1   **Consistency in migration strategies and habitat preferences of brown skuas over two**
2   **different years, a decade apart**

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4   Running page head: Consistency in skua migration

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24   ABSTRACT: At-sea movements and activity patterns of brown skuas *Stercorarius*

25   *antarcticus lonnbergi* from South Georgia were analysed in two winters, a decade apart, to

26   examine the degree of consistency in migration strategies and habitat preferences during the

27   non-breeding and pre-laying exodus periods. Oceanographic habitat preferences of tracked

28   skuas were determined using a robust model accounting for availability. At the population

29   level, brown skuas were broadly consistent in their choice of wintering areas and habitat

30   preferences, although the distribution extended further east in 2012 than in 2002. Skuas

31   preferred areas associated with static oceanography (bathymetric features) both during the

32   non-breeding and pre-laying periods, which may explain the consistency between years in

33   habitat use. There was no significant effect of year on departure dates from South Georgia,

34   but birds returned earlier to the colony in 2002. Migration schedules varied according to

35   breeding status, with failed birds departing earlier than birds that bred successfully. Although

36   failed birds travelled further from the colony, there was little variation in dates of return. In

37   general the timing of movements was similar between sexes, but females were more likely

38   than males to engage in a pre-laying exodus. Brown skuas spent a much higher proportion

39   of time sitting on the water than other seabirds during both the non-breeding and pre-laying

40   exodus periods, and the number of flight bouts per day was surprisingly low. The selection of

41   static features by brown skuas may indicate that skuas may have less flexibility to track

42   environmental changes than species that use dynamic cues.

43   KEY WORDS: Annual variability, biologging, GAMs, geolocation, GLS, habitat selection,

44   modelling, seabird

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INTRODUCTION

Seabirds spend most of their lives at sea, only returning to land to breed. Understanding the factors that influence their marine distribution and habitat preferences is therefore essential for mitigating threats at sea, including the establishment of an effective, evolving network of protected areas that will safeguard against future biodiversity loss (Block et al. 2011, Frederiksen et al. 2012). The open ocean is a dynamic environment, and seabirds frequently target areas of higher prey availability (Pinaud & Weimerskirch 2005, Nur et al. 2011, Quillfeldt et al. 2013). These regions are often characterised by local physical features or processes, including eddies, frontal systems, upwelling zones and shelf breaks, that increase primary production or serve to aggregate animals at higher trophic levels (Wakefield et al. 2009, Kappes et al. 2010, Pinet et al. 2011, Louzao et al. 2011a). Reductions in size, and improvements in battery-life and functionality of tracking devices since the 1990s have greatly improved our knowledge of at-sea distribution patterns and behaviour of marine predators (Phillips et al. 2008). More recently, studies that combine tracking data with remotely sensed environmental data in habitat models have provided key insights into the oceanographic factors that drive the distribution of seabirds (Péron et al. 2010, Louzao et al. 2011b, Wakefield et al. 2011, Quillfeldt et al. 2015).

A limitation of many biologging studies is that data are available from relatively few individuals tracked over short periods of time (Žydelis et al. 2011). In addition, as most physical characteristics of the ocean are dynamic at varying temporal and spatial scales, prey, and hence predator, distributions are expected to vary accordingly (Pinaud et al. 2005, Žydelis et al. 2011, Quillfeldt et al. 2013). Although there is evidence in some species that individuals can change their non-breeding destination (e.g. Dias et al. 2011), the general trend appears to be for high regional site fidelity among migrant seabirds (Croxall et al. 2005, Phillips et al. 2005, 2006, Thiebot et al. 2011, Guilford et al. 2011, Yamamoto et al. 2014). There is also good evidence for high year-to-year consistency in migration schedules (timing and duration of events) for birds that are faithful to their winter destinations (Croxall et al. 2005, Phillips et al. 2005, Dias et al. 2011, Yamamoto et al. 2014). It is important to note, however, that in all these studies, individuals were tracked for successive years, when conditions may be more similar than after longer intervals.

Individuals from the same breeding population frequently use multiple regions or habitats during their non-breeding period (Phillips et al. 2005, Kopp et al. 2011, Dias et al. 2011). These alternative strategies are often associated with differences in age, breeding status, sex, or individual preferences (Phillips et al. 2005, Ramírez et al. 2013, Quillfeldt et al. 2015). Migration schedules can also vary, especially in relation to sex or prior breeding outcome

89   (Phillips et al. 2005, Bogdanova et al. 2011, Catry et al. 2013a). In addition, some non-

90   breeding regions may be used by a small minority of animals: only two of 34 black-browed

91   albatrosses *Thalassarche melanophris* tracked from South Georgia did not migrate to the

92   Benguela Upwelling but instead spent the non-breeding period on the Patagonian Shelf or in

93   Australian waters (Phillips et al. 2005); and, only two of 39 south polar skuas *Stercorarius*

94   *maccormicki* tracked from King George Island wintered in the southern hemisphere, one off

95   Peru and the other west of Gough Island (Kopp et al. 2011). Thus, to better identify core

96   areas for the entire population, and also to improve the accuracy of predicted distributions

97   based on observed habitat preferences accounting for future environmental changes,

98   tracking studies should ideally involve large numbers of individuals in multiple years (Hindell

99   et al. 2003, Soanes et al. 2013).

100   The brown skua *Stercorarius antarcticus lonnbergi* breeds on islands from the subantarctic

101   to the Antarctic continent, and is one of the main terrestrial consumers, primarily feeding on

102   other seabirds, and seal carrion (Phillips et al. 2004a, Carneiro et al. 2014, 2015). To date,

103   non-breeding ranges of brown skuas have been inferred from the distribution of just six birds

104   tracked from South Georgia during the winter of 2002 using global location sensors (GLS);

105   these birds dispersed over deep, subantarctic and mixed subantarctic-subtropical waters

106   within the Argentine Basin (Phillips et al. 2007). However, stable isotope analyses of

107   feathers from a larger sample suggested that some individuals may use continental shelf or

108   shelf-slope waters (Phillips et al. 2009). In the present study, GLS-immersion loggers were

109   deployed on adult brown skuas from the same population, but different individuals, in order

110   to: (1) assess if distribution or other aspects of migration strategies have changed in the ten

111   years since the first study, (2) identify key habitat preferences, (3) better characterise the

112   migration period in terms of timings, durations and travel distances, (4) investigate

113   differences in distribution and migration characteristics in relation to sex and recent breeding

114   performance, (5) compare at-sea activity patterns between male and female non-breeders,

115   and (6) describe the pre-laying exodus.

116

117   **MATERIALS AND METHODS**

118   This study was carried out during two non-breeding seasons a decade apart on brown skuas

119   at Bird Island, South Georgia (54° 00' S, 38° 03' W). Bird Island is probably the most

120   densely-populated colony of brown skuas in the world, with 132 nesting pairs per km^2

121   (Phillips et al. 2004a). A GLS-only logger (weight 7 g) or a combined GLS-immersion logger

122   (weight 9 g) was deployed in austral summer 2001/02 on 28 breeding adults. Combined

GLS-immersion loggers (weight 1.5 g) were deployed on 25 breeding adults, none of which were in the earlier sample, in the same study area in austral summer 2011/12. All loggers were attached with a cable-tie to a British Trust for Ornithology (BTO) metal ring on the tarsus and recovered after a year. Skuas were captured on the ground by hand or using a hand net or noose pole. Only data encompassing the non-breeding and pre-laying exodus periods are analysed here. The non-breeding period was defined as the time from the start of the outward migration to the return to the breeding grounds the following season, and was assessed for each individual using both location and activity data. Departure date was identified as that immediately prior to a directed movement away from South Georgia and consecutive nights thereafter that were spent largely on the water, whereas return date was that preceding the first night spent dry (on land). As skuas with eggs or chicks at South Georgia never forage at sea, after the initial return from migration, subsequent periods of consecutive days with intervening nights spent largely on the water were classified as pre-laying trips (Phillips et al. 2007, Carneiro et al. 2014).

Light data were analysed using the BASTrak suite based on times of sunset and sunrise estimated from thresholds in light curves; latitude was derived from day (night) length, and longitude from the time of local midday (midnight) in relation to Greenwich Mean Time and day of the year, providing two locations per day with an average accuracy of 186 ± 114 km (Phillips et al. 2004b). Locations were excluded for 2 to 4 weeks around the equinoxes, when latitudes were unreliable. All other analyses were carried out using R software (R Core Team 2014). A hierarchical state-space model fitted to data from multiple animals was used to filter and correct observed locations for logger error (Jonsen et al. 2013, Gutowsky et al. 2014). Estimates of uncertainty for each latitude and longitude are required in order to fit state-space models (Winship et al. 2012). As there are no relevant published data for skuas from double-tagging experiments, a fixed geolocation error (SD of latitudinal and longitudinal error: 1.66° and 1.82°, respectively; Phillips et al. (2004b)) derived from concurrent deployment of satellite-transmitters and GLS loggers on albatrosses was used as an estimate of uncertainty. The state-space model was fitted using Markov Chain Monte Carlo (MCMC) sampling in the bsam package (Jonsen et al. 2015). Two chains of 5,000 samples from the joint posterior probability distribution were obtained after discarding the initial burn-in period of 100,000 samples, and retaining every 20th of the remaining samples. Convergence was assessed visually by checking trace, density and autocorrelation plots (Pollet et al. 2014). After processing, locations derived from curves with apparent interruptions around sunset and sunrise which were not filtered by the state-space model were removed after visualisation in ArcGIS v. 10.2.2.

158 Changes in the spatial distribution of brown skuas between non-breeding and pre-laying
159 periods in 2002 and 2012 were investigated by producing 95 % (general use) and 40 %
160 (core) utilization distributions (UDs) for each individual using kernel analysis with a cell size
161 of 50 km and a fixed smoothing parameter (h) of 200 km (Phillips et al. 2006). The 40 %
162 density contour was selected by noting where the relationship began to increase
163 exponentially when incremental changes in UDs were plotted against the size of the total
164 area identified, which is considered to be a reliable approach for defining core areas of
165 activity (Lascelles et al. 2016). Population core and general use areas were created by
166 merging individual UDs, assigning them equal weighting. Individual overlaps were quantified
167 using Bhattacharyya's affinity, which ranges from 0 (no overlap) to 1 (identical UDs) and is
168 considered to be the most appropriate index for quantifying the degree of similarity among
169 UD estimates (Fieberg & Kochanny 2005). Kernel analysis and individual overlap
170 calculations were carried out using the adehabitatHR package (Calenge 2006). Analyses of
171 similarity (ANOSIM) were used to test for significant differences in the 95 % and 40 %
172 overlaps by year, sex, and breeding status (failed or successful birds in the year of
173 deployment) using the vegan package (Oksanen et al. 2015). The dissimilarities between the
174 UDs were included in a distance matrix (also known as a dissimilarity matrix). ANOSIM uses
175 a bootstrap randomization procedure to test for differences between groups; if two groups
176 are different, then dissimilarities between the groups should be greater than those within the
177 groups (Oksanen et al. 2015). R values from ANOSIM are equivalent to a correlation
178 coefficient and range from -1 to 1, with 0 indicating completely random grouping.

179 Oceanographic habitat preferences of the tracked skuas during the non-breeding and pre-
180 laying periods were determined using a case-control approach in binomial generalized
181 additive models (GAMs). For each animal location, we simulated 50 temporally-matched
182 pseudo-absences (controls) representing accessible areas where animals could potentially
183 have travelled (see e.g. Wakefield et al. 2011, Žydelis et al. 2011, Raymond et al. 2015).
184 These were created using correlated random walks (CRWs), based on the distribution of
185 observed turning angles and distances between successive locations, using the
186 adehabitatLT package (Calenge 2006). A constraint function defined by the minimum convex
187 polygon (MCP) of all observed locations, increased by a 200 km buffer to account for GLS
188 logger error was used to restrict the CRWs (Žydelis et al. 2011). The number of simulated
189 locations was determined by measuring changes in x^2 values of each parameter by running
190 global models with all observed locations and varying numbers of simulated pseudo-
191 absences (Žydelis et al. 2011). Fifty CRWs were sufficient for most parameters, even though
192 a few would have ideally required even more CRWs. However, and given the computational

193   requirements associated with large numbers of CRWs, we used 50 for all our models (see
194   electronic supplementary material, S1).

195   A set of oceanographic variables were included as candidate predictors in the habitat
196   models on the basis of their biological relevance, i.e., their potential influence on skua
197   distribution. To account for geolocation error, a buffer of 200 km was created around each
198   observed and simulated location. A spatially weighed average of all oceanographic data was
199   calculated for each of those locations. Potential predictors were: (1) depth (a proxy for
200   coastal or pelagic domains), extracted from ETOPO1 at a spatial resolution of 0.01°,
201   downloaded from https://www.ngdc.noaa.gov/mgg/global/global.html, and, for 2002 and
202   2012, (2) chlorophyll *a* (CHL *A*, a surrogate of marine productivity), 8-day composites
203   derived from SeaWIFS and Aqua MODIS, respectively, with a 0.09° spatial resolution, (3)
204   sea surface temperature (SST, a proxy for water mass), a product from NOAA Pathfinder
205   Advanced Very High Resolution Radiometer (AVHRR) v. 5.2 at 0.04° spatial and daily
206   temporal resolutions, (4) eddy kinetic energy (EKE) and (5) sea level anomaly (SLA), which
207   are indices of mesoscale activity, were daily delayed time AVISO DUACS products with a
208   0.3° spatial resolution. All remotely-sensed variables were extracted using the Marine
209   Geospatial Ecology Tools (MGET) for ArcGIS v. 10.2.2 (Roberts et al. 2010). As the volume
210   of missing data prevented the use of daily composites, an average of three 8-day or 24 1-
211   day composites centred on the date of the location was created for the dynamic predictors.
212   After creating the composites, values for CHL *A* were still missing for ~ 24 % of locations.
213   Such a large proportion is likely to affect inference because of the systematic pattern in the
214   occurrence of missing values (Wakefield et al. 2011), therefore, CHL *A* was discarded as a
215   predictor in the analyses. All composites were created from customized functions and the
216   raster package in R. Additionally, spatial gradients of SST (SST gradient, an indicator of the
217   presence of frontal systems) and depth (depth slope, a proxy for topographic features) were
218   calculated as the standard deviation of the mean.

219   Prior to GAM analysis, predictors were tested for colinearity by calculating all pairwise
220   Spearman rank correlations (r_s), and when $|r_s| > 0.5$, predictors were not included in the
221   same model. Habitat selection was examined using GAMs because data exploration
222   indicated potentially non-linear relationships between response and predictors. GAMs take
223   into account non-linear relationships using non-parametric smoothers to fit flexible curves to
224   data (Aarts et al. 2008), and were implemented within the mgcv package (Wood 2006).
225   Smooth functions for model predictors were specified using cubic regression splines with
226   shrinkage to avoid overparameterization and to identify the most parsimonious number of
227   knots (Wood 2006). The number of knots, representing maximum degrees of freedom of

228   each smooth, was manually limited by k = 4 to avoid excessive flexibility and model

229   overfitting that would have no ecological meaning (Mannocci et al. 2014). Due to the

230   dynamic nature of oceanographic predictors and possible changes in habitat preferences,

231   year, but not sex or breeding status, was included as an interaction in the models.

232   The best minimum models were determined by forward selection using k-fold cross-

233   validation (Wakefield et al. 2011), testing the goodness of fit of each individual, in turn,

234   against the prediction based on the other 24 individuals. Cross-validation was preferred over

235   information criteria, e.g. the Akaike Information Criterion (AIC), as the latter can lead to

236   overparameterized models because of violation of the independence assumption inherent

237   within tracking datasets (Aarts et al. 2008, Cleasby et al. 2015). Cross-validation prevents

238   overparameterization by using a set of data for fitting the model and another set for

239   assessing predictive performance (Aarts et al. 2008). Each model was trained on 24 folds

240   and tested, in turn, on the remaining, withheld fold which represented an individual. Model

241   selection was based on the predictive ability of the model using the area under the receiver

242   operating curve (AUC) averaged across the 25 sets of results (i.e., individuals) using the

243   pROC package (see Raymond et al. 2015). AUC values between 0.5-0.7 indicate poor

244   model predictive ability, values from 0.7-0.9 indicate reasonable model discrimination ability,

245   and values higher than 0.9 indicate very good model discrimination (Pearce & Ferrier 2000).

246   The forward selection procedure consisted initially of fitting all possible single predictor

247   models with and without the year-interaction and ranking those models according to AUC.

248   The best ranking model was chosen, and then, each of the remaining predictors was added

249   in turn; the best model among this new set was then retained if the AUC increased

250   significantly. This process was continued until there was no further increase in the AUC. The

251   significance of the increase in AUC between two models was tested with a paired t-test.

252   Using cross-validation and paired t-tests to compare AUCs is somewhat conservative;

253   however, we considered this approach to be the best solution to avoid overparameterization,

254   as it prevents adding parameters that only contribute trivially to increasing AUC. Habitat

255   preference models were fitted separately for the non-breeding and pre-laying periods.

256   Timing (departure and return dates, and duration), the size of the core and general use

257   areas (40 % and 95 % UDs), travel speeds and distances (summed great circle distances

258   between the locations) were compared between birds of different sex and breeding status

259   during the pre-laying exodus and migration periods. The effect of year was included in

260   models for the migration but not pre-laying period because of the reduced sample size (only

261   two birds engaged in a pre-laying exodus in 2002). All main effects and interactions were

262   tested in linear models. AIC values were used to rank all possible models according to their

263   degree of parsimony; the best model was the one with the lowest AIC. If two or more models

264   were within 2 AIC units from the best-supported model, differed by one parameter and had a

265   similar maximized log-likelihood value, only the most parsimonious model was selected. The

266   latter suggests that improvements in model fit have not been enough to overcome the

267   penalty of an additional parameter (Burnham & Anderson 2002, Arnold 2010). Unless

268   indicated otherwise, all data are presented as mean ± SD.

269

270   **At-sea activity analysis**

271   The combined GLS-immersion loggers tested for saltwater immersion every three seconds.

272   The number of positive tests was recorded for each 10-min period, providing a value that

273   ranged from 0 (continuously dry) to 200 (continuously wet). Each 10-min period was

274   categorised as daylight or darkness using sunset and sunrise times estimated from the

275   thresholds in light curves recorded by the same loggers. The activity data were used to

276   determine the proportion of time spent flying during daylight and darkness, and daily (each

277   consecutive light and dark period). The proportion of the total time spent on water, and time

278   spent in flight in each day that occurred during darkness, as well as the duration and number

279   of flight bouts per day, were also calculated. A flight bout was defined as any continuous

280   sequence of 10-min periods of completely dry (0) values. This method is likely to

281   underestimate the number of flight bouts as birds may engage in multiple short periods of

282   flight within 10 minutes. However, Phalan et al. (2007) found a close correlation between

283   bouts derived from lower and higher resolution loggers (which record immersion every 10

284   seconds), indicating that bouts are adequate as proxies of activity. At-sea activity

285   characteristics were compared between sexes, and between daylight *vs.* darkness using

286   linear mixed-effect models with individual identity included as a random effect. Year was not

287   included in the models because of the limited sample size for 2001/02 (only three birds for

288   the non-breeding period and two birds for the pre-laying exodus). Proportion data were

289   arcsine transformed. Models including all combinations of variables as well as their

290   interactions were tested using AIC values following the approach described above.

291

292   **RESULTS**

293   Eight out of 28 breeding adults (29 %) fitted with loggers in summer 2001/02 returned to

294   breed in 2002; seven loggers were retrieved (one bird was not recaptured), of which one

295   failed to download. Immersion data were only available for three of the loggers. The low

return rate of instrumented birds was attributed to the accretion of goose barnacles *Lepas*
spp. to the self-amalgamating tape wrapped around the logger causing an increase in load
on the leg, and is discussed in Phillips et al. (2007). Of 25 birds fitted with a logger in
2011/12, 22 returned to breed in the following season, from which 19 loggers were retrieved
(three loggers were lost). Return rates were higher for birds with devices (22 of 25; 88 %)
than for control birds (60 of 82; 73 %), all fitted with a plastic colour-ring with a unique alpha-
numeric sequence in the first season, but the difference was not statistically significant
(Fisher's exact test, P = 0.18).

Non-breeding period

Tracked skuas started their outward migration on 4 March ± 19 days (range: 3 February to
22 April, n = 24). There was no significant effect of year on mean departure date (Table 1),
but birds returned to South Georgia ca. 10 days earlier in 2002, on 5 October ± 8 days
(range: 30 September to 15 October, n = 3), compared with 16 October ± 10 days (range: 26
September to 4 November, n = 19) in 2012. The migration period lasted ca. 225 ± 20 days
(range: 192 to 270, n = 22), and was similar between years (Table 1). Departure dates and
durations of the migration period, but not return dates, varied according to breeding status
and sex (Table 1). Excluding one bird that failed in early February and only started its
outward migration on 4 April, failed birds departed earlier than birds that bred successfully,
on 21 February ± 16 days (range: 3 February to 31 March, n = 12) and 16 March ± 15 days
(range: 1 March to 22 April, n = 12), respectively (Table 1). Males departed 3 to 4 weeks
later than females, on 17 March ± 18 days (range: 19 February to 22 April, n = 10),
compared with 23 February ± 14 days (range: 3 February to 22 March, n = 15; Table 1);
however, the effect of sex probably only reflects differences associated with breeding status,
as the proportion of tracked males that bred successfully was higher than the proportion of
females (60 % *vs.* 40 %). The mean distance travelled during migration was 391.9 ± 71.6 km
per day (range: 272.9 to 540.2 km, n = 24), with no effect of year, sex or breeding status
(Table 1). Maximum distances from the colony varied according to breeding status, ranging
from 1,824 to 5,066 km (3,009 ± 1,043, n = 13) for failed birds, and from 1,445 to 3,363 km
(2,400 ± 489 km, n = 11) for successful birds. There was no difference in the maximum
distance travelled from the colony between 2002 and 2012, nor between males and females
(Table 1).

Skuas were distributed over a wide area (95 % UDs) during the non-breeding period,
ranging from 2,437,500 to 9,455,000 km^2 (4,442,500 ± 1,470,068 km^2, n = 24; Fig. 1). The

330   distribution was limited to waters between the northern extent of the Subtropical Front and

331   the southern boundary of the Antarctic Circumpolar Current, and between the Argentine and

332   Agulhas basins. Core areas were 717,396 ± 244,662 km^2 (range: 370,000 to 1,597,500 km^2,

333   n = 24; Fig. 1). Although the non-breeding range appeared to be more extensive in 2012

334   than 2002, there was no significant effect of year, sex or breeding status on distribution

335   according to the results of the ANOSIM (R = 0.0 – 0.1, P > 0.05), nor did these factors affect

336   the size of individual 95 % and 40 % UDs (Table 1).

337   The best model predicting skua distribution from oceanographic variables during the non-

338   breeding period achieved an accuracy of AUC = 0.76 (reasonable discrimination ability).

339   However, the predictive accuracy when calculated separately for each individual varied from

340   AUC = 0.50 (no discrimination) to AUC = 0.91 (very good discrimination). The most

341   important predictors of habitat use by the tracked skuas were, in order of decreasing

342   importance, depth and depth slope. Model response curves indicated that probability of

343   occurrence was higher in both shallow and deep water (i.e., lowest in mid-depths), and in

344   areas with steeper depth slopes (Fig. 2). There was no effect of year on habitat preference

345   during the non-breeding period, nor did the tracked birds prefer areas according to SST,

346   SST gradient, EKE or SLA.

347

348   **Pre-laying exodus**

349   After the return to South Georgia, two out of three (67 %) and 10 out of 19 (53 %) brown

350   skuas that returned to breed in 2002 and 2012, respectively, engaged in a pre-laying

351   exodus. No characteristic of the pre-laying exodus (start and return dates, duration, distance

352   travelled per day and maximum range from the colony) differed significantly between males

353   and females, nor between birds that bred successfully or failed in the previous season

354   (Table 1). However, the majority (75 %) of pre-laying trips were performed by females.

355   Skuas departed to sea on 30 October ± 9 days (range: 18 October to 15 November, n = 12),

356   which was 16 ± 8 days (range: 8 to 39 days, n = 12) after their first return to the colony, for a

357   pre-laying exodus that lasted six to nine days (7 ± 1 days, n = 12). All trips were to the north

358   of South Georgia, ranging from 772 to 2,636 km from the colony (1,553 ± 580 km, n = 12).

359   Trips were to subantarctic and mixed subantarctic-subtropical waters (Fig. 1). The tracked

360   birds covered 455 ± 212 km per day (range: 195.5 to 953 km per day, n = 12). Individual

361   core areas and 95 % UDs during the pre-laying exodus ranged from 195,000 to 402,500 km^2

362   (256,250 ± 61,158 km^2, n = 12) and from 1,105,000 to 2,360,000 km^2 (1,538,333 ± 345,694

363   km^2, n = 12), respectively. There were no significant effects of sex or breeding status on

364   distributions (ANOSIM results, R = -0.1 – 0.2, P > 0.05), nor on the size of individual core

365   and general use areas according to linear models (Table 1).

366   Depth was the main predictor of skua distribution during the pre-laying period. The best

367   model had reasonable discrimination ability (AUC = 0.77). Variation among individuals,

368   however, was considerable, with predictive accuracies ranging from none (AUC = 0.50) to

369   very high (AUC = 0.93). Probability of occurrence of brown skuas increased in areas with

370   greater water depth (Fig. 3). Habitat selection by tracked skuas was not affected by year,

371   SST, SST gradient, EKE, SLA, and depth slope.

372

373   **At-sea activity patterns**

374   Given the few birds sampled in 2002, immersion data from both years were pooled. Brown

375   skuas from South Georgia spent a considerably smaller percentage of time in flight than on

376   the water during both the non-breeding and pre-laying exodus periods (Tables 2 and 3).

377   During the non-breeding period, females spent more time than males in flight during

378   darkness, probably as a consequence of longer, but not more frequent, flight bouts (Tables 2

379   and 3). Skuas were more active (i.e., performed more flight bouts), during daylight than

380   darkness; however, the bouts in daylight were shorter. During the pre-laying exodus,

381   although the proportion of time spent in flight appeared to be higher in daylight than

382   darkness, this was not reflected in the best model, nor in this case, was there a significant

383   difference between males and females (Tables 2 and 3). Flight bout duration, however, was

384   longer during darkness, and females engaged in more flight bouts per day than males. There

385   was no difference in the number of flight bouts per day between daylight and darkness, nor

386   in the duration of flight bouts between males and females during the pre-laying exodus

387   (Tables 2 and 3).

388

389   **DISCUSSION**

390   **Distribution and habitat use**

391   With the inclusion of the new, large sample from 2012, this study represents the most

392   detailed published analysis of movements and activity patterns of brown skuas during the

393   non-breeding and pre-laying exodus periods. Although habitat use of brown skuas was

394   described previously in terms of differences in bathymetry, sea surface temperature and

395   chlorophyll *a* concentrations between core and peripheral areas (Phillips et al. 2007), this is

12

the first study to present a robust model of habitat preference, accounting for availability. The loggers deployed in summer 2011/12 had no deleterious effect on adult survival; indeed, return rates were higher, but not statistically significant, for birds with devices than for control birds. Although some birds in the larger sample tracked in winter 2012 travelled to areas east of those used in winter 2002, there were no statistically significant differences in distribution, the size of the core and general use areas, nor in habitat preferences, despite the decade that had elapsed between the two series of deployments. Similarly, northern hemisphere skuas (great *Stercorarius skua* and long-tailed *S. longicaudus* skuas) tracked during two or three consecutive years migrated to the same general regions, and had similar migration schedules (Sittler et al. 2011, Magnusdottir et al. 2012, Gilg et al. 2013).

The brown skuas tracked in this study were not limited to any specific water mass; however, most of their core areas were in subantarctic and mixed subantarctic subtropical waters during both the non-breeding season and the pre-laying exodus. They preferred regions with either shallow or deep waters, and increasing depth slopes, during the migration period, whereas in the pre-laying exodus, they selected habitat based solely on water depth. This confirms the inference from stable isotope analysis that a minority of brown skuas winter in shelf-slope waters (Phillips et al. 2007, 2009). Depth gradients are steeper at seamounts, and where shelf-edge fronts form, which are zones of intense mixing and enhanced primary production (Bost et al. 2009, Louzao et al. 2011b, Wakefield et al. 2011, Scales et al. 2014). Also, several studies have shown associations of seabirds with frontal systems influenced by bathymetric features (Phillips et al. 2005, 2006, Paiva et al. 2010a, Paiva et al. 2010b, Louzao et al. 2011b, Rayner et al. 2012).

In the present study, the core areas of several individuals (as well as the composite 40 % UDs for the population) overlapped extensively with regions of steeper slopes around the Falkland Escarpment, which forms the boundary between the Falkland Plateau and the Argentine Basin (Fig. 1). The Falkland Escarpment is a region subject to high frontal probability during the austral autumn, winter and spring, mostly associated with the presence of eddies from the Brazil-Malvinas Confluence, where the warm Brazil Current and the cold Malvinas Current meet (Saraceno et al. 2004). Moreover, five birds targeted areas of shallower bathymetry around the Discovery Rise and its associated seamounts during their migration in 2012, whilst one bird travelled as far as the Agulhas Basin, reaching turbulence zones from the Agulhas Return Current, where primary productivity is enhanced.

Although the skuas showed a preference for oceanographic characteristics that are often found in areas with abundant and predictable prey, it is noteworthy that much of the Argentine Basin, which was one of the main wintering areas, is not particularly productive

431 based on chlorophyll *a* concentrations (Phillips et al. 2007). This suggests that bathymetric

432 features alone cannot entirely explain the observed distribution of brown skuas. Quillfeldt et

433 al. (2013) suggested that the occurrence of Antarctic prions *Pachyptila desolata* in deep

434 waters to the east of the Patagonian Shelf may be to avoid competition with larger seabirds.

435 The same may be true for brown skuas, as the Patagonian Shelf is used year-round by

436 numerous albatross and petrel populations from Tristan da Cunha, Gough, the Falkland

437 Islands, South Georgia, and New Zealand (Croxall & Wood 2002, Phillips et al. 2006, Catry

438 et al. 2013b, Copello et al. 2013). The ranges of the tracked brown skuas still overlapped to

439 some extent with non-breeding Falkland skuas *S. antarcticus antarcticus* (Phillips et al.

440 2007), and even more with wandering albatrosses *Diomedea exulans*, year-round (Jiménez

441 et al. in press). However, inter-specific competition between these taxa may be alleviated by

442 trophic partitioning of resources or differences in behaviour. Whilst $\delta^{13}C$ values are similar

443 for wandering albatrosses and brown skuas, $\delta^{15}N$ values in feathers from wandering

444 albatrosses are much higher, and their activity patterns differ (Phalan et al. 2007, Phillips et

445 al. 2009, Ceia et al. 2012). Therefore, although the tracking and isotope data indicate that

446 they occur in the same general area, wandering albatrosses feed at substantially higher

447 trophic levels. Although $\delta^{15}N$ values in brown skuas are significantly higher than in non-

448 breeding Antarctic prions, this is not by a full trophic level, suggesting there is some diet

449 overlap (Phillips et al. 2007, 2009). Antarctic prions feed on a wider range of small

450 zooplankton taxa, whereas brown skuas probably have a mixed diet that includes

451 zooplankton, low trophic level squid or fish (Phillips et al. 2007, Grecian et al. 2015). Finally,

452 skuas breeding at the Falkland Islands occur closer to the Patagonian shelf-break and to a

453 lesser extent in open waters than brown skuas (Phillips et al. 2007).

454 As brown skuas select habitats based mainly on static oceanography (water depth), their

455 return to the same general area each year is not surprising, assuming that prey preferences

456 are also consistent. Similarly, the use of neritic waters and areas of steeper bathymetric

457 relief by black-browed albatrosses varied very little over multiple breeding seasons (Pinaud

458 & Weimerskirch 2005, Wakefield et al. 2011, Catry et al. 2013b). The recurrent use of similar

459 areas may increase familiarity with feeding conditions, including fine-scale resource

460 distribution, and potentially help reduce inter-specific competition (Quillfeldt et al. 2013,

461 Ramírez et al. 2015). Although habitat preferences were consistent between years, the

462 tracked skuas had multiple migration destinations in 2012, which should ensure that a

463 proportion of the population would escape from detrimental changes during winter if those

464 are constrained spatially (Phillips et al. 2009, Dias et al. 2011). At the population level, core

465 and general use areas did not differ significantly between years, but a few individuals in

466 2012 travelled to regions east of those exploited in 2002 (Fig. 1). Two birds in this latter

group remained exclusively in the Agulhas Basin or in waters around the Discovery Rise, whereas another four birds used areas around the Discovery Rise and in the Argentine Basin. The existence of several non-breeding destinations for the same population has been confirmed for many seabird species, including south polar and great skuas (Phillips et al. 2005, Kopp et al. 2011, Dias et al. 2011, Magnusdottir et al. 2012, Tranquilla et al. 2013, Ramírez et al. 2015). That the minority strategies were not detected in brown skuas from South Georgia in the first set of deployments probably reflects the modest sample size rather than indicates that birds have explored new environments in the subsequent decade. This is supported by the stable isotope data which suggests that some birds sampled in 2001/02 had exploited neritic or shelf-slope waters in the previous winter (see above), and by the lack of any substantial differences between years in distribution based on randomizations, or in habitat preferences (this study). Regardless, the two tracking datasets provide an adequate representation of the distribution of the majority of individuals. Indeed, in an analysis of 15 years of tracking data, Bogdanova et al. (2014) suggested that one or two years of data is usually sufficient to identify a considerable proportion of the long-term foraging areas for species which feed on spatially stable habitats. Furthermore, the distributions of general (95 % UD) and core areas (40 %) of the tracked skuas were not influenced by sex or breeding status, which are complicating factors in other studies (Bogdanova et al. 2011, 2014).

Migration schedules

Failed birds departed from the breeding grounds earlier than successful birds, in line with other studies (Phillips et al. 2005, Bogdanova et al. 2011, Quillfeldt et al. 2015). If migration commences earlier, more time may be allocated to undertake farther movements. Indeed, maximum distance from the colony was higher for failed than for successful breeders. Failed birds may also be in better condition to undertake longer migrations, as costs associated with breeding have been lower (Bogdanova et al. 2011). The latter is particularly likely for skuas at South Georgia, which are able to exploit abundant seal carrion only in December and January; thereafter, the availability of carrion declines steeply and breeding birds are forced to target other, less profitable prey (Phillips et al. 2004a, Anderson et al. 2009, Carneiro et al. 2014). Therefore, a movement away from the breeding grounds to areas with more favourable conditions should be expected for failed birds that are no longer under central-place constraints.

The mean date of return to South Georgia, however, was similar for all tracked individuals within the same year, suggesting that previous breeding outcome ceased to be important at

501   some stage during the migration period (Phillips et al. 2005). Similar arrival dates may

502   decrease the chances of nest site usurpation by prospectors seeking to adopt a vacant site

503   (Furness 1987). Indeed, it has been suggested that nesting habitat in the study area is

504   saturated, with few opportunities for the establishment of new territories (Phillips et al.

505   2004a). The explanation for the later return of tracked birds to the colony in 2012 than 2002

506   is less clear. Shifts in phenology are expected as a response to climate change, and in the

507   Southern Ocean, dates of arrival and of the first egg have been later for a number of species

508   (Barbraud & Weimerskirch 2006). In summer 2002/03, brown skuas at South Georgia laid

509   later, and had lower hatching success, fledging success and chick growth rates than in the

510   mid-1980s (Phillips et al. 2004a). Later arrival in 2012 than 2002 may therefore be indicative

511   of poorer environmental conditions during the preceding winter, potentially reflecting a

512   longer-term trend, but this would need to be confirmed by more extensive tracking. There

513   was no consistent effect of sex on timing of movements, in accordance with previous studies

514   of arrival times of brown skuas at the South Orkney Islands, and of migration schedules of

515   long-tailed skuas in the high Arctic (Burton 1968, Gilg et al. 2013).

516   Prior to egg-laying and after returning from migration, ca. 55 % of tracked skuas travelled to

517   waters to the north of South Georgia in a pre-laying exodus. Although timings and distances

518   travelled were unaffected by sex and previous breeding status, a pre-laying exodus was

519   more commonly performed by females. At this time of year, food resources accessible on

520   land for skuas are likely to be limited. There is very little carrion available from seals, and

521   most burrow-nesting petrels have yet to return (Carneiro et al. 2014). Skuas arrive earlier at

522   their breeding grounds to defend their territories and (re)establish pair bonds, but it is

523   possible that to acquire enough resources for egg formation, females have to return to feed

524   at sea. In most seabird species, females are generally away for longer periods or travel

525   further to reach more productive waters (Guilford et al. 2009, Hedd et al. 2014, Quillfeldt et

526   al. 2014, but see Pinet et al. 2012). Moreover, given the exceptionally high nesting density at

527   South Georgia, loss of the territory to conspecifics is more likely if the breeding site is

528   unattended for longer periods, suggesting it may be beneficial for one member of the pair to

529   remain close to the colony. Indeed, high attendance rates and fewer joint nest absences

530   have been reported for skuas at South Georgia during incubation and chick-rearing when

531   compared to sites elsewhere (Pietz 1987, Catry & Furness 1999, Caldow & Furness 2000,

532   Carneiro et al. 2014).

533

534   **At-sea activity patterns**

535 Brown skuas spend much less time flying during the non-breeding and pre-laying periods

536 than albatrosses and petrels, particularly during daylight (Phillips et al. 2007, this study). The

537 number of flight bouts per day was surprisingly low. This suggests that birds may forage

538 opportunistically using a sit-and-wait strategy as previously described for other species,

539 including white-chinned petrels *Procellaria aequinoctialis*, grey-headed albatrosses

540 *Thalassarche chrysostoma*, and Desertas petrels *Pterodroma deserta* (Catry et al. 2004,

541 Mackley et al. 2010, Péron et al. 2010, Ramírez et al. 2013). Alternatively, brown skuas may

542 feed on large items of carrion or moribund prey, as they do on land during the breeding

543 season (Phillips et al. 2004a, Anderson et al. 2009, Carneiro et al. 2014). Amongst

544 procellariids, the species with activity patterns during the non-breeding season that are most

545 similar (i.e., low flight activity) to those of wintering brown skuas are wandering albatrosses

546 and white-chinned petrels, which to some extent also rely on scavenging (Xavier et al. 2004,

547 Mackley et al. 2010, 2011). These two species nonetheless spend considerably more time in

548 flight, possibly because they use dynamic soaring to reduce flight costs, whereas skuas

549 usually flap continuously in cruising flight and so would expend more energy if travelling long

550 distances between prey patches (Pennycuick 1987, Catry et al. 2011, Gutowsky et al. 2014).

551 Although both sexes were more active during daylight, females spent proportionally more

552 time flying during darkness than males in the non-breeding season. This reflects their longer,

553 but not more frequent, flight bouts. As females have higher wing loading and less

554 manoeuvrability than males (Phillips et al. 2002, Carneiro et al. 2014), they might land less

555 frequently because of the greater cost of taking off (Shaffer et al. 2001, Phillips et al. 2004c).

556 The greater manoeuvrability of males would also be an advantage during daylight when

557 feeding by kleptoparasitism (Phillips et al. 2002), but the limited time spent flying suggests

558 that either this foraging mode is rare, or that when used, it is highly successful. Although in

559 theory, darkness should tend to limit movements, as aerial detection and capture of prey is

560 more difficult (Phalan et al. 2007, Mackley et al. 2011), this seems not to affect females to

561 the same degree as males, but it could explain their longer flight durations at night. The

562 number of flight bouts per day during the pre-laying exodus was also higher for females,

563 suggesting that they increase their foraging effort to acquire enough resources for egg

564 formation.

565

566 **CONCLUSIONS**

567 Although seabird distributions are expected to vary temporally and spatially according to the

568 dynamic nature of the marine environment, the population of brown skuas tracked from

569   South Georgia during migration and the pre-laying exodus visited the same general area and
570   showed similar habitat preferences between 2002 and 2012. They preferred habitats
571   associated with static features (i.e., bathymetry), which may explain the consistency found
572   between years. Further studies comparing years of contrasting foraging conditions would
573   reveal whether skuas are able to change their foraging strategies to compensate for
574   environmental changes. In addition, this study highlighted the need for large sample sizes to
575   detect strategies used by a small proportion of the population. The existence of multiple non-
576   breeding destinations may be advantageous given increasing anthropogenic impacts on
577   marine ecosystems.

578

586

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Table 1: Summary of linear models for the effects of sex, breeding status (successful or failed) and year on characteristics of the non-breeding period and pre-laying exodus of brown skuas tracked from South Georgia in winter 2002 and 2012. + indicates predictors that were retained by the most parsimonious models, n/a (not applicable) indicates predictors that were not retained in the analysis. Interactions are not shown because they were not retained in the best models.

	Sex	Status	Year	d.f.	AICc	ΔAICc
Non-breeding period						
Departure dates	+	+		4	193.6	0.0
Return dates			+	3	169.2	0.0
Duration	+	+		4	175.3	0.0
Size of core area (40% UD)				2	667.2	0.0
Size of general use area (95% UD)				2	753.3	0.0
Distance travelled per day				2	-11.7	0.0
Max. distance from colony		+		3	10.8	0.0
Pre-laying exodus						
Departure dates			n/a	2	-46.6	0.0
Return dates			n/a	2	90.6	0.0
Duration			n/a	2	38.0	0.0
Size of core area (40% UD)			n/a	2	1.6	0.0
Size of general use area (95% UD)			n/a	2	1.3	0.0
Distance travelled per day			n/a	2	19.1	0.0
Max. distance from colony			n/a	2	85.5	0.0

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Table 2: Summary of activity patterns of brown skuas tracked from South Georgia during the non-breeding period and pre-laying exodus in winter 2002 and 2012.Values are presented as mean ± SD (range).

	Daylight		Darkness	
	Male	Female	Male	Female
Non-breeding period				
% time in flight				
2002	25.9 ± 0.0 (25.9 - 25.9)	19.8 ± 6.9 (14.9 - 24.7)	11.4 ± 0.0 (11.4 - 11.4)	15.1 ± 1.4 (14.1 - 16.1)
2012	24.8 ± 4.5 (18.8 - 33.0)	25.9 ± 5.4 (17.9 - 37.5)	16.9 ± 3.9 (12.1 - 22.7)	24.5 ± 7.9 (9.2 - 42.0)
Total time in flight (h per day)				
2002	3.0 ± 0.0 (3.0 - 3.0)	2.3 ± 0.8 (1.7 - 2.9)	1.4 ± 0.0 (1.4 - 1.4)	1.9 ± 0.2 (1.8 - 2.1)
2012	2.6 ± 0.5 (2.0 - 3.5)	2.9 ± 0.7 (1.9 - 4.1)	2.2 ± 0.5 (1.6 - 3.1)	3.2 ± 1.1 (1.2 - 5.6)
Total time on water (h per day)				
2002	8.5 ± 0.0 (8.5 - 8.5)	9.3 ± 0.8 (8.7 - 9.9)	11 ± 0.0 (11.0 - 11.0)	10.5 ± 0.2 (10.4 - 10.6)
2012	8.0 ± 0.5 (7.2 - 8.6)	8.3 ± 0.8 (6.9 - 9.5)	11.2 ± 0.5 (10.6 - 11.7)	9.7 ± 1.2 (7.7 - 11.7)
No. flight bouts per day				
2002	2.3 ± 0.0 (2.3 - 2.3)	2.0 ± 1.0 (1.3 - 2.7)	0.9 ± 0.0 (0.9 - 0.9)	1.3 ± 0.1 (1.2 - 1.4)
2012	1.8 ± 0.8 (0.9 - 2.7)	2.2 ± 0.7 (1.0 - 3.7)	1.3 ± 0.3 (1.0 - 1.9)	1.4 ± 0.4 (0.9 - 2.0)
Duration flight bouts (min)				
2002	29.1 ± 0.0 (29.1 - 29.1)	32.9 ± 4.4 (29.8 - 36.0)	85.9 ± 0.0 (85.9 - 85.9)	89.7 ± 1.5 (88.7 - 90.8)
2012	30.8 ± 2.2 (28.6 - 35.1)	46.1 ± 29.3 (33.4 - 135.7)	95.6 ± 15.4 (81.6 - 119.3)	119.7 ± 43.7 (57.6 - 188.9)
Pre-laying exodus				
% time in flight				
2002	23.4 ± 0.0 (23.4 - 23.4)	11.5 ± 0.0 (11.5 - 11.5)	1.4 ± 0.0 (1.4 - 1.4)	0.3 ± 0.0 (0.3 - 0.3)
2012	13.6 ± 3.3 (11.3 - 15.9)	19.1 ± 9.0 (12.6 - 40.0)	9.9 ± 6.1 (5.6 - 14.2)	17.8 ± 10.0 (5.2 - 33.0)
Total time in flight (h per day)				
2002	3.6 ± 0.0 (3.6 - 3.6)	1.7 ± 0.0 (1.7 - 1.7)	0.2 ± 0.0 (0.2 - 0.2)	0.0 ± 0.0 (0.0 - 0.0)
2012	2.0 ± 0.4 (1.7 - 2.3)	2.6 ± 1.4 (1.1 - 5.6)	0.9 ± 0.6 (0.5 - 1.3)	1.9 ± 1.2 (0.4 - 4.0)
Total time on water (h per day)				
2002	12.0 ± 0.0 (12.0 - 12.0)	13.6 ± 0.0 (13.6 - 13.6)	8.1 ± 0.0 (8.1 - 8.1)	8.6 ± 0.0 (8.6 - 8.6)
2012	12.4 ± 0.7 (11.9 - 12.9)	10.6 ± 2.2 (7.9 - 13.5)	8.6 ± 0.8 (8.1 - 9.1)	8.8 ± 2.4 (6.1 - 13.0)

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N. flight bouts per day					
	2002	2.0 ± 0.0 (2.0 - 2.0)	1.1 ± 0.0 (1.1 - 1.1)	0.5 ± 0.0 (0.5 - 0.5)	0.1 ± 0.0 (0.1 - 0.1)
	2012	0.5 ± 0.2 (0.3 - 0.7)	2.0 ± 1.9 (0.7 - 6.1)	0.8 ± 0.2 (0.7 - 1.0)	1.4 ± 1.0 (0.3 - 3.4)
Duration flight bouts (min)					
	2002	46.0 ± 0.0 (46.0 - 46.0)	34.4 ± 0.0 (34.4 - 34.4)	63.3 ± 0.0 (63.3 - 63.3)	28.2 ± 0.0 (28.2 - 28.2)
	2012	23.7 ± 2.7 (21.8 - 25.6)	40.5 ± 18.4 (26.1 - 77.5)	62.3 ± 6.8 (57.5 - 67.1)	67.5 ± 40.8 (24.9 - 147.2)

Table 3: Summary of linear mixed-effects models of activity patterns of brown skuas tracked from South Georgia in 2002 and 2012 during the non-breeding period and pre-laying exodus. + indicates predictors retained in the most parsimonious models.

Non-breeding period	LightDark	Sex	LightDark:Sex	d.f.	AICc	ΔAICc
% of time spent in flight	+	+	+	6	-1399.6	0.0
No. of flight bouts per day	+			3	-3.7	0.0
Duration of flight bouts	+	+		4	373.1	0.0
Pre-laying exodus						
% of time spent in flight				3	-82.9	0.0
No. of flight bouts per day		+		3	50.0	0.0
Duration of flight bouts	+			3	32.0	0.0

Fig. 1: Utilization distributions (40 % and 95 %) of individual brown skuas tracked from South Georgia during the non-breeding season in 2002 [a] and 2012 [c]. Composite of individual utilization distributions (40 % and 95 %) during non-breeding and pre-laying exodus in 2002 [b] and 2012 [d] overlaid on bathymetric map. Black lines correspond to STF (Subtropical Front), SAF (Subantarctic Front), PF (Polar Front), and SACCF (Southern Antarctic Circumpolar Current Front).
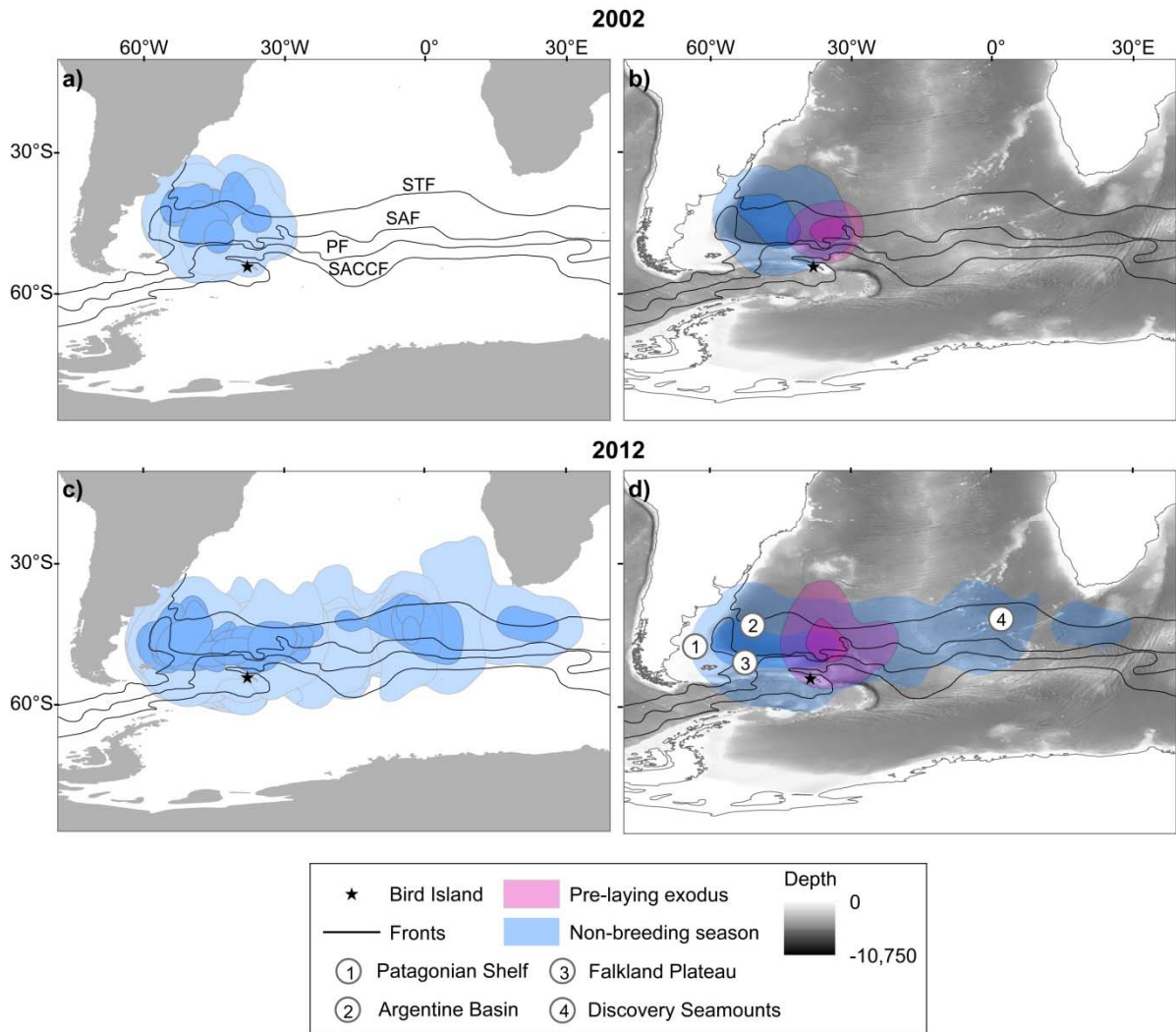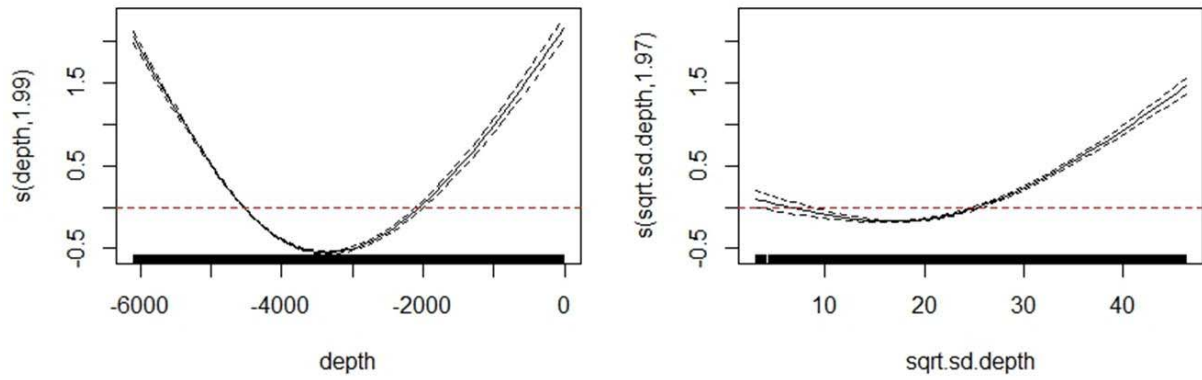
876 Fig. 2: Response curves of predictors retained in the most parsimonious habitat model for
877 brown skuas during the non-breeding period. Dashed lines indicate estimated 95 %
878 confidence intervals, with covariate values as a rug along the bottom of the figure.
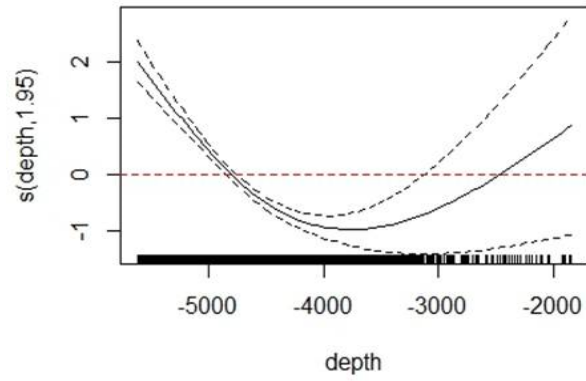

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Fig. 3: Response curves of predictors retained in the most parsimonious habitat model for

894   brown skuas during the pre-laying exodus. Dashed lines indicate estimated 95 % confidence

895   intervals, with covariate values as a rug along the bottom of the figure.

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Supplement 1

Effects of different numbers of correlated random walks (CRWs) on model performance. Number of simulations was tested by running global models with all observed locations and varying numbers of simulated pseudo-absences. The number of simulations was determined by measuring changes in x^2 values of each parameter, being set when x^2 stabilized. SST refers to sea surface temperature, SLA to sea level anomaly, and EKE to eddy kinetic energy.