

Male and female contributions to provisioning rates of thin-billed prions, *Pachyptila belcheri*, in the South Atlantic

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Abstract We recorded individual provisioning patterns of male and female thin-billed prions in the largest known colony on New Island (Falkland Islands, South Atlantic Ocean), to determine male and female contributions to provisioning rates and to compare them with data from their other main breeding site, on Kerguelen, in the Southern Indian Ocean. Both male and female birds from New Island undertook trips of 1–8 days' duration (median 3 days), similar to those on Kerguelen, although we did not observe a clear distinction between long and short trips. Meal sizes increased with longer trips but did not differ between male birds and female birds. Thus, as on Kerguelen, male and female thin-billed prions on New Island contributed equally to chick provisioning. The proportion of short trips was comparable to those observed in a more favourable year, and was higher than those in a poor year, on Kerguelen. In order to avoid potential disturbance to the birds in the colony by frequent capture and handling, we used miniature radio-tags to record the presence of individuals in the colony and to evaluate the influence of transmitter load on the birds. Despite generally deteriorating conditions towards the end of the breeding season, chicks of tagged adults were fed normally, indicating that the method is adequate.

Keywords Procellariiformes · Foraging · Monitoring · Sexual division of parental care · Nest attendance

Introduction

Although most bird species have bi-parental care (Lack 1968; Cockburn 2006), male and female parents do not always contribute equally to food provisioning. Sexual differences in provisioning rates of parents have been recorded in a number of sexually size-dimorphic birds, including passerines (Morse 1968; Aho et al. 1997), raptors (Newton 1979; Marquiss and Newton 1982) and seabirds (Table 1 in Lewis et al. 2002), and, recently, also in birds showing no sexual size dimorphism (Wiggins and Morris 1987; Gray and Hamer 2001; Lewis et al. 2002; Fraser et al. 2002; Bradley et al. 2002).

Most Procellariiformes (e.g. albatrosses, petrels, shearwaters) are highly pelagic and provision their chicks after feeding trips of various days' duration. Among the procellariiform seabirds, although equal parental effort by both sexes appears to be the norm (e.g. Simons 1981), sexual differences in provisioning rates of parents have been reported in a few species, e.g. Manx shearwaters *Puffinus puffinus* (Gray and Hamer 2001; Quillfeldt et al. 2004) and wandering albatross *Diomedea exulans* (Tickell 1968).

During the chick-rearing period, pelagic seabirds face time and energy constraints, because they have to feed their chicks as often as possible, and forage far from their breeding site, while also maintaining a good body condition in order not to jeopardize their survival. Several pelagic Procellariiformes resolve this conflict by using a twofold provisioning strategy, first described by Chaurand and Weimerskirch (1994) and Weimerskirch et al. (1994).

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During the chick-rearing period, they alternate short trips in coastal waters with long trips in pelagic waters (e.g. Weimerskirch and Cherel 1998; Ropert-Coudert et al. 2004; Congdon et al. 2005). While adults mainly use short trips for chick provisioning, they lose body reserves. In contrast, long trips are used to rebuild the adults' body reserves, and the per-day gain for chicks is lower than during short trips. Long trips are thus viewed as an investment in adult survival (e.g. Weimerskirch 1998; Duriez et al. 2000).

The thin-billed prion *Pachyptila belcheri* is a small and abundant sub-Antarctic seabird, known to breed in two main areas: on Crozet and Kerguelen in the Southern Indian Ocean, and on the Falkland Islands (and possibly on some islands of Tierra del Fuego in the Southern Atlantic Ocean) (Clark et al. 1984; Cox 1980). The life cycle and basic biology of thin-billed prions have been described by Strange (1980). The author also provided a first growth curve for the body mass development of chicks. More recently, studies of the biology of thin-billed prions have been carried out on Kerguelen, including studies of sexual dimorphism of voice and morphology (Genevois and Bretagnolle 1995), feeding ecology (Cherel et al. 2002; Chastel and Bried 1996) and parental investment (Duriez et al. 2000; Weimerskirch et al. 1995). On Kerguelen, there was no difference between male and female thin-billed prions in provisioning effort (Weimerskirch et al. 1995), as both carried out trips 1–9 days long, and alternated long and short trips (with ca. 60% short trips of 1–4 days' duration). On New Island, recent studies have explored variability in provisioning and parent–chick interactions (Quillfeldt et al. 2003, 2006, 2007).

The aim of the present study was to record individual provisioning patterns of male and female thin-billed prions in the largest known colony on New Island (Falkland Islands), to determine male and female contributions to provisioning rates and compare them with the data from the Southern Indian Ocean. We aimed to avoid potential disturbance to the birds in the colony by frequent capture and handling and the use of trap doors (e.g. Weimerskirch et al. 1995). Instead, we used miniature radio-tags to record the presence of birds in the colony and to evaluate the influence of transmitter load on the birds.

Methods

Study site and study species

The study was carried out on New Island, Falkland Islands (51°43' S, 61°17' W), from January to March 2006. Thin-billed prions breed on the Falkland Islands, Crozet and Kerguelen, New Island being the most important known breeding site (Catry et al. 2003).

Thin-billed prions show the typical procellariiform pattern of a single-egg clutch and slow chick development, with an average fledging period of 50 days (Strange 1980). Thin-billed prions are burrow nesters, and we reached chicks in their nest chambers via short access tunnels in the roof of each burrow, capped with removable stone lids. This system facilitated rapid access to chicks, reducing overall disturbance. Marked nests were monitored for eggs and hatching chicks.

Chick measurements

When eggs were found, the hatching date was estimated from the egg density (see Quillfeldt et al. 2003), and the nest was not visited again until 3 days after the estimated hatching date.

If chicks were present on our first visit, we determined the hatching dates of chicks (to the nearest day) by calibrating wing length against wing growth in chicks of known age. Chicks were weighed daily at 0730 hours and 1930 hours to the nearest 1 g, with a digital balance. Wing length was measured every 3 days, to the nearest 1 mm, with a stopped wing rule. Tarsus length was measured every 3 days, to the nearest 0.1 mm, with callipers. An index of chick body condition at 1930 hours each evening was calculated relative to the mean mass for chicks of each age over the seasons 2003–2006 (m_{mean}), with the following formula: $BC = m \times 100/m_{\text{mean}}$.

Meal sizes and feeding frequencies were estimated from the evening and morning weights, by correction of the mass differences for metabolic mass loss, with the equations given in Quillfeldt et al. (2003). Meal sizes were defined to represent one feeding for meal sizes up to 50 g and two feedings for meal sizes larger than 50 g (approximately half of the maximum food delivered by two parents). Only nights of single feeds were included in the analyses, to ensure correct calculation of meal sizes from periodic weighing ($N = 28$ meals from male parents, 19 meals from female parents).

Transmitter attachment and detection

We caught one or both adults at 18 and 7 study nests, respectively (32 adults in total) over a period of 9 nights from 3 February. Chicks were 30–40 days old at this time, and adult weights ranged between 114 g and 137 g (without food loads). Adults were fitted with a VHF radio-transmitter (Biotrack, Dorset, UK.). The transmitters weighed 1.2 g (<1% of body mass) and measured 17 mm × 8 mm × 5 mm, with an external aerial measuring 240 mm × 0.6 mm. They were attached to two central tail feathers with self-amalgamating tape, which formed a seal over the feathers and transmitter and was covered by

the surrounding feathers (a method previously used in Manx shearwaters, e.g. Quillfeldt et al. 2004). The aerial was thin and flexible and extended ca. 140 mm beyond the tail. The process from capture to returning a bird to its burrow took no longer than 10 min.

We monitored visits of tagged birds to the colony for 18 consecutive nights (8–26 February), using a scanning logger (Televilt, Sweden) with a three-element Yagi antenna located on a hillside directly above the area of the study nests. Trials at the colony indicated that the range of this system was <1 km, so we were confident that signals received were from birds in the colony and not at sea. Signals were detected mainly before birds entered their nests or when they left the colony. We monitored attendance overnight from 2200 hours (before the first adults returned) until 0600 hours (after the last adults had left the colony).

Signals from four of the attached transmitters were not recorded, and checks confirmed that the transmitters had been lost by shedding of the central tail feathers. Of the remaining 28 birds, 16 were male and 12 were female. Although we recorded for a total of 18 nights, some adults were recorded for a shorter period, because either the chick had fledged before the end of the observed period, or the transmitter had stopped signalling. Thus, in total, we recorded up to six trips per adult (between three and four trips for most adults, but only one trip for two male birds and two female birds each). The total number of recorded trips was 53 for male birds and 29 for female birds.

Molecular sexing

We plucked one small body contour feather for molecular sex determination. DNA was extracted using the DNeasy tissue kit (Qiagen, Hilden), and DNA was eluted in 50 µl of buffer. Sexing of birds is based on differences in length between introns in the CHD-Z and CHD-W genes (Fridolfsson and Ellegren 1999), and we used the primers developed by Fridolfsson and Ellegren (1999: 2550F/2718R). All samples were run on a 2% agarose gel and checked for the presence of a single or double band representing a male bird or a female bird, respectively.

Data analysis

For statistical tests we used SPSS 11.0 (SPSS, Chicago, IL, USA). General linear models (GLMs) are given with *t* values to indicate the direction (positive or negative) of the correlation to the covariable, and, as a measure of effect sizes, we included partial eta-squared values (η^2 , i.e. the proportion of the effect + error variance that is attributable to the effect). The sum of the partial eta-squared values are not additive (e.g. http://www.web.uccs.edu/lbecker/SPSS/glm_effectsize.htm).

Results

Male and female birds’ trip lengths

We registered trip durations of 1–8 days, in both male and female birds (Fig. 1). There was no clear distinction between long and short trips, as medium trip durations were very common. The most frequent trip length (29.3% of cases, Fig. 1) was 1 night; however, only 9.3% of the total foraging time was spent on 1-day trips, while trips of medium and long duration (3–7 days) occupied most of the foraging time (Fig. 2). Male birds and female birds had a similar median trip length of 3 days (Mann–Whitney rank sum test, $U_{29,53} = 1249.5$, $P = 0.659$). Using the cut-off point of Weimerskirch et al. (1995), we distinguished short trips of 1–4 days and long trips of 5–8 days. Male birds and female birds used long trips at similar rates

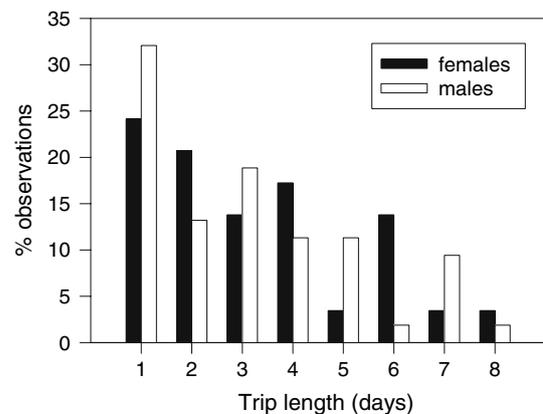


Fig. 1 Distribution of trip lengths of male and female thin-billed prions during chick-provisioning, observed by radio-tracking ($N = 53$ trips of male birds and 29 trips of female birds)

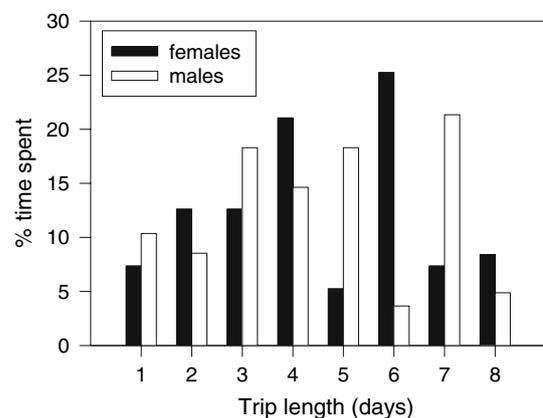


Fig. 2 Allocation of total time observed to trip lengths of male and female thin-billed prions during chick-provisioning ($N = 53$ trips of male birds and 29 trips of female birds)

female 1			8	1	1			6	1
female 2		3		4			6	2	2
female 3			4	3			6		4
male 1	2	1		5	1		3		4
male 2		3		5		2		4	
male 3			7			4		3	

Fig. 3 Examples of tracked thin-billed prions (three female and three male), showing the trips undertaken in the study period of 18 consecutive nights (8–26 February). Numbers indicate the observed trip length, and long trips (5–8 nights) are marked grey

(24.5% vs 24.1% of registered trips, $\chi^2 = 0.053$, $P = 0.181$) and spent a similar fraction of their time on long trips (48.2% vs 46.3% of registered time, $\chi^2 = 0.025$, $P = 0.874$). All registered long trips were followed by one or several short trips (for example, see Fig. 3), but some individuals (e.g. female 3 and male 3 in Fig. 3) never returned after 1 or 2 nights but used only long and intermediate trips.

Meal sizes in relation to trip length

Meal sizes increased with longer trip lengths, and male birds and female birds delivered similar meals (Fig. 4, GLM with meal size as dependent variable, sex as categorical variable (“factor”) and trip duration as covariate; influence of sex $F = 0.6$, $P = 0.447$, $\eta^2 = 0.013$; influence of trip duration $F = 13.7$, $P < 0.001$, $\eta^2 = 0.237$, $t = 3.7$).

Evaluation of influence of transmitter load

To test whether chicks of tagged adults were fed normally, we compared the development of their body condition with that of control chicks, for all chicks with a minimum of 6 nights before and after the time of transmitter attachment ($n = 11$ controls and 22 chicks with tagged adults). Control chicks were regularly weighed, but their adults were not

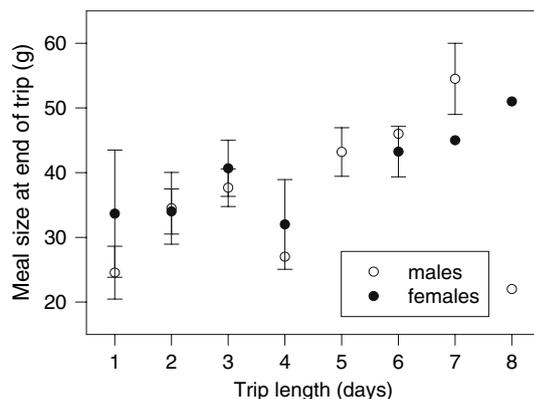


Fig. 4 Sizes of meals delivered to thin-billed prion chicks after trips of variable duration by male and female parents. Only nights of single feeds were included, to enable the calculation of meal sizes from periodic weighing ($N = 28$ meals from male parents, 19 meals from female parents)

captured. Both control and studied chicks decreased their body condition in relation to the mean for 2003–2006, on average, but the mean change was similar (-4.2 ± 2.6 for controls vs -5.9 ± 2.8 ; $t = 0.41$, $df 31$, $P = 0.687$, Fig. 5). Within the group of tagged birds, we observed no difference between pairs where one or two adults were carrying a transmitter (Fig. 5, $t = 0.51$, $df 22$, $P = 0.616$).

Discussion

During the present study we used a novel technique to record provisioning patterns of male and female thin-billed prions in the largest known colony on New Island (Falkland Islands).

Evaluation of radio-tracking as monitoring method

In order to avoid potential disturbance to the birds at the colony by frequent capture and handling, we used miniature radio-tags to record the presence of birds in the colony, and we evaluated the influence of transmitter load on the birds. Despite generally deteriorating conditions towards the end of the breeding season, all except one chick of tagged adults were fed normally, indicating that the method is adequate, at least for use over a short period.

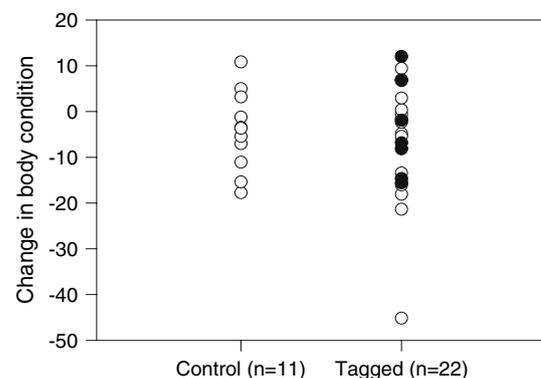


Fig. 5 Change in body condition of thin-billed prion chicks during the time the parents carried transmitters, calculated from the average body condition of the chick before and after the transmitter attachment. Within the “tagged” group, black circles indicate chicks where both adults were tagged

The outlier was a chick with only one tagged parent, and the chick probably experienced competition, as we found a second, well-fed chick in the nest. The focal chick starved and died. The adult was recorded only once, 5 days after transmitter attachment, but, during this period, the chick had not been fed. We cannot exclude the possibility that, in addition to the deteriorating conditions, in this single case the extra load of the transmitter contributed to chick abandonment. However, Weimerskirch et al. (1995) found that single and handicapped birds were capable of rearing chicks to fledging, and, as only one parent of this chick carried a transmitter, we think it more likely that the adults experienced predation or lost their nest to the parents of the second chick. Moreover, within the group of tagged birds, we observed no difference between pairs where one or two adults were carrying a transmitter (Fig. 5).

Foraging patterns

We found that male and female parents contributed equally to chick provisioning, as both trip durations and meal sizes were indistinguishable. Similar contributions by the sexes had also been observed previously in the Southern Indian Ocean (Weimerskirch et al. 1995). Furthermore, the relationship between trip length and meal size (i.e. the slope in Fig. 4) was similar between male and female parents.

Thin-billed prions are slightly sexually dimorphic in bill and tarsus but not in body weight or wing measurements (Genevois and Bretagnolle 1995). Thus, the costs of flight are similar for both sexes. It remains to be established, however, whether the sexes use similar foraging areas, and how both sexes respond to better foraging conditions than those observed.

The results resemble observations on Kerguelen (Weimerskirch et al. 1995), except that we observed a less clear distinction between long and short trips as reported for Kerguelen; alternate long and short trips were common, but, in many cases, several short trips were observed in succession, before the next long trip. This pattern was, therefore, similar to that observed for birds of experimentally increased demand (single parents) or flight costs (handicapped parents) on Kerguelen (Weimerskirch et al. 1995) but, also, for a season of good food availability (Duriez et al. 2000). The birds in the present study used slightly more “short trips” (trips of 1–4 days’ duration) than did the birds on Kerguelen in 1992 (76% vs 60%), but this was comparable to the observation on Kerguelen during the more favourable chick-rearing season of 1997 (73%, Duriez et al. 2000). It had been noted earlier (Quillfeldt et al. 2003, 2007) that feeding rates of thin-billed prions on the Falklands are, in general, higher than in the Southern Indian Ocean, which would be supported by this observation. It will also be instructive to follow

provisioning patterns over several stages of chick development, to study how provisioning patterns are adjusted to variable chick demand.

Zusammenfassung

Wir registrierten individuelle Füttermuster von männlichen und weiblichen Dünnschnabel-Walvögeln in ihrer größten bekannten Kolonie, auf New Island (Falklandinseln, Südatlantik), um männliche und weibliche Anteile an der Kükenfütterrate zu bestimmen, und mit Daten vom anderen Hauptbrutort auf Kerguelen (südlicher Indischer Ozean) zu vergleichen. Sowohl Männchen als auch Weibchen von New Island unternahmen Nahrungsflüge von einem bis acht Tagen Dauer (Median drei Tage). Dies war vergleichbar mit Kerguelen, obwohl wir keine klare Trennung zwischen langen und kurzen Nahrungsflügen beobachten konnten. Die Füttermenge stieg mit der Flugdauer an, aber unterschied sich nicht zwischen Männchen und Weibchen. Daher erbringen männliche und weibliche Dünnschnabel-Walvögeln auf New Island, genau wie in Kerguelen, gleiche Anteile an der Kükenfütterrate. Der Anteil kurzer Nahrungsflüge war vergleichbar mit dem in einer besseren Brutsaison, und höher als der in einem schlechteren Jahr, in Kerguelen. Um mögliche Störungen durch häufigen Fang der Vögel zu vermeiden, registrierten wir die Anwesenheit der Vögel in der Kolonie mit Hilfe von Miniatur-Radiosendern, und untersuchten daher, ob das Gewicht der Sender die Vögel beeinflusste. Trotz sich verschlechternder Nahrungsverfügbarkeit zum Ende der Brutsaison wurden die Küken der besenderten Walvögel normal gefüttert, so dass wir keinen Kurzzeiteinfluss der Sender auf das Verhalten der Vögel feststellen konnten und die Methode als für diese Art angemessen einschätzen.

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