Colony attendance and at-sea distribution of thin-billed prions during the early breeding season

Petra Quillfeldt1,*, Richard A. Phillips2, Melanie Marx1 and Juan F. Masello1

1 Justus Liebig University Giessen, Department of Animal Ecology and Systematics, 35392 Giessen, Germany
2 British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

*Correspondence: Petra Quillfeldt, Justus Liebig University Giessen, Department of Animal Ecology and Systematics, Heinrich-Buff-Ring 38, 35392 Giessen, Germany. E-mail: Petra.Quillfeldt@bio.uni-giessen.de

Running title: Thin-billed prion early breeding season

Abstract

Procellariiform seabirds have extreme life histories; they are very long-lived, first breed when relatively old, lay single egg clutches, both incubation and chick-rearing are prolonged and chicks exhibit slow growth. The early part of the breeding season is crucial, when pair bonds are re-established and partners coordinate their breeding duties, but is a difficult period to study in burrow-nesting species. Miniature geolocators (Global Location Sensors or GLS loggers) now offer a way to collect data on burrow attendance, as well as determine at-sea movements. We studied the early breeding season in thin-billed prions Pachyptila belcheri breeding at New Island, Falkland Islands. Males and females arrived back at the colony at similar times, with peak arrival in the last days of September. However, males spent more time on land during the pre-laying period, presumably defending and maintaining the burrow and maximising mating opportunities. Males departed later than females, and carried out a significantly shorter pre-laying exodus. Males took on the first long incubation shift, whereas females returned to sea soon after egg laying. During the pre-laying exodus and incubation, males and females travelled at similar speeds (>250km per day) and were widely distributed over large areas of the Patagonian Shelf. Inter-annual differences in oceanographic conditions were stronger during the incubation than during the pre-laying exodus and were matched by stronger differences in distribution. The study thus suggests that extended trips and flexible
distribution enable thin-billed prions to meet the high energy demands of egg production and incubation despite low productivity in waters around the colony during the early summer.

**Keywords**

Pachyptila belcheri, South-west Atlantic, breeding schedule, central-place forager, foraging ecology, tracking

**Introduction**

Seabirds are central place foragers during the breeding season, often nesting on islands at some distance from the most productive feeding sites. Procellariiformes (petrels, shearwaters, albatrosses) are the most pelagic of the seabirds, and have evolved physiological and morphological adaptations, including the reduction of ingested prey to an energy-rich stomach oil, a low cost of flight, slow growth and long fasting capacity of chicks, that allow the efficient exploitation of distant foraging areas (Phillips & Hamer 1999, Weimerskirch et al. 2000). This enables them to take on very long incubation shifts and use a bimodal foraging strategy with alternating long and short trips during chick provisioning (e.g. Chaurand & Weimerskirch 1994, Catard & Weimerskirch 2000, Baduini & Hyrenbach 2003, Congdon et al. 2005).

Most Procellariiformes lay annually and have a well-demarcated breeding season that begins in the spring. They are usually migratory, and thus absent from waters around the breeding colony for part of the year (Brooke 2004). The transition from the non-breeding to the breeding season starts with the re-occupation of the nest site, pair-bond re-establishment and mating. During this phase, birds spend a high proportion of their time ashore, and therefore lose weight (Brooke 2004). To recover body condition, it is often more efficient to fly long distances to areas of high resource abundance than to feed in the vicinity of the colonies. Thus, an extended foraging trip before laying - the pre-laying exodus or ‘honeymoon period’ - the length of which varies among species from a few days to nearly two months, is a common characteristic of both male and female petrels (Warham 1990). As soon as the female returns from the pre-laying exodus, she lays a single egg, and then often the male takes the first long incubation shift (Brooke 2004).

The movements of medium to small species of seabird, including petrels, have become increasingly well-known in recent years with the deployment of miniaturized geolocators or Global Location Sensor (GLS) loggers (Egevang et al. 2010, Harris et al. 2010 Rayner et al. 2012, Quillfeldt et al. 2013). Because the locations provided by these loggers have a large associated error, they are mostly used to study large-scale movements such as migration during the non-breeding season;
however, the raw light data, often in combination with concurrent data on salt-water immersion recorded by the same device, can be used to deduce periods spent on land in burrow-nesting species, including small petrels, and hence to infer various aspects of breeding phenology (Phillips et al. 2006, Guilford et al. 2012, Rayner et al. 2012).

The aim of the present study was to study the early part of the breeding season in a small burrow-nesting petrel, the Thin-billed prion *Pachyptila belcheri*, from the arrival to the colony to the first incubation shift. Using geolocation loggers, we specifically aimed to: (i) compare colony attendance patterns and trip durations of males and females, (ii) determine the foraging areas used by the two sexes during the pre-laying exodus and early incubation, and (iii) examine annual variation in timing and destinations of pre-laying and incubation trips.

Materials and methods

Study species and sites

Thin-billed prions breed on islands off South America and in the Indian Ocean; there are several million birds in the Falkland and Kerguelen islands, a smaller population on Isla Noir (southern Chile) and a very small number (10–20 pairs) on the Crozet Islands (Marchant & Higgins, 1990). They show the typical procellariiform pattern of a single-egg clutch and slow chick development, with an average fledging period of 50–54 days (Quillfeldt et al., 2010a). Thin-billed prions feed mainly on crustaceans during the breeding season and show some flexibility in diet within and between years; small squid are dominant during incubation and amphipods during chick-rearing, with euphausiids and copepods also taken in variable amounts (Quillfeldt et al., 2010b).

To investigate spatial movements and activity patterns, we attached small leg-mounted geolocators (developed by the British Antarctic Survey, Cambridge, UK) to 25 thin-billed prions in austral summer 2009/10 and 20 thin-billed prions in summer 2010/11 at New Island, Falkland/Malvinas Islands (51°43′S, 61°18′W). Nests were selected according to accessibility and the presence of individuals known from previous years to maximize the chances of recapture. The birds were captured by hand at marked nests during incubation. The geolocators weighed 1 g (<1% of the mean body mass - 130g - of thin-billed prions) and were fixed to plastic leg bands. Tagged individuals were marked with numbered steel rings on the other leg. Burrows were revisited and devices retrieved during incubation in the following seasons. Twenty devices (80%) were recovered from thin-billed prions in December 2010, and 14 devices (70%) in December 2011, of which, respectively, 20 and 9 downloaded successfully, and a further 5 partial datasets were recovered from loggers with failed batteries.
In the present analysis, we included data from a single pre-laying period (October to December) for each individual. Because several datasets terminated several months before device recovery, the final samples sizes were 20 birds in 2010 (10 males and 10 females, Fig. 1) and 9 birds in 2011 (4 males and 5 females, Fig. 1). At least one complete incubation trip was recorded for all but one bird (whose device was recovered after its return from the pre-laying exodus).

A detailed study found no evidence for any substantial impact of the geolocators on thin-billed prions: breeding performance was unaffected in the season of attachment or following recovery; eco-physiological measurements suggested that adults adapted to the higher load; and the similarity in stable isotope ratios in blood and feathers of instrumented adults and controls indicated that general diet and distribution was unaffected (Quillfeldt et al., 2012a).

**Data processing**

Geolocators provide two positions per day based on light levels, with an accuracy of approximately 186 ± 114 km (Phillips et al., 2004). Light data were analysed using the BASTrak software suite (British Antarctic Survey, Cambridge, UK). TransEdit was used to check for integrity of light curves and to determine dawn and dusk times, and Locator to estimate the latitude from day length and longitude from the time of local mid-day relative to Greenwich Mean Time. We assumed a sun elevation angle of -3.5°, based on known positions obtained during pre- and post-deployment calibration of the loggers at the colony. All estimated locations were examined visually in a geographical information system (GIS) and any unrealistic positions – either associated with interference to light curves at dawn or dusk, or in proximity to equinoxes when latitudes are unreliable - were excluded from further analyses.

Trips to sea were distinguished from periods in the burrow by examining the light data, with incubation shifts apparent as periods of continuous darkness during daylight hours. The pre-laying exodus was an obvious phase lasting 14−41 days when the bird was at sea, which preceded the first incubation shift. It was also possible to determine the day of first arrival in the colony, the period from first arrival to the start of the pre-laying exodus (hereafter, the “pre-exodus phase”), and the total number and proportion of days spent in the burrow during this phase. Days away from the nest during the incubation shifts indicated egg neglect (also termed intermittent incubation), a common strategy in petrels and some other offshore feeders (e.g. Schreiber & Burger 2002).

Changes in distribution between phases of the breeding season were examined using kernel analysis of filtered locations (Phillips et al., 2004). The non-parametric fixed kernel density estimator was used to determine density contours. Kernel densities do not require serial independence of observations when estimating foraging ranges (de Solla et al., 1999). Kernel analyses were performed...
in a Lambert equal-area azimuthal projection centred on the South Pole using ARCGIS 9.3 (ESRI, Redlands, CA, USA) and HAWTH’S ANALYSIS TOOLS (Beyer, 2004). The total distance travelled during foraging trips was calculated in the same projection.

Statistical data analyses

Statistical analyses were conducted using SPSS 11.0. We tested for normality using Kolmogorov-Smirnov tests and by checking plots of the data. Means are given with standard errors. Mixed linear models (GLMMs) based on Type III sum of squares were used to test for differences in the timing and distribution of each parameters among years and sexes. We carried out a separate GLMM for each timing and distribution parameter, with sex and year included as categorical independent variables ("factor"). Initially, we included the interaction between the two factors, but this was removed if non-significant (e.g. Engqvist 2005). As a measure of effect sizes we used partial Eta-Square values (η²; i.e. the proportion of the effect + error variance that is attributable to the effect) in case of variables and covariates tested with a GLM. The sums of the partial Eta-Square values are non-additive (e.g. [http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm](http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm)). Differences between pairs of means were assessed via pairwise t tests.

Sea surface temperature anomaly (SSTA) data in the Falkland current area adjacent to the Falkland Islands (50-52°S, 61-63°W, an area used frequently by the prions) were downloaded from [http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/weekly/ssta/](http://ingrid.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/weekly/ssta/). Anomalies were chosen in order to compare the effects of abnormally cold or warm water within and between seasons.

RESULTS

Return to breeding colony

Thin-billed prions arrived back at the colony from 24 September to 16 October 2010 (mean: 1 October 2010 ± 1 day) and from 16 September to 13 October 2011 (mean: 26 September 2011 ± 2 days). There were noticeable peaks in arrival on 28–29 September 2010 (8 of 20 birds) and 24–26 September 2011 (7 of 9 birds; Fig. 1). The arrival date did not differ between years or sexes (Table 1).

The pre-exodus phase (i.e. from first arrival at the colony to departure for the pre-laying exodus) lasted 2–36 days (mean 26 ± 2 days), with no significant effect of year or sex (Table 1). The pre-exodus phase consisted of shifts of 1–7 days in the burrow (Fig. 1), alternating with foraging trips lasting 1–8 days (Fig. 1).
Both colony attendance (cumulative number of days) and the proportion of days spent in the burrow between arrival and the pre-laying exodus were greater in males than females (Table 1). Males spent a cumulative period of 14.0 ± 1.6 days and 17.0 ± 0.9 days on land in 2010 and 2011, respectively, equivalent to 54 and 51% of the total pre-exodus phase, whereas females spent a cumulative time of 11.1 ± 1.5 days and 9.6 ± 1.8 days on land in 2010 and 2011, respectively, equivalent to 48 and 41% of the total pre-exodus phase.

Pre-laying exodus

All 14 males and 15 females engaged in a pre-laying exodus (Fig. 1). Females departed first, on 22 October 2010 (± 2 days) and 20 October 2011 (± 2 days). Males departed on average on 28 October (± 1 day) in both years. The departure date differed between sexes, but not between years (Table 2). Females engaged in pre-laying exoduses of 27.1 ± 2.4 days in 2010 and 28.5 ± 2.2 days in 2011, and males in significantly shorter trips, of 18.9 ± 1.1 days in 2010 and 18.5 ± 1.1 days in 2011 (Fig. 1, Table 2). The longer trip duration in females compensated for the earlier departure, such that females and males returned to the colony on similar dates: males on 15 November and females on 18 November on average, in both years (Table 2). The slightly later date was due to three very late females: two in 2010 and one in 2011 returned as late as 28 November (Fig. 1). When these were removed, the mean female arrival date was 15 November (i.e. similar to that of males).

During the pre-laying exodus, males travelled 5055 ± 354 km in 2010, and 4574 ± 603 km in 2011, which was less than the travel distances of females, which were 7667 ± 607 km in 2010 and 7021 ± 524 km in 2011 (Table 2). However, the exoduses of females were longer in duration, and overall, the mean daily travel speeds were very similar; 274 ± 11 km/day and 261 ± 10 km/day.

All birds except one female foraged over the Patagonian Shelf, in waters north and west of the Sub-Antarctic Front (Fig. 2). One of ten females in 2010 crossed the Drake Passage to forage in Antarctic waters south of the Polar Front (Fig. 2). At-sea distributions during the two seasons were largely overlapping (Fig. 3a).

Incubation

Females departed earlier on the first incubation trip, after spending 3.7 ± 0.9 days on average in the burrow in 2010 and 2.6 ± 0.8 days in 2011. Incubation trips by females started on 21 November (± 2 days) on average in the two years. Males covered the first incubation shift, thus spending longer than females in the burrow (10.2 ± 0.8 days in 2010 and 8.9 ± 1.2 days in 2011; Table 3). Males then departed on average on 26 November 2010 (± 1 day) and 25 November 2011 (± 1 day) for their first incubation trip to sea. The departure date differed between sexes but not years (Table 3).
Incubation trips of males and females were of similar mean duration in both years (males: 7.1 ± 0.4 days, females: 7.2 ± 0.4 days), and total distance (males: 2676 ± 170 km in 2010, 2293 ± 230 km in 2011, females: 2702 ± 307 km in 2010, 2299 ± 122 km in 2011) (Table 3). Daily travel speeds of males and females were also similar (362 ± 20 km/day and 370 ± 20 km/day, respectively) and were faster than during the pre-laying exodus (paired sample t-test: t=6.7, d.f. 27, P < 0.001).

Thin-billed prions mostly foraged over the Patagonian Shelf in waters north and west of the Sub-Antarctic Front during incubation (Fig. 3b, Fig. 4). However, one male and one female in 2010 crossed the Drake Passage to forage in Antarctic waters south of the Polar Front (Fig. 4). The distributions during the two seasons overlapped in the area to the west of New Island, but additional southerly areas were used extensively in 2010 and more northerly areas in 2011 (Fig. 3b).

In 2010 only, egg neglect by males was observed (Figure 1).

**DISCUSSION**

We used geolocators to compare pre-laying attendance patterns and distributions of male and female thin-billed prions from the large colony on New Island over two years. Overall, we found little if any difference in timing of movements or foraging distributions of tracked birds between 2010 and 2011. This might reflect a rather fixed breeding schedule, as observed in other species at New Island (e.g. southern rockhopper penguins *Eudyptes c. chrysocome*, Strange 1982) or, given that a longer-term study recorded significant annual variation in timing of breeding, with earlier hatching in warmer seasons (Quillfeldt *et al.* 2007), that the two years in the present study were relatively similar in terms of sea surface temperatures at the beginning of the season. In both years, moderately cold waters (SSTA around -0.5°C) prevailed during the arrival period (Fig. 5). These conditions may have favoured similar phenologies in the two years.

**Return to breeding**

Petrels return to colonies prior to egg laying in order to defend and repair nests or burrows, (re)establish pair bonds and maximise mating opportunities, both within pair and extra-pair copulations (e.g. Quillfeldt *et al.* 2012b). Little is known about behavior during this period in many burrow-nesting species, including exactly when individuals return, pre-laying attendance patterns, and the characteristics of the pre-laying exodus. In some migratory species, the numbers of birds visiting the breeding colony increases gradually, but in others is well synchronized (Brooke 2004). For example, all Antarctic petrels *Thalassoica antarctica* from one colony arrived within the same 36 hour period (Pryor 1968). Thin-billed prions in the present study showed what is perhaps a typical arrival phenology: although a high percentage returned during a peak period of a few days, other individuals
returned considerably later or earlier. The timing of arrival recorded here (Fig. 1) appears to be later than the dates reported in the late 1970s, when large numbers were observed by 10 September, and maximum numbers by about 18 September (Strange 1980). However, the use of geolocators would not allow the discrimination of visits that last only a few hours at night, which could account for the observed activity in the colony in early to mid September, especially as it is not until the period from late September to the third week in October that pairs were frequently recorded in the burrows during daylight hours in the earlier study (Strange 1980), which is similar to the dates observed here.

It has been suggested that if one sex arrives earlier, it is usually the male, with a typical difference of a few days in small species and 10−11 days in the great albatrosses Diomedea spp. (Warham 1990). Contrary to this, female and male thin-billed prions in the present study did not differ in their arrival time. Similarly, no difference was found in the arrival of Chatham petrel males and females using GLS (Rayner et al. 2012).

Nest attendance in the pre-laying period of petrels is usually higher for males than females (Brooke 2004). Our results for thin-billed prion corroborate this: males spent more time in the burrow and less time at sea during the pre-exodus period from first return to the start of the pre-laying exodus. The explanation for this is not certain, but it is likely that males take a greater share in defending the burrow from conspecifics. Alternatively, males may show a greater presence due to a necessity for mate guarding. Copulations must take place during this phase, as the female lays shortly after return from the pre-laying exodus, and in an earlier study thin-billed prions showed a relatively high incidence of extra-pair paternity (Quillfeldt et al. 2012b). Thus, it would be instructive to study how individual attendance patterns may be involved in safeguarding paternity or pursuing extra-pair copulations. At New Island, mating thin-billed prions were observed from 15–26 October 1977 with peaks on 24 and 26 October, just before departure on the pre-laying exodus (Strange 1980).

The pre-laying exodus

Many procellariiform species leave their breeding areas for periods of a few days to several weeks, often travelling to distant foraging areas to gather resources for egg production and incubation. In a few species, the feeding areas have been identified, and may be the same as those used during the nonbreeding period in relatively short-distance migrants. For example, white-chinned petrels Procellaria aequinoctialis from South Georgia fly 2000 km northwest to the Patagonian Shelf off central Argentina, which is also a major wintering area for the same birds (Phillips et al. 2006) and Barau’s petrels ranged up to 3800 km during the pre-laying exodus (Pinet et al. 2012). Thin-billed prions in the present study mainly used the Patagonian Shelf during the pre-laying exodus, with only a
single bird foraging south of the Drake Passage. Thus, the prions did not return to their wintering area, which is ca. 3000 km further east in the south Atlantic (Quillfeldt et al. 2013).

In most petrel species, both sexes undertake a pre-laying exodus as each needs to accumulate reserves to fuel periods of fasting during incubation (Mallory et al. 2008). The female must also produce the single large egg, which is formed while at sea. In thin-billed prions at New Island, egg-laying dates in 1977 and 1978 were in the period from 8–22 November (Strange 1980), and were thus very similar to the mean arrival date of 15 November in the present study. The tracked females spent only three days on average in the burrow after their return from the pre-laying exodus, suggesting that they lay the egg very soon after arrival, as in other procellariids (Warham 1990).

Males of many petrel species also appear to require a prolonged foraging period to recover from greater nest attendance in the pre-exodus phase, and to fuel the first major incubation stint. For example, male Barau’s petrel *Pterodroma baraui* foraged further from the colony, in waters with greater surface chlorophyll concentration, and spent more time in flight than females during the pre-laying exodus (Pinet et al. 2012). However, in most species, females are away for longer than males, and some taxa do not undertake a pre-laying exodus (e.g. Balearic shearwaters, Guildford et al. 2012). In the present study, female thin-billed prions left earlier and stayed away longer on their pre-laying exodus than males, and thus show a typical behaviour for a petrel. There was no obvious sex difference in their at-sea distribution (Fig. 2) and only a slight inter-annual difference (Fig. 3).

**Incubation**

In most petrels, the first incubation stint is taken by the male, while the female returns to sea, presumably to recover from the energetic demands of egg production. Results from other recent studies of birds fitted with geolocators confirms this, e.g. male Barau’s petrels systematically took the first incubation shift (Pinet et al. 2012). Similarly, female thin-billed prions left for an extended foraging trip soon after the pre-laying exodus, leaving the male to incubate.

In 2010, half of the males (5 of 10) showed some egg neglect (marked black in Fig. 1). Egg neglect (also termed intermittent incubation), is common in petrels and some other offshore feeders (e.g. Schreiber & Burger 2002). It allows incubating adults more time to forage, but on the other hand the incubation period is lengthened, as embryonic development is arrested (Vleck & Kenagy 1980).

Temporary egg neglect is common in thin-billed prions in the second half of the incubation period (own unpubl. data), as well as in related blue petrels *Halobaena caerulea* (Chaurand & Weimerskirch 1994). In the latter, the decision to leave the egg unattended is taken soon after sunset, and is triggered by low body mass (Ancel et al. 1998). Although it is generally assumed that temporary
egg neglect occurs when a partner is overdue, male thin-billed prions in the present study only left for one day, and then returned to the nest the following night to resume incubation.

As observed for the pre-laying exodus, there was no obvious sex difference in the areas used during the first incubation trip by our tracked birds (Fig. 4). Similarly, the distribution of males and females showed a high overlap during the winter (Quillfeldt et al. 2013). Previously, a stable isotope analysis had suggested that male thin-billed prions foraged at a higher trophic level and further north than females during courtship and chick feeding (Quillfeldt et al. 2008). However, this was based on analyses of blood samples from a single breeding season (2004/05), when conditions were exceptionally poor (see Quillfeldt et al. 2010b). Therefore, the inferred degree of sexual segregation might need reappraisal in light of the current results.

The inter-annual differences were considerably higher during the incubation than during the pre-laying exodus (Fig. 3). This was most likely in response to stronger inter-annual differences in oceanographic conditions during the incubation that during the pre-laying exodus (Fig. 5). It would therefore be instructive to study the flexibility in distribution over a larger range of conditions in subsequent years.

ACKNOWLEDGEMENTS

Fieldwork at New Island was supported by the New Island Conservation Trust with assistance from Ian, Maria and Georgina Strange. The work was approved by the Falkland Islands Government (Environmental Planning Office), and funded by grants provided by the German Science Foundation DFG (Qu 148/1ff). We are grateful to Hendrika van Noordwijk for assistance in the field, and Ina Hampel and Lisa Kleemann for assistance with data analyses.

REFERENCES


Congdon, B. C., Krockenberger, A. and Smithers, B. 2005. Dual-foraging and coordinated provisioning in a tropical Procellariiform, the wedge-tailed shearwater. – Marine Ecology Progress Series 301: 293–301.


Table 1. Effect of year and sex on timing of arrival and pre-laying attendance patterns during the pre-exodus phase. Significant p-values are marked bold. As a measure of effect sizes, we report partial Eta-Square values ($\eta^2$). None of the interactions were significant. d.f. = 28 (based on 29 birds).

<table>
<thead>
<tr>
<th>Dependent</th>
<th>Independents</th>
<th>F</th>
<th>P</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arrival date</td>
<td>Year</td>
<td>3.8</td>
<td>0.060</td>
<td>0.130</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>0.4</td>
<td>0.546</td>
<td>0.014</td>
</tr>
<tr>
<td>Total duration of pre-exodus phase (days)</td>
<td>Year</td>
<td>1.3</td>
<td>0.261</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>2.3</td>
<td>0.144</td>
<td>0.080</td>
</tr>
<tr>
<td>Cumulative period spent in the burrow (days)</td>
<td>Year</td>
<td>0.1</td>
<td>0.732</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>6.5</td>
<td>0.017</td>
<td>0.201</td>
</tr>
</tbody>
</table>
Table 2. Effects of year and sex on timing and duration of the pre-laying exodus in thin-billed prions. Significant p-values are marked bold. As a measure of effect sizes we report partial Eta-Square values ($\eta^2$). None of the interactions were significant. d.f. = 28 (based on 29 birds).

<table>
<thead>
<tr>
<th>Dependent</th>
<th>Independents</th>
<th>F</th>
<th>P</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Departure date</td>
<td>Year</td>
<td>0.3</td>
<td>0.601</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>11.7</td>
<td><strong>0.002</strong></td>
<td>0.310</td>
</tr>
<tr>
<td>Trip duration (days)</td>
<td>Year</td>
<td>0.1</td>
<td>0.802</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>19.1</td>
<td><strong>&lt;0.001</strong></td>
<td>0.423</td>
</tr>
<tr>
<td>Return date</td>
<td>Year</td>
<td>0.1</td>
<td>0.842</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>2.8</td>
<td>0.106</td>
<td>0.098</td>
</tr>
<tr>
<td>Cumulative travel distance (km)</td>
<td>Year</td>
<td>1.0</td>
<td>0.336</td>
<td>0.036</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>22.7</td>
<td><strong>&lt;0.001</strong></td>
<td>0.466</td>
</tr>
<tr>
<td>Travel speed (km/day)</td>
<td>Year</td>
<td>3.2</td>
<td>0.088</td>
<td>0.108</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>1.1</td>
<td>0.301</td>
<td>0.041</td>
</tr>
</tbody>
</table>
Table 3. Effects of year and sex on timing and duration of the first incubation trip of thin-billed prions. Significant p-values are marked bold. As a measure of effect sizes we report partial Eta-Square values ($\eta^2$). None of the interactions were significant. d.f. = 27 (based on 28 birds).

<table>
<thead>
<tr>
<th>Dependent</th>
<th>Independents</th>
<th>F</th>
<th>P</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period in the burrow after pre-laying exodus</td>
<td>Year</td>
<td>1.4</td>
<td>0.250</td>
<td>0.052</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>44.9</td>
<td>&lt;0.001</td>
<td>0.642</td>
</tr>
<tr>
<td>Departure date</td>
<td>Year</td>
<td>2.3</td>
<td>0.143</td>
<td>0.084</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>4.9</td>
<td>0.036</td>
<td>0.164</td>
</tr>
<tr>
<td>Trip duration (days)</td>
<td>Year</td>
<td>0.2</td>
<td>0.643</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>0.5</td>
<td>0.843</td>
<td>0.002</td>
</tr>
<tr>
<td>Cumulative travel distance (km)</td>
<td>Year</td>
<td>1.9</td>
<td>0.185</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>&lt;0.1</td>
<td>0.983</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Travel speed (km/day)</td>
<td>Year</td>
<td>2.0</td>
<td>0.174</td>
<td>0.073</td>
</tr>
<tr>
<td></td>
<td>Sex</td>
<td>0.1</td>
<td>0.793</td>
<td>0.003</td>
</tr>
</tbody>
</table>
Fig. 1. Early breeding season chronology of thin-billed prions from arrival to the colony (first yellow block) until the end of the second foraging trip in incubation (in grey). Four birds, marked with #, were recaptured earlier, three after the first incubation foraging trip (in green) and one after the pre-laying exodus (in pink). Colony attendance before the pre-laying exodus consisted of shifts of 1–7 days in the burrow (in yellow) alternating with foraging trips of 1–8 days (in turquoise). In 2010, half of the males (5 of 10) showed some egg neglect (marked black), lasting for a single day (birds left one night and returned the subsequent night) in four cases, and two days and one night in one case.

Fig. 2. Pre-laying exoduses of male and female thin-billed prions tracked using geolocators from New Island (marked red) during October–November 2010 (a) and 2011 (b).

Fig. 3. Distribution (kernel density contours) of thin-billed prions tracked using geolocators from New Island (marked black) during (a) the pre-laying exodus, and (b) the first incubation trip, in two breeding seasons.

Fig. 4. Incubation trips of male and female thin-billed prions tracked using geolocators from New Island (marked red) during November-December 2010 (a) and 2011 (b).

Fig. 5. Sea surface temperature anomaly (SSTA) data in the Falkland current area adjacent to the Falkland Islands (50-52°S, 61-63°W) over the two breeding seasons, with important phases marked in colour.
Fig. 1.
Fig. 2. (a) Pre-laying exodus 2010
- Sub-antarctic Front
- Polar Front
- Males 2010
- Females 2010

(b) Pre-laying exodus 2011
- Sub-antarctic Front
- Polar Front
- Males 2011
- Females 2011
Fig. 3.

(a) (b)

Pre-laying exodus
Kernel densities:
- 2010 - 80%
- 60%
- 40%
- 2011 - 80%
- 60%
- 40%

New Island
Polar Front
Sub-antarctic Front

Incubation
Kernel densities:
- 2010 - 80%
- 60%
- 40%
- 2011 - 80%
- 60%
- 40%

New Island
Polar Front
Sub-antarctic Front
Fig. 5: Weekly SSTA (°C) for Thin-billed prion early breeding season:
- Arrival (mid September to mid October)
- Pre-laying exodus
- First incubation trips

Year 1 (2010) and Year 2 (2011) highlighted on the graph.