



Sea surface temperatures and behavioural buffering capacity in thin-billed prions *Pachyptila belcheri*: breeding success, provisioning and chick begging

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Seabirds are important predators in marine ecosystems and are commonly used to monitor the productivity of their marine environments. However, different measures of seabird breeding success differ in their sensitivity to environmental conditions. Here, we present an analysis of provisioning rates and chick growth as well as hatching and fledging success, in thin-billed prions *Pachyptila belcheri* at New Island, Falkland Islands between 2003 and 2005 and relate these patterns to ocean climate. During the study period, SST were rising within and between breeding seasons and were negatively correlated with provisioning frequencies of thin-billed prions. Chick mass was reduced and begging intensities increased at low feeding frequencies, but overall breeding success and fledging success were not affected, because most chicks survived to fledging despite poor provisioning rates. Chick numbers and survival therefore may not be sensitive indicators of environmental conditions in all seabird species and ranges of food abundance. Monitoring behavioural buffering mechanisms, such as feeding rates, may be more effective in some ranges of food abundance and time scales and provide an earlier warning of ecological change. As a novel technique, the use of begging intensities as indicator of chick body condition is proposed in species where repeated handling causes disturbance. The present data suggest that begging rates can serve as a non-invasive method to monitor chick condition.

Food availability for seabirds varies both in time and space, requiring physiological and behavioural mechanisms to regulate the storage of excess energy and enable the use of stores during energy shortfall. This applies to both adult birds and their dependent young. Seabirds have evolved behavioural buffer mechanisms to cope with natural fluctuations in food supply (Furness 1996), which may include flexible time budgets in adults and flexible growth rates in chicks (Burger and Piatt 1990). Poorly fed chicks may retard growth processes and decrease metabolic rates in response to dietary restrictions. As a result, they may still fledge successfully despite severe food shortages during their development (Cherel et al. 1988, Øyan and Anker-Nilssen 1996).

Seabirds are commonly used to monitor the productivity of their marine environments (Montevicchi 1993, for a bibliography on the topic see Harding et al. 2005), based on the assumption that at least part of the variation in prey abundance and/or availability is reflected in the productivity of the top predators (Croxall and Prince 1979, CCAMLR 1985, 1988, Ainley et al. 1995, Barrett 2002). However, different components of parental behaviour, offspring mortality and offspring condition may not reflect environmental conditions equally sensitively (Cairns 1987, Gill et al. 2002). In particular, the occurrence of flexible growth rates suggests that chick survival may be a very insensitive measure of food abundance. On the other hand, food intake rates of chicks are limited, such that

feeding rates are possibly insensitive on the upper end of the scale of prey abundance. Clearly, differences between species in patterns of adult attendance, chick growth and other parameters will influence the usefulness for monitoring (Croxall et al. 1999). We here use data of three breeding seasons in the Falkland Islands to assess the effect of prey abundance on different components of parental and chick behaviour, offspring mortality and offspring condition.

The cold, mineral-rich waters of the Falkland current provide food for large breeding colonies of seabirds in the southwest Atlantic, from the Falkland Island 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 minerals by 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 (Acha et al. 2004). There are only few series of long-term data on any level of the food chain in the Falkland Islands (Clausen and Pütz 2002, Pütz et al. 2003), and therefore our understanding about the influence of environmental variability in the Falkland Current marine ecosystem is still very limited. A succession of poor seasons in the Falkland archipelago, but also a long-term decline in seabird productivity in various parts of the southern ocean (Croxall et al. 2002, Weimerskirch et al. 2003), generated growing concern about human influence in the form of global warming on the Antarctic and related ecosystems and in the form of fishery. A better understanding of the variability of conditions and the impact on the various parts of the food chain is needed.

Thin-billed prions *Pachyptila belcheri* are small sub-Antarctic petrels that attend their chicks at night. The absence of adults from the nest burrow during the day provides the opportunity to collect data on chick provisioning with relatively low disturbance to the birds. Thin-billed prions feed on the same type of prey that most of the commercially targeted squid and fish prey on, on small crustaceans such as euphausiids and amphipods (Strange 1980, Cherel et al. 2002). Thin-billed prions are thus potentially suitable for assessing amphipod and euphausiid abundance. They have flexible foraging strategies, using short foraging trips as well as long trips of up to 8 days (Weimerskirch et al. 1995), and measures of feeding rates can serve as a real-time monitor of food availability.

The aims of the present study are: 1) to describe feeding rates, breeding success and chick growth of thin-billed prions on New Island, Falkland Islands, in the breeding seasons 2002–2003, 2003–2004 and 2004–2005, 2) to study the influence of sea-surface temperatures on feeding frequencies within and be-

tween the breeding seasons, and 3) to assess how sensitively different components of parental behaviour, offspring mortality and offspring condition reflect environmental conditions.

Methods

The study was carried out at New Island, Falkland Islands, from 8 January to 4 February 2003, from 8 January to 10 March 2004 and from 18 Jan to 8 March 2005. Nests were checked annually before our arrival at the field site by experienced fieldworkers, to establish the presence of eggs. Thin-billed prions breed in the Falkland Islands, Crozet and Kerguelen. New Island is the most important known breeding site for thin-billed prions. Up to 2 million pairs were estimated to breed on this island in 2001–2002 (Cstry et al. 2003).

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 were carried out in Kerguelen, including studies of sexual dimorphism of voice and morphology (Genevois and Bretagnolle 1995), feeding ecology (Chastel and Bried 1996, Cherel et al. 2002), parental investment (Chastel et al. 1995, Weimerskirch et al. 1995, Duriez et al. 2000), and demographic studies in relation to environmental variability (Nevoux and Barbraud 2006). 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. 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 07.30 and 19.30 h to the nearest 1 g using a digital balance. Wing length was measured every three days to the nearest 1 mm with a stopped wing rule. Tarsus length was measured every three days to the nearest 0.1 mm using callipers. In 2003, nests were also checked once towards the end of the nestling season, to control chick survival after the end of our field season.

Meal sizes and feeding frequencies were estimated from the evening and morning weights, by correcting the mass differences for metabolic mass loss, using 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 (about half of the maximum food delivered by two parents). An index of chick body condition at 19.30 h each evening was calculated relative to the mean mass for study chicks of each age (m_{mean}), using the following formula: $BC = m \times 100/m_{\text{mean}}$.

Begging rates were recorded as described previously for burrow-nesting Procellariiformes (Quillfeldt 2002, Quillfeldt and Masello 2004, Quillfeldt et al. 2004), by placing a portable tape recorder or digital voice recorder outside the nest entrance and an external microphone with a 2 m connection in the nest entrance close to the nest chamber. The recorders were switched on at 23.00 h each night (before the first adults returned) and recorded at low speed until the end of the tape (*ca.* 95 min in tape recorders and 6 hrs in digital recorders). We included only first begging sessions of each chick and night in the analyses of begging behaviour, and included only chicks from 10 days of age. This way, daily variation in begging behaviour reflected the chick's need at the time of adult arrival. From the recorded begging sessions, we recorded the duration (in min), the total number of calls in the session, the mean call rate

(call/min), and the maximum call rate sustained for one minute (calls/min).

Means are given with standard errors. The main inter-annual comparisons of meal size and feeding frequency use only January data, because only these were available for all three years. 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://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.weekly/.ssta/. We obtained Multivariate ENSO Index (MEI) data from: <http://www.cdc.noaa.gov/people/klaus.wolter/MEI> and analysed the relationship with sea surface temperature in the potential main foraging area.

Results

Breeding success

Overall breeding success differed between the three seasons (Table 1). The fledging success (relative to nests) was 50% lower in 2002–2003 than in 2003–2004 and 60% lower than in 2004–2005 due to the combined effect of lower hatching rates of eggs and lower chick survival rates (Table 1). The proportion of

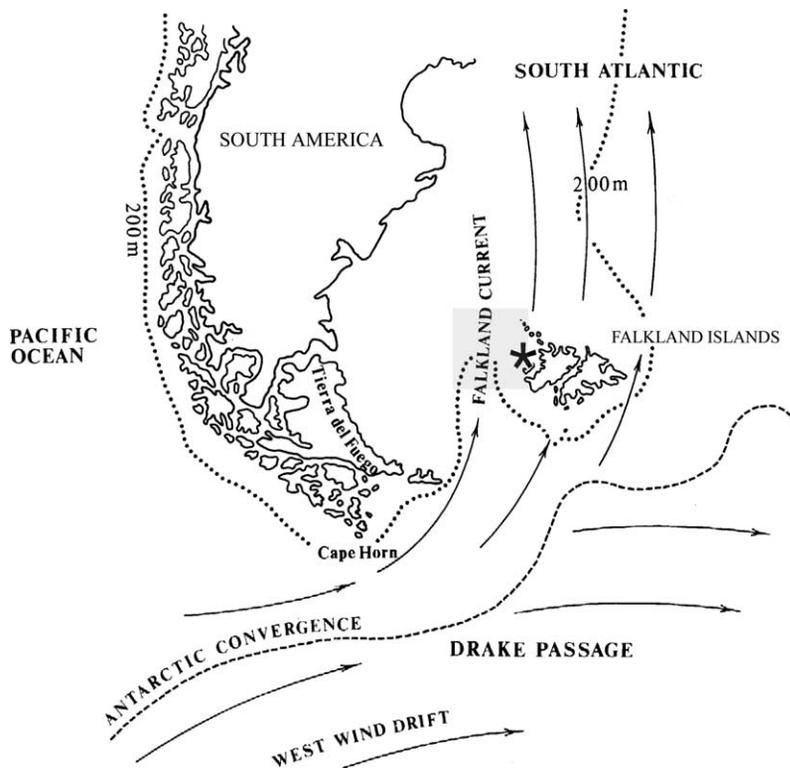


Fig. 1. Map of the study area: note that New Island (marked with “*”) is directly exposed to the western branch of the Falkland current, and is adjacent to the area of measurements of sea surface temperature (marked grey).

Table 1. Variation in timing and success of breeding thin-billed prions at New Island, Falkland Islands. χ^2 tests of raw data were used to test for differences between proportions (breeding success data), while ANOVA was used to compare median hatching dates. For the latter, all pair-wise post-hoc tests were also statistically significant (Tukey Test): 2003 vs. 2005 $P < 0.001$, 2003 vs. 2004 $P = 0.006$, 2004 vs. 2005 $P = 0.012$.

Year	2002–2003	2003–2004	2004–2005	Test
Laying success	60%	68%	72%	$\chi^2 = 0.74$, $P = 0.691$
Total nests with eggs	70	77	80	
Hatching period (days)	25 (30 Dec. 2002–23 Jan 2003)	25 (24 Dec. 2003–17 Jan 2004)	18 (26 Dec. 2004–12 Jan 2005)	
Median day of hatching	8 Jan	5 Jan	2 Jan	$F_{167,2} = 18.6$, $P < 0.001$
No. of eggs hatched	40	60	74	
Hatching success (of eggs)	57%	78%	93%	$\chi^2 = 3.58$, $P = 0.167$
Laying \times Hatching (Hatching success of nests)	34%	53%	67%	$\chi^2 = 7.87$, $P = 0.020$
No. chicks fledged	27	54	66	
Fledging success (of chicks)	68%	90%	89%	$\chi^2 = 1.03$, $P = 0.597$
Hatching \times Fledging (Fledging success of eggs)	39%	70%	83%	$\chi^2 = 7.68$, $P = 0.021$
Laying \times Hatching \times Fledging (Fledging success of nests)	23%	48%	59%	$\chi^2 = 13.28$, $P = 0.001$
No. chicks starved	9	4	4	
No. chicks predated	2	2	4	
No. chicks died from flooding	2	0	0	

occupied nests, i.e. laying success, did not differ between the years (Table 1). The hatching period spanned 18–25 days (Fig. 2, Table 1), with a maximal difference of 6 days between the mean hatching dates (Table 1). The main chick mortality was caused by starvation, while up to three chicks each season were predated by striated caracaras *Phalacrocorax australis*, and we found one possible case of predation by a rodent (*Rattus rattus* or *Mus musculus*) in 2004–2005. Additionally, two chicks died in 2002–2003 from nest flooding after heavy rain.

Chick feeding and sea surface temperatures

Feeding rates and feeding frequencies were higher in 2003 than in 2004, and lowest in 2005, and correspondingly the interval between feedings was shortest in 2003 (Table 2, ANOVA of means of chicks for January 2003, 2004 and 2005; feeding rates: $F_{104,2} = 21.1$, $P < 0.001$, feeding frequencies: $F_{104,2} = 15.4$, $P < 0.001$, interval between feedings: $F_{104,2} = 21.2$, $P < 0.001$).

In 2004 and 2005, the feeding rates declined and the mean interval between feedings increased from January to February (Table 2), a tendency that was statistically significant in 2004 (t-test of means of chicks January 2004 vs. February 2004: $t_{38} = -2.2$, $P = 0.032$). In 2003, we did not observe any torpid chicks, while this was regularly encountered in malnourished chicks in 2004 and 2005. In 2003, the interval to the next feeding was short (1–2 days) in 95% of the observations while in 2004, 15% of the feeding intervals were three days or longer and in 2005 the proportion of long trips was 19%. The distribution of long and short intervals varied between years ($\chi^2 = 22.4$, $P \leq 0.001$). Furthermore,

the maximum observed interval between feedings was 4 days in 2003, but 8 days in 2004 and 9 days in 2005.

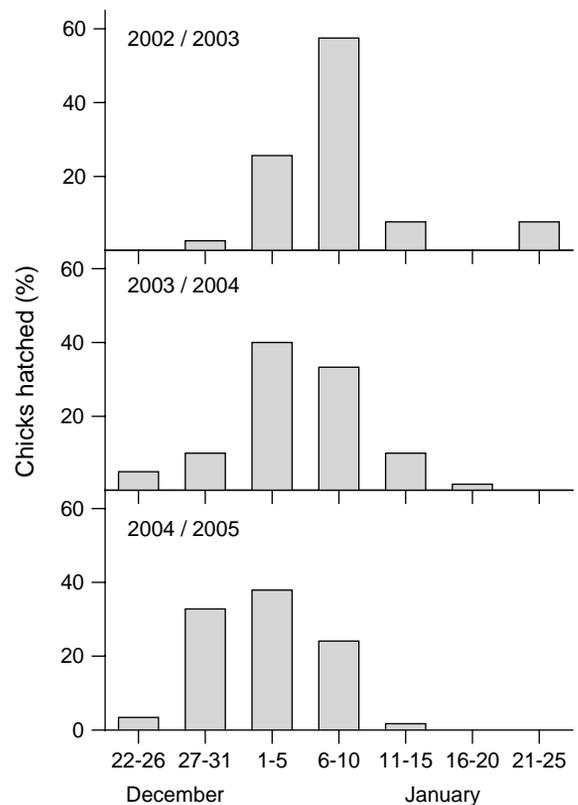


Fig. 2. Distribution of hatch dates of thin-billed prions in the breeding seasons 2002–2003 ($n = 40$), 2003–2004 ($n = 60$) and 2004–2005 ($n = 74$).

Table 2. Feeding frequencies of thin-billed prions at New Island, Falkland Islands. The frequency of nights with 0, 1 or 2 feeds are given and the average feeding rates and frequencies, calculated from chick means ($n = 20$ for 2003 and 46 for 2004 and 2005). Chicks older than 9 days were included.

Month	Feeds			Feeding frequency (feeds/night)	Feeding rate (g/night)	Mean interval to next feeding (days)
	0	1	2			
January 2003	82	223	58	0.93 ± 0.03	31.7 ± 0.7	1.39 ± 0.06
January 2004	220	310	89	0.79 ± 0.02	27.6 ± 0.6	1.58 ± 0.04
February 2004	369	309	158	0.77 ± 0.02	25.6 ± 0.8	1.76 ± 0.07
January 2005	222	234	70	0.71 ± 0.03	24.3 ± 0.8	1.71 ± 0.05
February 2005	486	376	159	0.70 ± 0.02	24.1 ± 1.0	1.80 ± 0.05

Sea surface temperatures were elevated in December 2002, February 2004 and during the breeding season of 2004–2005 (Figs. 3 and 4). The weekly data of sea surface temperature were negatively correlated to the weekly feeding frequency (Fig. 5; $R = -0.84$, $n = 15$, $P < 0.001$). However, Fig. 3 shows that the elevated sea surface temperatures were not above those observed in other, more productive seasons.

SSTA were not related to the monthly Multivariate ENSO Index (MEI) over the last 24 years ($R = -0.01$, $n = 284$, $P = 0.823$), or to MEI one year before ($R = -0.08$, $n = 286$, $P = 0.197$), or three years before SSTA measurement ($R = -0.02$, $n = 286$, $P = 0.763$). However, SSTA were correlated with the MEI two years before SSTA measurement ($R = 0.31$, $n = 286$, $P < 0.001$), indicating a 2-year lag in water temperatures between the Pacific Ocean and the South-west Atlantic (Fig. 3).

Chick response to food supply: growth, fledging periods, begging behaviour

During the study period of three years, the body masses and body conditions of chicks were low compared to

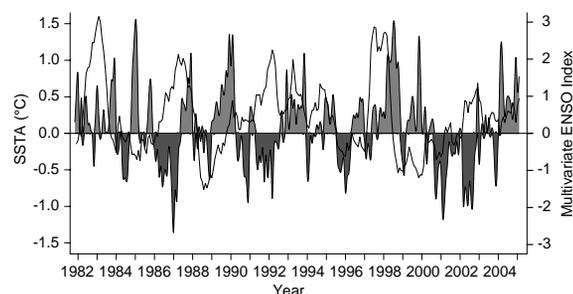


Fig. 3. Monthly sea-surface temperature anomaly, shown in grey shades for negative anomalies (cold water) and positive anomalies (warm water) in the area adjacent to the Falkland Islands ($50-52^{\circ}\text{S}$, $61-63^{\circ}\text{W}$) from November 1981 to March 2005 (ticks are set in January of the corresponding year). The line without shading indicates Multivariate ENSO Index (MEI) data from <http://www.cdc.noaa.gov/people/klaus.wolter/MEI>, to illustrate temporal sequence with local temperature data.

the data of thin-billed prions at New Island during a previous season (Figs. 6 and 7, ANOVA for body condition 2003–2005: $F_{84,2} = 6.5$, $P = 0.002$). In 2004, the chicks fledged at $51.30 \pm .5$ days of age ($n = 31$, range 47–59 days). Chicks in 2005 fledged two days older on average at 53.5 ± 0.5 days ($n = 37$, range 48–61 days; t -test 2004 vs 2005: $t_{66} = 3.2$, $P = 0.002$). The fledging dates spanned 21 days in 2004 (15 February to 6 March), and 19 days in 2005 (16 February to 6 March).

The mean peak mass and the mean fledging mass of chicks were 22 g lower in 2005 than in 2004 (Table 3). Tarsus growth was affected, with higher growth rates in the year of best provisioning, and a shorter final tarsus length at fledging in the poorest season (Table 3). We did not find differences in wing growth between 2004 and 2005, but the tail growth was more rapid in the better of the two seasons for which data are available. The tail lengths and wing lengths at fledging did not differ between the seasons, which may be due to the longer fledging period in the poorer season.

Between years, chicks varied in their begging (Fig. 7). The highest begging call number recorded in 2003 was 539 calls, but 1256 calls in 2004 and 3082 calls in 2005 (Fig. 7, ANOVA for total call numbers 2003–2005: $F_{84,2} = 26.1$, $P < 0.001$). The mean duration of begging sessions was also increased from 13.4 ± 0.9 min in 2003, to 17.1 ± 1.3 min in 2004 and 40.5 ± 4.6 min in 2005

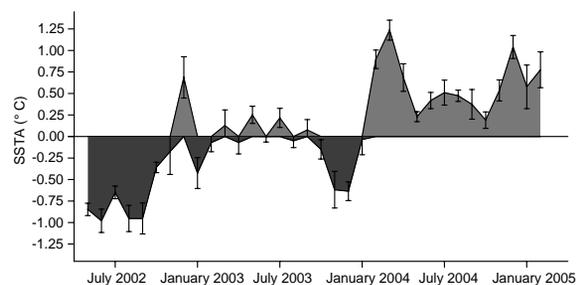


Fig. 4. Monthly sea-surface temperature anomaly in the area adjacent to the Falkland Islands ($50-52^{\circ}\text{S}$, $61-63^{\circ}\text{W}$), during the study seasons.

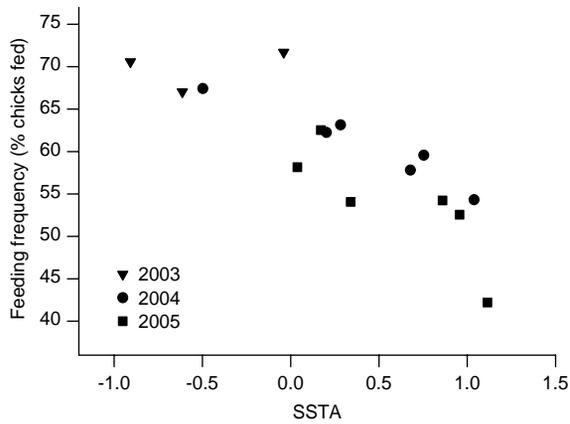


Fig. 5. Correlation between weekly sea-surface temperature anomalies ($50\text{--}52^{\circ}\text{S}$, $61\text{--}63^{\circ}\text{W}$) during three breeding seasons and corresponding mean feeding frequencies of thin-billed prions. Feeding frequency was calculated as the proportion of chicks fed each night, and mean weekly values are given.

(Fig. 7, ANOVA for session duration 2003–2005: $F_{84,2} = 25.5$, $P < 0.001$). The maximum duration observed in 2003 was 21 min, but 37 min in 2004 and 110 min in 2005. There was no statistically significant difference in the mean call rate (Fig. 7; 25.3 ± 1.0 calls/min in 2003 vs. 28.1 ± 1.3 calls/min in 2004 and 30.6 ± 1.7 calls/min in 2005; ANOVA for mean call rates 2003–2005: $F_{84,2} = 2.6$, $P = 0.08$), while the maximal call rates were increased in the latter years (Fig. 7; 39.4 ± 1.4 calls/min in 2003 vs. 42.3 ± 1.5 calls/min in 2004 and 51.5 ± 1.9 calls/min in 2005; ANOVA for maximum begging rates 2003–2005: $F_{84,2} = 13.2$, $P < 0.001$).

The weekly data of begging were correlated to the data of adult provisioning (Fig. 8, Pearson correlation of chick feeding rate with total begging call number: $R_p = -0.696$, $n = 13$, $P = 0.008$; with maximal begging call rate: $R_p = -0.841$, $n = 13$, $P < 0.001$). The weekly data of begging were also correlated to SSTA (Pearson correlation of SSTA with total begging call number: $R_p = 0.654$, $n = 13$, $P = 0.015$; with maximal begging call rate: $R_p = 0.730$, $n = 13$, $P = 0.005$).

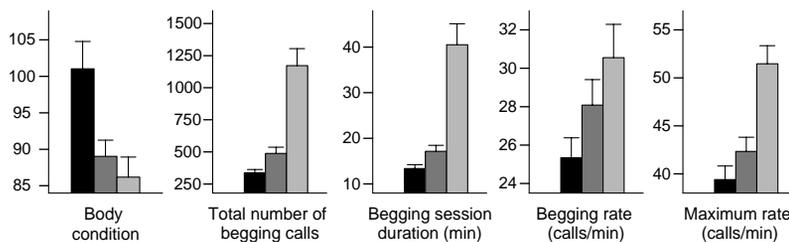


Fig. 7. Body conditions and begging call parameters of thin-billed prion chicks ($n = 20$ chicks in 2003, 37 chicks in 2004 and 28 chicks in 2005) during three breeding seasons. Bars show yearly means \pm SE (black bars: 2003, dark grey bars: 2004, light grey bars: 2005).

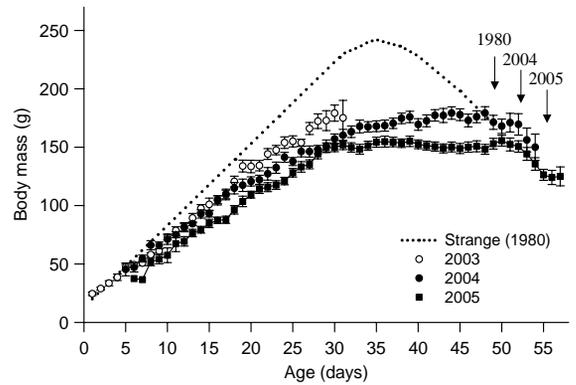


Fig. 6. Chick growth curves of thin-billed prions during three breeding seasons, with a reconstruction of the mean growth curve reported by Strange (1980) for comparison. In 2002–2003, we included data of 29 chicks that survived at least until 4 February. The chicks did not fledge at this time, but due to the limited duration of the field season later data were not recorded. In 2003–2004 and 2004–2005, 36 and 46 chicks, respectively, were recorded to fledging. The arrows show the mean age at fledging.

Discussion

We found that chick mass, feeding frequencies and begging intensities vary inter-annually in thin-billed prions with changes in sea surface temperature (SST), presumably because prey availability varies. In contrast, overall breeding and fledging success were insensitive to the variation in conditions encountered in the present study. Fledging and breeding success integrate longer timescales than the behavioural measures, and may therefore be influenced by countervailing conditions, which may mask some effects. In particular, low breeding success may be caused by poor conditions in the early part of the season, when adults tend to desert more readily than later (see year 2003 in Table 1). It therefore appears recommendable to measure feeding rates and to use begging intensities as indicator of chick body condition in this species, which are potentially more sensitive and provide an earlier warning of ecological

Table 3. Variation in parameters of chick growth of thin-billed prions at New Island, Falkland Islands. All parameters except tarsus growth rate were available in only two years, and were compared by t-tests. Tarsus growth rates and wing growth were determined during the approximately linear growth phase (10–25 days of age for tarsus and 20–40 days for wing growth). ANOVA was used to compare tarsus growth rates. For the latter, pair-wise post-hoc tests indicated that the difference was caused by the high rate in 2003 (Tukey Test): 2003 vs 2005 $P=0.040$, 2003 vs 2004 $P=0.072$, 2004 vs 2005 $P=0.979$). Peak mass is the highest mass recorded for each chick.

	2003	2004	2005	Test
Peak mass (g)		216.5 ± 3.6	194.3 ± 3.7	$t_{64}=4.15$, $P<0.001$
Fledging mass (g)		160.4 ± 3.5	137.8 ± 4.0	$t_{60}=4.02$, $P<0.001$
Tarsus growth (mm/day)	0.69 ± 0.03	0.59 ± 0.03	0.59 ± 0.02	$F_{2,59}=3.3$, $P=0.043$
Fledging tarsus (mm)		34.1 ± 0.2	33.5 ± 0.2	$t_{68}=2.05$, $P=0.044$
Wing growth (mm/day)		4.5 ± 0.1	4.6 ± 0.1	$t_{71}=-0.74$, $P=0.460$
Fledging wing (mm)		179.7 ± 1.3	178.1 ± 1.1	$t_{58}=0.99$, $P=0.324$
Tail growth (mm/day)		3.0 ± 0.1	2.4 ± 0.1	$t_{64}=4.78$, $P<0.001$
Fledging tail (mm)		80.8 ± 1.0	79.5 ± 0.8	$t_{52}=0.89$, $P=0.376$

change. Further research is required as to their utility with other ranges of food abundance and other taxa. Measures of begging intensity in other species of seabirds need to be tested.

Sea surface temperatures and provisioning rates of thin-billed prions

We found that sea surface temperatures (SST) during the study period were raising within and between breeding seasons and were negatively correlated with provisioning frequencies of thin-billed prions. A recent demographic study of this species (Nevoux and Barbraud 2006) indicated that SST in Antarctic waters were negatively related with hatching success and total breeding success of thin-billed prions at Kerguelen, while local SST had no influence on the parameters measured. Similarly, in Antarctic prions *Pachyptila desolata*, the distance of Antarctic waters were associated with feeding trip lengths (Weimerskirch et al. 1999). Our data indicate that elevated local SST are also important, and may correlate with lowered productivity and less available prey. Chick mass, feeding frequency data and begging intensities, but not overall breeding success and fledging success reflected periods of elevated SST in the chick-rearing period adequately, because most chicks in survived to fledging despite poor provisioning rates.

Long-term studies of seabirds in the Pacific Ocean indicate that inter-annual decreases in fledging success are correlated with SST above long-term averages as observed in El Niño years (Schreiber and Schreiber 1984, Ainley et al. 1988, Schreiber 1994). Similarly, in the South Atlantic, El Niño conditions affect the reproductive performance of most seabird species with a delay in time over the effect experienced in the tropical Pacific (Prince 1985, Croxall et al. 1988).

Peck et al. (2004) showed that elevated SSTs may influence seabird reproduction at finer time scales, i.e. within a breeding season. They found that changes in foraging success (meal size and feed frequency) and chick growth of wedge-tailed shearwater *Puffinus pacificus* were negatively correlated with daily variations in SST both within and among seasons. Our results are in line with these observations, as we observed a strong

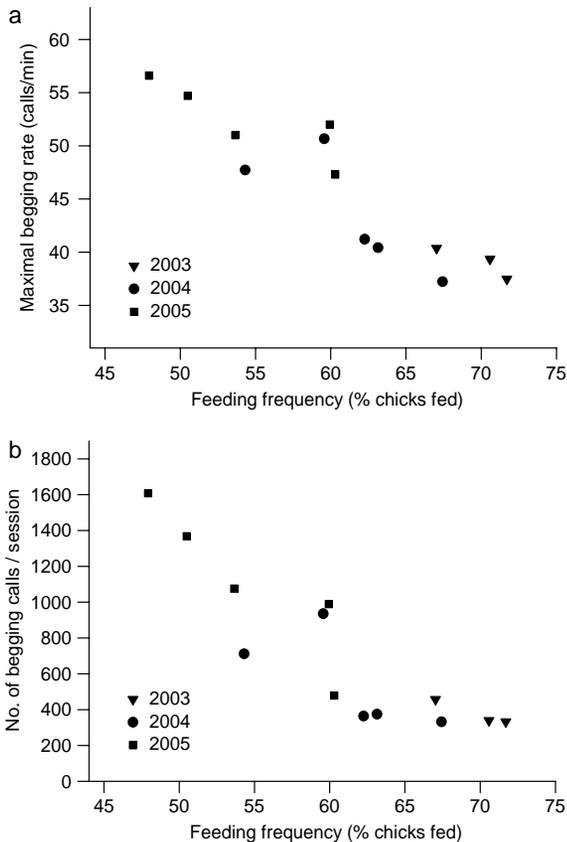


Fig. 8. Correlation between the weekly feeding frequency and two parameters of begging rate: (a) the maximum number of begging calls per minute and (b) the total number of calls in a begging session of thin-billed prions at New Island, Falkland Islands in 3 seasons.

negative relationship between SST and thin-billed prion provisioning frequencies both within and among seasons. These data suggest that nutrient-rich low-temperature waters were more distant on average when sea surface temperature were elevated, such that thin-billed prions had to engage in long foraging trips. In the breeding season 2002–2003, the desertion of thin-billed prions and other seabirds coincided with a rapidly elevated SST, a phenomenon also observed during the poorest part of the chick-rearing season in February–March 2004 and 2005.

Two mechanisms have been proposed to explain SST anomalies observed in the South Atlantic: 1) SST anomalies appear to be transferred from the Pacific to the Atlantic via the Antarctic Circumpolar Current. Anomalies associated with ENSO (El Niño Southern Oscillation) in the Pacific may propagate around the globe via the Antarctic Circumpolar Wave (ACW, Peterson and White 1998), and equatorward via the Atlantic circulation. Links were seen at a lag of 2 yr between the Pacific and southern Patagonian shelf (present analysis and Waluda et al. 1999). This is consistent with high SST observed after January 2004, which may be a reflection of the El Niño event of the southern winter 2002–2003. 2) The atmospheric influence of El Niño anomalies may also contribute to SST anomalies observed in the South Atlantic. El Niño conditions result in rainfalls up to 10 times higher than average in an area along the Atlantic coast from Southern Brazil to northeast Patagonia in Argentina (Holmgren et al. 2001). This may result in a greater outflow of water from rivers such as the Río de la Plata (confluence of the river systems Uruguay and Paraná), and the river Río Negro, Argentina, and greater amounts of coastal rain with an increase in warmer and less saline water.

Thin-billed prions in the Falklands prey mainly on amphipods (Strange 1980, own obs.). The data of thin-billed prion provisioning rates in the present study are in line with low fisheries catch statistics in the seasons of 2002, 2004 and 2005 (for data see: <http://www.fis.com/falklandfish>), suggesting that the abundance of macrozooplankton was low.

Since 1981, when the SST data set started, elevated sea surface temperature in excess of that of the last season was observed several times, for example in the seabird breeding seasons 1984–85 and 1989–90 (Fig. 3). Within this period, widespread starvation of seabirds in the Falkland Islands was reported only once previously (rockhopper penguins *Eudyptes chrysocome* and gentoo penguins *Pygoscelis papua* in the breeding season 1985–1986; Lyster 1986a,b, Keymer et al. 2001). Thus, elevated water temperature alone may not be responsible for recently observed low productivity in the area and we need to consider other human and natural factors as well.

Responses of chicks to low feeding rates and implications for monitoring

In the present study, we found that in a situation of increased SST, chick provisioning was compromised but chick mortality was not increased. Chick numbers and survival do not appear to be sensitive indicators of environmental conditions. Thus, monitoring behavioural buffering mechanisms, such as provisioning and growth rates, may be more useful than monitoring numbers and breeding success. This is in line with ecological theory, suggesting that only an extreme reduction in food supply would affect seabird population sizes (Cairns 1987, 1992a, b). Empirical evidence for buffering against variable food supply has been collected for many species of seabirds (e.g. reviewed by Furness 1996), but is missing for other species. More sensitive parameters may provide an earlier warning of ecological change, and therefore more information on such parameters is needed.

Contrary to expectation, overall breeding success of thin-billed prions at New Island was highest in the season with poorest feeding rates, 2005, and lowest in the season with the highest feeding rates, 2003. In 2003, chick mortality was initially high, but due to improving conditions those chicks that survived the first week, had a very good chance of fledging. In 2004 and 2005, chick survival was high despite decreased provisioning rates. Compared with Strange (1980), the average peak weights of chicks during 2003–2005 were low, but survival to fledging was hardly affected. Chicks of procellariiform seabirds typically reach a pronounced mass peak in their nestling stage, before losing mass again prior to fledging, a process known as mass recession (Brooke 2004). In the present study, in contrast, growth was near asymptotic in 2004 and 2005, without reaching an obvious peak. In procellariiform chicks, body stores accumulated before the mass peak are used to complete structural and feather growth before fledging, and less stores may lead to fledging at lower weight and hence with a higher risk of post-fledging mortality. In gentoo penguins, fledging weight was not a good indicator of feeding rates, because poorly provisioned, and thus light chicks were more likely to die (Williams and Croxall 1990). In our sample, this was not the case, as the peak mass and the fledging mass of chicks were lower during poor provisioning (Table 3), indicating that the influence of mortality on fledging weight was small.

We also found evidence that the length of the fledging period was affected. According to Strange (1980), chicks fledged at 43 to 54 days of age, the average being 49–50 days. The fledging period was from 14 February to 4 March. In 2004 and 2005, many chicks fledged older (up to 59 days in 2004, and 61

days in 2005) and later in the season, the last chick leaving on 10 March 2004.

Of the other parameters studied, tarsus growth seemed to vary with provisioning, with better-provisioned chicks growing tarsi more rapidly and reaching longer final tarsus lengths. Tail growth was also more rapid, but tail lengths and wing lengths at fledging did not differ between the seasons, possibly due to the longer fledgling period in the poorer season.

Compared with feeding frequencies reported for thin-billed prions breeding in Kerguelen (Weimerskirch et al. 1995, Cherel et al. 2002), the feeding frequencies in 2003 were relatively high. Adults in Kerguelen made only 50% short trips (1–4 days), and long trips lasted for up to 8 days (Weimerskirch et al. 1995), similar to the situation observed in the late part of the breeding season 2003–2004. Cherel et al. (2002) observed similarly low feeding rates: in three seasons on Kerguelen, 53, 52 and 45% of chicks were fed, comparable with the lowest values for attendance observed in 2003–2004 (Fig. 5). Although the thin-billed prions of the present study had masses much below those previously reported for New Island (Strange 1980), nearly all larger chicks survived, and mortality by starvation was mainly observed in young, possibly not thermally fully regulating chicks. Despite cases of torpidity, the low mortality and comparison with the feeding rates of the same species in Kerguelen suggests that the chicks were still sufficiently well fed to fledge, although the consequences for post-fledging survival are unknown.

Buffering ability and behavioural responses of seabirds to food availability vary among species (e.g. for a review see Furness 1996). In thin-billed prions, flexible growth rates, flexible foraging ranges and long maximal foraging ranges seem to provide an effective buffer mechanism against spatial and temporal environmental instability. Different sensitivity of parameters of breeding success to environmental conditions has also been recognized in previous studies, for example, in penguins. Here, the use of the length of incubation shifts and foraging trips, and analysis of chick and adult weights has been recommended in addition to the more widely recorded measure of breeding output/pair (Trivelpiece et al. 1990, CCAMLR 1985, 1988).

The gathering of some measures, such as chick weights, induces different degrees of disturbance to the animals, which may not only stress the animals, but also influence the measurements themselves. In many burrowing species, periodic chick weighing can be employed to estimate feeding rates, because the chicks are unattended during the day and caught with relatively little handling effects. However, other species are more sensitive to capture, handling may attract predation or breeding adults in the colony may be disturbed. In such situations in particular, alternative

non-invasive methods should be used such as the analysis of feeding rates from video and direct observations and the use of presence data of adults in the colony. As a novel technique, the use of begging calls would probably be feasible for many open-nesting and burrow-nesting seabird species. Because begging call rates indicate chick body condition (Quillfeldt 2002, Quillfeldt and Masello 2004, Quillfeldt et al. 2004), they may be used to monitor the productivity of the marine environment. Begging calls can be recorded without handling the chicks, although initial calibration may involve some chick weighing or recording of feeding rates. It further has to be tested, whether begging rates in the species involved reaches an upper limit, above which it is no longer a sensitive parameter (as observed in Cory's shearwaters *Calonectris diomedea*; Quillfeldt and Masello 2004). The collection of several parameters simultaneously, including adult body condition (eg. Chastel et al. 1995), can furthermore strengthen our interpretive ability over a range of food abundances.

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