

1 Environmental drivers of foraging behaviour during long-distance foraging trips of
2 male Antarctic fur seals

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9 Received 21 May 2021

10 Initial acceptance 24 September 2021

11 Final acceptance 25 October 2021

12 MS number 21-00317

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16 Animals may use long-distance foraging trips to capitalize on spatiotemporal variation
17 in food availability, allowing individuals to maximize resource gain from foraging
18 effort. This is particularly important for dimorphic species with polygynous mating
19 where males face strong selection pressures to attain large size and access to
20 reproductive females. We tracked 17 male Antarctic fur seals, *Arctocephalus gazella*,
21 during their prolonged postbreeding trips and assessed links between their movements
22 and environmental predictors of profitable feeding areas. Males made one of two types
23 of trips: a long trip to the Antarctic ice edge or shorter trips to areas where the southern

24 Antarctic Circumpolar Current fronts generate high biological activity. The trip type
25 was not determined by body size but was related to departure date from the breeding
26 area, suggesting that males must trade off opportunities at the breeding area
27 (reproductive, social interactions) and foraging opportunities between breeding
28 seasons. Regardless of trip structure, males focused search effort far from foraging
29 areas of central-place foraging seabirds and seals including female Antarctic fur seals
30 provisioning offspring. Males showed clear spatiotemporal patterns in dive behaviour,
31 with deep dives in shelf waters during the day and predominantly shallower dives in
32 pelagic waters at night. Diel dive patterns showed monthly changes in photoperiod and
33 lunar phase, consistent with feeding on vertically migrating prey. However, males did
34 not use area-restricted search to focus dive effort, instead performing a mix of foraging
35 and nonforaging behaviour within and between restricted search areas. We discuss the
36 scale and type of inference that can be made from movement models, given the
37 behavioural constraints that govern long-distance trips in vast, heterogeneous
38 environments like the Southern Ocean.

39 Keywords

40 Antarctic Circumpolar Current, area-restricted search, biologging, competition, dive
41 behaviour, sea-ice, spatial heterogeneity

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44 Long-distance movements for foraging, dispersing or migrating are ubiquitous
45 throughout the animal kingdom and key for many ecological and evolutionary
46 processes (Bowler & Benton, 2005). The causes and consequences can be examined by
47 investigating animals before and after the movements (Liedvogel et al., 2013) but

48 advances in animal telemetry now allow researchers to record the movements and
49 behaviour of animals throughout their long-distance trips; this has been pivotal for our
50 understanding of the mechanisms that drive this behaviour (Ropert-Coudert & Wilson,
51 2005). Seasonal, long-distance movements are often an adaptation to capitalize on
52 spatiotemporal variation in resource availability (Alerstam et al., 2003). Intraspecies
53 variation is common, and may be explained by intrinsic factors such as age, sex, body
54 size, personality, constraints imposed by physiological ability, reproductive roles and
55 energy requirements (Alerstam et al., 2003) or by intrinsic individual differences
56 (Patrick et al., 2014). However, characterizing the movements of predators and linking
57 them to resource availability remains difficult due to a limited capacity for directly
58 observing both the predator's foraging behaviour and the prey's distribution in the wild,
59 particularly for long-distance movements across vast ocean expanses.

60 Oceanic food resources are distributed heterogeneously in space and time (Nakata et
61 al., 2004) and consequently animals may cover great distances to satisfy their energy
62 needs (Block et al., 2011; Sequeira et al., 2018). Marine predators often consume prey
63 at depth, making it particularly difficult to observe and quantify their foraging
64 behaviour at sea (Kuhn & Costa, 2006). Foraging theory predicts that animals should
65 increase their search effort in areas where resources are abundant (MacArthur & Pianka,
66 1966), depending on predation risk and nutrient requirements (Pyke et al., 1977). It also
67 predicts that animals should continue to search within profitable areas until the capture
68 rate in the foraging patch falls to the average rate for the habitat (Charnov, 1976). While
69 identifying these search type movement patterns in tracking data can be challenging
70 (Turchin, 1998), analytical methods can distinguish movements that are slow and
71 sinuous, indicative of area-restricted search (ARS; or a resident state), from faster and
72 more linear movements (i.e. a directed state) along an animal's foraging path

73 (Barraquand & Benhamou, 2008; Jonsen et al., 2005; Pinaud, 2008). ARS by marine
74 predators often coincides with environmental features that stimulate biological activity,
75 such as upwellings, currents and frontal systems (Block et al., 2011). It has also been
76 linked to periods of intense feeding behaviour (Weimerskirch et al., 2007), suggesting
77 that ARS may provide an indication of profitable feeding areas during movements at
78 sea. Subsequently, ARS analysis has been used to identify areas of ecological
79 importance (Hindell et al., 2011) important for conservation and management efforts
80 (Hays et al., 2019; Tancell et al., 2013). However, the inferences drawn from ARS
81 methods applied to two-dimensional horizontal movement can be limited for animals
82 that feed in dynamic, three-dimensional habitats (Bailleul et al., 2008; Bestley et al.,
83 2015).

84 In marine environments, spatiotemporal variability in resource distribution occurs in
85 horizontal and vertical space. The foraging strategies predators use to exploit these
86 dynamic resources can be inferred from changes in their movement behaviour recorded
87 using fine-scale sensors, such as dive recorders and accelerometers (Carroll et al., 2014;
88 Harcourt et al., 2000; Yoshino et al., 2020). These sensors have revealed how marine
89 predators allocate their time to different foraging (i.e. diving) and nonforaging (i.e. rest,
90 recovery and prey processing) behaviours throughout long-distance trips (Boyd, 1996;
91 Russell et al., 2015). However, to combine sensors that record vertical and horizontal
92 movement behaviour often requires a compromise between device size, battery
93 longevity and the need to recover the device to access the data (McIntyre, 2014;
94 Wilmers et al., 2015). Consequently, assessments of vertical and horizontal movement
95 behaviour have been limited to certain taxa and are often difficult to achieve throughout
96 long-distance trips.

97 Long-distance trips are common among pinnipeds when unconstrained to a terrestrial
98 site for breeding or moulting; this is particularly the case for males after their summer
99 breeding period, when females are solely responsible for parental care (Boyd et al.,
100 1998; Hückstädt et al., 2014; Salton et al., 2021; Salton et al., 2019). Males in sexually
101 dimorphic, polygynous species, like otariids (fur seals and sea lions; Weckerly, 1998),
102 are under high selection pressure to reach a large size so they can acquire and maintain
103 access to breeding territory, and so might be particularly likely to need to find the most
104 productive foraging areas (Lindenfors et al., 2002). Indeed, it is well known that male
105 otariids make lengthy trips at sea (Baylis et al., 2018; Boyd et al., 1998; Campagna et
106 al., 2001; Lowther et al., 2013; Page et al., 2006; Salton et al., 2019; Weise et al., 2010)
107 to recover condition from fasting when ashore and to acquire resources for growth and
108 reproduction. While the movements of male otariids are well studied, how long-
109 distance movement patterns relate to individual factors such as body size or how
110 environmental variation is linked to profitable feeding habitat remains unclear.

111 This study investigated the long-distance movements of male Antarctic fur seals,
112 *Arctocephalus gazella*, a sexually dimorphic and polygynous pinniped. Male Antarctic
113 fur seals establish and defend breeding territories during October to December; while
114 this gives them access to females to mate with it means they must fast (McCann, 1980),
115 losing weight at up to 1.5 kg/day (Boyd & Duck, 1991), and risk lethal injuries (Baker
116 & McCann, 1989). Most pups (90%) are born between 29 November and 25 December,
117 but as late as 8 January (Page et al., 2003), and females come into oestrus and are mated
118 7 days postpartum (Duck, 1990). After breeding, male Antarctic fur seals spend most
119 of their time at sea (Doidge et al., 1986) and can disperse widely to areas far from their
120 sub-Antarctic breeding sites, presumably to access higher quality feeding areas. At this
121 time, their foraging locations are segregated from those of lactating females (which

122 remain close to the breeding site), perhaps due to local depletion of food by females or
123 because males can forage more successfully in more distant regions (Boyd et al., 1994).
124 In East Antarctica, males on long-distance trips use distant, productive ice edge habitat
125 (Patterson et al., 2016; Raymond et al., 2015) as well as open water (Bestley et al.,
126 2015), yet the drivers behind intraspecific variation in the use of these habitats (e.g. age,
127 body size, reproductive status) are unknown. Male Antarctic fur seals are known to
128 adopt ARS behaviour and rest while at sea (Bestley et al., 2016; Bestley et al., 2015),
129 but how ARS behaviour relates to the spatiotemporal distribution of resources is
130 unknown. There is less information on their dive behaviour postbreeding, but they
131 appear to undertake a combination of deep and shallow dives, depending on habitat
132 (Green, 1997; Lowther et al., 2020).

133 The objectives of this study were to (1) characterize the behaviour of male Antarctic
134 fur seals during their long-distance, postbreeding trips and identify drivers of individual
135 variation (e.g. body size, date of departure from the breeding site); (2) determine
136 whether their ARS behaviour is consistent with targeting profitable feeding areas, as
137 indicated by key environmental parameters (e.g. frontal zones and different ice habitat);
138 and (3) establish whether dive behaviour is related to spatiotemporal patterns in
139 environmental features that drive prey availability (habitat and diel changes in light).
140 Following foraging theory, we expected ARS and dives to be more frequent while seals
141 were away from our study site (Heard Island), as close to the island intra- and
142 interspecies competition is likely to be high in the mid to late austral summer because
143 of the many seabirds and seals foraging close to the breeding area on similar prey
144 (Green et al., 1998; Hindell et al., 2011; Patterson et al., 2016; Woehler & Green, 1992).
145 We also expected ARS and dives to be more frequent in habitats with abundant prey,
146 such as the ice edge, where melting sea ice releases ice algae and allows increased light

147 penetration, enhancing primary productivity and biological activity (Brierley &
148 Thomas, 2002), particularly in January–February when light levels and ice melt rate are
149 favourable for phytoplankton (Arrigo et al., 2008). Moreover, we expected variation in
150 dive depth to closely align with diel changes in solar illumination and lunar phase, as
151 light levels map diel vertical movements of dominant Southern Ocean prey for marine
152 predators (Bost et al., 2002; Croxall et al., 1985; Duhamel et al., 2000).

153 <H1>METHODS

154 <H2>*Tag Deployment*

155 We used telemetry data collected from 17 male Antarctic fur seals that were captured
156 and sedated while hauled out at Heard Island (53° 10' S, 73° 30' E) between 18
157 December 2003 and 14 January 2004 (for further details see Ethical Note and Frydman
158 & Gales, 2007). The males were likely to have been breeders (or at least competitors of
159 territory) given their proximity to the breeding area, their body size and the timing of
160 capture which was prior to the arrival of itinerant males (Boyd & Duck, 1991; Page et
161 al., 2003). Males were weighed with a spring balance (200 ± 0.1 kg, Salter Australia
162 Ltd, Rowville, Victoria, Australia) and their standard body length (nose to tail) was
163 measured (±1 cm) before either a satellite relay data logger (SRDL, $N = 5$; Sea Mammal
164 Research Unit, University of St Andrews, St Andrews, U.K.) or a Kiwisat ($N = 12$;
165 Sirtrack Ltd, Havelock North, New Zealand) tag was attached (see Ethical Note for
166 further capture and handling details). Data were collected until the battery of the tag
167 failed or the tag fell off, which was between 31 and 183 days (see Appendix Table A1
168 for details).

169 The SRDL and Kiwisat tags collected location information via the ARGOS system
170 (CLS, Saint-Agne, France). Location data were obtained at irregular time intervals
171 (median interval of 30 min) and included Argos location estimates of classes 3, 2, 1, 0,
172 A and B (with decrease degree of location accuracy, Argos, 1989). The SRDL tags also
173 had pressure and salinity sensors, with onboard data processing, and were used to
174 transmit a summary of data on three categorized behaviours: diving (>5 m depth),
175 cruising (<5 m depth and no dives for 5 min) and hauled out (dry for 10 min),
176 summarized as percentages of time within 6 h periods (Fedak et al., 2002). Cruising
177 may encompass multiple behaviours such as travelling and resting at the surface. The
178 SRDL tags also transmitted an optimized and unbiased sample of individual dive
179 records (Bestley et al., 2015; Fedak et al., 2002). These records included information
180 on dive characteristics, such as maximum dive depth (m) and dive duration (s). A third
181 dive characteristic, ‘dive residuals’, was derived from the other two characteristics (i.e.
182 residuals from a linear model of duration relative to depth), and used to identify
183 relatively long-duration dives for a given depth (i.e. relatively higher effort; following
184 Bestley et al. 2015).

185 <H2>*Postbreeding Trip Characteristics*

186 To address our first objective and characterize the behaviour of male Antarctic fur seals
187 during their long-distance, postbreeding trips, the location data were interrogated and
188 processed. Investigating the time at sea showed some males made local trips around
189 Heard and Kerguelen Islands (collectively referred to as the ‘breeding area’) before
190 they undertook clear movements away from the breeding area, off the Kerguelen
191 Plateau and towards the Antarctic continent (the postbreeding trip). Only postbreeding
192 trips were analysed. Trip start time was identified from the last location recorded on
193 land before a trip was initiated. The end time was the time of the first on-land location

194 recorded when the seal returned to the breeding area (a ‘complete trip’; mean \pm SD: 89
195 \pm 56 days, $N = 11$ individuals), or the time of the last location transmitted at sea for that
196 seal. Individuals started their postbreeding trips 1–49 days after tag deployment (mean
197 \pm SD: 16 ± 13 d, $N = 17$ individuals; Appendix Table A1) with trips initiated between
198 29 December 2003 and 5 February 2004.

199 A hierarchical switching state-space model (SSSM) was used to predict the most likely
200 movement path and associated behavioural states from the error-prone Argos locations
201 (Bestley et al., 2015; Breed et al., 2009). This model estimates locations at a specified,
202 regular time step and also the probability of being in one of two unobserved movement
203 states: faster, linear movements (‘directed’) and slower, more sinuous movements
204 (‘resident’), which we refer to as residence probabilities (Jonsen et al., 2005). The
205 SSSM was implemented as described by Bestley et al. (2015) with a 3 h time step, and
206 individual tracks were processed in batches based on similar trip duration and
207 formation. The SSSM was fitted using the software package WINBUGS (freely
208 available online: [https://www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-](https://www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-winbugs)
209 [winbugs](https://www.mrc-bsu.cam.ac.uk/software/bugs/the-bugs-project-winbugs)). We used the diagnostics outlined by Bestley et al. (2015) to assess the
210 goodness-of-fit.

211 The SSSM location estimates were used to calculate four parameters that summarized
212 each male’s postbreeding trip: maximum distance from Heard Island (Great Circle
213 distance using trip R package v1.1-17; Sumner, 2013), total distance travelled during a
214 trip, trip duration and minimum latitude (i.e. furthest south). It was not possible to
215 accurately calculate the four parameters when tags ceased transmitting at sea, and we
216 therefore only used males that made a complete trip ($N = 11$) in the following grouping
217 analysis. Based on these parameters, individuals were grouped using a classification
218 tree (binary recursive partitioning model) using the tree R package v1.0-35 (Ripley,

219 2014). This identified that while all males moved in a southerly direction, their trips
220 could be categorized into two types based on whether they crossed 65.65°S: either a
221 long postbreeding trip ('long trip') or a short postbreeding trip ('short trip'). This
222 information was used to categorize incomplete trips. Two-sample *t* tests were then
223 applied to assess whether body mass, body length, body condition (mass adjusted for
224 length, kg/m, Arnould, 1995) and trip start date differed between males that made long
225 versus short trips.

226 <H2>*Spatial Predictors of ARS Behaviour*

227 To assess our second objective and determine whether ARS patterns were consistent
228 with targeting profitable feeding areas, we investigated competition and biological
229 activity as potential drivers of ARS behaviour. The distance a male travelled from
230 Heard Island was deemed an indicator of competition avoidance (Kuhn et al., 2014;
231 Weber et al., 2021).

232 To estimate the relative importance of biological activity, nine habitats were defined
233 based on environmental features known to influence biological activity (Bestley et al.,
234 2020; Moore & Abbott, 2000). 'Shelf' habitat defined locations over the shallow
235 section of the Kerguelen Plateau (0–500 m) using bathymetry from GEBCO (global 30
236 arc-second grid, GEBCO 2014). Beyond the shelf, locations were categorized
237 according to frontal zones identified by Sokolov and Rintoul (2009) extracted at a daily
238 resolution using raadtools v0.3.1.9001 (Sumner, 2014). These frontal zones were Polar
239 Front (north: 'PF_N'; middle: 'PF_M'; south 'PF_S'), Southern Antarctic Circumpolar
240 Current Front (north: 'SACCF_N'; south: 'SACCF_S') and Southern Boundary
241 Current ('SB'). The 'ice' habitat was defined from daily sea ice concentration and the
242 approximate ice edge (15% concentration) derived from Nimbus-7 SMMR and DMSP

243 SSM/I-SSMIS Passive Microwave Data (Cavalieri et al., 2015). Locations were
244 allocated within ice habitat if the ice concentration was greater than zero, the location
245 was south of the ice edge or less than 50 km from the ice edge (to account for the
246 spatiotemporal accuracy of the ice and seal data). This classification should encapsulate
247 locations where the dominant driving force of biological activity is the ice. Some
248 locations were not assigned to a habitat: they typically occurred between the southern
249 extent of the Sokolov and Rintoul (2009) frontal zones and the ice habitat. We expected
250 these locations to have a similar biological distribution to the Southern Boundary
251 Current and defined them as ‘SB/near-ice’. For the SRDL tags, we could identify when
252 seals were hauled out on ice. Therefore, for the analysis of dive data from SRDL tags
253 (see Spatiotemporal predictors of diving) we divided ice habitat into two categories: ice
254 habitat where males were known to have hauled out (Ice_Haul) and were known not to
255 have hauled out (Ice_NoHaul).

256 Dynamic air–sea physical processes that affect ice concentration, distribution and decay
257 subsequently influence biological activity within ice habitat (Brierley & Thomas, 2002;
258 Smith Jr, 1987). We therefore conducted a separate analysis specifically for males in
259 ice habitat that assessed whether within-ice habitat dynamics might explain changes in
260 movement state while males were within the vicinity of the ice. Four variables were
261 derived from the product of sea ice concentration and ice edge (outlined above) and
262 used to predict the movement state of the males when they were south of 62°S: distance
263 to ice edge (km), ice concentration (log transformed), time since the ice melted (days)
264 and ice melt rate (calculated as a north-to-south first difference from the time-since-
265 melt raster, providing a spatial gradient in the rate of ice retreat; Andrews-Goff et al.,
266 2018).

267 Generalized additive mixed models (GAMM; Wood 2006) were used to assess whether
268 the probability of animals being in a resident state was explained by each of these
269 drivers independently: distance from Heard Island (continuous variable), habitat
270 (factor) and features of the ice environment (continuous). The continuous variables
271 were fitted as smoothing functions to account for expected nonlinear trends. To account
272 for repeated measures, all models were fitted with individual as a random effect
273 (intercept only, to elevate convergence issues with the modes) including an AR1
274 autoregressive correlation structure nested within individual to account for the serial
275 time dependence. These residence probability models were fitted with a binomial error
276 distribution and a logit link function, implemented using the mgcv R package v1.7.28
277 (Wood, 2011). All model selection and parameter inference approaches are described
278 at the end of the Methods.

279 ARS behaviour may also be associated with seal behaviours other than foraging.
280 Antarctic fur seals are known to spend periods hauled out on ice (Ribic et al., 1991) and
281 it is likely that, like other fur seals, they also spend prolonged periods at sea at the
282 water's surface, either resting or digesting prey (Bestley et al., 2016; Ladds et al., 2018).
283 To assess whether these behaviours influence ARS probabilities, the duration of two
284 SRDL data summary behaviours, cruising and hauled out, were calculated within
285 directed and resident states for each habitat. Each 6 h period with behavioural data was
286 assigned a location estimate from the SSSM using the middle time step of the 6 h period.
287 If a seal was hauled out away from the breeding area, the duration of the period hauled
288 out was quantified by summing the number of consecutive 6 h periods with 100% time
289 spent hauled out. Any nonconsecutive periods spent hauled out were excluded, such
290 that these calculations are minimum estimates. Similarly, the duration of 6 h summaries
291 that had consecutive 100% cruise time were calculated.

292 <H2>*Spatiotemporal Predictors of Diving*

293 Our third objective was to establish whether seal dive behaviour was related to
294 spatiotemporal patterns in environmental features that drive prey availability. Only the
295 SRDL tags ($N = 5$ individuals) collected dive data. Associating the three dive
296 characteristics (dive depth; dive duration; dive residuals) with profitable foraging areas
297 required estimating the dive location. This was achieved by cross-referencing the time
298 a dive occurred with the times of the estimated SSSM locations and, where necessary,
299 applying a linear interpolation between locations. To test the effect of habitat on the
300 dive characteristics, six linear mixed models (LMM) were fitted using the nlme R
301 package v3.1-108 (Pinheiro et al., 2013) to assess whether each of the three dive
302 characteristics varied among habitat types, separately for directed and resident
303 movement states. Dive depth and duration were log transformed to normalize the
304 residuals and the estimates were presented back transformed to their original units. All
305 models included individual as random effect (intercept only, to elevate convergence
306 issues with the models) to account for repeated measure of dives per male ($N = 5$
307 individuals).

308 We also examined changes in light levels that are likely to influence diurnal movement
309 of prey. We assessed whether dive frequency ($N = 5$ SRDL tags only) differed with diel
310 light levels by using solar position at a seal's location as a proxy for solar illumination.
311 Solar position (continuous variable) is calculated using solar azimuth and elevation
312 based on location, local date and time (Indian/Kerguelen time zone: UTC +5 h), using
313 the mapproj R package v0.8-29 (Bivand & Lewin-Koh, 2014). From solar position, a
314 categorical variable for diel period was defined with four levels: positive values of solar
315 elevation angle identified 'day'; values between zero and -12 deg below the horizon
316 identified nautical twilight ('dusk' from 0 to -12 and 'dawn' from -12 to 0); and values

317 below -12 deg identified ‘night’. The length of diel periods dramatically changes from
318 summer to winter and not all SRDL tags transmitted data into the austral winter months
319 (some tags fell off earlier than others). Therefore, to assess changes in dive frequency
320 we included a variable for month and used only a subset of the data, from January to
321 March, where dives were recorded for all seals with SRDL tags. To investigate lunar
322 phase effects on the diel pattern we calculated a categorical predictor for lunar phase.
323 Lunar phase is based on the fraction of the moon illuminated, as defined in equation
324 32.2 of Meeus (1982). The fractional part illuminated was calculated based on location
325 and local time using the `oce` R package v0.9-13. (Kelley, 2014). These values were
326 categorized into lunar phases using even sampling intervals centred on the fractional
327 part that defines each lunar phase. Therefore, values 0.875 to 1 and 0 to 0.125 were
328 categorized as ‘new’, 0.125 to 0.375 as ‘waxing’, 0.375 to 0.625 as ‘full’ and 0.625 to
329 0.875 as ‘waning’.

330 We tested for temporal change in both dive frequency and dive behaviour using diel
331 periods and solar position, respectively. The categorical predictors for month and lunar
332 phase were incorporated into models as interaction terms. Dive frequency was the
333 number of dives recorded for an individual within each of the categorized diel periods
334 (four-level factor) within a given month (three-level factor) or lunar phase (four-level
335 factor). Generalized linear mixed models (GLMMs) were fitted to these dive frequency
336 models using the `lme4` R package v0.999999.0 (Bates et al., 2012) with a random effect
337 for individual (intercept only, to elevate convergence issues with the models) and a
338 Poisson error distribution with a log link function. An offset was included in the model
339 that accounted for the average duration of the diel period for an individual within each
340 month or moon phase (i.e. longer days during high summer months). Dive
341 characteristics were tested against predictor variables of solar illumination (continuous)

342 and its interaction with lunar phase (four-level factor) using LMMs. Dive depth and
343 duration were log transformed to normalize the residual errors and the estimates were
344 presented back transformed to their original units. These LMMs also included
345 individual male as the random effect (intercept only, to elevate convergence issues with
346 the models).

347 <H2>*Model Selection and Parameter Inference*

348 For GAMMs examining residence probabilities, a separate model was fitted for each of
349 the three sets of predictor variables (distance to Heard Island, habitat and features of
350 the ice environment). Inference about whether or not the predictor(s) was informative
351 was based on P values that were calculated using the Bayesian estimated covariance
352 matrix of the parameter estimates (Wood, 2011).

353 The LMMs and the GLMMs (dive frequency) were initially fitted with maximum-
354 likelihood estimation and Akaike's information criterion (AIC) was used to compare
355 the full model with each reduced model (e.g. without the interaction term and
356 competing fixed effects), including the null (no fixed effects; Zuur et al., 2009).
357 Inference about the suitability of models was drawn from the differences in AIC relative
358 to the model with the lowest AIC (i.e. ΔAIC). The best model had the lowest AIC and
359 highest Akaike weight (w_i). Factor level comparisons were based on modelled estimates
360 and associated P values that were calculated using restricted maximum likelihood, to
361 correct for biases in the estimates (Zuur et al., 2009).

362 Models that included habitat as a predictor and movement state (response or predictor)
363 were fitted to a subset of the data: exclusively movements within habitats in which more
364 than one male adopted a resident movement state. The subset was necessary to allow
365 model convergence. Given that distinct trip structures were observed (i.e. long and short

366 trips), it was also important to account for biases in habitat use among males with
367 different trip structures (i.e. some males did not use ice habitat). To do this, separate
368 models were implemented for males that adopted the two different trip structures,
369 including a separate model for males that made second postbreeding trips. This
370 accounted for the different males being only able to use certain habitats, and distinct
371 temporal changes in the spatial distribution of habitats due to the seasonal advance of
372 the sea ice. This method was chosen over the use of interactions because we were
373 ultimately interested in how the response variable differed between the habitats. A
374 slight modification of this approach was required when we assessed habitat effects on
375 dive behaviour: there were too few individuals with dive data to fit separate models for
376 males with different trip structures. The test statistics represent differences in habitat
377 levels relative to a reference habitat level, which we specified as the most northern
378 habitat where both movement states were recorded: the northern extension of the
379 southern Antarctic Circumpolar Current front (SACCF).

380 All analyses were conducted in R v2.15.1 (R Development Core Team, 2012). All
381 parameter estimates are reported as back-transformed estimates to the original units
382 along with their standard errors. The parameter test statistics and log-ratio tests were
383 considered significant at $P < 0.05$.

384 <H2>*Ethical Note*

385 The 17 male Antarctic fur seals were captured while hauled out on Heard Island. Each
386 seal was approached as it rested and was netted with a handheld hoop net (Furhman
387 Diversified Inc, Seabrook, TX, U.S.A.), after which three people physically restrained
388 the animal by holding the pectoral flippers to the side of the body and the head and neck
389 to the ground. The net was designed with a hole at the apex large enough to allow the

390 snout to protrude for unimpeded breathing and enable mask induction of gas
391 anaesthetic, while keeping the eyes covered with sufficient net material to block the
392 vision of the animal. Isoflurane and oxygen were delivered through a mask connected
393 to a vaporizer (Isotec III, Ohmeda Ltd, Hatfield, U.K.) and Bain nonrebreathing circuit
394 in a similar system to that described by Gales et al. (2005). Isoflurane anaesthesia was
395 maintained using the mask delivery system, during which time the tag was glued
396 (Araldite 2017 epoxy adhesive, Araldite, Basel, Switzerland) to the mid-dorsal pelage
397 between the scapulae, and standard body measurements were recorded (Committee on
398 Marine Mammals, 1967). The devices weighed <700 g and were equivalent to <1% of
399 the seal's weight and < 1% of adult seals' body cross-section, making them unlikely to
400 significantly adversely affect swimming and diving (Skinner et al., 2012). Once the
401 glue became reasonably set (5–10 min) the anaesthesia ceased, and the animals were
402 released and observed during recovery. All animal handling procedures were approved
403 and carried out under the guidelines of the University of Tasmania Animal Ethics
404 Committee and the Australian Antarctic Animal Ethics Committee.

405 <H1>RESULTS

406 <H2>*Characteristics of Postbreeding Trips*

407 Eight males made long and nine made short postbreeding trips from Heard Island
408 (Appendix Table A1). Complete long trips ($N = 4$) lasted 157 ± 25 days during which
409 time males spent 29–55% of their time associated with the ice (Fig. 1a). Males on long
410 trips typically returned to the breeding area mid-year (mean \pm SD = 9 June \pm 27 days,
411 $N = 4$ trips). In contrast, short trips ($N = 7$) lasted 50 ± 6 days and did not reach the ice;
412 the males returned to the breeding area around 3 months earlier (mean \pm SD = 10 March
413 \pm 10 days, $N = 7$ trips; Fig. 1b). Some males that made a short trip were recorded

414 undertaking a second short trip, after a period hauled out at Heard Island (mean \pm SD
415 = 18 ± 4 days hauled out, $N = 4$ trips), when they again moved south to comparable
416 latitudes (by which time the ice had advanced north) and adopted resident states in ice
417 habitat (Fig. 1c).

418 Whether a male made a long or short trip was not associated with body mass, body
419 length or body condition (i.e. mass/length; Appendix Table A2). However, the males
420 that made a long trip departed the breeding area earlier (mean \pm SD = 6 January \pm 9
421 days, $N = 8$ individuals) than those that made a short trip (mean \pm SD = 20 January \pm 8
422 days, $N = 9$ individuals; Appendix Table A1). Long trips reached a greater maximum
423 distance from Heard Island, entailed a longer time at sea and traversed greater total
424 distances compared to short trips (Appendix Table A1). Males alternated between
425 directed and resident states throughout postbreeding trips. All males displayed lengthy
426 directed periods at the start and end (for complete trips) of the trip, and with more
427 resident states at the southern extent (Fig. 2). Consequently, males on long trips spent
428 a greater proportion of time in a resident state than those on short trips (Appendix Table
429 A1).

430 <H2>*Spatial Predictors of ARS Behaviour*

431 Males rarely entered a resident state during the initial traverse away from the breeding
432 area or in the return phase of their trip (i.e. through the Kerguelen shelf habitat and
433 polar frontal zones; Fig. 2). Residence probabilities were strongly positively related to
434 distance travelled from Heard Island (GAMM: $P < 0.001$; Table 1, Model 1) and
435 influenced by habitat type, but were dependent on the type of trip (i.e. long versus short;
436 Table 1, Models 2.1, 2.2 and 2.3).

437 Males on long trips had high residence probabilities in Southern Boundary/near-ice
 438 habitat and ice habitat (59–60%), and similar probabilities in other habitats (38–41%;
 439 Table 1, Model 2.1). Males on long trips adopted at least one resident state prior to
 440 reaching the ice, and all arrived at the ice by 8 February (mean \pm SD = 27 ± 2 days after
 441 departing the breeding area, $N = 8$ individuals). Males on short trips also had a higher
 442 residence probability in their southernmost habitat (SB/near-ice 68%), and similar
 443 probabilities in other habitats (47–50%; Table 1, Model 2.2). However, later in the
 444 season once the ice had advanced north, the four individuals that made a second short
 445 trip had equivalent residence probabilities in all habitats south of the polar front (47–
 446 50%; Table 1, Model 2.3; Fig. 2). For all males that used ice habitat ($N = 12$
 447 individuals), none of the sea ice features examined (distance to ice, ice concentration,
 448 time since ice melt or ice melt rate) explained variation in residence probabilities
 449 (GAMM: $|T| < -0.48$, $|P| > 0.07$; Table 1, Model 3).

450 During postbreeding trips, males with SRDL tags ($N = 5$ individuals) dived during both
 451 resident and directed states (Appendix Table A2) but overall spent relatively little time
 452 diving (13–22%) and more time cruising (55–88%) or hauled out (11–47%). Two of
 453 the SRDL-tagged males made long trips and recorded periods hauled out while in ice
 454 habitat, for up to 2 days at a time (Fig. 2, Appendix Table A2). These short periods
 455 hauled out in the ice habitat occurred during directed and resident states.

456 <H2>*Spatiotemporal Predictors of Diving*

457 A total of 16 317 dives were recorded for males with SRDL tags and the dive
 458 characteristics varied among habitats. Males were capable of diving down to 232 m and
 459 for up to 12.3 min, but most dives were within the upper 40 m of the water column
 460 (mean \pm SD: $89 \pm 4\%$ of an individual's dives, $N = 5$ individuals) and lasted less than

461 2 min (mean \pm SD: $85 \pm 3\%$ of an individual's dives, $N = 5$ individuals). The deepest
462 dives (i.e. >200 m, $N = 10$ dives) all occurred in shelf habitat (i.e. close to the sea floor),
463 and while in shelf habitat few dives were <40 m ($N = 2$ of 49 dives in shelf habitat).
464 Only 268 dives were recorded in the Polar Frontal zones and most of these dives were
465 in the top 40 m ($N = 172$ dives; 64%). South of the Polar Front, dives were
466 predominantly within the upper 40 m of the water column ($N = 14\,397$ of 16 000 dives;
467 90%). Variation in dive depth and duration among habitats south of the Polar Front was
468 notably small, particularly during resident states (Appendix Table A3). Both positive
469 and negative dive residuals occurred south of the Polar Front, with significantly
470 negative residuals (i.e. shorter dive durations than expected for a given depth) within
471 the Southern Boundary Current near ice habitat and ice habitat without periods hauled
472 out (Appendix Table A3).

473 Dives occurred on almost all days of postbreeding trips (80–100% of days per
474 individual). Day length varied by month from January to March (depending on location;
475 mean \pm SD: 17 ± 0.5 h to 14 ± 0.7 h, respectively). Accordingly, the number of hours
476 during night, dusk and dawn increased from January to March, at which time most dives
477 were recorded at high latitudes near the ice. Dives consistently occurred during the
478 darkest part of the 24 h cycle, regardless of the month (GLMM, significant interaction,
479 Δ AIC -322.51; Table 2, Fig. 3). In January, dives were more likely to occur during
480 dawn and dusk, and, despite the short night, were more likely to occur at night than
481 during the day (mean \pm SD: dawn: 21.8 ± 0.1 dives/h; dusk: 26.7 ± 0.1 dives/h; night:
482 9.1 ± 0.1 dives/h; day: 4.2 ± 0.4 dives/h). By March, the frequency of dives was greatest
483 during the night and dusk, with fewer occurring during dawn and daytime (mean \pm SD
484 night: 19.9 ± 0.1 dives/h; dusk: 19.0 ± 0.2 dives/h; dawn: 8.0 ± 0.2 dives/h; day: $1.7 \pm$
485 0.2 dives/h).

486 The frequency of dives in different diel periods was dependent on lunar phase (GLMM,
487 significant interaction, $\Delta\text{AIC} -142.18$). Night dives were least frequent under a full
488 moon compared with any other lunar phase (mean \pm SD: full: 16 ± 0.1 dives/h; new: 41
489 ± 0.1 dives/h; waxing: 39 ± 0.1 dives/h; waning: 33 ± 0.1 dives/h). In addition, all three
490 dive characteristics (dive depth, dive duration and dive residuals) were influenced by
491 solar illumination and this relationship was dependent on lunar phase. Dives were
492 deeper and longer at higher light values, consistent with the deepest dives occurring
493 during daylight (78% of dives deeper than 100 m occurred during the day and 18% at
494 dawn, $N = 45$ dives). There was a significant lunar phase influence on night diving
495 (Table 3). At low values of solar illumination, night dives were shallower, and they
496 lasted longer under a new moon than under a full moon (dive depth: new moon intercept
497 = 2.88, slope = 0.01; full moon, intercept = 2.85, slope = 0.006; dive duration: new
498 moon, intercept = 3.96, slope = 0.004; full moon, intercept = 3.98, slope = 0.007). Under
499 a new moon, night dive residuals were also more likely to be positive (i.e. greater
500 duration for a given depth; dive residuals: new moon, intercept = -0.02, slope = -0.01;
501 full moon, intercept = 0.09, slope = 0.01).

502 <H1>DISCUSSION

503 The foraging behaviour of postbreeding male Antarctic fur seals is not constrained by
504 offspring provisioning which frees them to undertake long-distance trips to highly
505 productive feeding habitats. Tracked male Antarctic fur seals showed two distinct trip
506 types, either a long trip south to the marginal ice zone or short trip(s) within oceanic
507 waters. Trip type was related to departure date but not to body size. Resident states were
508 more likely to occur away from the breeding area and within habitats at the southern
509 extent in ice habitat during long trips and in southern Antarctic Circumpolar Current

510 front habitat during short trips. Dive behaviour varied among habitats and followed a
511 diel pattern amplified by changes in solar and lunar light. These findings suggest that
512 date of departure from the breeding ground has consequences for postbreeding habitat
513 use, including dive behaviour, and that during the postbreeding period these males
514 forage for prey whose behaviour is influenced by solar and lunar illumination.

515 The two trip types offered different foraging opportunities. Long trips to ice habitat are
516 consistent with animals targeting the highly productive marginal ice zone (Bailleul et
517 al., 2007; Bost et al., 2004; Labrousse et al., 2015; Lawton et al., 2008). Blooms at the
518 marginal ice zone can be several magnitudes more productive than blooms in open
519 water (Arrigo et al., 2008; Smith & Nelson, 1986) providing important feeding grounds
520 for marine predators (Ainley & DeMaster, 2013). We found significant negative dive
521 residuals in ice habitats suggesting relatively efficient prey encounters in that habitat.
522 Further north, where the Southern Boundary Current and Southern Antarctic
523 Circumpolar Current Front interact with the southern extent of the Kerguelen Plateau,
524 persistent phytoplankton blooms also occur (Schallenberg et al., 2018; Sokolov &
525 Rintoul, 2007). The productivity of these blooms can also be several magnitudes higher
526 than the surrounding waters (Sullivan et al., 1993), and there is evidence of other marine
527 predators including migratory humpback whales, *Megaptera novaeangliae* (Bestley et
528 al., 2019) foraging in this area. Notably though, short postbreeding trips of male
529 Antarctic fur seals included a relatively high proportion of directed state movement
530 behaviour. An earlier comparison between directed and resident states for these males
531 suggested that the directed state is more costly, in terms of horizontal and vertical
532 movement (Bestley et al., 2015), and may therefore result in a lower prey encounter
533 rate for males on short trips. This suggests that while both long and short trips provide
534 opportunities to feed in highly productive habitats, opportunity costs may differ

535 between trip types. For example, by remaining at the breeding area longer, males
536 undertaking short trips may have a lower prey encounter rate but gain other benefits
537 such as increased reproductive opportunities, see below.

538 Trip duration in some otariids has been associated with body size (Salton et al., 2019;
539 Weise et al., 2010), but this was not the case for Antarctic fur seals (this study),
540 Australian sea lions, *Neophoca cinerea* (Lowther et al., 2013) or New Zealand fur seals,
541 *Arctocephalus forsteri* (Page et al., 2006). Rather, the distinction between males making
542 a long or short trip arose from their departure date from the breeding area: seals that
543 made long trips departed earlier. Late departures may allow males to gain access to
544 receptive females that come into oestrus later in the breeding season (Page et al., 2003;
545 Shaughnessy & Goldsworthy, 1990), but it seems that by doing so these males cannot
546 reach the ice in time for the February peak of productivity at the marginal ice zone
547 (Arrigo et al. 2008). Instead, these individuals must concentrate feeding further north
548 in the food web supported by the bloom associated with the southern Kerguelen Plateau.
549 It seems males may make a trade-off between accessing foraging areas and other
550 opportunities gained from remaining closer to the breeding area (e.g. foraging,
551 reproductive, social).

552 The spatial distribution of ARS behaviour at sea is consistent with male seals passing
553 through areas of low profitability and focusing their effort on more productive foraging
554 areas. During the austral summer, seabirds and seals provisioning offspring on Heard
555 Island are largely constrained to foraging in local waters (Hindell et al., 2011). This
556 may lead to depletion of local resources (Ashmole, 1963; Birt et al., 1987; Kuhn et al.,
557 2014) and increase local foraging competition (Green et al., 1998; Hindell et al., 2011;
558 Woehler & Green, 1992). This could reduce the rate of energy return for fur seal males
559 foraging in local habitats, and from their behaviour it seems that it is more profitable

560 for them to forage in areas beyond the reach of most provisioning seals and seabirds.
561 The residence probabilities were highest in the southern extent of the Southern
562 Antarctic Circumpolar Current Front, the Southern Boundary Current and near the sea
563 ice. By focusing their search efforts in these productive areas, males may increase their
564 rate of energy return, help to restore condition lost while they fasted during breeding
565 (Boyd & Duck, 1991) and prepare for their annual moult (Page et al., 2003). Similar
566 long-distance foraging patterns are seen in other marine predators at Heard Island that
567 are not constrained to central-place foraging (Labrousse et al., 2015; Patterson et al.,
568 2016).

569 Although ice habitat appears important on a large scale, the specific ice environment
570 features we examined did not show any relationship with residence probabilities, which
571 could reflect processes that operate at different scales within a hierarchical patch system
572 (Fauchald, 1999). Foraging animals have been shown to adjust their behaviour in
573 response to hierarchical spatial distributions of food resources and environmental
574 factors (Benoit-Bird et al., 2013; Fritz et al., 2003; Weimerskirch et al., 2005). The
575 ability to distinguish a behavioural response at different hierarchical scales is limited
576 by the spatiotemporal precision at which animal foraging behaviour is measured (Fritz
577 et al., 2003). The location data used in this study have a resolution ranging from
578 hundreds of metres to several kilometres, which limits inferences about movement
579 behaviour (Hays et al., 2001). While the SSM approach used here can improve
580 inferences drawn from tracking data (Breed et al., 2012), the spatial resolution of our
581 approach seems best suited for detecting behavioural responses to regional scale
582 processes, and less adequate for within-region processes. Within-ice features at a larger
583 scale, such as polynyas, can be used to predict habitat use of male Antarctic fur seals
584 (Raymond et al., 2015). The within-ice features examined in this study, relating to sea

585 ice dynamics, influence biological processes at a relatively fine spatiotemporal scale:
586 perhaps as fine as tens of metres and hours (Massom & Stammerjohn, 2010).
587 Identifying behavioural responses of marine predators to these dynamic processes may
588 require movement measurements at a comparable scale, and ideally integration of the
589 dive behaviour, as shown for southern elephant seals, *Mirounga leonina* (Bailleul et al.,
590 2008; Labrousse et al., 2015), or finer-scale environmental features, as shown for
591 emperor penguins, *Aptenodytes forsteri* (Labrousse et al., 2019). This highlights the
592 importance of grounding inferences from movement data to comparable hierarchical
593 spatial scales of food resources and environmental factors.

594 Patterns of diving behaviour were consistent with seals capitalizing on spatiotemporal
595 variability in prey distributions throughout their wide-ranging postbreeding trips and
596 can provide information on targeted prey. Males made deeper dives over the shelf
597 during the day when photoperiod was longest (i.e. in summer) suggesting that they were
598 targeting benthopelagic prey, such as mackerel icefish, *Champsocephalus gunnari*,
599 which form deep shoals (100–250 m) at dawn and during the day (Frolkina, 2002), and
600 that was a dominant prey species found in Antarctic fur seal scats at Heard Island during
601 austral summer 1987–1988 (Green et al., 1989). As photoperiod decreased, and the
602 nights lengthened, seals moved into pelagic habitats and dived to shallow depths at
603 night. The longer duration dive for a given depth at night, particularly under a new
604 moon, also suggests that males invested more effort in their dives under low ambient
605 light levels. This diel pattern indicates feeding upon vertically migrating prey, such as
606 myctophids and krill (Boyd & Croxall, 1992; Croxall et al., 1985; Horning & Trillmich,
607 1999; Lea et al., 2002; Lea et al., 2009), which aggregate at shallow depths during
608 periods of low ambient light levels (Bost et al., 2002; Duhamel et al., 2000; Hays,
609 2003). For air-breathing marine vertebrates, shallow dives are more cost effective than

610 deeper dives (Butler & Jones, 1997). By foraging on shallow aggregations of prey,
611 particularly as photoperiod decreases, males are more likely to maximize their rate of
612 energy return and thereby restore condition lost during breeding (Boyd & Duck, 1991).

613 Although animal movement patterns are driven by the distribution of resource patches,
614 wide-ranging predators may forage opportunistically, and other factors can motivate
615 residency. To sustain directed movement between breeding and distant foraging areas,
616 wide-ranging predators like male Antarctic fur seals may need to feed opportunistically
617 while travelling. After reaching a profitable feeding area, marine predators will also
618 need to rest at some point, to recover from diving and process prey (Boyd, 1996; Russell
619 et al., 2015; Sparling et al., 2007; Weimerskirch & Guionnet, 2002). Ideally resting
620 behaviours should occur close to the foraging area, to minimize travel costs. Resting
621 could occur on the ice or at the surface of the water: the latter would be consistent with
622 the long cruise periods undertaken by males while in open-water habitat. Males may
623 also haul out on ice to evade predators such as killer whales, *Orcinus orca* (Pitman &
624 Durban, 2012; Ribic et al., 1991). The relatively short periods spent hauled out while
625 at the ice edge habitat is consistent with maximizing foraging time and/or primarily
626 resting in surface waters.

627 In conclusion, the large sexual size dimorphism and highly polygynous mating system
628 of otariids means males of these species are under strong selection pressures to attain
629 large size and sufficient energy storage to successfully retain a territory during
630 breeding. Consequently, these males must seek highly productive foraging areas
631 between breeding seasons to restore condition lost during breeding. Male Antarctic fur
632 seals appear to achieve this by avoiding areas with high competition for food resources
633 and focusing their foraging effort in areas of high biological activity further away. The
634 two types of postbreeding trips observed in this study may reflect males making a trade-

635 off between prime postbreeding foraging opportunities associated with sea ice and
636 reproductive opportunities gained by remaining in the breeding area after other males
637 leave.

638

639 **Author Contributions**

640 S.B., M.S., R.H. conceived and designed the study. N.G. provided historic tag data. S.B.
641 collated and pre-processed tracking and habitat data. M.S. & S.B. analysed data. M.S.
642 wrote the manuscript. R.H., S.B., N.G. provided useful comments on the organization
643 and the writing of the manuscript.

644 **Declaration of Interest**

645 None.

646 **Acknowledgments**

647 This project was funded through an Australian Antarctic Science project (ASAC Project
648 2388). M. Salton was supported by an Australian Postgraduate Award. S. Bestley was
649 supported by an Australia Research Council Super Science Fellowship (Project
650 FS110200057).

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1143 Appendix

1144

Long-distance trips of male Antarctic fur seals

1145 Table 1 Summary of generalized additive mixed models that assessed three types of
 1146 predictors of residence probabilities (pResident) for male Antarctic fur seals on postbreeding
 1147 trips from Heard Island

Model	Response (subset)	Predictor	Estimate (%) (SE)	<i>t/F</i>	<i>P</i>
1	pResident	Distance to HI	0.003 (0.0004)	69.99	<0.001
2.1	pResident (long trip)	[SACCF_N]	38 (22)	-2.15	0.03
		SACCF_S	41 (13)	0.94	0.35
		SB	41 (23)	0.46	0.64
		SB/near-ice	59 (19)	4.36	< 0.001
		Ice	60 (19)	4.65	< 0.001
2.2	pResident (short trip 1st)	[SACCF_N]	47 (23)	-0.58	0.56
		SACCF_S	48 (8)	0.47	0.64
		SB	50 (19)	0.74	0.46
		SB/near-ice	68 (34)	2.56	0.01
		Ice	NIL	NIL	NIL
2.3	pResident (short trip 2nd)	[SACCF_N]	54 (35)	0.49	0.62
		SACCF_S	49 (20)	-1.08	0.28
		SB	50 (27)	-0.68	0.49
		SB/near-ice	50 (29)	-0.64	0.52
		Ice	47 (26)	-1.08	0.28
3	pResident	[Intercept]	0.339	3.29	0.001
		Distance to ice	-0.351	-1.89	0.06
		Ice	0.071	1.47	0.14
		concentration			

Foraging behaviour during long-distance trips

Time since melt	-0.075	-1.25	0.21
Melt rate	-0.008	-0.48	0.63

1148 The first model tested the effect of a continuous variable for distance to Heard Island
1149 (HI). The second model tested a factor variable for habitat, with factor level
1150 comparisons to a reference level (SACCF_N; for habitat abbreviations see Fig. 1). The
1151 second model was fitted on three subsets of the data, based on trip structure: long trips;
1152 short trips 1st; short trips 2nd. The third model tested four continuous variables relating
1153 to features of the ice environment: distance to ice, ice concentration, time since the ice
1154 melted and ice melt rate. Each model was fitted with binomial errors and logit link, a
1155 random effect for individual male (to account for repeated measures), and an
1156 autoregressive correlation structure to account for serial dependence in the switching
1157 state-space model time series. NIL: did not encounter the ice habitat.

1158

Long-distance trips of male Antarctic fur seals

1159 Table 2 Model selection to test for the effects of diel period and month (Model 1) and diel
 1160 period and lunar phase (Model 2) on the frequency of dives by male Antarctic fur seals

Model	Response	Fixed effects	logLik	AIC	Δ AIC	w_i
1	Dive frequency	Diel + Month + Diel*Month + offset	-1069.9	2175.4	0	1
		Diel + Month + offset	-1240.7	2497.9	322.5	0
		Diel + Month + Diel*Month	-1372.1	2779.7	604.3	0
		Diel + Month	-1959.0	3934.6	1759.2	0
		Month	-1984.6	3978.1	1802.7	0
		Diel + offset	-4242.5	8496.4	6320.9	0
		Month + offset	-4824.9	9658.7	7483.3	0
		Diel	-5460.5	10 932.4	8756.9	0
		Null	-5486.1	10 976.5	8801.1	0
		Offset	-8013.9	16 032.1	13 856.7	0
2	Dive frequency	Diel + Lunar + Diel*Lunar + offset	-851.1	1746.3	0	1
		Diel + Lunar + offset	-935.1	1888.4	142.1	0
		Diel + offset	-1074.3	2159.4	413.1	0
		Diel + Lunar + Diel*Lunar	-11719	2387.9	641.6	0
		Diel + Lunar	-1289.7	2597.4	851.1	0
		Diel	-1369.8	2750.5	1004.1	0
		Lunar	-1383.5	2777.8	1031.4	0
		Lunar + offset	-1459.2	2922.6	1176.3	0
		Null	-4689.7	990.3	7643.9	0
		Offset	-4795.2	9594.5	7848.2	0

1161 An offset was used to account for different length diel periods that are typical of high-latitude
 1162 environments and as seals moved latitudinally over time. logLik: log-likelihood; AIC: Akaike
 1163 information criterion; Δ AIC: difference in AIC; w_i : Akaike weight (see Methods). $N = 5$
 1164 individuals, 16 317 dives.

Foraging behaviour during long-distance trips

1165 Table 3 Model selection to test for the effects of solar illumination (Solar) and lunar phase
 1166 (Lunar) on dive depth (Model 1), dive duration (Model 2) and dive residuals (Model 3) for
 1167 male Antarctic fur seals

Model	Response	Fixed effects	logLik	AIC	Δ AIC	w_i
1	Dive depth	Solar + Lunar + Solar: Lunar	-16 416.5	32 853.0	0	1
		Solar + Lunar	-16 436.9	32 888.0	34.9	0
		Solar	-16 451.2	32 910.3	57.3	0
		Lunar	-16 654.3	33 320.7	467.6	0
		Null	-16 668.4	33 342.9	489.9	0
2	Dive duration	Solar + Lunar + Solar*Lunar	-20 069.2	40 158.3	0	1
		Solar	-20 084.5	40 177.0	18.6	0
		Solar + Lunar	-20 082.7	40 179.5	21.1	0
		Null	-20 109.6	40 225.1	66.8	0
		Lunar	-20 107.5	40 227.0	68.6	0
3	Dive residuals	Solar + Lunar + Solar*Lunar	-21 380.5	42 781.1	0	1
		Solar + Lunar	-21 461.7	42 937.5	156.4	0
		Solar	-21 521.7	43 051.5	270.1	0
		Lunar	-21 567.5	43 147.1	365.9	0
		Null	-21 624.8	43 255.5	474.4	0

1168 logLik: log-likelihood; AIC: Akaike information criterion; Δ AIC: difference in AIC;
 1169 w_i : Akaike weight (see Methods). $N = 5$ individuals, 16 317 dives.

Long-distance trips of male Antarctic fur seals

1170 Table A1 Summary of animal measurements and postbreeding trip(s) characteristics for 17
 1171 male Antarctic fur seals from Heard Island

ID (trip number)	Mass (kg)	Lengt (m)	Body condit ion (kg/m)	Trip start date	Com plete trip	Max imu m dista nce (km)	Total distan ce (km)	Trip dur atio n (da ys)	Minim um latitude (S)	Time in resident state (%)
FM03 (1)	82.7	1.63	50.7	29 Dec	×	1649	6874	115	67.60	40.3
FM07-S (1)	118.9	1.66	71.6	29 Dec	×	1524	6907	147	66.49	58.1
FM06 (1)	67.8	1.39	48.8	30 Dec	✓	1520	11 859	175	66.35	50.8
FM05 (1)	100.8	1.67	60.4	31 Dec	✓	1504	9608	166	66.49	60.6
FM12 (1)	106.4	1.7	62.6	3 Jan	✓	1556	6773	120	66.01	66.8
FM19-S (1)	87.1	1.69	51.5	14 Jan	×	1529	2724	54	66.79	60.4
FM20 (1)	104.6	1.75	59.8	16 Jan	✓	1487	9122	169	66.22	64.7
FM15 (1)	91.2	1.63	56.0	18 Jan	×	1510	4375	72	66.59	34.4
Mean ± SE	95 ± 16	1.6 ± 0.1	58 ± 8	6 Jan ± 9 days						60.7 ± 3.5
FM04 (1)	73.8	1.6	46.1	11 Jan	✓	1474	3857	54	63.70	48.4
FM08 (1)	96.7	1.7	56.9	12 Jan	✓	1346	3966	52	64.35	33.4
FM18 (1)	74.3	1.6	46.4	13 Jan	×	1230	1758	28	61.98	58.4
FM10-S (1)	97.2	1.59	61.1	16 Jan	✓	1423	3432	45	62.41	23.1
FM11-S (1)	98.55	1.64	60.1	19 Jan	×	1350	1831	39	62.29	60.7

Foraging behaviour during long-distance trips

FM02 (1)	110.7	1.73	64.0	20 Jan	✓	1090	3518	56	62.63	48.8
FM17-S (1)	70.1	1.55	45.2	25 Jan	✓	1088	2651	44	60.98	55.4
FM13 (1)	116.7	1.64	71.2	27 Jan	✓	1109	2837	42	60.16	41.1
FM01 (1)	114.6	1.56	73.5	5 Feb	✓	1350	3778	55	61.66	58.9
Mean ± SE	95 ± 18	1.6 ± 0.1	58 ± 11	20 Jan days						44 ± 4.7
FM08 (2)	96.7	1.70	24	21 Dec	×	1338	3897	60	64.92	62.3
FM04 (2)				28 Mar	×	1806	2393	32	63.20	36.4
FM13 (2)				28 Mar	×	1547	2845	45	63.67	50
FM02 (2)				30 Mar	×	1446	2233	33	65.32	32.9
<i>df</i>	15	10.7	14.4	14.434						8.97
<i>t</i>	0.02	0.38	-0.14	3.3214						2.79
<i>P</i>	0.981	0.708	0.893	0.005						0.021

1172 Animal identities with ‘-S’ are those that carried an SRDL tag. Complete trips are
 1173 those that returned to the breeding area (see Methods). Seals that made a ‘long trip’
 1174 are presented first, in order of their start date, and then the seals that made a ‘short
 1175 trip’. The mean ± SE for five test variables and the results of Welch two-sample tests
 1176 between the groups (long versus short trips) are presented. Maximum distance is from
 1177 Heard Island, and percentage of time in resident state (rather than directed state) is
 1178 from a switching state-space model.

Long-distance trips of male Antarctic fur seals

1179 Table A2 Summary of foraging (i.e. diving) and nonforaging (i.e. cruising and hauled out)
 1180 behaviours that occurred during each movement state throughout the postbreeding trips of
 1181 five male Antarctic fur seals with SRDL tags

1182

ID (Trip type)	Stat e	No. of states	State duratio n (days)	No. of dives	Time diving (%)*	Time cruising (%)*	Time haule d out (%)*	Duration cruising (days)	Durat ion haule d out (days)
FM19- S (long)	D	3	7 ± 2 [4–8]	182 ± 127	22 ± 8	74 ± 11	11	0.5 ± 0.2 [0.2–0.7]	0.5
	R	3	15 ± 4 [12–18]	766 ± 692	19 ± 12	54 ± 26	54	0.4 ± 0.2 [0.3–0.5]	2
FM07- S (long)	D	15	4 ± 3 [1–14]	226 ± 203	15 ± 6	67 ± 24	38 ± 28	0.4 ± 0.1 [0.3–0.5]	0.9 ± 0.5 [0.2– 2]
	R	15	6 ± 7 [1–29]	443 ± 583	18 ± 7	56 ± 25	47 ± 17	0.4 ± 0.2 [0.3–0.7]	0.8 ± 0.5 [0.2– 2]
FM17- S (short)	D	4	4 ± 3 [1–9]	176 ± 123	16 ± 10	88 ± 11	NA	0.6 ± 0.1 [0.5–0.7]	NA

Foraging behaviour during long-distance trips

	R	3	7 ± 9	449 ±	16 ± 5	84 ± 5	NA	0.5 ± 0.0	NA
			[1 – 18]	632				[0.5–0.5]	
FM10-	D	4	8 ± 6	307 ±	16 ± 8	83 ± 6	NA	0.9 ± 0.9	NA
S			[1–16]	217				[0.5–2]	
(short)									
	R	3	5 ± 5	170 ±	22 ± 8	78 ± 8	NA	0.4 ± 0.2	NA
			[1–8]	223				[0.3–0.5]	
FM11-	D	2	7 ± 3	56 ± 5	13 ± 0	87 ± 0	NA	0.5 ± 0.0	NA
S			[5–9]					[0.5–0.5]	
(short)									
	R	2	11 ± 11	262 ±	18 ± 7	84 ± 7	NA	0.5 ± 0.0	NA
			[3–18]	344				[0.5–0.5]	

1183 Males are grouped according to trip type (long or short trip). Variables include the number of
 1184 movement states (D = directed; R= resident), number of dives, percentage of time in a
 1185 behaviour (diving, cruising or hauled out; see Methods) and the duration of behaviours (see
 1186 Methods). Means are presented ± SD and calculations of duration include the range (within
 1187 brackets). Behaviour summary data were available for a portion of each movement state:
 1188 mean ± SD = 76.86 ± 25.48 [0–99% coverage]. NA: not available.

1189 *Percentage of total behaviour summary data recorded during each movement state
 1190 that was allocated to that behaviour.

1191

1192 Table A3 Summary of factor level comparisons for six linear mixed models that assessed
 1193 whether three dive characteristics (dive depth; dive duration; dive residuals) varied among
 1194 habitat types, separately for when male Antarctic fur seals were in directed or resident states

		Directed state			Resident state		
Response	Habitat	Estimate	<i>t</i>	<i>P</i>	Estimate	<i>t</i>	<i>P</i>
		(SE)			(SE)		

Long-distance trips of male Antarctic fur seals

Dive	[SACCF_	36.3	27.71	< 0.001	16.1	32.04	< 0.001
depth (m)	N]	(0.13)			(0.09)		
	SACCF_S	20.4	-11.57	< 0.001	18.2	1.53	0.13
		(0.05)			(0.08)		
	SB	21.7	-8.60	< 0.001	13.7	-1.75	0.08
		(0.06)			(0.09)		
	SB/near-	13.2	-11.38	< 0.001	15.1	-0.73	0.46
	ice	(0.09)			(0.09)		
	Ice_Haul	10.1	-14.92	< 0.001	12.7	-2.93	0.003
		(0.09)			(0.08)		
	Ice_NoHa	14.2	-10.80	< 0.001	23.8	4.75	< 0.001
	ul	(0.09)			(0.08)		
Dive	[SACCF_	1.63	34.8	< 0.001	0.81	31.25	< 0.001
duration	N]	(0.13)			(0.12)		
(min)	SACCF_S	0.98	-8.08	< 0.001	0.92	1.18	0.24
		(0.06)			(0.11)		
	SB	1.07	-5.60	< 0.001	0.73	-0.91	0.36
		(0.07)			(0.12)		
	SB/near-	0.82	-6.32	< 0.001	0.64	-2.03	0.04
	ice	(0.11)			(0.12)		
	Ice_Haul	0.78	-8.79	< 0.001	0.97	-1.46	0.14
		(0.11)			(0.11)		
	Ice_NoHa	0.65	-6.94	< 0.001	0.69	1.62	0.10
	ul	(0.11)			(0.11)		
Dive	[SACCF_	0.02	0.17	0.868	0.15	1.09	0.28
residuals	N]	(0.12)			(0.14)		

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SACCF_S	-0.14	-1.92	0.06	-0.08	-1.60	0.11
	(0.07)			(0.14)		
SB	-0.14	-1.54	0.12	0.003	-1.05	0.29
	(0.09)			(0.15)		
SB/near-ice	0.23	1.89	0.06	-0.36	-3.39	< 0.001
	(0.12)			(0.15)		
Ice_Haul	-0.001	2.67	0.01	0.07	-0.58	0.57
	(0.12)			(0.14)		
Ice_NoHaul	0.32	-0.01	0.99	-0.56	-4.90	< 0.001
	(0.12)			(0.14)		

1195 Dive depth and duration were log transformed to normalize the residuals and the
 1196 estimates are presented back transformed to their original units. All models included a
 1197 random effect to account for repeated measure of dives per male ($N = 5$ individuals),
 1198 which accounted for 65–89% of the variance explained by the models. The northern
 1199 SACCF level [SACCF_N] was used as a reference for factor level comparisons. For
 1200 habitat abbreviations see Fig. 1. Ice_Haul: ice habitat where males were known to
 1201 have hauled out; Ice_NoHaul: ice habitat where males were known not to have hauled
 1202 out.
 1203

Long-distance trips of male Antarctic fur seals

1204 Figure 1 Postbreeding trips for male Antarctic fur seals departing Heard Island ($N = 16$
1205 males) and Kerguelen Island ($N = 1$ male) from 29 December 2003 to 3 July 2004.
1206 Males made either (a) a single ‘long’ trip ($N = 8$) or (b, c) multiple short trips: (b) first
1207 short trip ($N = 9$) and (c) second short trip ($N = 4$). Lines indicate directed movement
1208 states and enlarged sections along lines indicate resident movement state from a
1209 switching state-space model. Habitats encountered during trips (see inset legend): shelf;
1210 Polar Front zones (north: PF_N; middle: PF_M; south: PF_S), Southern Antarctic
1211 Circumpolar Current Front zones (north: SACCF_N; south: SACCF_S), Southern
1212 Boundary Current (SB), near-ice/Southern Boundary Current (SB/near-ice) and ice.
1213 Bathymetry (GEBCO) is shaded at four intervals: 0–500 m, 500–1000 m, 1000–2000
1214 m and >2000 m depth.

1215 Figure 2 Latitudinal movements during postbreeding trips of male Antarctic fur seals.
1216 Individuals (IDs are shown above each panel) made (a – e) a single short trip, (f – i)
1217 multiple short trips or (j – q) a single long trip. Locations were derived from a switching
1218 state-space model, with dots indicating resident states. For habitat abbreviations see
1219 Fig. 1. The solid horizontal line identifies the latitude of the deployment site, and the
1220 dotted horizontal line represents the boundary between long and short trips. For the five
1221 males with SRDL tags, (a), (b), (d), (n) and (o), green vertical lines show the occurrence
1222 of 6 h periods hauled out (derived from the 6 h binned behaviour data).

1223 Figure 3 Temporal pattern in dives of male Antarctic fur seals ($N = 5$) relative to the
1224 position of the sun during their postbreeding trips. IDs are shown at the top of each
1225 panel. Vertical bars indicate daily dive frequency and are separated into diel periods by
1226 colour (from white to black: day, dawn, dusk, night). The black wave line is the solar
1227 position through time relative to an individual’s location throughout its trip, with dives
1228 indicated as coloured points (coloured according to their depth). Positive values of solar

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1229 position indicate daylight, values between 0 and -12 (solid and dotted horizontal lines,
1230 respectively) indicate nautical twilight and values below -12 indicate night. Black and
1231 red horizontal rectangles above the black wave line indicate changes in movement state
1232 (directed and resident, respectively).