

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

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16 17 **Abstract**

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

34 distribution enable thin-billed prions to meet the high energy demands of egg production and
35 incubation despite low productivity in waters around the colony during the early summer.

36

37 **Keywords**

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

40

41 **Introduction**

42

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

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

63 The movements of medium to small species of seabird, including petrels, have become
64 increasingly well-known in recent years with the deployment of miniaturized geolocators or Global
65 Location Sensor (GLS) loggers (Egevang et al. 2010, Harris et al. 2010 Rayner et al. 2012, Quillfeldt
66 et al. 2013). Because the locations provided by these loggers have a large associated error, they are
67 mostly used to study large-scale movements such as migration during the non-breeding season;

68 however, the raw light data, often in combination with concurrent data on salt-water immersion
69 recorded by the same device, can be used to deduce periods spent on land in burrow-nesting species,
70 including small petrels, and hence to infer various aspects of breeding phenology (Phillips et al. 2006,
71 Guilford et al. 2012, Rayner et al. 2012).

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

78

79 **Materials and methods**

80

81 **Study species and sites**

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

90 To investigate spatial movements and activity patterns, we attached small leg-mounted
91 geolocators (developed by the British Antarctic Survey, Cambridge, UK) to 25 thin-billed prions in
92 austral summer 2009/10 and 20 thin-billed prions in summer 2010/11 at New Island,
93 Falkland/Malvinas Islands (51°43'S, 61°18'W). Nests were selected according to accessibility and the
94 presence of individuals known from previous years to maximize the chances of recapture. The birds
95 were captured by hand at marked nests during incubation. The geolocators weighed 1 g (<1% of the
96 mean body mass - 130g - of thin-billed prions) and were fixed to plastic leg bands. Tagged individuals
97 were marked with numbered steel rings on the other leg. Burrows were revisited and devices retrieved
98 during incubation in the following seasons. Twenty devices (80%) were recovered from thin-billed
99 prions in December 2010, and 14 devices (70%) in December 2011, of which, respectively, 20 and 9
100 downloaded successfully, and a further 5 partial datasets were recovered from loggers with failed
101 batteries.

102 In the present analysis, we included data from a single pre-laying period (October to
103 December) for each individual. Because several datasets terminated several months before device
104 recovery, the final samples sizes were 20 birds in 2010 (10 males and 10 females, Fig. 1) and 9 birds in
105 2011 (4 males and 5 females, Fig. 1). At least one complete incubation trip was recorded for all but
106 one bird (whose device was recovered after its return from the pre-laying exodus).

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

112

113 *Data processing*

114 Geolocators provide two positions per day based on light levels, with an accuracy of approximately
115 186 ± 114 km (Phillips *et al.*, 2004). Light data were analysed using the BASTrak software suite
116 (British Antarctic Survey, Cambridge, UK). TransEdit was used to check for integrity of light curves
117 and to determine dawn and dusk times, and Locator to estimate the latitude from day length and
118 longitude from the time of local mid-day relative to Greenwich Mean Time. We assumed a sun
119 elevation angle of -3.5° , based on known positions obtained during pre- and post-deployment
120 calibration of the loggers at the colony. All estimated locations were examined visually in a
121 geographical information system (GIS) and any unrealistic positions – either associated with
122 interference to light curves at dawn or dusk, or in proximity to equinoxes when latitudes are unreliable
123 - were excluded from further analyses.

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

132 Changes in distribution between phases of the breeding season were examined using kernel
133 analysis of filtered locations (Phillips *et al.*, 2004). The non-parametric fixed kernel density estimator
134 was used to determine density contours. Kernel densities do not require serial independence of
135 observations when estimating foraging ranges (de Solla *et al.*, 1999). Kernel analyses were performed

136 in a Lambert equal-area azimuthal projection centred on the South Pole using ARCGIS 9.3 (ESRI,
137 Redlands, CA, USA) and HAWTH'S ANALYSIS TOOLS (Beyer, 2004). The total distance travelled
138 during foraging trips was calculated in the same projection.

139

140 *Statistical data analyses*

141 Statistical analyses were conducted using SPSS 11.0. We tested for normality using Kolmogorov-
142 Smirnov tests and by checking plots of the data. Means are given with standard errors. Mixed linear
143 models (GLMMs) based on Type III sum of squares were used to test for differences in the timing and
144 distribution of each parameters among years and sexes. We carried out a separate GLMM for each
145 timing and distribution parameter, with sex and year included as categorical independent variables
146 ("factor"). Initially, we included the interaction between the two factors, but this was removed if non-
147 significant (e.g. Engqvist 2005). As a measure of effect sizes we used partial Eta-Square values (η^2 ; i.e.
148 the proportion of the effect + error variance that is attributable to the effect) in case of variables and
149 covariates tested with a GLM. The sums of the partial Eta-Square values are non-additive (e.g.
150 http://web.uccs.edu/lbecker/SPSS/glm_effectsize.htm). Differences between pairs of means were
151 assessed via pairwise t tests.

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

157

158

159 **RESULTS**

160

161 *Return to breeding colony*

162 Thin-billed prions arrived back at the colony from 24 September to 16 October 2010 (mean: 1 October
163 2010 \pm 1 day) and from 16 September to 13 October 2011 (mean: 26 September 2011 \pm 2 days). There
164 were noticeable peaks in arrival on 28–29 September 2010 (8 of 20 birds) and 24–26 September 2011
165 (7 of 9 birds; Fig. 1). The arrival date did not differ between years or sexes (Table 1).

166 The pre-exodus phase (i.e. from first arrival at the colony to departure for the pre-laying
167 exodus) lasted 2–36 days (mean 26 \pm 2 days), with no significant effect of year or sex (Table 1). The
168 pre-exodus phase consisted of shifts of 1–7 days in the burrow (Fig. 1), alternating with foraging trips
169 lasting 1–8 days (Fig. 1).

170 Both colony attendance (cumulative number of days) and the proportion of days spent in the
171 burrow between arrival and the pre-laying exodus were greater in males than females (Table 1). Males
172 spent a cumulative period of 14.0 ± 1.6 days and 17.0 ± 0.9 days on land in 2010 and 2011,
173 respectively, equivalent to 54 and 51% of the total pre-exodus phase, whereas females spent a
174 cumulative time of 11.1 ± 1.5 days and 9.6 ± 1.8 days on land in 2010 and 2011, respectively,
175 equivalent to 48 and 41% of the total pre-exodus phase.

176

177 *Pre-laying exodus*

178 All 14 males and 15 females engaged in a pre-laying exodus (Fig. 1). Females departed first, on 22
179 October 2010 (± 2 days) and 20 October 2011 (± 2 days). Males departed on average on 28 October (\pm
180 1 day) in both years. The departure date differed between sexes, but not between years (Table 2).
181 Females engaged in pre-laying exoduses of 27.1 ± 2.4 days in 2010 and 28.5 ± 2.2 days in 2011, and
182 males in significantly shorter trips, of 18.9 ± 1.1 days in 2010 and 18.5 ± 1.1 days in 2011 (Fig. 1,
183 Table 2). The longer trip duration in females compensated for the earlier departure, such that females
184 and males returned to the colony on similar dates: males on 15 November and females on 18
185 November on average, in both years (Table 2). The slightly later date was due to three very late
186 females: two in 2010 and one in 2011 returned as late as 28 November (Fig. 1). When these were
187 removed, the mean female arrival date was 15 November (i.e. similar to that of males).

188 During the pre-laying exodus, males travelled 5055 ± 354 km in 2010, and 4574 ± 603 km in
189 2011, which was less than the travel distances of females, which were 7667 ± 607 km in 2010 and
190 7021 ± 524 km in 2011 (Table 2). However, the exoduses of females were longer in duration, and
191 overall, the mean daily travel speeds were very similar; 274 ± 11 km/day and 261 ± 10 km/day.

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

196

197 *Incubation*

198 Females departed earlier on the first incubation trip, after spending 3.7 ± 0.9 days on average in the
199 burrow in 2010 and 2.6 ± 0.8 days in 2011. Incubation trips by females started on 21 November (± 2
200 days) on average in the two years. Males covered the first incubation shift, thus spending longer than
201 females in the burrow (10.2 ± 0.8 days in 2010 and 8.9 ± 1.2 days in 2011; Table 3). Males then
202 departed on average on 26 November 2010 (± 1 day) and 25 November 2011 (± 1 day) for their first
203 incubation trip to sea. The departure date differed between sexes but not years (Table 3).

204 Incubation trips of males and females were of similar mean duration in both years (males: $7.1 \pm$
205 0.4 days, females: 7.2 ± 0.4 days), and total distance (males: 2676 ± 170 km in 2010, 2293 ± 230 km in
206 2011, females: 2702 ± 307 km in 2010, 2299 ± 122 km in 2011) (Table 3). Daily travel speeds of
207 males and females were also similar (362 ± 20 km/day and 370 ± 20 km/day, respectively) and were
208 faster than during the pre-laying exodus (paired sample t-test: $t=6.7$, d.f. 27, $P < 0.001$).

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

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

215

216 **DISCUSSION**

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

227

228 *Return to breeding*

229 Petrels return to colonies prior to egg laying in order to defend and repair nests or burrows,
230 (re)establish pair bonds and maximise mating opportunities, both within pair and extra-pair
231 copulations (e.g. [Quillfeldt et al. 2012b](#)). Little is known about behavior during this period in many
232 burrow-nesting species, including exactly when individuals return, pre-laying attendance patterns, and
233 the characteristics of the pre-laying exodus. In some migratory species, the numbers of birds visiting
234 the breeding colony increases gradually, but in others is well synchronized ([Brooke 2004](#)). For
235 example, all Antarctic petrels *Thalassoica antarctica* from one colony arrived within the same 36 hour
236 period ([Pryor 1968](#)). Thin-billed prions in the present study showed what is perhaps a typical arrival
237 phenology: although a high percentage returned during a peak period of a few days, other individuals

238 returned considerably later or earlier. The timing of arrival recorded here (Fig. 1) appears to be later
239 than the dates reported in the late 1970s, when large numbers were observed by 10 September, and
240 maximum numbers by about 18 September (Strange 1980). However, the use of geolocators would not
241 allow the discrimination of visits that last only a few hours at night, which could account for the
242 observed activity in the colony in early to mid September, especially as it is not until the period from
243 late September to the third week in October that pairs were frequently recorded in the burrows during
244 daylight hours in the earlier study (Strange 1980), which is similar to the dates observed here.

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

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

261

262 *The pre-laying exodus*

263 Many procellariiform species leave their breeding areas for periods of a few days to several weeks,
264 often travelling to distant foraging areas to gather resources for egg production and incubation. In a
265 few species, the feeding areas have been identified, and may be the same as those used during the
266 nonbreeding period in relatively short-distance migrants. For example, white-chinned petrels
267 *Procellaria aequinoctialis* from South Georgia fly 2000 km northwest to the Patagonian Shelf off
268 central Argentina, which is also a major wintering area for the same birds (Phillips *et al.* 2006) and
269 Barau's petrels ranged up to 3800 km during the pre-laying exodus (Pinet *et al.* 2012). Thin-billed
270 prions in the present study mainly used the Patagonian Shelf during the pre-laying exodus, with only a

271 single bird foraging south of the Drake Passage. Thus, the prions did not return to their wintering area,
272 which is ca. 3000 km further east in the south Atlantic (Quillfeldt *et al.* 2013).

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

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

289

290 *Incubation*

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

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

300 Temporary egg neglect is common in thin-billed prions in the second half of the incubation
301 period (own unpubl. data), as well as in related blue petrels *Halobaena caerulea* (Chaurand &
302 Weimerskirch 1994). In the latter, the decision to leave the egg unattended is taken soon after sunset,
303 and is triggered by low body mass (Ancel *et al.* 1998). Although it is generally assumed that temporary

304 egg neglect occurs when a partner is overdue, male thin-billed prions in the present study only left for
305 one day, and then returned to the nest the following night to resume incubation.

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

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

319

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326

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406
407

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

Dependent	Independents	F	P	Effect size
Arrival date	Year	3.8	0.060	0.130
	Sex	0.4	0.546	0.014
Total duration of pre-exodus phase (days)	Year	1.3	0.261	0.048
	Sex	2.3	0.144	0.080
Cumulative period spent in the burrow (days)	Year	0.1	0.732	0.005
	Sex	6.5	0.017	0.201

411

412

413 Table 2. Effects of year and sex on timing and duration of the pre-laying exodus in thin-billed prions.
 414 Significant p-values are marked bold. As a measure of effect sizes we report partial Eta-Square values
 415 (η^2). None of the interactions were significant. d.f. = 28 (based on 29 birds).

Dependent	Independents	F	P	Effect size
Departure date	Year	0.3	0.601	0.011
	Sex	11.7	0.002	0.310
Trip duration (days)	Year	0.1	0.802	0.002
	Sex	19.1	<0.001	0.423
Return date	Year	0.1	0.842	0.002
	Sex	2.8	0.106	0.098
Cumulative travel distance (km)	Year	1.0	0.336	0.036
	Sex	22.7	<0.001	0.466
Travel speed (km/day)	Year	3.2	0.088	0.108
	Sex	1.1	0.301	0.041

416

417

418 Table 3. Effects of year and sex on timing and duration of the first incubation trip of thin-billed prions.
 419 Significant p-values are marked bold. As a measure of effect sizes we report partial Eta-Square values
 420 (η^2). None of the interactions were significant. d.f. = 27 (based on 28 birds).

Dependent	Independents	F	P	Effect size
Period in the burrow after pre-laying exodus	Year	1.4	0.250	0.052
	Sex	44.9	<0.001	0.642
Departure date	Year	2.3	0.143	0.084
	Sex	4.9	0.036	0.164
Trip duration (days)	Year	0.2	0.643	0.009
	Sex	0.5	0.843	0.002
Cumulative travel distance (km)	Year	1.9	0.185	0.069
	Sex	<0.1	0.983	<0.001
Travel speed (km/day)	Year	2.0	0.174	0.073
	Sex	0.1	0.793	0.003

421

422

423 Fig. 1. Early breeding season chronology of thin-billed prions from arrival to the colony (first
424 yellow block) until the end of the second foraging trip in incubation (in grey). Four birds, marked with
425 #, were recaptured earlier, three after the first incubation foraging trip (in green) and one after the pre-
426 laying exodus (in pink). Colony attendance before the pre-laying exodus consisted of shifts of 1–7
427 days in the burrow (in yellow) alternating with foraging trips of 1–8 days (in turquoise). In 2010, half
428 of the males (5 of 10) showed some egg neglect (marked black), lasting for a single day (birds left one
429 night and returned the subsequent night) in four cases, and two days and one night in one case.

430

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

433

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

437

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

440

441 Fig. 5. Sea surface temperature anomaly (SSTA) data in the Falkland current area adjacent to the
442 Falkland Islands (50–52°S, 61–63°W) over the two breeding seasons, with important phases
443 marked in colour.

444

445 Fig. 1.
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447

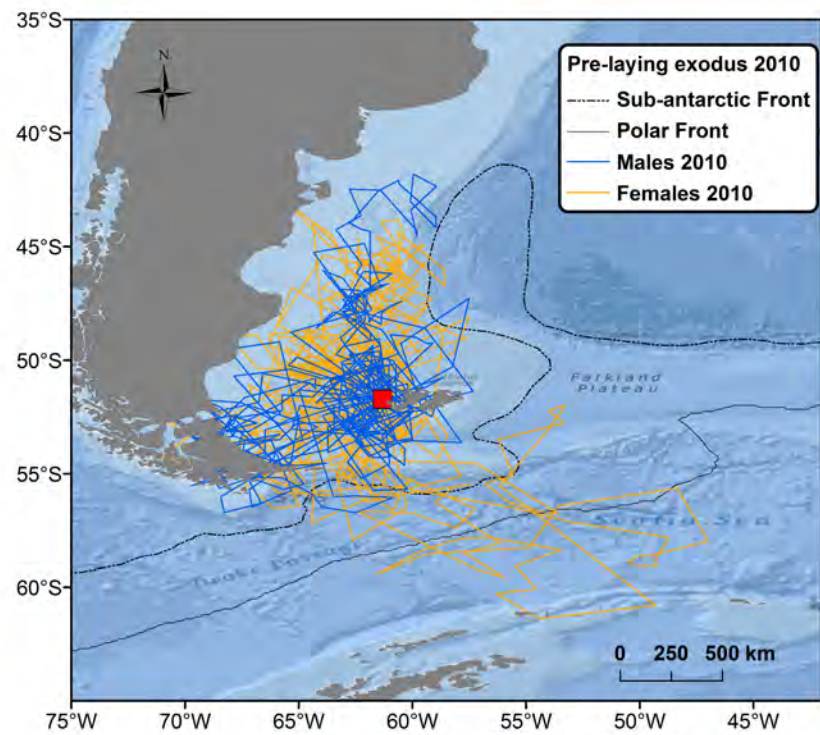


448
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451 Fig. 2.

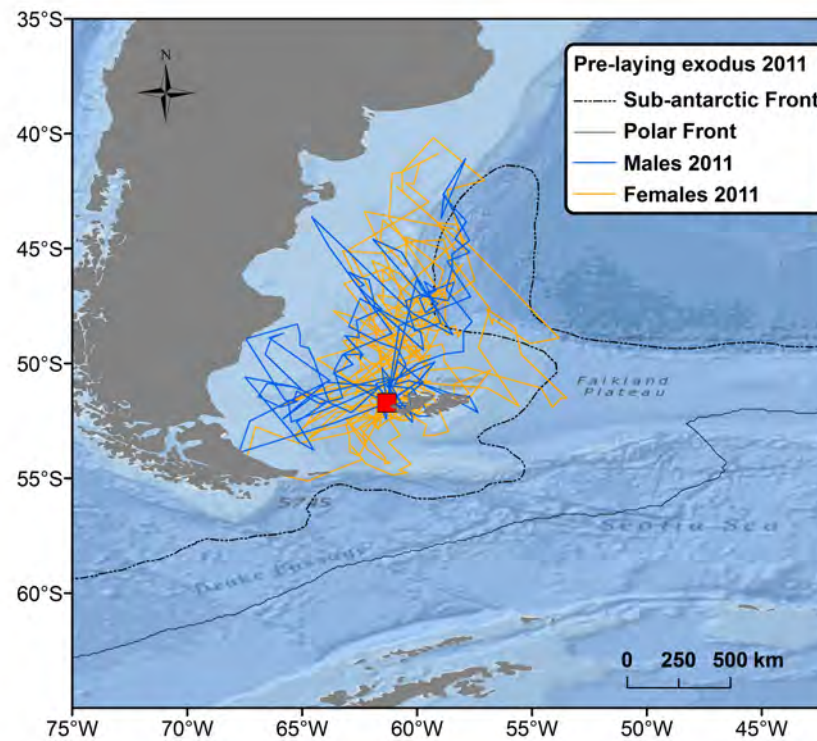
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453 (a)



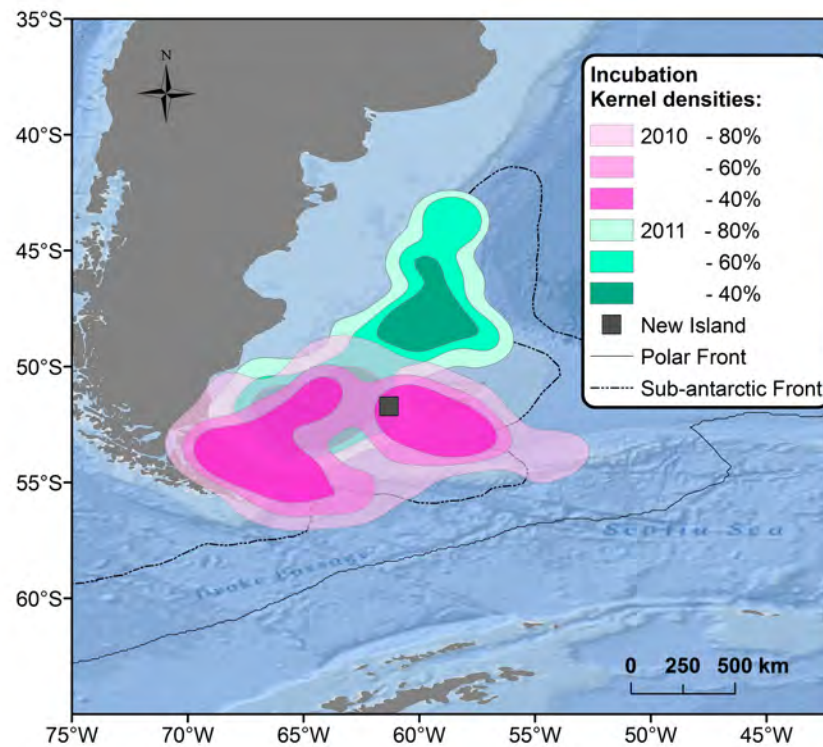
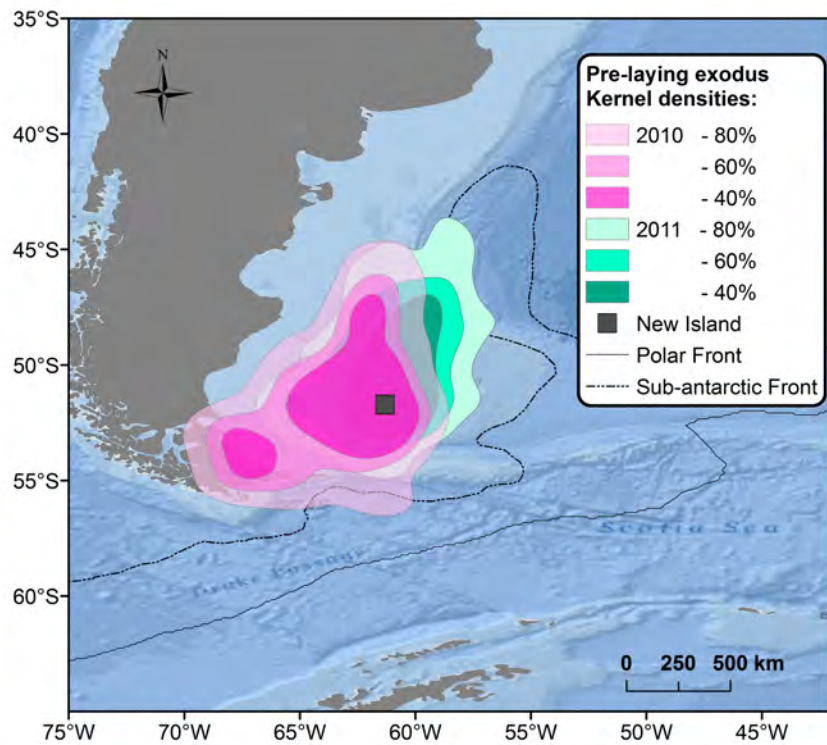
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(b)



456 Fig. 3.
457
458 (a)

(b)

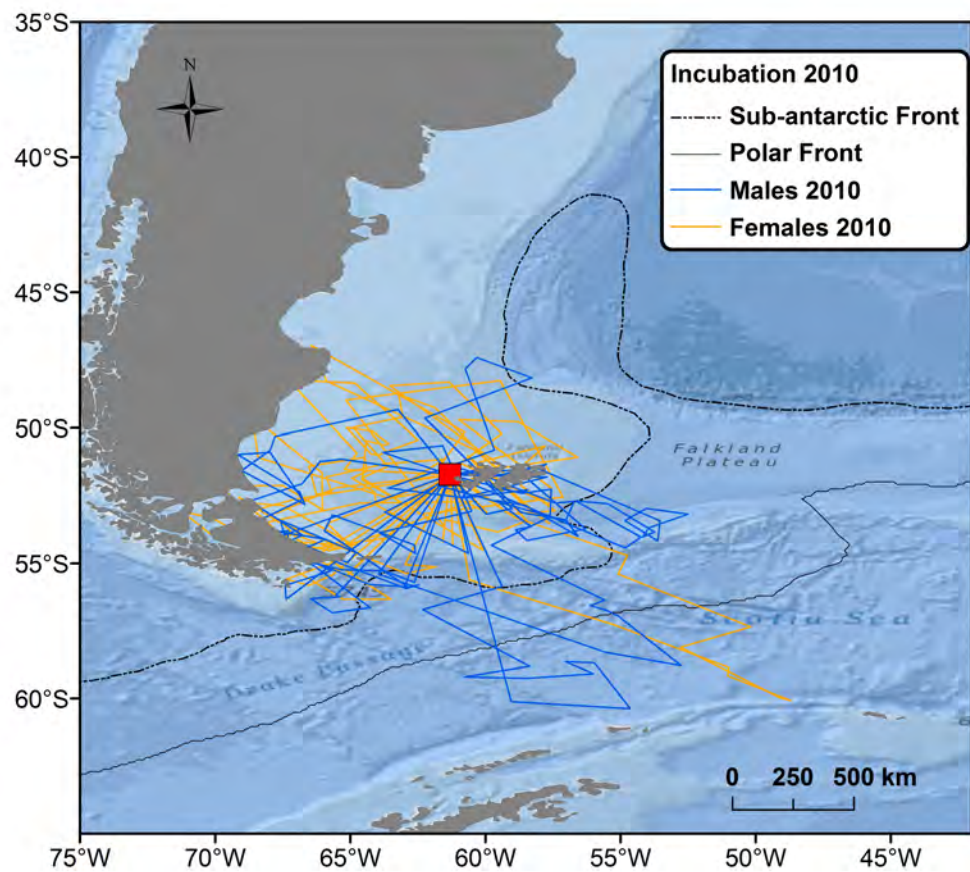


459
460
461

462 Fig. 4.

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464 (a)



(b)

