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Title: Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, *Mirounga leonina*

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Abstract: Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, *Mirounga leonina*

Long-term fidelity to foraging areas may have fitness benefits to individuals, particularly in unpredictable environments. However, such strategies may result in short-term energetic losses and delay responses to fast environmental changes. We used satellite tracking data and associated diving data to record the habitat use of nine individual southern elephant seals (*Mirounga leonina*) over 34 winter migrations. By assessing overlap in two- and three-dimensional home ranges we illustrate strong long-term (up to seven year) fidelity to foraging habitat. Furthermore, a repeatability statistic and hierarchical clustering exercise provided evidence for individual specialization of foraging migration strategies. We discuss the possible influences of stable long-term foraging migration strategies on the adaptability of individual elephant seals to rapid environmental change. Our results further illustrate the need for more long-term longitudinal studies to quantify the influence of individual-level site familiarity, fidelity and specialization on population-level resource selection and population dynamics.

Title: Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, *Mirounga leonina*

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Editor
Animal Behaviour

Dear Editor

SUBMISSION OF REVISED MANUSCRIPT

Appended please find the revised manuscript now entitled: **“Slow to change? Individual fidelity to three-dimensional foraging habitats in southern elephant seals, *Mirounga leonina*”**.

We have now completed a revision of the above-mentioned manuscript and addressed all of the editor’s remarks as follows:

1. Put keywords in alphabetical order.

>> **Done – please see Abstract document**

2. Take the figures out of the text and upload them separately. Similarly, put all the tables together after the references. Figure captions should be collected together and placed after the references and tables in the manuscript. They must not be on the same page as the figure or uploaded as figures.

>> **Done - please refer to the highlighted document.**

3. Tables should have a short one-sentence title above the table and other information should be placed below the table.

>> **Done - please refer to the highlighted document.**

4. 'N' should be a capital letter in italics.

>> **Done - all places where this was done are highlighted in the highlight document.**

5. Table 2. Remove the internal horizontal line.

>> **Done. However, we retained an underlining of the “50% 3D-UD” for clarity. Please advise should you require any further amendments here.**

6. Use double line spacing in the references.

>> **Done.**

7. For software references such as Calenge 2015 add the website address.

>> **Done - please refer to the highlighted reference list.**

We also attach a version of the new manuscript, highlighting the changes/corrections made, as well as a ‘clean’ version of the revised manuscript.

We trust that we have adequately addressed the all comments and wish to thank you again for your attention to this manuscript.

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Highlights

- We recorded the oceanic behaviour of focal elephant seals over multiple years
- Seals displayed long-term fidelity to three-dimensional migration strategies
- Individual specialization was evident in foraging migrations
- The reported high fidelity may limit the adaptability of individuals

1 **Introduction**

2 Many species display foraging site fidelity, returning repeatedly to the same foraging areas
3 (e.g. Augé, Chilvers, Moore, & Davis, 2014; Weber et al., 2015), even when habitat quality is
4 sub-optimal (Krebs, 1971; Merkle, Cherry, & Fortin, 2015). Fidelity to foraging areas may
5 have long-term advantages for individual fitness, particularly in unpredictable environments
6 (Switzer, 1993). For example, animals may return to foraging areas because they are familiar
7 with resources (Greenwood, 1980) and able to exploit comparatively productive areas,
8 resulting in long-term energetic gains. Animals may also return to certain areas because they
9 are familiar with potential refuges and able to avoid predation (Clarke et al., 1993; Forrester,
10 Casady, & Wittmer, 2015). The benefits of long-term site fidelity may have short-term costs
11 if sufficient food cannot be found in temporally heterogeneous environments (Bradshaw,
12 Hindell, Sumner, & Michael, 2004). More significant fitness costs of site fidelity may be
13 incurred when animals are unable to respond to short- and medium term changes in food
14 availability by switching between foraging patches (e.g. Newell, 1999; Whisson, Dixon,
15 Taylor, & Melzer, 2016). Once an individual has learned a behaviour it may be hesitant to
16 change or to adopt new foraging strategies, especially if the associated risks are great. The
17 risks of looking for new foraging patches may be particularly great if foraging patches are far
18 apart or are of unpredictable quality.

19

20 Individual animals sometimes display individual-level foraging fidelity, where the
21 intra-individual variation in space use is less than the inter-individual variation in space use
22 within a population (Wakefield et al., 2015). Individual-level foraging fidelity may be a type
23 of individual specialization, best explained by phenotypic trade-offs when specialization in
24 one strategy results in the inability to efficiently perform an alternative strategy (Bolnick et
25 al., 2003). Various foraging behaviours such as prey recognition, capture ability, digestive

26 capacity and predator avoidance strategies may be affected. The existence of individual-level
27 specialization, in terms of site fidelity and dietary specialization, has long been recognized
28 but rarely explicitly considered in ecological studies (Piper, 2011).

29
30 Foraging site fidelity has been widely illustrated in marine vertebrates, including
31 marine birds (e.g. Baylis et al., 2015), turtles (e.g. Carman et al., 2016), fish (e.g. Gannon et
32 al., 2015) and marine mammals (e.g. Vermeulen et al., 2016). Pinnipeds in particular often
33 display high levels of foraging site fidelity (e.g. Arthur et al., 2015; Baylis et al., 2015; Wege,
34 Tosh, de Bruyn, & Bester, 2016). Fidelity to large-scale foraging areas was demonstrated for
35 southern elephant seals (*Mirounga leonina*), but individual seals that were faithful to foraging
36 areas did not show mass gain benefits (Bradshaw et al., 2004). However, it was proposed that
37 returning to generally more productive areas could result in benefits over longer timescales
38 (Bradshaw et al., 2004). Also, Authier et al. (2012) illustrated that lower variation in the
39 isotopic foraging niche of male southern elephant seals covaried positively with estimated
40 lifespans, thereby suggesting lifetime fitness benefits associated with foraging fidelity in this
41 species. While these reports provide valuable insights, little information is available
42 regarding the foraging area fidelity of individual elephant seals over the long term (3+ years)
43 and no information exists on fidelity to specific foraging strategies used to exploit the vertical
44 dimension.

45
46 Animal space use is typically quantified in two dimensions, despite the fact that
47 most animals also use space in a vertical dimension (i.e. by flying, diving or burrowing).
48 Incorporating the vertical component into representations of space use may provide novel
49 ecological insights and have conservation management benefits (Tracey et al., 2014). Habitat
50 use studies have attempted to incorporate the vertical dimension through separate analyses of

51 vertical metrics without incorporating spatial position (2-dimensions). Some recent studies,
52 particularly on marine predators, have incorporated the vertical behaviour component (e.g.
53 spherical first-passage time, Bailleul, Lesage, & Hammill, 2010). More recently, three
54 dimensional utilization distributions (3D UDs) quantified vertical space use and home range
55 overlap of sharks (Simpfendorfer, Olsen, Heupel, & Moland, 2012) and birds (Cooper,
56 Sherry, & Marra, 2014).

57

58 Southern elephant seals have a circumpolar distribution and their foraging behaviour
59 is closely linked to their specific haul-out sites (Hindell et al., 2016). Elephant seals display a
60 high degree of fidelity to their haul-out sites (Hofmeyr, Kirkman, Pistorius, & Bester, 2012),
61 which may be an important indication of learned behaviour in these animals. Here we assess
62 (1) the persistence of migration site fidelity in southern elephant seals; (2) fidelity to a three-
63 dimensional environment, particularly the water depths exploited; and (3) the individual
64 repeatability and specialization of migration strategies. We predicted that foraging site
65 fidelity in elephant seals would decay over the long-term, due to the spatiotemporally patchy
66 nature of their prey distribution (i.e. that site fidelity would persist only as long as prey
67 patches persist – Kamil, 1983). Fidelity to three-dimensional environments was expected to
68 be lower, both as a result of variation in the vertical distribution of prey items, as well as the
69 influences of physiological development and ageing on the dive capacity of seals. Finally, the
70 propensity for Marion Island’s elephant seals to forage in deep ocean areas, south-west of the
71 island (Hindell et al., 2016; Oosthuizen, Bester, Altwegg, McIntyre, & de Bruyn, 2015) led to
72 a prediction of limited individual-level specialization in migration strategies.

73

74 **Methods**

75 *Ethical Note*

76 The research described refers to an Antarctic seal species, the southern elephant seal. It
77 conforms to Antarctic Treaty legislation and to the SCAR Code of Conduct for the Use of
78 Animals for Scientific Purposes in Antarctica (ATCM XXXIV 2011). We adhere to the
79 ‘Guidelines for the use of animals in research’ as published in *Animal Behaviour* (1990, 41,
80 183–186) and the laws of the country where the research was conducted. All flipper tagging
81 and satellite device deployment/retrieval procedures were reviewed and approved by the
82 Animal Use and Care Committee and more recently the renamed Animal Ethics Committee
83 of the University of Pretoria (AUCC 040827-024; AUCC 040827-023 and EC077-15), and
84 fieldwork was performed under Prince Edward Island’s Research Permits R8-04 and R04-08.
85 All dive and track data are available via the PANGAEA Data Publisher for Earth &
86 Environmental Science ([doi:10.1594/PANGAEA.871448](https://doi.org/10.1594/PANGAEA.871448)).

87

88 *Track data and filtering*

89 As part of a series of tracking projects between April 2004 and February 2013, we deployed
90 95 satellite-relay data loggers (either Series 9000 SRDLs, or CTD-SRDLs, Sea Mammal
91 Research Unit, University of St Andrews, Scotland) on southern elephant seals of both sexes
92 hauled out at sub-Antarctic Marion Island (46° 54’S; 37° 45’E). These instruments provided
93 track locations (obtained via Service Argos estimates), basic time-depth profiles of
94 approximately 20 dives per day and a maximum of four temperature-depth profiles per day
95 (Boehme et al., 2009).

96

97 Uniquely marked (de Bruyn, Tosh, Oosthuizen, Phalanndwa, & Bester, 2008) seals
98 were immobilized using a handheld syringe, extended by a length of drip-tubing, to deliver a
99 calculated dose of ketamine based on a visual estimation of the seal’s mass (Bester, 1988).

100 Seals were then observed from a distance until the anticipated end of the induction period

101 (about 20 min post-injection), and then approached for the first time to assess the depth of
102 anaesthesia by evaluating reactions to stimuli (e.g. slight noise and touch) (Bornemann et al.,
103 2013). As soon as the seals tolerated physical stimuli, their eyes were covered with a towel to
104 protect against solar radiation and minimise unnecessary stimuli. Transmitters were glued
105 onto the fur of the heads of the seals using a quick-setting epoxy resin (Field et al., 2012).
106 The heaviest of these devices (CTD-SRDLs) weighed 545 g, representing 0.19% of the
107 average post-moult departure mass of female elephant seals from this population (Postma,
108 Bester, & De Bruyn, 2013). After their post-migration return to the island, data transmitting
109 devices were either removed from sedated animals by shaving them off the fur or shed
110 naturally with the pelage during the annual moult. No short-term deleterious effects were
111 evident with immobilization, device deployment or retrieval, while tracking devices attached
112 to elephant seals are known not to affect individual mass gain or survival in the long term
113 (McMahon, Field, Bradshaw, White, & Hindell, 2008). We report on a subset of the resultant
114 dataset, after retaining data from 34 post-moult migrations (as opposed to post-breeding
115 migrations, Le Boeuf & Laws, 1994) from nine individual seals (two males and seven
116 females) that successfully carried instruments over multiple winter migrations (Table 1).
117 Only tracks with data for a minimum period of 30 days were included. Seals in this sample
118 provided tracking and dive data for a median of three migrations (range: 2 – 7), each
119 migration covering a median period of 223 days (range: 38 – 292).

120

121 All statistical analyses were undertaken in the R programming environment (Team,
122 2016). Track data were filtered to remove estimated locations that required swim speeds in
123 excess of 3.5 m/s and/or creating spikes in the track with angles smaller than 15° and 25°
124 with extensions greater than 2,500 m and 5,000 m, respectively (Freitas, Lydersen, Fedak, &
125 Kovacs, 2008).

126

127 *Inter-annual and multi-year fidelity*

128 Fidelity to home ranges was expressed as the overlap in 95% kernel density utilization
129 distributions (UD) of two dimensional location data (latitude and longitude) and three
130 dimensional diving data (latitude, longitude and dive depth). The two dimensional UD's were
131 calculated using an *ad hoc* smoothing parameter, which assumes a bivariate normal UD in the
132 R package '*adehabitatHR*' (Calenge, 2015). Overlap of two-dimensional UD's was calculated
133 following Arthur et al. (Arthur et al., 2015), using Bhattacharyya's affinity (BA) for a general
134 measure of similarity between UD estimates.

135

136 Daily median dive depth values were calculated for each two dimensional location
137 to create a three dimensional dataset. We divided the datasets into daytime and nocturnal
138 dives, as southern elephant seals often display diel vertical migration (e.g. Biuw et al., 2010;
139 McIntyre, Bornemann, Plötz, Tosh, & Bester, 2011). Three dimensional kernel density
140 utilisation distributions (3D-UD) were estimated in the '*ks*' package (Duong, 2016), using a
141 two-stage plug-in method, developed by Duong and Hazelton (2003) and applied by
142 Simpfendorfer et al. (2012) and Cooper et al. (2014) amongst others. We calculated overlap
143 in 95% 3D-UD's both inter-annually and over multiple years (multi-year) for individual seals,
144 following Simpfendorfer et al. (2012). Inter-annual overlap is the overlap for tracks from
145 consecutive years (e.g. overlap between 2006 and 2007; 2007 and 2008 etc.), while multi-
146 year overlap was calculated between tracks separated by a year or more (e.g. overlap between
147 2006 and 2008; 2006 and 2009 etc.).

148

149 *Repeatability*

150 We applied a repeatability statistic to a series of track and behavioural metrics to assess
151 individual behavioural consistency compared to the behaviours displayed by all the seals in
152 the dataset. This repeatability statistic was calculated, making use of an intra-class correlation
153 coefficient (Wolak, Fairbairn, & Paulsen, 2012), following McFarlane Tranquila et al.
154 (2014). Accordingly, among-groups variance (s_A^2) and within-individual variance
155 components (s^2) are derived from a linear mixed-effects model (R package ‘*psychometric*’).
156 Repeatability (r) was then calculated as:

$$r = \frac{s_A^2}{(s^2 + s_A^2)}$$

157 where high r values (> 0.5) indicate consistent individual behaviours.

158

159 The repeatability statistic was applied to the following track and behavioural
160 metrics: (1) the daytime and nocturnal 95% and 50% 3D-UDs incorporating the dive depths
161 of tracked seals; (2) the maximum distance travelled away from Marion Island per migration
162 and (3) the bearing of the location at the maximum distance away from Marion Island.

163

164 *Hierarchical clustering*

165 We explored the possibility of individually specific migration strategies (consistent long term
166 behaviour) using a hierarchical clustering approach. A principal components analysis (PCA)
167 was first applied to a series of track- and dive metrics to generate a single metric
168 representative of an overall strategy. Six daily metrics were included in the PCA: (1) median
169 daytime dive depth; (2) median night-time dive depth; (3) diel vertical migration (defined as
170 the difference between daytime and night-time median dive depths); (4) distance from
171 Marion Island; (5) bearing from Marion Island; and (6) mean speed of travel (mean speed of
172 travel between all locations associated with a specific day). The first five principal
173 components explained 93.7% of the variance. The relative contribution of each principal

174 component to a single, weighted metric was determined from the loadings of the PCA output.
175 This value was used in a hierarchical clustering analysis, using Ward's clustering criterion
176 (Ward, 1963) on a Euclidean distance matrix.

177

178 **Results**

179 *Home range overlap*

180 Seven of the nine seals tracked over multiple migrations had overlapping 95% UD that
181 encompassed more than 50% of their home ranges (UD overlap > 0.5) (Fig. 1). Two
182 individual seals tracked twice in non-consecutive years (RR217:2009, 2011 and
183 YY039:2008, 2011), had comparatively disparate UDs, characterised by small areas of
184 overlap (0.31 and 0.19 respectively, Table 1). Mean inter-annual overlap of 95% UDs was
185 0.73 ± 0.14 (Table 1). Overlap of UDs for multi-year periods were slightly lower at $0.61 \pm$
186 0.18 . Inter-annual overlap of 95% UDs was consistently high for individuals tracked over
187 consecutive migrations, with a minimum overlap of 0.65 ± 0.17 (maximum of 0.91 ± 0.03).
188 Multi-year overlap was more variable, ranging from 0.19 to 0.92 (Table 1).

189

190 *Three-dimensional UD overlap*

191 The mean inter-annual overlap of 95% 3D-UDs was 0.54 ± 0.15 for daytime dives and $0.57 \pm$
192 0.15 for nocturnal dives. Overlap was slightly lower for multi-year periods at 0.45 ± 0.17 for
193 daytime dives and 0.47 ± 0.15 for nocturnal dives. Five of the six seals that were tracked in
194 consecutive years, recorded 95% 3D-UDs that overlapped by 60% - 71%. Individual
195 variation was evident, with some seals using very similar three-dimensional spaces over long
196 time periods (e.g. YY189, Fig. 2, Table 2), while others used slightly different depths
197 between years (e.g. GG335, Fig. 2, Table 2) and others used completely different depths (e.g.
198 PO225, Fig. 2, Table) despite substantial overlap in the two dimensional 95% UD (Fig. 1).

199 Areas of restricted movement or 50% 3D-UDs overlapped much less and was more variable
200 between seals (Table 2), although two seals (PO043 and OO052) had similar areas of
201 restricted movement and diving behaviours in consecutive years (50% 3D-UDs overlap =
202 approximately 60%).

203

204 Two seals (PO225 and GG335) used similar oceanographic areas (2-D UD) (Fig. 1)
205 but had very different diving behaviours (3-D –UD) (Fig. 2) in their subsequent migrations.
206 GG335 dived to varied depths but maintained a substantial overlap in 3D-UDs over the 5
207 years that it was tracked. This seal employed two general diving strategies, performing
208 deeper dives in the last two migrations (2011, 2012), compared to the preceding three years
209 (Fig. 2). PO225 dived to variable depths during its 2007 migration but used more specific
210 depth layers in 2011.

211

212 *Repeatability*

213 All repeatability (r) values were larger than 0.5 (Table 3), suggesting consistency in
214 individual behaviours. The lowest value (0.53) was calculated for track bearings of the point
215 furthest away from Marion Island, indicating least consistency for this metric. All other r
216 values were equal to or larger than 0.6 (Table 3), indicating high levels of consistency in the
217 three-dimensional area sizes used by seals and distances travelled away from Marion Island.

218

219 *Hierarchical clustering*

220 Five principal components (PCs) explained 93.7% of the variance in our dataset and included
221 both horizontal movement and vertical dive behaviour metrics. PC1 was most strongly
222 associated with DVM, PC2 with distance and bearing from Marion Island + night-time dive

223 depths, PC3 with daytime dive depths, PC4 with travel speed and PC5 with bearing and
224 distance.

225

226 Hierarchical clustering revealed three distinct migration strategies used by the
227 tracked seals (Fig. 3), and multiple tracks of individual seals tended to group together in the
228 same clusters (e.g. OO052, GG335). Two individuals (WW061 and RR217) grouped in two
229 different clusters. Seals grouping into specific clusters generally foraged in the same areas.
230 For example, GG335 (2007) and WW061 (2008) both travelled in a westerly direction away
231 from Marion Island (and further), compared to their other migrations (Fig. 1). These
232 migrations clustered with all of the migrations recorded for OO021 (Fig. 3), which used a
233 similar spatial area (Fig. 1).

234

235 Migrations in cluster 1 (C1) covered a wide latitudinal range, from the Subtropical
236 Front in the north to south of the APF (Fig. 3). Migrations in cluster 3 (C3) were
237 characterised by the greatest distances away from Marion Island, but restricted to latitudes
238 south of the Subantarctic Front, with many of the tracks concentrated south of the Antarctic
239 Polar Front (APF). Cluster two (C2) comprised of tracks from one seal (OO052), which used
240 a small area adjacent to Marion Island during all five of its post-moult migrations.

241

242 **Discussion**

243 Studies of fidelity to migration strategies over long-distances and long time periods, are often
244 restricted to few migrations (e.g. two or three) (Mingozzi, Mencacci, Cerritelli, Giunchi, &
245 Luschi, 2016), although a few recent studies have successfully tracked seasonally migrating
246 birds over multiple years (e.g. Berthold et al., 2002; Lopez-Lopez et al., 2014; Vardanis,
247 Nilsson, Klaassen, Strandberg & Alerstam, 2016). Similarly, individual foraging site fidelity

248 in elephant seals has only been studied from a small number of migrations, not separated by
249 more than one or two years (e.g. Bradshaw et al., 2004; Simmons, 2008). In one study, a
250 single northern elephant seal, *M. angustirostris*, followed the same path in 2006 as it did 11
251 years previously in 1995; although the North American continent predisposes migration by
252 this species to a westerly bearing away from haulout sites (Costa, Breed, & Robinson, 2012).
253 Our study followed a small number of individual seals and reports on continued fidelity over
254 long distances and time periods not reported before. Seals tracked in our sample showed high
255 overlap in 95% UD, even over extended periods of up to seven years – averaging more than
256 60% for both consecutive and non-consecutive migrations (Table 1). The long-term fidelity
257 to oceanographic areas used by seals included their use of the vertical environment, and
258 overlap in 95% 3D-UDs averaged more than 45% over multi-year comparisons and more
259 than 50% for consecutive years.

260

261 Individual-level flexibility in inter-annual migration routes has been illustrated for
262 some migrating birds known to forage on prey items that are variably distributed (Vardanis,
263 Nilsson, Klaassen, Strandberg & Alerstam, 2016), although the drivers of such flexibility
264 remain unknown. Bradshaw et al. (2004) were unable to link foraging success of tracked
265 southern elephant seals to the likelihood that they would alter their foraging strategies,
266 suggesting that elephant seals do not follow the win-stay/lose-switch rule (Shields, Cook,
267 Hebblethwaite, & Wiles-Ehmann, 1988) over shorter time periods. Alternatively, they
268 suggested that elephant seals would benefit over longer periods by returning to areas with
269 generally increased productivity. While the condition of seals tracked in our sample is
270 unknown and we were unable to assess the impacts of migration strategies, the long-term
271 fidelity to migration patterns and oceanographic areas apparently supports the hypothesis of
272 Bradshaw et al. (2004) that the win-stay/lose-switch rule does not apply over multiple

273 migrations in elephant seals. However, the reasonably small sample size we report on here
274 does not exclude the possibility that tracked seals rarely encountered such poor foraging
275 success as to prompt any switches in strategy.

276

277 Two seals in our sample (PO225 and GG335) displayed much more overlap in
278 their 2D UD_s, compared to their 3-D UD_s (Figs. 1 and 2). GG335 evidently switched its
279 depth use strategy once between 2010 and 2011, performing deeper dives in 2011 and 2012
280 when compared to the earlier tracks. The two migrations of PO225 (2007; 2011) were 3 years
281 apart, limiting any hypotheses on the development of dive behaviour. However, it is unlikely
282 that the observed differences in diving behaviour are due to ontogenic development of diving
283 capacity (Bennett, McConnell, & Fedak, 2001), because this seal was first tracked as an
284 adult, eight year old male and diving capacity does not develop substantially once a seal
285 reaches maturity (Grundling, 2014). Elephant seal dive strategies may change within-
286 migrations (e.g. Bester, Bornemann, & McIntyre, in press; Biuw et al., 2010; McIntyre,
287 Ansoerge, et al., 2011), indicating that elephant seals are often able to exploit localised prey
288 patches at different depths. The dissimilar diving behaviour seen in different migrations of
289 PO225 and GG335 further suggests an element of inter-annual plasticity in foraging
290 strategies. Long-term longitudinal tracking investigations are needed to explore these shifts in
291 diving strategies.

292

293 Seal behaviours in our study showed high levels of individual repeatability (*r*).
294 Combined with the outputs of the clustering exercise, these results suggest a high level of
295 individual specialization in migration behaviour. Individual variation in southern elephant
296 seal behaviours, and other marine predators, has been acknowledged and recently accounted
297 for in behavioural modelling exercises (e.g. Farnsworth et al., 2015; Massie et al., 2016;

298 Stillfried, Belant, Svoboda, Beyer, & Kramer-Schadt, 2015). Moreover, recent studies have
299 illustrated consistency and specialization in individual behaviour (e.g. Wakefield et al.,
300 2015). Southern elephant seals employ various foraging strategies, exploiting shallow water
301 masses associated with the Kerguelen Plateau, and the Antarctic Peninsula, or using deep,
302 open water regions in the Southern Ocean (Hindell et al., 2016). Female elephant seals in the
303 Antarctic Peninsula region display individual behavioural and foraging niche specialization
304 with substantial within-migration behavioural plasticity (Hückstädt et al., 2012). Similarly,
305 Marion Island elephant seals use three broad migration strategies (clusters) (Fig. 3), which
306 were identified from diel vertical migration patterns, dive depths, and distance and bearing
307 from Marion Island.

308

309 *Implication of long-term fidelity and individual specialization*

310 The Southern Ocean is rapidly changing with a generally warming and freshening trend
311 leading to expected poleward shifts in the distribution of lower trophic level consumers
312 (Constable et al., 2014). The long-term spatial fidelity of elephant seals, including three-
313 dimensional environments (this study), has potential implications for our understanding of
314 their behavioural response to disturbance. The origin of fidelity described here is unknown
315 and is not analysed in detail. However, site familiarity and fidelity may develop if juvenile
316 elephant seals are successful during their first foraging migration (Bradshaw et al., 2004).
317 This would suggest that environmental conditions experienced in early migrations may have
318 consequences for future migration strategies (Dall, Bell, Bolnick, & Ratnieks, 2012). Juvenile
319 southern elephant seals tracked from Marion Island generally travel due west, irrespective of
320 year, and focus their foraging behaviour along bathymetric features, frontal zones and meso-
321 scale eddies (Tosh et al., 2012; 2015), adding to their familiarity of the surrounding ocean.
322 While the intra-migration dive behaviour of southern elephant seals is known to respond to

323 changes in the temperature structure of the water column and associated changes in the
324 distribution of potential prey items (Guinet et al., 2014; McIntyre, Ansorge, et al., 2011), the
325 long-term fidelity to foraging areas and diving behaviour may limit coarser-scale movement
326 and behavioural adaptations of individual elephant seals to rapid environmental changes,
327 although this requires further investigation. Similarly, other taxa such as seabirds and marine
328 turtles, which rely on site-specific information gained early in life, may be more vulnerable to
329 rapid environmental change and other anthropogenic disturbances (Hipfner, 2008; Vander
330 Zanden et al., 2016; Wakefield et al., 2015). Future research needs to elucidate the role of
331 long-term behavioural adaptations in individual elephant seals in response to rapid
332 environmental change, particularly through long-term longitudinal monitoring of fitness
333 consequences associated with behavioural changes in relation to environmental differences.

334

335 Our results show the value of long-term data on known individuals for illustrating
336 individual repeatability, and potentially specialization, in the migration strategies of animals.
337 Tracking studies are often used for conservation planning and environmental management
338 purposes (e.g. Jabour et al., 2016). Such studies can benefit from incorporating seasonal
339 variation in habitat use of target species (Braham et al., 2015), as well as samples
340 representing substantial spatial variation (Mazor, Beger, McGowan, Possingham, & Kark,
341 2016). However, while the influence of individual differences on our understanding of animal
342 ecology is recognised (Dall et al., 2012), it is seldom implemented in population-level
343 studies. Bolnick et al (2011) highlights that individual specialisation or phenotypic expression
344 can have serious implications for studies on the ecology, evolution and conservation of
345 populations. For example, resource selection models which assume foragers are informed
346 about their total surroundings to select the most favourable areas would benefit from
347 incorporating effects associated with individual familiarity and fidelity (Wakefield et al.,

348 2015). Our study provides further support to the call for long-term longitudinal research
349 quantifying the influence of site familiarity, site fidelity and resource specialization on animal
350 population dynamics.

351

352

353

354 **References**

Comment [TM1]: Spacing revised to double-spacing throughout the reference list

- 355 Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., ... Lea, M.-A.
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591

592 Tables

593 **Table 1: Elephant seals tracked over multiple migrations.**

Tag	Sex	N	Age at deployments	Years successfully tracked	Inter-annual UD overlap	Multi-year UD overlap
GG335	F	6	7,8,9,10,11,12	2007,2008,2009,2010,2011,2012	0.65 ± 0.17	0.57 ± 0.15
OO021	F	3	5,6,7	2007,2008,2009	0.91 ± 0.03	0.92
OO052	M	5	4,5,6,9,11	2006,2007,2008,2011,2013	0.74 ± 0.09	0.64 ± 0.19
PO043	F	3	8,9,10	2007,2008,2009	0.69 ± 0.13	0.48
PO225	M	2	8,12	2007,2011	-	0.74
RR217	F	2	4,6	2009,2011	-	0.31
WW061	F	4	7,10,11,12	2008,2011,2012,2013	0.87 ± 0.09	0.58 ± 0.19
YY039	F	2	4,7	2008,2011	-	0.19
YY189	F	7	2,3,4,5,6,8,9	2006,2007,2008,2009,2010,2012,2013	0.71 ± 0.09	0.64 ± 0.19

594 Mean (± SD) overlap in inter-annual utilization distributions, as well as mean (± SD) overlap

595 in multiple-year utilization distributions, are reported. Only tracks over periods of more than

596 30 days (median: 223, range: 38 – 292) were included.

597

598 **Table 2: Inter-annual and multi-year overlap in 95% and 50% three-dimensional utilization**
 599 **distributions (3D-UDs) for southern elephant seals.**

<i>Tag</i>	<i>N</i>	<u>95% 3D-UD</u>			
		<i>Inter-annual</i>		<i>Multi-year</i>	
		<i>Day</i>	<i>Night</i>	<i>Day</i>	<i>Night</i>
GG335	6	0.43 ± 0.1	0.51 ± 0.15	0.41 ± 0.15	0.48 ± 0.11
OO021	3	0.56 ± 0.09	0.58 ± 0.14	0.38	0.5
OO052	5	0.66 ± 0.2	0.63 ± 0.24	0.47 ± 0.16	0.45 ± 0.13
PO043	3	0.71	0.71	-	-
PO225	2	-	-	0.3	0.29
RR217	2	-	-	0.23	0.25
WW061	4	0.56	0.66	0.28 ± 0.07	0.35 ± 0.01
YY039	2	-	-	0.09	0.04
YY189	7	0.61 ± 0.14	0.62 ± 0.11	0.51 ± 0.17	0.52 ± 0.15
		0.54 ± 0.15	0.57 ± 0.15	0.45 ± 0.17	0.47 ± 0.15
		<u>50% 3D-UD</u>			
GG335	6	0.12 ± 0.07	0.25 ± 0.22	0.14 ± 0.17	0.19 ± 0.15
OO021	3	0.38 ± 0.05	0.44 ± 0.02	0.21	0.26
OO052	5	0.57 ± 0.04	0.62 ± 0.41	0.29 ± 0.31	0.24 ± 0.27
PO043	3	0.62	0.62	-	-
PO225	2	-	-	0.07	0.08
RR217	2	-	-	0	0
WW061	4	0.22	0.56	0.02 ± 0.03	0
YY039	2	-	-	0	0
YY189	7	0.37 ± 0.22	0.44 ± 0.14	0.22 ± 0.2	0.3 ± 0.19
		0.31 ± 0.21	0.39 ± 0.23	0.2 ± 0.22	0.22 ± 0.2

601 **Table 3: Repeatability (*r*) values of habitat use parameters.**

Parameter	Repeatability (<i>r</i>)
Daytime 95% 3D UD (kernel volume)	0.62
Night-time 95% 3D UD (kernel volume)	0.60
Daytime 50% 3D UD (kernel volume)	0.61
Night-time 50% 3D UD (kernel volume)	0.67
Maximum distance travelled from MI	0.62
Bearing of maximum distance point from MI	0.53

602 **Repeatability (*r*) values were calculated from intra-class correlation coefficients.**

603

604

605 **Figure captions.**

606

607 **Figure 1:** Post-moult track locations for nine southern elephant seals tracked over multiple
608 years. The grey-shaded polygon represents the overlap between the 95% kernel density
609 utilization distributions for all tracks.

610

611 **Figure 2:** Three-dimensional kernel density utilization distributions (3D-UDs) over multiple
612 years for five southern elephant seals. Darker shading indicates 50% 3D-UDs and lighter
613 shading 95% 3D-UDs.

614

615 **Figure 3:** Hierarchical cluster analysis of migration strategies of southern elephant seals
616 tracked over multiple post-moult migrations, illustrating the three identified behavioural
617 clusters (C1-C3). Locations of migrations identified in each of the clusters are presented in
618 the three maps. Positions of all track locations not within a particular cluster are illustrated in
619 light grey. PO225 is represented in only one migration, due to a comparatively low number of
620 recorded daytime dive depths in 2007. STF = Subtropical Front, SAF = Subantarctic Front,
621 APF = Antarctic Polar Front. Frontal locations were determined from Swart & Speich (2010).

1 **Introduction**

2 Many species display foraging site fidelity, returning repeatedly to the same foraging areas
3 (e.g. Augé, Chilvers, Moore, & Davis, 2014; Weber et al., 2015), even when habitat quality is
4 sub-optimal (Krebs, 1971; Merkle, Cherry, & Fortin, 2015). Fidelity to foraging areas may
5 have long-term advantages for individual fitness, particularly in unpredictable environments
6 (Switzer, 1993). For example, animals may return to foraging areas because they are familiar
7 with resources (Greenwood, 1980) and able to exploit comparatively productive areas,
8 resulting in long-term energetic gains. Animals may also return to certain areas because they
9 are familiar with potential refuges and able to avoid predation (Clarke et al., 1993; Forrester,
10 Casady, & Wittmer, 2015). The benefits of long-term site fidelity may have short-term costs
11 if sufficient food cannot be found in temporally heterogeneous environments (Bradshaw,
12 Hindell, Sumner, & Michael, 2004). More significant fitness costs of site fidelity may be
13 incurred when animals are unable to respond to short- and medium term changes in food
14 availability by switching between foraging patches (e.g. Newell, 1999; Whisson, Dixon,
15 Taylor, & Melzer, 2016). Once an individual has learned a behaviour it may be hesitant to
16 change or to adopt new foraging strategies, especially if the associated risks are great. The
17 risks of looking for new foraging patches may be particularly great if foraging patches are far
18 apart or are of unpredictable quality.

19

20 Individual animals sometimes display individual-level foraging fidelity, where the
21 intra-individual variation in space use is less than the inter-individual variation in space use
22 within a population (Wakefield et al., 2015). Individual-level foraging fidelity may be a type
23 of individual specialization, best explained by phenotypic trade-offs when specialization in
24 one strategy results in the inability to efficiently perform an alternative strategy (Bolnick et
25 al., 2003). Various foraging behaviours such as prey recognition, capture ability, digestive

26 capacity and predator avoidance strategies may be affected. The existence of individual-level
27 specialization, in terms of site fidelity and dietary specialization, has long been recognized
28 but rarely explicitly considered in ecological studies (Piper, 2011).

29

30 Foraging site fidelity has been widely illustrated in marine vertebrates, including
31 marine birds (e.g. Baylis et al., 2015), turtles (e.g. Carman et al., 2016), fish (e.g. Gannon et
32 al., 2015) and marine mammals (e.g. Vermeulen et al., 2016). Pinnipeds in particular often
33 display high levels of foraging site fidelity (e.g. Arthur et al., 2015; Baylis et al., 2015; Wege,
34 Tosh, de Bruyn, & Bester, 2016). Fidelity to large-scale foraging areas was demonstrated for
35 southern elephant seals (*Mirounga leonina*), but individual seals that were faithful to foraging
36 areas did not show mass gain benefits (Bradshaw et al., 2004). However, it was proposed that
37 returning to generally more productive areas could result in benefits over longer timescales
38 (Bradshaw et al., 2004). Also, Authier et al. (2012) illustrated that lower variation in the
39 isotopic foraging niche of male southern elephant seals covaried positively with estimated
40 lifespans, thereby suggesting lifetime fitness benefits associated with foraging fidelity in this
41 species. While these reports provide valuable insights, little information is available
42 regarding the foraging area fidelity of individual elephant seals over the long term (3+ years)
43 and no information exists on fidelity to specific foraging strategies used to exploit the vertical
44 dimension.

45

46 Animal space use is typically quantified in two dimensions, despite the fact that
47 most animals also use space in a vertical dimension (i.e. by flying, diving or burrowing).
48 Incorporating the vertical component into representations of space use may provide novel
49 ecological insights and have conservation management benefits (Tracey et al., 2014). Habitat
50 use studies have attempted to incorporate the vertical dimension through separate analyses of

51 vertical metrics without incorporating spatial position (2-dimensions). Some recent studies,
52 particularly on marine predators, have incorporated the vertical behaviour component (e.g.
53 spherical first-passage time, Bailleul, Lesage, & Hammill, 2010). More recently, three
54 dimensional utilization distributions (3D UD) quantified vertical space use and home range
55 overlap of sharks (Simpfendorfer, Olsen, Heupel, & Moland, 2012) and birds (Cooper,
56 Sherry, & Marra, 2014).

57

58 Southern elephant seals have a circumpolar distribution and their foraging behaviour
59 is closely linked to their specific haul-out sites (Hindell et al., 2016). Elephant seals display a
60 high degree of fidelity to their haul-out sites (Hofmeyr, Kirkman, Pistorius, & Bester, 2012),
61 which may be an important indication of learned behaviour in these animals. Here we assess
62 (1) the persistence of migration site fidelity in southern elephant seals; (2) fidelity to a three-
63 dimensional environment, particularly the water depths exploited; and (3) the individual
64 repeatability and specialization of migration strategies. We predicted that foraging site
65 fidelity in elephant seals would decay over the long-term, due to the spatiotemporally patchy
66 nature of their prey distribution (i.e. that site fidelity would persist only as long as prey
67 patches persist – Kamil, 1983). Fidelity to three-dimensional environments was expected to
68 be lower, both as a result of variation in the vertical distribution of prey items, as well as the
69 influences of physiological development and ageing on the dive capacity of seals. Finally, the
70 propensity for Marion Island's elephant seals to forage in deep ocean areas, south-west of the
71 island (Hindell et al., 2016; Oosthuizen, Bester, Altwegg, McIntyre, & de Bruyn, 2015) led to
72 a prediction of limited individual-level specialization in migration strategies.

73

74 **Methods**

75 *Ethical Note*

76 The research described refers to an Antarctic seal species, the southern elephant seal. It
77 conforms to Antarctic Treaty legislation and to the SCAR Code of Conduct for the Use of
78 Animals for Scientific Purposes in Antarctica (ATCM XXXIV 2011). We adhere to the
79 ‘Guidelines for the use of animals in research’ as published in *Animal Behaviour* (1990, 41,
80 183–186) and the laws of the country where the research was conducted. All flipper tagging
81 and satellite device deployment/retrieval procedures were reviewed and approved by the
82 Animal Use and Care Committee and more recently the renamed Animal Ethics Committee
83 of the University of Pretoria (AUCC 040827-024; AUCC 040827-023 and EC077-15), and
84 fieldwork was performed under Prince Edward Island’s Research Permits R8-04 and R04-08.
85 All dive and track data are available via the PANGAEA Data Publisher for Earth &
86 Environmental Science (doi:10.1594/PANGAEA.871448).

87

88 *Track data and filtering*

89 As part of a series of tracking projects between April 2004 and February 2013, we deployed
90 95 satellite-relay data loggers (either Series 9000 SRDLs, or CTD-SRDLs, Sea Mammal
91 Research Unit, University of St Andrews, Scotland) on southern elephant seals of both sexes
92 hauled out at sub-Antarctic Marion Island (46° 54’S; 37° 45’E). These instruments provided
93 track locations (obtained via Service Argos estimates), basic time-depth profiles of
94 approximately 20 dives per day and a maximum of four temperature-depth profiles per day
95 (Boehme et al., 2009).

96

97 Uniquely marked (de Bruyn, Tosh, Oosthuizen, Phalanndwa, & Bester, 2008) seals
98 were immobilized using a handheld syringe, extended by a length of drip-tubing, to deliver a
99 calculated dose of ketamine based on a visual estimation of the seal's mass (Bester, 1988).

100 Seals were then observed from a distance until the anticipated end of the induction period

101 (about 20 min post-injection), and then approached for the first time to assess the depth of
102 anaesthesia by evaluating reactions to stimuli (e.g. slight noise and touch) (Bornemann et al.,
103 2013). As soon as the seals tolerated physical stimuli, their eyes were covered with a towel to
104 protect against solar radiation and minimise unnecessary stimuli. Transmitters were glued
105 onto the fur of the heads of the seals using a quick-setting epoxy resin (Field et al., 2012).
106 The heaviest of these devices (CTD-SRDLs) weighed 545 g, representing 0.19% of the
107 average post-moult departure mass of female elephant seals from this population (Postma,
108 Bester, & De Bruyn, 2013). After their post-migration return to the island, data transmitting
109 devices were either removed from sedated animals by shaving them off the fur or shed
110 naturally with the pelage during the annual moult. No short-term deleterious effects were
111 evident with immobilization, device deployment or retrieval, while tracking devices attached
112 to elephant seals are known not to affect individual mass gain or survival in the long term
113 (McMahon, Field, Bradshaw, White, & Hindell, 2008). We report on a subset of the resultant
114 dataset, after retaining data from 34 post-moult migrations (as opposed to post-breeding
115 migrations, Le Boeuf & Laws, 1994) from nine individual seals (two males and seven
116 females) that successfully carried instruments over multiple winter migrations (Table 1).
117 Only tracks with data for a minimum period of 30 days were included. Seals in this sample
118 provided tracking and dive data for a median of three migrations (range: 2 – 7), each
119 migration covering a median period of 223 days (range: 38 – 292).

120

121 All statistical analyses were undertaken in the R programming environment (Team,
122 2016). Track data were filtered to remove estimated locations that required swim speeds in
123 excess of 3.5 m/s and/or creating spikes in the track with angles smaller than 15° and 25°
124 with extensions greater than 2,500 m and 5,000 m, respectively (Freitas, Lydersen, Fedak, &
125 Kovacs, 2008).

126

127 *Inter-annual and multi-year fidelity*

128 Fidelity to home ranges was expressed as the overlap in 95% kernel density utilization
129 distributions (UD) of two dimensional location data (latitude and longitude) and three
130 dimensional diving data (latitude, longitude and dive depth). The two dimensional UD were
131 calculated using an *ad hoc* smoothing parameter, which assumes a bivariate normal UD in the
132 R package '*adehabitatHR*' (Calenge, 2015). Overlap of two-dimensional UD was calculated
133 following Arthur et al. (Arthur et al., 2015), using Bhattacharyya's affinity (BA) for a general
134 measure of similarity between UD estimates.

135

136 Daily median dive depth values were calculated for each two dimensional location
137 to create a three dimensional dataset. We divided the datasets into daytime and nocturnal
138 dives, as southern elephant seals often display diel vertical migration (e.g. Biuw et al., 2010;
139 McIntyre, Bornemann, Plötz, Tosh, & Bester, 2011). Three dimensional kernel density
140 utilisation distributions (3D-UD) were estimated in the '*ks*' package (Duong, 2016), using a
141 two-stage plug-in method, developed by Duong and Hazelton (2003) and applied by
142 Simpfendorfer et al. (2012) and Cooper et al. (2014) amongst others. We calculated overlap
143 in 95% 3D-UDs both inter-annually and over multiple years (multi-year) for individual seals,
144 following Simpfendorfer et al. (2012). Inter-annual overlap is the overlap for tracks from
145 consecutive years (e.g. overlap between 2006 and 2007; 2007 and 2008 etc.), while multi-
146 year overlap was calculated between tracks separated by a year or more (e.g. overlap between
147 2006 and 2008; 2006 and 2009 etc.).

148

149 *Repeatability*

150 We applied a repeatability statistic to a series of track and behavioural metrics to assess
151 individual behavioural consistency compared to the behaviours displayed by all the seals in
152 the dataset. This repeatability statistic was calculated, making use of an intra-class correlation
153 coefficient (Wolak, Fairbairn, & Paulsen, 2012), following McFarlane Tranquilla et al.
154 (2014). Accordingly, among-groups variance (s_A^2) and within-individual variance
155 components (s^2) are derived from a linear mixed-effects model (R package ‘*psychometric*’).
156 Repeatability (r) was then calculated as:

$$r = \frac{s_A^2}{(s^2 + s_A^2)}$$

157 where high r values (> 0.5) indicate consistent individual behaviours.

158

159 The repeatability statistic was applied to the following track and behavioural
160 metrics: (1) the daytime and nocturnal 95% and 50% 3D-UDs incorporating the dive depths
161 of tracked seals; (2) the maximum distance travelled away from Marion Island per migration
162 and (3) the bearing of the location at the maximum distance away from Marion Island.

163

164 *Hierarchical clustering*

165 We explored the possibility of individually specific migration strategies (consistent long term
166 behaviour) using a hierarchical clustering approach. A principal components analysis (PCA)
167 was first applied to a series of track- and dive metrics to generate a single metric
168 representative of an overall strategy. Six daily metrics were included in the PCA: (1) median
169 daytime dive depth; (2) median night-time dive depth; (3) diel vertical migration (defined as
170 the difference between daytime and night-time median dive depths); (4) distance from
171 Marion Island; (5) bearing from Marion Island; and (6) mean speed of travel (mean speed of
172 travel between all locations associated with a specific day). The first five principal
173 components explained 93.7% of the variance. The relative contribution of each principal

174 component to a single, weighted metric was determined from the loadings of the PCA output.
175 This value was used in a hierarchical clustering analysis, using Ward's clustering criterion
176 (Ward, 1963) on a Euclidean distance matrix.

177

178 **Results**

179 *Home range overlap*

180 Seven of the nine seals tracked over multiple migrations had overlapping 95% UD's that
181 encompassed more than 50% of their home ranges (UD overlap > 0.5) (Fig. 1). Two
182 individual seals tracked twice in non-consecutive years (RR217:2009, 2011 and
183 YY039:2008, 2011), had comparatively disparate UD's, characterised by small areas of
184 overlap (0.31 and 0.19 respectively, Table 1). Mean inter-annual overlap of 95% UD's was
185 0.73 ± 0.14 (Table 1). Overlap of UD's for multi-year periods were slightly lower at $0.61 \pm$
186 0.18 . Inter-annual overlap of 95% UD's was consistently high for individuals tracked over
187 consecutive migrations, with a minimum overlap of 0.65 ± 0.17 (maximum of 0.91 ± 0.03).
188 Multi-year overlap was more variable, ranging from 0.19 to 0.92 (Table 1).

189

190 *Three-dimensional UD overlap*

191 The mean inter-annual overlap of 95% 3D-UD's was 0.54 ± 0.15 for daytime dives and $0.57 \pm$
192 0.15 for nocturnal dives. Overlap was slightly lower for multi-year periods at 0.45 ± 0.17 for
193 daytime dives and 0.47 ± 0.15 for nocturnal dives. Five of the six seals that were tracked in
194 consecutive years, recorded 95% 3D-UD's that overlapped by 60% - 71%. Individual
195 variation was evident, with some seals using very similar three-dimensional spaces over long
196 time periods (e.g. YY189, Fig. 2, Table 2), while others used slightly different depths
197 between years (e.g. GG335, Fig. 2, Table 2) and others used completely different depths (e.g.
198 PO225, Fig. 2, Table) despite substantial overlap in the two dimensional 95% UD (Fig. 1).

199 Areas of restricted movement or 50% 3D-UDs overlapped much less and was more variable
200 between seals (Table 2), although two seals (PO043 and OO052) had similar areas of
201 restricted movement and diving behaviours in consecutive years (50% 3D-UDs overlap =
202 approximately 60%).

203

204 Two seals (PO225 and GG335) used similar oceanographic areas (2-D UD) (Fig. 1)
205 but had very different diving behaviours (3-D –UD) (Fig. 2) in their subsequent migrations.
206 GG335 dived to varied depths but maintained a substantial overlap in 3D-UDs over the 5
207 years that it was tracked. This seal employed two general diving strategies, performing
208 deeper dives in the last two migrations (2011, 2012), compared to the preceding three years
209 (Fig. 2). PO225 dived to variable depths during its 2007 migration but used more specific
210 depth layers in 2011.

211

212 *Repeatability*

213 All repeatability (r) values were larger than 0.5 (Table 3), suggesting consistency in
214 individual behaviours. The lowest value (0.53) was calculated for track bearings of the point
215 furthest away from Marion Island, indicating least consistency for this metric. All other r
216 values were equal to or larger than 0.6 (Table 3), indicating high levels of consistency in the
217 three-dimensional area sizes used by seals and distances travelled away from Marion Island.

218

219 *Hierarchical clustering*

220 Five principal components (PCs) explained 93.7% of the variance in our dataset and included
221 both horizontal movement and vertical dive behaviour metrics. PC1 was most strongly
222 associated with DVM, PC2 with distance and bearing from Marion Island + night-time dive

223 depths, PC3 with daytime dive depths, PC4 with travel speed and PC5 with bearing and
224 distance.

225

226 Hierarchical clustering revealed three distinct migration strategies used by the
227 tracked seals (Fig. 3), and multiple tracks of individual seals tended to group together in the
228 same clusters (e.g. OO052, GG335). Two individuals (WW061 and RR217) grouped in two
229 different clusters. Seals grouping into specific clusters generally foraged in the same areas.
230 For example, GG335 (2007) and WW061 (2008) both travelled in a westerly direction away
231 from Marion Island (and further), compared to their other migrations (Fig. 1). These
232 migrations clustered with all of the migrations recorded for OO021 (Fig. 3), which used a
233 similar spatial area (Fig. 1).

234

235 Migrations in cluster 1 (C1) covered a wide latitudinal range, from the Subtropical
236 Front in the north to south of the APF (Fig. 3). Migrations in cluster 3 (C3) were
237 characterised by the greatest distances away from Marion Island, but restricted to latitudes
238 south of the Subantarctic Front, with many of the tracks concentrated south of the Antarctic
239 Polar Front (APF). Cluster two (C2) comprised of tracks from one seal (OO052), which used
240 a small area adjacent to Marion Island during all five of its post-moult migrations.

241

242 **Discussion**

243 Studies of fidelity to migration strategies over long-distances and long time periods, are often
244 restricted to few migrations (e.g. two or three) (Mingozzi, Mencacci, Cerritelli, Giunchi, &
245 Luschi, 2016), although a few recent studies have successfully tracked seasonally migrating
246 birds over multiple years (e.g. Berthold et al., 2002; Lopez-Lopez et al., 2014; Vardanis,
247 Nilsson, Klaassen, Strandberg & Alerstam, 2016). Similarly, individual foraging site fidelity

248 in elephant seals has only been studied from a small number of migrations, not separated by
249 more than one or two years (e.g. Bradshaw et al., 2004; Simmons, 2008). In one study, a
250 single northern elephant seal, *M. angustirostris*, followed the same path in 2006 as it did 11
251 years previously in 1995; although the North American continent predisposes migration by
252 this species to a westerly bearing away from haulout sites (Costa, Breed, & Robinson, 2012).
253 Our study followed a small number of individual seals and reports on continued fidelity over
254 long distances and time periods not reported before. Seals tracked in our sample showed high
255 overlap in 95% UD_s, even over extended periods of up to seven years – averaging more than
256 60% for both consecutive and non-consecutive migrations (Table 1). The long-term fidelity
257 to oceanographic areas used by seals included their use of the vertical environment, and
258 overlap in 95% 3D-UD_s averaged more than 45% over multi-year comparisons and more
259 than 50% for consecutive years.

260

261 Individual-level flexibility in inter-annual migration routes has been illustrated for
262 some migrating birds known to forage on prey items that are variably distributed (Vardanis,
263 Nilsson, Klaassen, Strandberg & Alerstam, 2016), although the drivers of such flexibility
264 remain unknown. Bradshaw et al. (2004) were unable to link foraging success of tracked
265 southern elephant seals to the likelihood that they would alter their foraging strategies,
266 suggesting that elephant seals do not follow the win-stay/lose-switch rule (Shields, Cook,
267 Hebblethwaite, & Wiles-Ehmann, 1988) over shorter time periods. Alternatively, they
268 suggested that elephant seals would benefit over longer periods by returning to areas with
269 generally increased productivity. While the condition of seals tracked in our sample is
270 unknown and we were unable to assess the impacts of migration strategies, the long-term
271 fidelity to migration patterns and oceanographic areas apparently supports the hypothesis of
272 Bradshaw et al. (2004) that the win-stay/lose-switch rule does not apply over multiple

273 migrations in elephant seals. However, the reasonably small sample size we report on here
274 does not exclude the possibility that tracked seals rarely encountered such poor foraging
275 success as to prompt any switches in strategy.

276

277 Two seals in our sample (PO225 and GG335) displayed much more overlap in
278 their 2D UD_s, compared to their 3-D UD_s (Figs. 1 and 2). GG335 evidently switched its
279 depth use strategy once between 2010 and 2011, performing deeper dives in 2011 and 2012
280 when compared to the earlier tracks. The two migrations of PO225 (2007; 2011) were 3 years
281 apart, limiting any hypotheses on the development of dive behaviour. However, it is unlikely
282 that the observed differences in diving behaviour are due to ontogenic development of diving
283 capacity (Bennett, McConnell, & Fedak, 2001), because this seal was first tracked as an
284 adult, eight year old male and diving capacity does not develop substantially once a seal
285 reaches maturity (Grundling, 2014). Elephant seal dive strategies may change within-
286 migrations (e.g. Bester, Bornemann, & McIntyre, in press; Biuw et al., 2010; McIntyre,
287 Ansorge, et al., 2011), indicating that elephant seals are often able to exploit localised prey
288 patches at different depths. The dissimilar diving behaviour seen in different migrations of
289 PO225 and GG335 further suggests an element of inter-annual plasticity in foraging
290 strategies. Long-term longitudinal tracking investigations are needed to explore these shifts in
291 diving strategies.

292

293 Seal behaviours in our study showed high levels of individual repeatability (r).
294 Combined with the outputs of the clustering exercise, these results suggest a high level of
295 individual specialization in migration behaviour. Individual variation in southern elephant
296 seal behaviours, and other marine predators, has been acknowledged and recently accounted
297 for in behavioural modelling exercises (e.g. Farnsworth et al., 2015; Massie et al., 2016;

298 Stillfried, Belant, Svoboda, Beyer, & Kramer-Schadt, 2015). Moreover, recent studies have
299 illustrated consistency and specialization in individual behaviour (e.g. Wakefield et al.,
300 2015). Southern elephant seals employ various foraging strategies, exploiting shallow water
301 masses associated with the Kerguelen Plateau, and the Antarctic Peninsula, or using deep,
302 open water regions in the Southern Ocean (Hindell et al., 2016). Female elephant seals in the
303 Antarctic Peninsula region display individual behavioural and foraging niche specialization
304 with substantial within-migration behavioural plasticity (Hückstädt et al., 2012). Similarly,
305 Marion Island elephant seals use three broad migration strategies (clusters) (Fig. 3), which
306 were identified from diel vertical migration patterns, dive depths, and distance and bearing
307 from Marion Island.

308

309 *Implication of long-term fidelity and individual specialization*

310 The Southern Ocean is rapidly changing with a generally warming and freshening trend
311 leading to expected poleward shifts in the distribution of lower trophic level consumers
312 (Constable et al., 2014). The long-term spatial fidelity of elephant seals, including three-
313 dimensional environments (this study), has potential implications for our understanding of
314 their behavioural response to disturbance. The origin of fidelity described here is unknown
315 and is not analysed in detail. However, site familiarity and fidelity may develop if juvenile
316 elephant seals are successful during their first foraging migration (Bradshaw et al., 2004).
317 This would suggest that environmental conditions experienced in early migrations may have
318 consequences for future migration strategies (Dall, Bell, Bolnick, & Ratnieks, 2012). Juvenile
319 southern elephant seals tracked from Marion Island generally travel due west, irrespective of
320 year, and focus their foraging behaviour along bathymetric features, frontal zones and meso-
321 scale eddies (Tosh et al., 2012; 2015), adding to their familiarity of the surrounding ocean.
322 While the intra-migration dive behaviour of southern elephant seals is known to respond to

323 changes in the temperature structure of the water column and associated changes in the
324 distribution of potential prey items (Guinet et al., 2014; McIntyre, Ansorge, et al., 2011), the
325 long-term fidelity to foraging areas and diving behaviour may limit coarser-scale movement
326 and behavioural adaptations of individual elephant seals to rapid environmental changes,
327 although this requires further investigation. Similarly, other taxa such as seabirds and marine
328 turtles, which rely on site-specific information gained early in life, may be more vulnerable to
329 rapid environmental change and other anthropogenic disturbances (Hipfner, 2008; Vander
330 Zanden et al., 2016; Wakefield et al., 2015). Future research needs to elucidate the role of
331 long-term behavioural adaptations in individual elephant seals in response to rapid
332 environmental change, particularly through long-term longitudinal monitoring of fitness
333 consequences associated with behavioural changes in relation to environmental differences.

334

335 Our results show the value of long-term data on known individuals for illustrating
336 individual repeatability, and potentially specialization, in the migration strategies of animals.
337 Tracking studies are often used for conservation planning and environmental management
338 purposes (e.g. Jabour et al., 2016). Such studies can benefit from incorporating seasonal
339 variation in habitat use of target species (Braham et al., 2015), as well as samples
340 representing substantial spatial variation (Mazor, Beger, McGowan, Possingham, & Kark,
341 2016). However, while the influence of individual differences on our understanding of animal
342 ecology is recognised (Dall et al., 2012), it is seldom implemented in population-level
343 studies. Bolnick et al (2011) highlights that individual specialisation or phenotypic expression
344 can have serious implications for studies on the ecology, evolution and conservation of
345 populations. For example, resource selection models which assume foragers are informed
346 about their total surroundings to select the most favourable areas would benefit from
347 incorporating effects associated with individual familiarity and fidelity (Wakefield et al.,

348 2015). Our study provides further support to the call for long-term longitudinal research
349 quantifying the influence of site familiarity, site fidelity and resource specialization on animal
350 population dynamics.

351

352

353

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590

591

592 **Tables**593 **Table 1:** Elephant seals tracked over multiple migrations.

Tag	Sex	N	Age at deployments	Years successfully tracked	Inter-annual UD overlap	Multi-year UD overlap
GG335	F	6	7,8,9,10,11,12	2007,2008,2009,2010,2011,2012	0.65 ± 0.17	0.57 ± 0.15
OO021	F	3	5,6,7	2007,2008,2009	0.91 ± 0.03	0.92
OO052	M	5	4,5,6,9,11	2006,2007,2008,2011,2013	0.74 ± 0.09	0.64 ± 0.19
PO043	F	3	8,9,10	2007,2008,2009	0.69 ± 0.13	0.48
PO225	M	2	8,12	2007,2011	-	0.74
RR217	F	2	4,6	2009,2011	-	0.31
WW061	F	4	7,10,11,12	2008,2011,2012,2013	0.87 ± 0.09	0.58 ± 0.19
YY039	F	2	4,7	2008,2011	-	0.19
YY189	F	7	2,3,4,5,6,8,9	2006,2007,2008,2009,2010,2012,2013	0.71 ± 0.09	0.64 ± 0.19

594 Mean (\pm SD) overlap in inter-annual utilization distributions, as well as mean (\pm SD) overlap
595 in multiple-year utilization distributions, are reported. Only tracks over periods of more than
596 30 days (median: 223, range: 38 – 292) were included.

597 **Table 2:** Inter-annual and multi-year overlap in 95% and 50% three-dimensional utilization
 598 distributions (3D-UDs) for southern elephant seals.

<i>Tag</i>	<i>N</i>	<u>95% 3D-UD</u>			
		Inter-annual		Multi-year	
		<i>Day</i>	<i>Night</i>	<i>Day</i>	<i>Night</i>
GG335	6	0.43 ± 0.1	0.51 ± 0.15	0.41 ± 0.15	0.48 ± 0.11
OO021	3	0.56 ± 0.09	0.58 ± 0.14	0.38	0.5
OO052	5	0.66 ± 0.2	0.63 ± 0.24	0.47 ± 0.16	0.45 ± 0.13
PO043	3	0.71	0.71	-	-
PO225	2	-	-	0.3	0.29
RR217	2	-	-	0.23	0.25
WW061	4	0.56	0.66	0.28 ± 0.07	0.35 ± 0.01
YY039	2	-	-	0.09	0.04
YY189	7	0.61 ± 0.14	0.62 ± 0.11	0.51 ± 0.17	0.52 ± 0.15
		0.54 ± 0.15	0.57 ± 0.15	0.45 ± 0.17	0.47 ± 0.15
<u>50% 3D-UD</u>					
GG335	6	0.12 ± 0.07	0.25 ± 0.22	0.14 ± 0.17	0.19 ± 0.15
OO021	3	0.38 ± 0.05	0.44 ± 0.02	0.21	0.26
OO052	5	0.57 ± 0.04	0.62 ± 0.41	0.29 ± 0.31	0.24 ± 0.27
PO043	3	0.62	0.62	-	-
PO225	2	-	-	0.07	0.08
RR217	2	-	-	0	0
WW061	4	0.22	0.56	0.02 ± 0.03	0
YY039	2	-	-	0	0
YY189	7	0.37 ± 0.22	0.44 ± 0.14	0.22 ± 0.2	0.3 ± 0.19
		0.31 ± 0.21	0.39 ± 0.23	0.2 ± 0.22	0.22 ± 0.2

600 **Table 3:** Repeatability (*r*) values of habitat use parameters.

Parameter	Repeatability (<i>r</i>)
Daytime 95% 3D UD (kernel volume)	0.62
Night-time 95% 3D UD (kernel volume)	0.60
Daytime 50% 3D UD (kernel volume)	0.61
Night-time 50% 3D UD (kernel volume)	0.67
Maximum distance travelled from MI	0.62
Bearing of maximum distance point from MI	0.53

601 Repeatability (*r*) values were calculated from intra-class correlation coefficients.

602

603 **Figure captions.**

604

605 **Figure 1:** Post-moult track locations for nine southern elephant seals tracked over multiple
606 years. The grey-shaded polygon represents the overlap between the 95% kernel density
607 utilization distributions for all tracks.

608

609 **Figure 2:** Three-dimensional kernel density utilization distributions (3D-UDs) over multiple
610 years for five southern elephant seals. Darker shading indicates 50% 3D-UDs and lighter
611 shading 95% 3D-UDs.

612

613 **Figure 3:** Hierarchical cluster analysis of migration strategies of southern elephant seals
614 tracked over multiple post-moult migrations, illustrating the three identified behavioural
615 clusters (C1-C3). Locations of migrations identified in each of the clusters are presented in
616 the three maps. Positions of all track locations not within a particular cluster are illustrated in
617 light grey. PO225 is represented in only one migration, due to a comparatively low number of
618 recorded daytime dive depths in 2007. STF = Subtropical Front, SAF = Subantarctic Front,
619 APF = Antarctic Polar Front. Frontal locations were determined from Swart & Speich (2010).

620

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Figure 1
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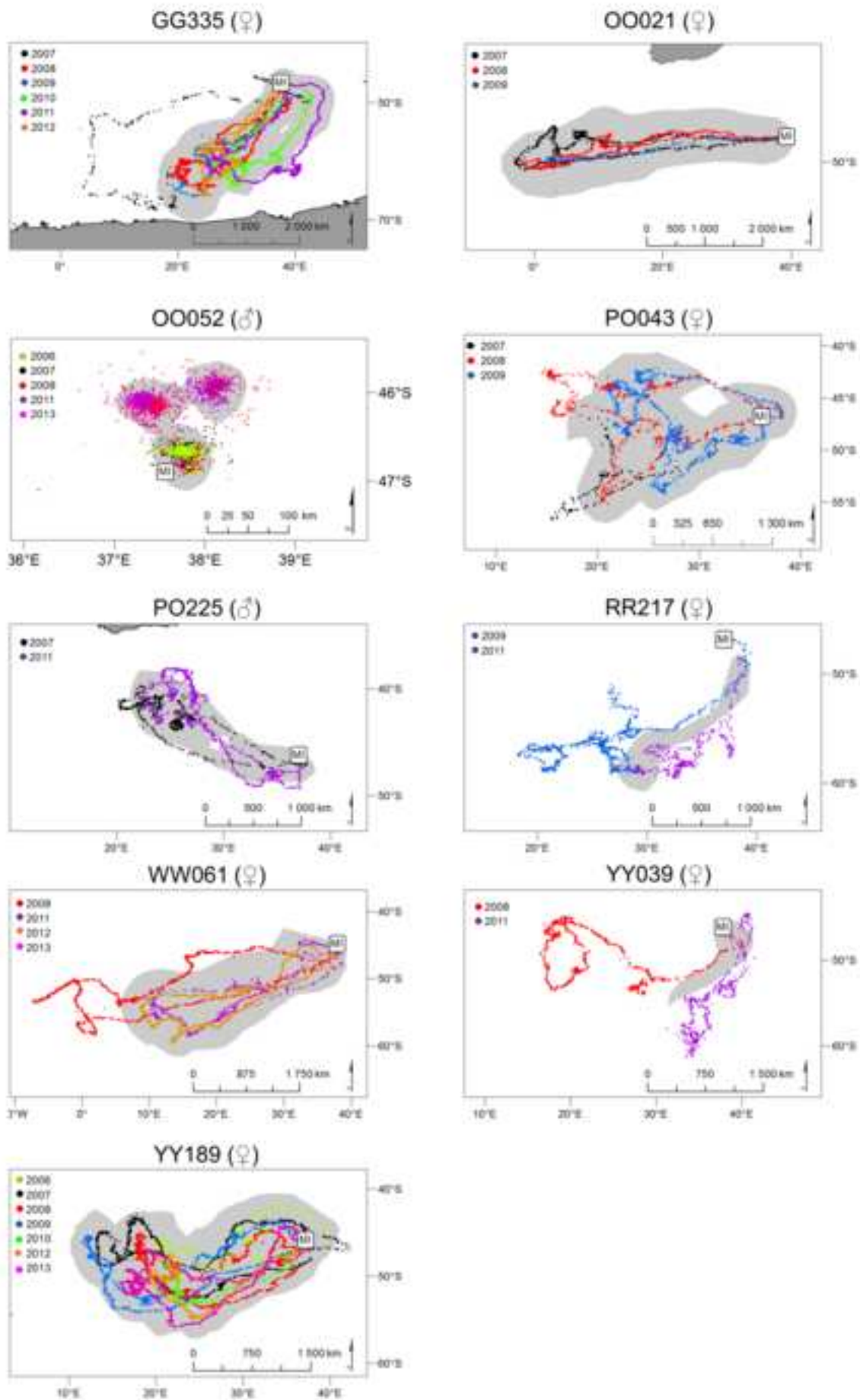
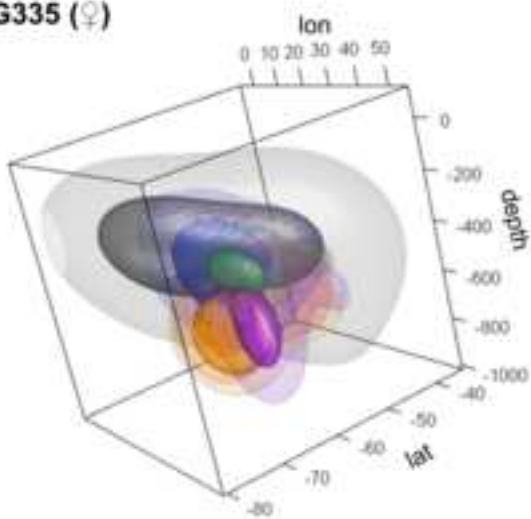
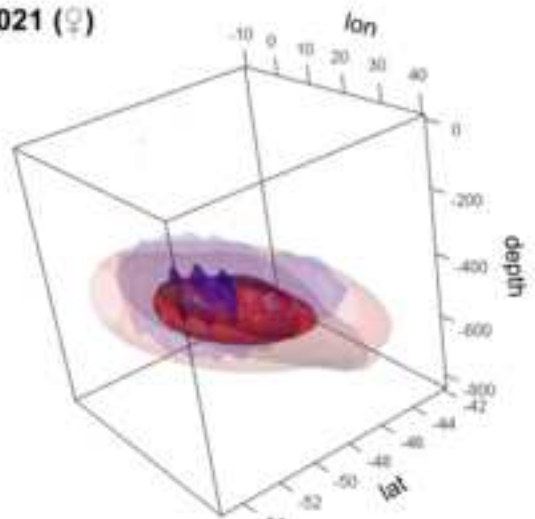


Figure 2
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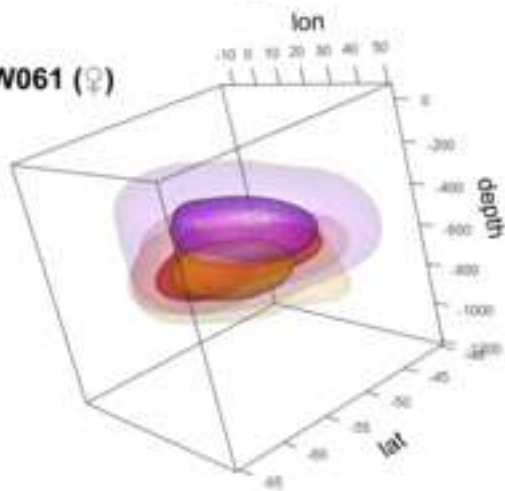
GG335 (♀)



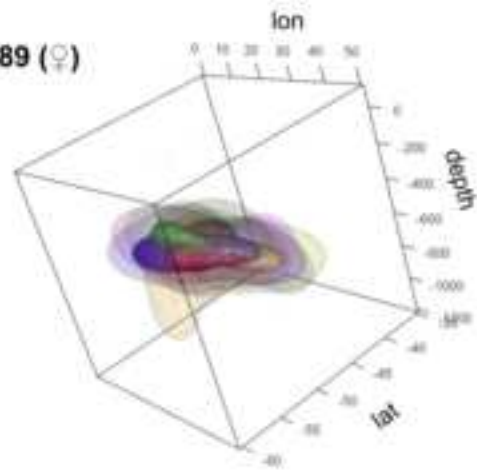
OO021 (♀)



WW061 (♀)



YY189 (♀)



PO225 (♂)

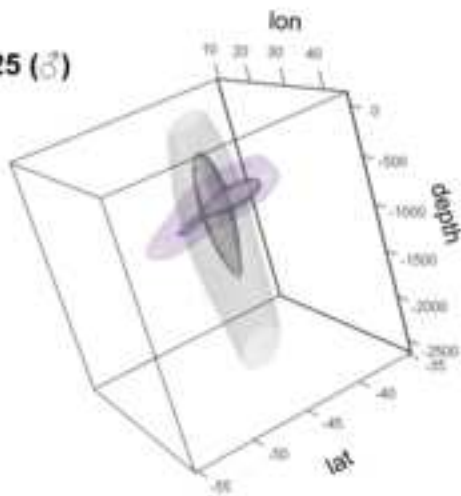


Figure 3
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