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Inter-annual changes in diet and foraging trip lengths in a small pelagic seabird, the thin-billed prion *Pachyptila belcheri*

Petra Quillfeldt · Andreas Michalik ·
Gritta Veit-Köhler · Ian J. Strange ·
Juan F. Masello

Abstract Central place foragers are constrained in their foraging distribution by the necessity to return to their nest site at regular intervals. In many petrels that feed on patchily distributed prey from the sea surface over large foraging areas, alternating long and short foraging trips are used to balance the demands of the chick with the requirements of maintaining adult body condition. When the local conditions are favourable for prey density and quality, adults should be able to reduce the number of long foraging trips. We studied the flexibility in foraging trip lengths of a small pelagic petrel, the thin-billed prion *Pachyptila belcheri*, over three breeding seasons with increasingly favourable, cold-water conditions. During a warm-water influx in February 2006, chicks were fed less frequently and adults carried out foraging trips of up to 8 days. When conditions became more favourable with colder water temperatures in 2007 and 2008, thin-billed prions decreased trip lengths, more often attended their chick every day, and long foraging trips of six to eight days

were not registered during 2008. Chick growth rates mirrored this, as chicks grew poorly during 2006, intermediate during 2007 and best during 2008. Thin-billed prions preyed mainly on squid during incubation and mainly on amphipods and euphausiids during chick-rearing. In the poorest season only, the diet was substantially supplemented with very small copepods. Together, the present results indicate that during warm-water conditions, thin-billed prions had difficulties in finding sufficient squid, amphipods or euphausiids and were forced to switch to lower trophic level prey, which they had to search for over large ocean areas.

P. Quillfeldt (✉) · A. Michalik · J. F. Masello
Max-Planck-Institut für Ornithologie, Vogelwarte Radolfzell,
Radolfzell, Germany
e-mail: petra.quillfeldt@gmx.de

A. Michalik
Department of Biology/Chemistry, Experimental Ecology
Group, University of Osnabrück, Osnabrück, Germany

G. Veit-Köhler
Deutsches Zentrum für Marine Biodiversitätsforschung,
Forschungsinstitut Senckenberg, Wilhelmshaven, Germany

I. J. Strange
New Island Conservation Trust, Stanley, Falkland Islands

Introduction

Food availability for top predators varies both in time and space. Seabirds show behavioural buffer mechanisms to cope with natural fluctuations in food supply, including flexible time budgets and prey choice (e.g., Furness 1996).

The cold, mineral-rich waters of the Falkland Current provide food for large breeding colonies of seabirds in the Southwest Atlantic, from the Falkland/Malvinas Islands archipelago to the Atlantic coast of Patagonia. Seabirds, predatory fish, squid and seals breeding at the Falkland Islands or visiting the area in summer are largely dependent, directly or indirectly, on the transport of plankton and nutrients from the Southern Ocean, which are brought to the surface along the Antarctic convergence zone and transported to lower latitudes by the water movements of the Falkland Current (e.g., Acha et al. 2004). For example, recent studies on thin-billed prions *Pachyptila belcheri* at New Island, Falkland Islands, suggest a link between time allocation patterns of breeding adults and ocean climate (Quillfeldt et al. 2007a). Sea-surface temperatures were

negatively correlated with provisioning frequencies to thin-billed prion chicks (Quillfeldt et al. 2007a).

The thin-billed prion is a small petrel, with a potentially very large foraging range, which feeds on small prey at or near the sea surface. Pennycuick (1982) recorded the flight speed of the closely related Antarctic prion *Pachyptila desolata* at South Georgia as 11 m/s (39.6 km/h). At this speed, the potential maximum foraging radius in 24 h would be 440 km. Although the actual foraging radii are smaller because birds spent time feeding or roosting, the foraging range of this small petrel is very extensive, given a mean incubation shift duration of 7 days and foraging trip durations of 1–8 days during chick feeding (Quillfeldt et al. 2007b).

The aim of the present study was to study the flexibility in time allocation and prey choice of chick-provisioning thin-billed prions in relation to ocean climate. We recorded chick growth, adult attendance and diet in three breeding seasons, and specifically addressed the following predictions:

1. in years with high sea surface temperatures, lower adult provisioning rate is caused by engaging in more long foraging trips, leading to poorer chick growth
2. thin-billed prions change diet between years with different environmental conditions (warm and cold water), with decreasing prevalence of *Themisto gaudichaudii* during warm-water conditions

Materials and methods

Study site and study species

The study was carried out at New Island Nature Reserve, Falkland/Malvinas Islands (51°43′S, 61°17′W), in the breeding seasons of the austral summers, between 2003 and 2008. We measured chick body conditions in the 6 years, while diet sampling and radiotracking were carried out in the breeding seasons 2005–2006, 2006–2007, and 2007–2008. The thin-billed prion is a small and abundant sub-Antarctic seabird, known to breed in two main areas: at Crozet and Kerguelen Islands in the Southern Indian Ocean, and at the Falkland Islands (and possibly on some islands off Tierra del Fuego: Clark et al. 1984; Cox 1980) in the Southern Atlantic Ocean.

The life cycle and basic biology of thin-billed prions have been described by Strange (1980). At New Island, recent studies explored variability in provisioning and parent–chick interactions (see reference list in Quillfeldt et al. 2009). 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).

Sea surface temperature anomaly (SSTA) data in the Falkland current area adjacent to the Falkland Islands (Fig. 1, 50–52°S, 61–63°W) were downloaded from http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/. EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/.ssta/.

Chick measurements

Thin-billed prions are burrow nesters, and we reached adults and 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, reducing overall disturbance. Marked nests were monitored for eggs and hatching chicks. 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 and tarsus length against wing growth in chicks of known age. Tarsus growth (mean over the
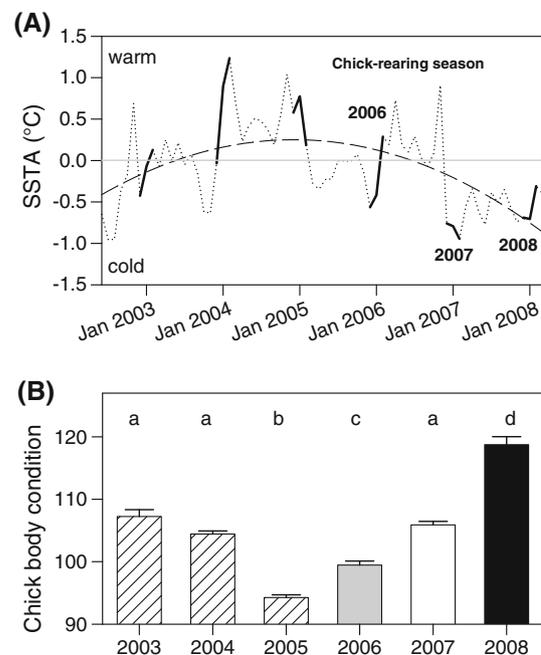

Fig. 1 a Sea surface temperature anomalies (SSTA) during 6 years, including the study period, with chick-rearing seasons (January–March) marked with *bold lines*. The *hatched trend line* shows a fitted quadratic regression, showing rising temperatures in the first 3 years, followed by gradually decreasing water temperatures. b Chick body conditions (mean ± SE) of thin-billed prions at New Island during 6 years (relative to mean data from 2003 to 2006), including the study period 2006–2008. Years with similar body condition (homogenous subsets determined by ANOVA) are marked with the *same letter*

seasons) was approximately linear until 30 days of age: Tarsus (mm) = 15.468 mm + 0.605 mm × age (days); ($R^2 = 0.93$, *df* 1,468, *F* = 19,036, *P* < 0.001). Wing growth until 30 days of age was best described by a quadratic regression: Wing (mm) = 19.415 mm − 0.569 mm × age (days) + 0.110 mm × age (days)^2; ($R^2 = 0.94$, *df* 1,498, *F* = 10,890, *P* < 0.001). The median hatch dates and ranges in the six seasons were 8 January 2003 (30 December–23 January), 5 January 2004 (24 December–17 January), 2 January 2005 (26 December–12 January), 2 January 2006 (23 December–8 January), 4 January 2007 (27 December–13 January) and 5 January 2008 (29 December–15 January). After hatch, chicks were brooded alternately by the parents for 3–8 days, before remaining in the nest on their own during the day. The parents return to feed their chicks at night, after feeding trips of 1–8 days (in 2005–2006; Quillfeldt et al. 2007b). Chicks were weighed daily to the nearest 1 g using a digital balance, during the duration of the field season. In 2004, 2005, and 2007, this included the entire chick-rearing period from hatching to fledging at the age 49–56 days, while only chicks up to ca. 30 days of age were measured in 2003 and 2008, and chicks from 20 days to fledging in 2006.

We calculated a body condition index for chicks of at least 10 days of age, using the observed body mass (m), relative to a multi-year (2003–2006) mean mass for chicks of each age (m_{mean}), using the formula: BC index = m/m_{mean} × 100 (e.g., Quillfeldt et al. 2006). m_{mean} was best described by the regression equation: m_{mean} (g) = $-0.0011\ g$ × age^3 + 0.0056 g × age^2 + 5.075 g × age + 22.917 g.

Radiotracking

We carried out radiotracking as described previously (Quillfeldt et al. 2007b), using VHF radiotransmitter (Biotrack, Dorset, UK). The transmitters weighed 1.2 g (<1% of body mass), and measured 17 × 8 × 5 mm, with an external aerial measuring 240 × 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. 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, 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 nest or when they left the colony. We monitored attendance overnight from 2200 h (before the first adults returned) until 0600 h (after the last adults had left the colony).

In 2006, we registered 82 foraging trips (28 birds, between 8 and 26 February 2006), in 2007 a total of 339 foraging trips (31 birds, 29 December 2006–18 February 2007), and in 2008 a total of 61 foraging trips (8 birds, 2 January–23 January 2008). Radiotracking data for males and females were pooled, as previous studies had not found any difference between males and females in provisioning effort at Kerguelen Islands (Weimerskirch et al. 1995) and New Island (Quillfeldt et al. 2007b). In 2007, we covered the complete chick-rearing season, and confirmed that the provisioning patterns did not differ for parents of younger and older chicks.

Diet sampling

We collected regurgitates and stomach contents in three successive field seasons. In February 2006, we collected 15 regurgitates from breeding adults returning to feed chicks, using mistnet captures and two stomachs of birds found dead (one adult and one chick).

In the 2006–2007, we collected samples opportunistically over the field season, whenever adults regurgitated during handling. We obtained 43 samples, of which three samples consisted mainly of green filamentous algae and were not included in the subsequent analyses. We removed algae from the analysis of volume of a further six samples that otherwise consisted mainly of cephalopods, suggesting that algae had been ingested incidentally with the latter. We were able to estimate volumes of prey types in 23 samples. The data were also separately analysed for two periods: incubation and brooding (19 December–9 January) and chick-rearing (25 January–19 February).

From 31 December 2007 to 14 January 2008, we collected 19 regurgitates from adults during handling. During a bad-weather event, 20 small chicks died from hypothermia when water ran into their nest burrows and were collected for stomach content analysis. The majority of chick stomach contents and some adult samples were too digested for volume estimates, and the total sample size was therefore 39 for prevalence data and 20 (12 adult and 8 chick samples) for volume data.

All samples were examined in the laboratory using a stereo microscope at 40× magnification. Prey taxa were determined with a reference collection and the help of experts (see acknowledgements). However, most food items were too digested for species determination. Therefore, we did not attempt to determine quantitatively to species level, but classed the diet in visually estimated volume % in seven groups: amphipods, euphausiids, *Munida gregaria*, copepods, cirripedia (adults and larvae),

squid, and fish (Table 1). As there were many observed values of less than five in *Munida gregaria*, copepods, cirripedia, and fish, we compared only the frequency of occurrence of the three main food items (amphipods, euphausiids, and squid), using chi-square tests.

Data analysis

Statistical tests were performed in SPSS 11.0 and SigmaStat 2.03. Normality was tested using Kolmogorov–Smirnov tests, and non-parametric tests were applied where appropriate. Significance was assumed at $P < 0.05$.

Results

Sea surface temperatures, chick condition and adult foraging trips

Prior to this study, sea surface temperature had increased between 2003 and 2005, and subsequently decreased during the 3 years in focus of this study (2006–2008) (Fig. 1a). These years can be classed according to their sea surface temperature as close to the long-term average, but showing increasing trend during the season (2006), recently turned cold (2007) and stable cold (2008).

The chick body conditions differed among the 6 years (ANOVA: $F = 116.6$, $df = 2$, $P < 0.001$, for homogenous subsets derived from Tukey post hoc tests, see Fig. 1b). During the study period, body conditions were lowest in 2006, intermediate in 2007, and highest in 2008 (Fig. 1b).

Foraging trip lengths differed between the three breeding seasons (Kruskal–Wallis ANOVA: $H = 18.3$, $df = 2$, $P < 0.001$). A multiple comparison procedure (Dunn's Method) isolated the year 2006, which differed from the other 2 years (2006 vs. 2007: $P = 0.002$, 2006 vs. 2008: $P < 0.001$, 2007 vs. 2008: $P = 0.177$). In 2006, thin-billed prions used fewer 1-day trips (Fig. 2) and spent considerably more time in long trips than in 2007 and 2008 (Fig. 2, inset).

Diet composition

A range of crustaceans were found in the diet. The overwhelmingly dominant amphipod in all years was *Themisto gaudichaudii*, with single specimens of *Phrosina* found in 2006 and *Lysianassoidea* in 2007. Krill was heavily digested, but fragments could be determined as belonging to *Euphausia vallentini*, with possible *E. lucens* and *E. longirostris* additionally found in 2008. Decapods *Munida gregaria* (lobster krill) of 6–10 mm size were regularly found. Larval stages of Cirripedia, the Cypris-larvae, were regularly ingested, especially in 2006 and 2007. In each of
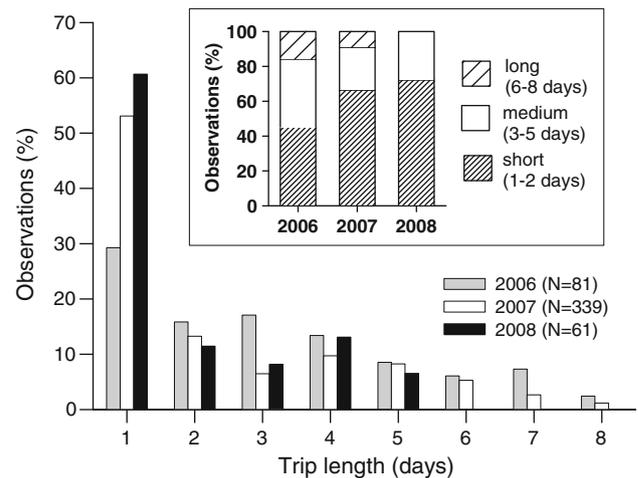

Fig. 2 Distribution of observed foraging trip lengths of thin-billed prions at New Island, Falkland Islands during chick provisioning. The *inset* shows foraging trip lengths classed as short (1–2 days), medium (3–5 days), and long trips (6–8 days)

these 2 years, we also obtained one sample containing adult Cirripedia of the family Lepadidae. In 2006, copepods were *Calanus* sp. (including *C. simillimus* and *C. australis*) of a size range of 2.5–3.6 mm, while the samples of 2008 contained *Neocalanus* sp. and further Calanidae, which were indeterminable. We were not able to determine fish bone remains, while all squid were determined from beaks as *Gonatus antarcticus*.

The frequency of occurrence of the three main food items (amphipods, euphausiids, and squid) differed between the incubation and the chick-rearing period (Table 1; Fig. 3, incubation vs. chick-rearing in 2006–2007: $\chi^2 = 7.4$, $df = 2$, $P = 0.024$). In contrast, there was no difference between years either in the incubation period (2006–2007 vs. 2007–2008: $\chi^2 = 1.0$, $df = 2$, $P = 0.598$) or in the chick-rearing period (2006 vs. 2007: $\chi^2 = 1.1$, $df = 2$, $P = 0.572$).

The estimated volumes of the prey groups also showed intra-year differences (Table 1; Fig. 3), with more squid taken in the incubation-brooding phase than during chick-rearing (Table 2), when amphipods became more important (Fig. 3; Table 2). The estimated volumes of minor food items, moreover, differed among the years. In particular, *Munida gregaria* and calanoid copepods only occurred in important quantities in some years, in particular during chick-rearing 2005–2006 (Fig. 3; Table 2).

Discussion

In the present study, we asked how thin-billed prions adapt their foraging behaviour to differences in food availability, related to ocean climate. Thin-billed prion adults were

Table 1 Diet of thin-billed prions at New Island, Falkland Islands, *F* (frequency of occurrence) is the percentage of samples in which prey items of each type were found, and Vol. is the average volume per sample

Season	Date		*N*	Crustacea					Squid (%)	Fish (%)
				Amphipods (*Themisto*) (%)	Euphausiids (%)	Decapods (*Munida*) (%)	Copepods (%)	Cirripedia (%)		
1. 2005–2006 (chick rearing)	February	*F*	17	88	65	47	41	18	12	–
		Vol.	17	32	31	17	17	1	2	–
2. 2006–2007		*F*	43	73	35	–	3	13	60	5
		Vol.	23	44	19	–	<1	<1	35	1
2a. Incubation + brooding	19 December– 9 January	*F*	27	63	6	–	–	1	78	–
		Vol.	10	35	1	–	–	<1	63	–
2b. Chick rearing	25 January– 19 February	*F*	13	92	62	–	8	15	23	15
		Vol.	11	57	29	–	<1	<1	11	3
3. 2007–2008 (incubation)	31 December– 14 January	*F*	39	49	33	28	3	3	77	3
		Vol.	20	9	12	15	3	<1	61	<1
4. 1977–1978	January	*F*	5	80	60	–	–	–	20	20
		Vol.	5	52	26	–	–	–	20	2
5a. 1986–1987 (incubation)*	10 December– 6 January	*F*	50	7	12	5	–	–	88	5
5b. 1986–1987 (chick rearing)	8–10 February	*F*	37	92	81	38	–	–	89	27
		Vol.	29	34	23	15	–	–	15	2

For comparison, diet analyses carried out in the same colony in 1977–1978 (Strange 1980) and in 1986–1987 (Thompson 1989) are included

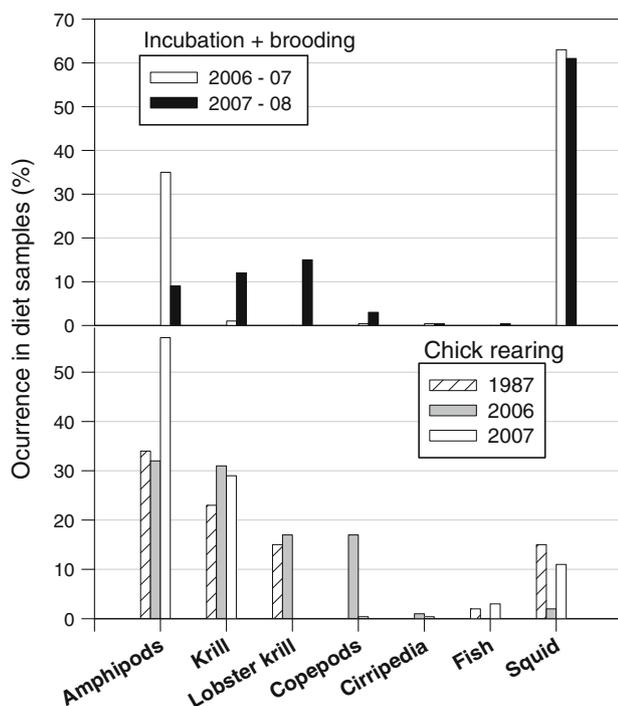* Volumes were not determined in these samples

Fig. 3 Diet composition of thin-billed prions at New Island, Falkland Islands, in volume %, in two periods of incubation to brooding, and three periods of chick provisioning. Data from 2006 to 2008 are from the present study, data of 1987 from Thompson (1989)

flexible both in their time allocation to long and short foraging trips and prey choice during chick-rearing. In a year of warmer sea surface water, adults engaged in more long foraging trips, and this caused lower chick provisioning rates and poorer chick growth.

Sea surface temperatures, chick condition and adult foraging trips

Procellariiformes can exploit vast ocean areas, by foraging over 1,000 km from the nest (Magalhaes et al. 2008; Waugh et al. 2000; Catard et al. 2000), and by alternating short trips in coastal waters with long trips in pelagic waters (e.g., Chaurand and Weimerskirch 1994; Weimerskirch and Cherel 1998; Catard et al. 2000; Congdon et al. 2005). To which extend procellariiform seabirds use long foraging trips depends on differences in food availability among sites (Waugh et al. 2000; Magalhaes et al. 2008), as well as among years (e.g.,Weimerskirch et al. 1999; Pinaud et al. 2005).

Our present results were in line with these results. Poor chick provisioning rates in February 2006 were caused by a high proportion of long foraging trips of parents, lasting up to 8 days. When conditions became more favourable in 2007 and 2008, thin-billed prions decreased trip lengths,

Table 2 Mann–Whitney tests for inter- and intra-year changes in the diet constituents of thin-billed prions at New Island, Falkland Islands, based on volume estimates

Effect	Crustacea					Squid	Fish
	Amphipods (*Themisto*)	Euphausiids	Decapods (*Munida*)	Copepods	Cirripedia		
Year (incubation period 06–07 vs. 07–08)	NS	NS	$P = 0.019$	NS	NS	NS	NS
Year (chick feeding 06 vs. 07)	NS	NS	$P = 0.005$	$P = 0.031$	NS	NS	NS
Incubation period vs. chick feeding 06–07	$P = 0.022$	NS	NS	NS	NS	$P = 0.039$	NS

more often attended their chick every day, and long foraging trips of 6–8 days were not registered at all during 2008 (Fig. 2). Thus, the present data add to and explain the results of a previous study including the seasons 2003–2005, the period immediately preceding this study (Quillfeldt et al. 2007a). Sea-surface temperatures were negatively correlated with provisioning frequencies and chick growth rates in thin-billed prion chicks (Fig. 1; Quillfeldt et al. 2007a), because adults use long trips during times of low food availability. Flexibility in foraging trip lengths was also observed for thin-billed prions at Kerguelen Islands, where the birds used more "short trips" (trips of 1–4 days duration) during a more favourable chick-rearing season (73% in 1997: Duriez et al. 2000 vs. 60% in 1992: Weimerskirch et al. 1995).

Both diet composition (e.g., Antarctic krill in 15% of diet samples of thin-billed prions at Kerguelen Islands; Cherel et al. 2002) as well as low carbon stable isotope signatures in thin-billed prion tissues (Cherel et al. 2002; Quillfeldt et al. 2008) indicate that the long foraging trips lead thin-billed prions predominantly to southern Antarctic waters, >1,000 km from the breeding colonies (Cherel et al. 2002).

Overall diet composition and intra-annual differences

Like Thompson (1989), we found a seasonal change in prey composition from tiny squid during the incubation period to mainly crustaceans during chick-rearing in thin-billed prions from New Island (Fig. 3; Table 2). The squid was predominantly of the species *Gonatus antarcticus* in our samples and previous studies (Thompson 1994), while the crustaceans were dominated by the amphipod *Themisto gaudichaudii* and euphausiids.

The squid *Gonatus antarcticus* has an Antarctic and sub-Antarctic distribution (Rodhouse et al. 1992) and is epi- to mesopelagic as juveniles, and meso- to bathypelagic as adults. The shelf/slope waters around the Falkland Islands are a possible nursery ground of this species (Rodhouse et al. 1992). Thin-billed prions, Rockhopper (*Eudyptes chrysocome*), Gentoo (*Pygoscelis papua*) and Magellanic (*Spheniscus magellanicus*) penguins in the Falkland Islands all took very small juvenile *Gonatus antarcticus* with

estimated dorsal mantle lengths of 17–66 mm (Thompson 1989, 1994). The prevalence of *Gonatus antarcticus* in the penguin diet was clearly higher in the west of the archipelago than eastern places, where *Gonatus antarcticus* might be replaced by the resident squid *Loligo gahi*. *Gonatus* specimens recorded in the penguin samples increased in body size from November to January, and had nearly disappeared from the penguin diets by March (Thompson 1994). The concurrent decline also in the diet of thin-billed prions (Fig. 3; Table 1) further supports the idea that after *Gonatus antarcticus* hatch in the vicinity of the Falkland Islands, a proportion of the juveniles are retained in the area, while the remainder are carried offshore in the Falkland Current (Rodhouse et al. 1992). Further studies on the ecology and abundance of *Gonatus antarcticus* might greatly enhance our understanding of seabird population dynamics in this area.

After hatching, Thompson (1989) found that Crustacea comprised ca. 85% by weight and 99.5% by number in the prey of thin-billed prions. Euphausiids (*Euphausia lucens* and *E. vallentini*) and amphipods (predominantly *Themisto gaudichaudii*) each comprised approximately 45% of the identified Crustacea with decapods, mainly *Munida*, making up the remainder. As in our present study, unidentified fish accounted for less than 2% of the total volume. The present result and data from thin-billed prions in other regions thus agree that chick-provisioning thin-billed prions feed mainly on the amphipod *Themisto gaudichaudii* and euphausiids at New Island (Table 1) and elsewhere.

Harper (1972) observed thin-billed prions feeding at dusk and overnight in the Southern Pacific ocean and found *Themisto gaudichaudii* to be the main prey item in the stomachs of birds collected at sea in that region. Likewise, Cherel et al. (2002) recorded *Themisto gaudichaudii* consistently as the dominant prey item over three consecutive chick-rearing periods 1995–1997 at Kerguelen Islands. There, *Themisto gaudichaudii* accounted for 57% of reconstituted mass of the diet of thin-billed prions, followed by euphausiids *Thyssanoessa macrura* and *Euphausia superba*.

Themisto gaudichaudii has a circumpolar distribution in the sub-Antarctic and Antarctic regions between the

sub-tropical convergence and the southern boundary of the West Wind Drift (Kane 1966). In sub-Antarctic waters it is most abundant during the summer months, i.e., the chick-feeding period, it has a high energy content (Williams and Robins 1979), and forms large surface swarms, particularly during the hours of darkness when the adults migrate towards the surface (Williams and Robins 1981). For these reasons, it is a suitable source of food during chick-rearing for a small surface-feeding petrel such as the thin-billed prion.

Inter-annual difference in diet composition

The present data suggest that during poor availability of their preferred food, thin-billed prions partly compensated their diet with alternative crustaceans. Similar prey switches have been observed in Antarctic prions, which took copepods when the favoured Antarctic krill were in short supply (Reid et al. 1997). Similarly, in the present study, changes were apparent in the prevalence of the less frequently taken decapod *Munida gregaria* (lobster krill) and copepods (Fig. 3; Table 2). As a minor food component, the *Munida gregaria* was also previously recorded in the diet of thin-billed prions (Thompson 1989), while we here recorded copepods and cirripedia (adults and Cypris-larvae) as additional, new dietary components for New Island thin-billed prions.

In 2006, adults brought the highest volume of copepods (17% estimated volume), and chick growth was poor. The copepods brought were very small (mainly *Calanus* spp. juveniles and adults of 2.5–3.6 mm), and thus, we consider them a replacement food item when the main food items (amphipods, euphausiids, squid) were scarce. Thin-billed prions feed principally by surface-seizing, picking off surface plankton in a manner resembling storm petrels (Hydrobatiidae, Harper 1987). While Antarctic and broad-billed prions scoop food off the surface with their bills, this is not observed in thin-billed prions (Harper 1987), as their bills lack the functional palatal lamellae in the maxilla necessary for sifting out food. Therefore, obtaining a high number of tiny copepods (e.g., 17% in 2006) is probably expensive in terms of time and energy demands.

Another consideration is foraging depth in relation to the prey depth. As stated earlier, thin-billed prions are epi-planktonic foragers, obtaining most of their food at or near the surface. In addition, they have been reported to dive to 7.5 m deep propelled by their wings (Chastel and Bried 1996). Further, it is important to note that thin-billed prions feed nearly exclusively at night (e.g., Harper 1987), possibly in adaptation to the diel migration of zooplankton to the surface at night.

Such diel migrations have been observed in many zoo-plankton species, including all crustacean prey species of thin-billed prions. During the afternoon or evening (depending on species), copepod juveniles and adults, as well as euphausiids and *T. gaudichaudii*, migrate upwards, to amass in the surface mixed layer. Of the copepods, *Calanus simillimus* (copepodids V and adults) was the species which was found closest to the surface compared to three other investigated larger Calanoida at South Georgia (Atkinson et al. 1992a, b). This finding might be an explanation for preferential ingestion of this comparably small copepod by the foraging thin-billed prions from New Island.

Calanoid copepods of the genus *Neocalanus* were found in stomach content samples from 2008. Of the three sub-Antarctic *Neocalanus*-species, two are possible prey for the thin-billed prions according to their depth distribution (Renz personal communication) *Neocalanus robustior* (epi-mesopelagic) and *Neocalanus tonsus* (0–500 m). The latter species had previously been found as the most important diet item (68% of mass) in the diet of Broad-billed prions *Pachyptila vittata* (Klages and Cooper 1992), but this is the to date first report of *Neocalanus* as prey for thin-billed prions.

Summary and conclusions

The present data support the high flexibility of thin-billed prion adults in their foraging behaviour, which make this species a sensitive monitor of the zooplankton availability in the sub-Antarctic waters adjacent to and south of the Falkland Islands (Quillfeldt et al. 2007b). Differences in foraging trip lengths and diet switches of this species indicated fluctuations in prey availability in relation to oceanographic conditions. Further studies on the ecology of the main prey items, *Themisto gaudichaudii* and *Gonatus antarcticus*, are needed in order to fully understand the complexity of ocean climate, food availability, and thus, adult foraging and chick growth.

References

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South

America: physical and ecological processes. J Mar Syst 44:83–105

Atkinson A, Ward P, Williams R, Poulet SA (1992a) Diel vertical migration and feeding of copepods at an oceanic site near South Georgia. Mar Biol 113:583–593

Atkinson A, Ward P, Williams R, Poulet SA (1992b) Feeding rates and diel vertical migration of copepods near South Georgia: comparison of shelf and oceanic sites. Mar Biol 114:49–56

Catard A, Weimerskirch H, Cherel Y (2000) Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. Mar Ecol Prog Ser 194:249–261

Chastel O, Bried J (1996) Diving ability of blue petrels and thin-billed prions. Condor 98:627–629

Chaurand T, Weimerskirch H (1994) The regular alternation of short and long foraging trips in blue petrel Halobaena caerulea: a previously undescribed strategy of food provisioning in a pelagic seabird. J Anim Ecol 63:275–282

Cherel Y, Bocher P, De Broyer C, Hobson KA (2002) Food and feeding ecology of the sympatric Thin-billed Pachyptila belcheri and Antarctic P. desolata prions at Iles Kerguelen, Southern Indian Ocean. Mar Ecol Prog Ser 228:263–281

Clark GS, Goodwin AJ, von Meyer AP (1984) Extension of the known range of some seabirds on the coast of southern Chile. Notornis 31:324

Congdon BC, Krockenberger AK, Smithers BV (2005) Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the Wedge-tailed shearwater. Mar Ecol Prog Ser 301:293–301

Cox JB (1980) Some remarks on the breeding distribution and taxonomy of the prions (Procellariidae: Pachyptila). J Southern Austral Mus 18:91–121

Duriez O, Weimerskirch H, Fritz H (2000) Regulation of chick provisioning in the Thin-billed prion: an interannual comparison and manipulation of parents. Can J Zool 78:1275–1283

Furness RW (1996) A review of seabird responses to natural and fisheries-induced changes in food supply. In: Greenstreet SPR, Tasker ML (eds) Aquatic predators and their prey. Fishing News Books, Blackwell Science Ltd., Oxford, pp 166–173

Harper PC (1972) The field identification and distribution of the Thin-billed prion (Pachyptila belcheri) and the Antarctic prion (Pachyptila desolata). Notornis 19:140–175

Harper PC (1987) Feeding behaviour and other notes on 20 species of Procellariiformes at sea. Notornis 34:169–192

Kane JE (1966) The distribution of Parathemisto gaudichaudii (Guer), with observations on its life-history in the 0° to 20° sector of the Southern Ocean. Discov Rep 34:163–198

Klages NTW, Cooper J (1992) Bill morphology and diet of a filter-feeding seabird: the Broad-billed Prion Pachyptila vittata at South Atlantic Gough Island. J Zool 227:385–396

Magalhaes MC, Santos RS, Hamer KC (2008) Dual-foraging of Cory's shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. Mar Ecol Prog Ser 359:283–293

Pennycuick CJ (1982) The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil Trans R Soc Lond B 300:75–106

Pinaud D, Cherel Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. Mar Ecol Prog Ser 298:295–304

Quillfeldt P, Masello JF, Strange IJ (2003) Breeding biology of the Thin-billed prion Pachyptila belcheri at New Island, Falkland Islands, in the poor season 2002/2003: egg desertion, breeding success and chick provisioning. Polar Biol 26:746–752

Quillfeldt P, Masello JF, Strange IJ, Buchanan KL (2006) Begging and provisioning of Thin-billed prions Pachyptila belcheri is related to testosterone and corticosterone. Anim Behav 71:1359–1369

Quillfeldt P, Strange IJ, Masello JF (2007a) Sea surface temperatures and behavioural buffering capacity in thin-billed prions Pachyptila belcheri: breeding success, provisioning and chick begging. J Avian Biol 38:298–308

Quillfeldt P, Strange IJ, Segelbacher G, Masello JF (2007b) Male and female contributions to provisioning rates of thin-billed prions Pachyptila belcheri in the South Atlantic. J Orn 148:367–372

Quillfeldt P, McGill R, Strange IJ, Masello JF, Weiss F, Brickle P, Furness RW (2008) Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of Thin-billed prions. Mar Ecol Prog Ser 373:137–148

Quillfeldt P, McGill R, Masello JF, Poisbleau M, van Noordwijk H, Demongin L, Furness RW (2009) Differences in the stable isotope signatures of seabird egg membrane and albumen—implications for non-invasive studies. Rapid Commun Mass Spectrom 23:3632–3636

Reid K, Croxall JP, Edwards TM (1997) Interannual variation in the diet of the Antarctic Prion Pachyptila desolata at South Georgia. Emu 97:126–132

Rodhouse PG, Symon C, Hatfield EMC (1992) Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Mar Ecol Prog Ser 89:183–195

Strange IJ (1980) The thin-billed prion, Pachyptila belcheri, at New Island, Falkland Islands. Gerfaut 70:411–445

Thompson KR (1989) An assessment of the potential for competition between seabirds and fisheries in the Falkland Islands. Brighton, Falkland Islands Foundation. Falkland Islands Foundation Project Report

Thompson KR (1994) Predation on Gonatus antarcticus by Falkland Islands seabirds. Antarct Sci 6:269–274

Waugh SM, Weimerskirch H, Cherel Y, Prince PA (2000) Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. Condor 102:804–813

Weimerskirch H, Cherel Y (1998) Feeding ecology of short-tailed shearwaters: breeding in Tasmania and foraging in the Antarctic? Mar Ecol Prog Ser 167:261–274

Weimerskirch H, Chastel O, Ackermann L (1995) Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion Pachyptila belcheri. Behav Ecol Sociobiol 36:11–16

Weimerskirch H, Fradet G, Cherel Y (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic Prion. J Avian Biol 30:165–174

Williams R, Robins D (1979) Calorific, ash, carbon and nitrogen content in relation to length and dry weight of Parathemisto gaudichaudi (Amphipoda, Hyperiidea) in the northeast Atlantic Ocean. Mar Biol 52:247–252

Williams R, Robins D (1981) Seasonal variability in abundance and vertical distribution of Parsthemisto gaudichaudii (Amphipoda: Hyperiidea) in the North East Atlantic Ocean. Mar Ecol Prog Ser 4:289–298