin Monitoring

Our study was conducted on Possession Island (46°25′S, 51°45′E, in 'La Grande Manchotière' colony) in the Crozet Archipelago. Since 1998, 10-month-old chicks have been randomly sampled each year during their moult, a few weeks before fledging, and have been fitted with subcutaneous passive transponder tags without any other external mark. The antennas buried under the usual and unique three transit pathways in and out of the ANTAVIA subcolony, which contains about 10 000 breeding pairs, allow for the continuous automatic collection of data on bird movements (Descamps et al. 2002; Le Bohec et al. 2007; Nesterova et al. 2010). This automatic identification system (Gendner et al. 2005) has major advantages. It does not require recapture, enables continuous monitoring whatever the climatic conditions and avoids the negative impact of flipper-bands, altogether producing a unique and reliable data set on nonbanded king penguins (see bias introduced by flipper-bands in Gauthier-Clerc et al. 2004; Le Maho et al. 2011; Saraux et al. 2011a).

Upon tagging, both flipper and beak lengths were measured (except for the first cohort tagged in 1998). These two morphological measurements are good descriptors of king penguin structural size and are highly repeatable (Fahlman et al. 2006). Flipper and beak measurements were correlated (Spearman rank correlation: $r_S = 0.40$, $N = 746$, $P < 0.001$), and we thus used a principal component analysis to obtain an integrative index of structural size. The first component explained 83% of the variance in these two variables, and we therefore used this component as a structural size index ($\mathrm{SSI} = 0.96 \times \mathrm{Flipper} + 0.26 \times \mathrm{Beak}$). Birds tagged after 2000 were also blood-sampled at tagging and sexed using microsatellite DNA analyses (adapted from Griffiths et al. 1998). In the absence of DNA samples, that is, for the first two cohorts, sex was determined by analysing the chronology of the sex-specific incubation shifts of their subsequent breeding cycles (Stonehouse 1960; Descamps et al. 2002).

King penguins become sexually mature at a minimum age of 3 or 4 years old but with an average age at first reproduction estimated at 6 years (Barrat 1976; Weimerskirch et al. 1992). To get a large enough sample of breeding king penguins, we analysed breeding data from 2003 to 2009. The breeding cycles and parameters of 801 known-aged birds (i.e. eight cohorts of birds tagged as 10-month-old chicks between 1998 and 2005 that reared a chick between 2003 and 2009) were established by interpreting their movements between the breeding area and the sea (see Descamps et al. 2002; Le Bohec et al. 2007 for details). As mentioned above, king penguins exhibit a unique breeding cycle in that it lasts more than a year from courtship to chick fledging. Successful birds are thus late for the next breeding attempt, leading to two main peaks of egg laying within a given breeding season (Stonehouse 1960; Barrat 1976). Breeders laying before 1 January are considered early breeders, while those breeding afterwards are the so-called late breeders.

Number of Chick-feeding Visits

Detections by the underground antennas enabled us to determine transits in and out of the colony for each bird with a transponder. As breeding king penguins come back on land to care for their chick, we investigated the number of entries into the colony as a proxy of parental feeding events. Newly hatched chicks cannot thermoregulate by themselves, so that parents have to keep them under the brood patch. Consequently, during this brooding period (the 31-day period after egg laying; Weimerskirch et al. 1992; Descamps et al. 2002), parents alternate between brooding shifts of several days within the colony and foraging trips at sea (5–9 days on average according to the brooding shift; Weimerskirch et al. 1992; Descamps et al. 2002). Because these brooding shifts are highly dependent on the partner's effort, feeding visits during this period might not be a useful proxy of the individual's parental effort. Indeed, by separating brooders and parents that were rearing thermally emancipated chicks (Appendix Fig. A1a), we observed a very low feeding rate estimated with our method in brooding birds, and thus only data on individuals rearing emancipated chicks are presented. Once king penguin chicks are thermally emancipated and mobile (gathered in crèches especially during winter; Le Bohec et al. 2005), parents do not remain with their chick continuously during the period they spend on land. Parents often wander around the colony, bathing in the bay and passing over the antennas several times a day. To avoid overestimating feeding visits, we thus only considered entries that were preceded by a trip out of the colony lasting for at least 3 days, since it allowed us to discriminate two peaks of visits that we respectively attributed to comings and goings and new feeding visits (Appendix Fig. A1b). The number of feeding visits was assessed for each monitored individual per period of 2 weeks throughout the breeding season (subsequently referred to as 'number of feeding visits').