Manuscript Number: ANBEH-D-16-00994R2

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

Article Type: UK Research paper

Corresponding Author: Dr. Trevor McIntyre,

Corresponding Author's Institution: University of Pretoria

First Author: Trevor McIntyre

Order of Authors: Trevor McIntyre; Marthán Bester; Horst Bornemann; Cheryl Tosh; Nico de Bruyn

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*

**Authors:** Trevor McIntyre[1] (corresponding author), Marthán N. Bester[1], Horst Bornemann[2], Cheryl A. Tosh[1], P. J. Nico de Bruyn[1]

**Addresses:**   1. Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield, 0028, South Africa.

2. Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Biosciences, Bentho-Pelagic Processes, PO Box 120161, 27515 Bremerhaven, Germany.

**Author for correspondence:**   Trevor McIntyre

e-mail: tmcintyre@zoology.up.ac.za

tel: +27 (0)12 420 4608

14 February 2017

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.

Trevor McIntyre & co-authors

Mammal Research Institute, Department of Zoology & Entomology
University of Pretoria, South Africa
Tel:              +27-12-4204608
Mobile:        +27-78-0243511
E-mail:          tmcintyre@zoology.up.ac.za

**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).

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

*Inter-annual and multi-year fidelity*

Fidelity to home ranges was expressed as the overlap in 95% kernel density utilization

distributions (UD) of two dimensional location data (latitude and longitude) and three

dimensional diving data (latitude, longitude and dive depth). The two dimensional UDs were

calculated using an *ad hoc* smoothing parameter, which assumes a bivariate normal UD in the

R package '*adehabitatHR*' (Calenge, 2015). Overlap of two-dimensional UDs was calculated

following Arthur et al. (Arthur et al., 2015), using Bhattacharyya's affinity (BA) for a general

measure of similarity between UD estimates.

Daily median dive depth values were calculated for each two dimensional location

to create a three dimensional dataset. We divided the datasets into daytime and nocturnal

dives, as southern elephant seals often display diel vertical migration (e.g. Biuw et al., 2010;

McIntyre, Bornemann, Plötz, Tosh, & Bester, 2011). Three dimensional kernel density

utilisation distributions (3D-UD) were estimated in the '*ks*' package (Duong, 2016), using a

two-stage plug-in method, developed by Duong and Hazelton (2003) and applied by

Simpfendorfer et al. (2012) and Cooper et al. (2014) amongst others. We calculated overlap

in 95% 3D-UDs both inter-annually and over multiple years (multi-year) for individual seals,

following Simpfendorfer et al. (2012). Inter-annual overlap is the overlap for tracks from

consecutive years (e.g. overlap between 2006 and 2007; 2007 and 2008 etc.), while multi-

year overlap was calculated between tracks separated by a year or more (e.g. overlap between

2006 and 2008; 2006 and 2009 etc.).

*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% UDs 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 $0.73 \pm 0.14$ (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 $0.65 \pm 0.17$ (maximum of $0.91 \pm 0.03$).

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 $0.54 \pm 0.15$ for daytime dives and $0.57 \pm$

192 0.15 for nocturnal dives. Overlap was slightly lower for multi-year periods at $0.45 \pm 0.17$ for

193 daytime dives and $0.47 \pm 0.15$ 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% UDs, 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 at 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 UDs, compared to their 3-D UDs (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

**References**

Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., … Lea, M.-A. (2015). Return customers: foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. *Plos One*, *10*, e0120888. doi:10.1371/journal.pone.0120888

ATCM (2011) SCAR's Code of Conduct for the Use of Animals for Scientific Purposes in Antarctica. IP53, Agenda Item CEP 8c, presented by SCAR during XXXIV Antarctic Treaty Consultative Meeting, Buenos Aires, Argentina, 20 June - 21 July 2011, 4pp. http://www.scar.org/scar_media/documents/science/atcm34_ip053_CofC_Animals.pdf

Augé, A. A., Chilvers, B. L., Moore, A. B., & Davis, L. S. (2014). Importance of studying foraging site fidelity for spatial conservation measures in a mobile predator. *Animal Conservation*, *17*, 61–71. doi:10.1111/acv.12056

Authier, M., Bentaleb, I., Ponchon, A., Martin, C., & Guinet, C. (2012). Foraging fidelity as a recipe for a long life: foraging strategy and longevity in male southern elephant seals. *PloS One*, *7*(4), e32026. doi:10.1371/journal.pone.0032026

Bailleul, F., Lesage, V., & Hammill, M. O. (2010). Spherical First Passage Time: A tool to investigate area-restricted search in three-dimensional movements. *Ecological Modelling*, *221*, 1665–1673.

Baylis, A. M. M., Orben, R. A., Arnould, J. P. Y., Peters, K., Knox, T., Costa, D. P., & Staniland, I. J. (2015). Diving deeper into individual foraging specializations of a large marine predator , the southern sea lion. *Oecologia*, *179*(4), 1053–1065. doi:10.1007/s00442-015-3421-4

Baylis, A. M. M., Orben, R. A., Pistorius, P., Brickle, P., Staniland, I., & Ratcliffe, N. (2015). Winter foraging site fidelity of king penguins breeding at the Falkland Islands. *Marine Biology*, *162*, 99–110. doi:10.1007/s00227-014-2561-0

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

379    Bennett, K. A., McConnell, B. J., & Fedak, M. (2001). Diurnal and seasonal variations in the

380         duration and depth of the longest dives in southern elephant seals (Mirounga leonina):

381         possible physiological and behavioural constraints. *Journal of Experimental Biology*,

382         *204*, 649–662.

383    Berthold, P., v. d. Bossche, W., Jakubiec, Z., Kaatz, C., Kaatz, M. & Querner, U. (2002).

384         Long-term satellite tracking sheds light upon variable migration strategies of White

385         Storks (*Ciconia ciconia*). *Journal of Ornithology*, *143*, 489-495.

386    Bester, M. N. (1988). Marking and monitoring studies of the Kerguelen stock of southern

387         elephant seals Mirounga leonina and their bearing on biological research in the Vestfold

388         Hills. *Hydrobiologia*, *165*, 269–277.

389    Bester, M. N., Bornemann, H., & McIntyre, T. (n.d.). Antarctic marine mammals and sea ice.

390         In D. N. Thomas & G. S. Dieckman (Eds.), *Sea Ice* (3rd ed.). Oxford: Wiley-Blackwell.

391    Biuw, M., Nøst, O. A., Stien, A., Zhou, Q., Lydersen, C., & Kovacs, K. M. (2010). Effects of

392         hydrographic variability on the spatial, seasonal and diel diving patterns of southern

393         elephant seals in the eastern Weddell Sea. *PLoS ONE*, *5*(11), e13816.

394         doi:10.1371/journal.pone.0013816

395    Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S. E., … Fedak, M.

396         (2009). Technical Note: Animal-borne CTD-Satellite Relay Data Loggers for real-time

397         oceanographic data collection. *Ocean Science*, *5*, 685–695.

398    Bolnick, D. I., Amarasekare, P., Araujo, M. S., R, B., Levine, J. M., Novak, M., … Vasseur,

399         D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in*

400         *Ecology and Evolution*, *26*(4), 183–192. doi:10.1016/j.tree.2011.01.009

401    Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., &

402         Forister, M. L. (2003). The ecology of individuals: incidence and implications of

403         individual specialization. *The American Naturalist*, *161*(1), 1–28.

404    Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays:

405        potential life history consequences of fidelity to marine foraging regions by southern

406        elephant seals. *Animal Behaviour*, *68*, 1349–1360.

407    Braham, M., Miller, T., Duerr, A. E., Lanzone, M., Fesnock, A., LaPre, L., … Katzner, T.

408        (2015). Home in the heat: Dramatic seasonal variation in home range of desert golden

409        eagles informs management for renewable energy development. *Biological

410        Conservation*, *186*, 225–232. doi:10.1016/j.biocon.2015.03.020

411    Calenge, C. (2015). Home Range Estimation in R : the adehabitatHR Package. Retrieved

412        from https://cran.r-project.org/web/packages/adehabitatHR/index.html

413    Carman, V. G., Bruno, I., Maxwell, S., Álvarez, K., Albareda, D., Acha, E. M., & Campagna,

414        C. (2016). Habitat use, site fidelity and conservation opportunities for juvenile

415        loggerhead sea turtles in the Río de la Plata, Argentina. *Marine Biology*, *163*.

416        doi:10.1007/s00227-015-2795-5

417    Clarke, M. F., da Silva, K. B., Lair, H., Pocklington, R., Kramer, D. L., & McLaughlin, R. L.

418        (1993). Site familiarity affects escape behaviour of the eastern chipmunk, Tamias

419        striatus. *Oikos*, *66*(3), 533–537.

420    Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes,

421        D. K. A., … Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I : how

422        changes in physical habitats directly affect marine biota. *Global Change Biology*.

423        doi:10.1111/gcb.12623

424    Cooper, N. W., Sherry, T. W., & Marra, P. P. (2014). Modeling three-dimensional space use

425        and overlap in birds. *Auk*, *131*, 681–693. doi:10.1642/AUK-14-17.1

426    Costa, D. P., Breed, G. A., & Robinson, P. W. (2012). New insights into pelagic migrations :

427        implications for ecology and conservation. *Annual Review of Ecology, Evolution, and

428        Systematics*, *43*, 73–96. doi:10.1146/annurev-ecolsys-102710-145045

429   Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary

430       ecology of individual differences. *Ecology Letters*, *15*, 1189–1198. doi:10.1111/j.1461-

431       0248.2012.01846.x

432   de Bruyn, P. J. N., Tosh, C. A., Oosthuizen, W. C., Phalanndwa, M. V, & Bester, M. N.

433       (2008). Temporary marking of unweaned southern elephant seal (Mirounga leonina L.)

434       pups. *South African Journal of Wildlife Research*, *38*(2), 133–137.

435   Duong, T. (2016). Package "ks". Retrieved from https://cran.r-

436       project.org/web/packages/ks/index.html

437   Duong, T., & Hazelton, M. (2003). Plug-in bandwidth matrices for bivariate kernel density

438       estimation. *Journal of Nonparametric Statistics*, *15*(1), 17–30.

439       doi:10.1080/10485250306039

440   Farnsworth, M. L., Dickson, B. G., Zachmann, L. J., Hegeman, E. E., Cangelosi, A. R.,

441       Jackson, T. G. J., & Scheib, A. F. (2015). Short-term space-use patterns of translocated

442       Mojave desert tortoise in southern California. *PLoS ONE*, *10*(9), e0134250.

443       doi:10.1371/journal.pone.0134250

444   Field, I. C., Harcourt, R. G., Boehme, L., Bruyn, P. J. N. De, Charrassin, J.-B., McMahon, C.

445       R., … Hindell, M. a. (2012). Refining instrument attachment on phocid seals. *Marine*

446       *Mammal Science*, *28*(3), E325–E332. doi:10.1111/j.1748-7692.2011.00519.x

447   Forrester, T. D., Casady, D. S., & Wittmer, H. U. (2015). Home sweet home: fitness

448       consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and*

449       *Sociobiology*, *69*, 603–612. doi:10.1007/s00265-014-1871-z

450   Freitas, C., Lydersen, C., Fedak, M., & Kovacs, K. M. (2008). A simple new algorithm to

451       filter marine mammal Argos locations. *Marine Mammal Science*, *24*(2), 315–325.

452   Gannon, R., Payne, N. L., Suthers, I. M., Gray, C. A., Meulen, D. E. Van Der, & Taylor, M.

453       D. (2015). Fine-scale movements , site fidelity and habitat use of an estuarine dependent

454     sparid. *Environmental Biology of Fishes*, *98*, 1599–1608. doi:10.1007/s10641-015-0385-

455     5

456 Greenwood, B. Y. P. J. (1980). Mating systems, philopatry and dispersal in birds and

457     mammals. *Animal Behaviour*, *28*, 1140–1162.

458 Grundling, A. (2014). *Ontogeny of southern elephant seal ( Mirounga leonina ) dive*

459     *behaviour*. B.Sc. hons. thesis, University of Pretoria.

460 Guinet, C., Vacquié-garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A. C., …

461     Bailleul, F. (2014). Southern elephant seal foraging success in relation to temperature

462     and light conditions : insight into prey distribution. *Marine Ecology Progress Series*,

463     *499*, 285–301. doi:10.3354/meps10660

464 Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., …

465     Charrassin, J.-B. (2016). Circumpolar habitat use in the southern elephant seal:

466     implications for foraging success and population trajectories. *Ecosphers*, *7*(May),

467     e01213. doi:10.1002/ ecs2.1213

468 Hipfner, J. M. (2008). Matches and mismatches: ocean climate, prey phenology and breeding

469     success in a zooplanktivorous seabird. *Marine Ecology Progress Series*, *368*, 295–304.

470     doi:10.3354/meps07603

471 Hofmeyr, G. J. G., Kirkman, S. P., Pistorius, P. A., & Bester, M. N. (2012). Natal site fidelity

472     by breeding female southern elephant seals in relation to their history of participation in

473     the winter haulout. *African Journal of Marine Science*, *34*(3), 373–382.

474 Hückstädt, L. A., Koch, P. L., McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P.

475     (2012). Stable isotope analyses reveal individual variability in the trophic ecology of a

476     top marine predator, the southern elephant seal. *Oecologia*, *169*(2), 395–406.

477     doi:10.1007/s00442-011-2202-y

478    Jabour, J., Lea, M.-A., Goldsworthy, S. D., Melcher, G., Sykes, K., & Hindell, M. A. (2016).

479        Marine telemetry and the conservation and management of risk to seal species in Canada

480        and Australia. *Ocean Development & International Law*, *47*(3), 255–271.

481        doi:10.1080/00908320.2016.1194094

482    Kamil, A. C. (1983). Optimal foraging theory and the psychology of learning. *American*

483        *Zoologist*, *23*(2), 291–302.

484    Krebs, J. R. (1971). Territory and breeding density in the Great Tit, Parus Major L. *Ecology*,

485        *52*(1), 2–22.

486    Le Boeuf, B. J., & Laws, R. M. (1994). *Elephant Seals: Population Ecology, Behavior, and*

487        *Physiology*. Berkeley: University of California Press.

488        doi:http://ark.cdlib.org/ark:/13030/ft7b69p131/

489    López-López, P., García-Ripollés, C. & Urios, V. (2014). Individual repeatability in timing

490        and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current*

491        *Zoology*, *60*(5), 642-652.

492    Massie, P. P., McIntyre, T., Ryan, P. G., Bester, M. N., Bornemann, H., & Ansorge, I. J.

493        (2016). The role of eddies in the diving behaviour of female southern elephant seals.

494        *Polar Biology*, *39*, 297–307. doi:10.1007/s00300-015-1782-0

495    Mazor, T., Beger, M., Mcgowan, J., Possingham, H. P., & Kark, S. (2016). The value of

496        migration information for conservation prioritization of sea turtles in the Mediterranean.

497        *Global Ecology and Biogeography*, *25*, 540–552. doi:10.1111/geb.12434

498    McFarlane Tranquilla, L. A., Montevecchi, W. A., Fifield, D. A., Hedd, A., Gaston, A. J.,

499        Robertson, G. J., & Phillips, R. A. (2014). Individual winter movement strategies in two

500        species of Murre (Uria spp.) in the Northwest Atlantic. *PLoS ONE*, *9*(4).

501        doi:10.1371/journal.pone.0090583

502  McIntyre, T., Ansorge, I. J., Bornemann, H., Plötz, J., Tosh, C. A., & Bester, M. N. (2011).

503  Elephant seal dive behaviour is influenced by ocean temperature: implications for

504  climate change impacts on an ocean predator. *Marine Ecology Progress Series*, *441*,

505  257–272. doi:10.3354/meps09383

506  McIntyre, T., Bornemann, H., Plötz, J., Tosh, C. A., & Bester, M. N. (2011). Water column

507  use and forage strategies of female southern elephant seals from Marion Island. *Marine*

508  *Biology*, *158*(9), 2125–2139. doi:10.1007/s00227-011-1719-2

509  McMahon, C. R., Field, I. C., Bradshaw, C. J. A., White, G. C., & Hindell, M. A. (2008).

510  Tracking and data–logging devices attached to elephant seals do not affect individual

511  mass gain or survival. *Journal of Experimental Marine Biology and Ecology*, *360*, 71–

512  77.

513  Merkle, J. A., Cherry, S. G., & Fortin, D. (2015). Bison distribution under conflicting

514  foraging strategies: site fidelity vs. energy maximization. *Ecology*, *96*(7), 1793–1801.

515  Mingozzi, T., Mencacci, R., Cerritelli, G., Giunchi, D., & Luschi, P. (2016). Living between

516  widely separated areas: Long-term monitoring of Mediterranean loggerhead turtles

517  sheds light on cryptic aspects of females spatial ecology. *Journal of Experimental*

518  *Marine Biology and Ecology*, *485*, 8–17. doi:10.1016/j.jembe.2016.08.007

519  Newell, G. R. (1999). Responses of Lumholtz's tree-kangaroo ( Dendrolagus lumholtzi ) to

520  loss of habitat within a tropical rainforest fragment. *Biological Conservation*, *91*, 181–

521  189.

522  Oosthuizen, W. C., Bester, M. N., Altwegg, R., McIntyre, T., & de Bruyn, P. J. N. (2015).

523  Decomposing the variance in southern elephant seal weaning mass: partitioning

524  environmental signals and maternal effects. *Ecosphere*, *6*(August), 1–22.

525  Piper, W. H. (2011). Making habitat selection more "familiar" : a review. *Behavioral Ecology*

526  *and Sociobiology*, *65*, 1329–1351. doi:10.1007/s00265-011-1195-1

527  Postma, M., Bester, M. N., & De Bruyn, P. J. N. (2013). Spatial variation in female southern

528      elephant seal mass change assessed by an accurate non-invasive photogrammetry

529      method. *Antarctic Science*, *25*(6), 731–740. doi:10.1017/S0954102013000059

530  R Core Team (2016). R: A language and environment for statistical computing. R Foundation

531      for Statistical Computing, Vienna, Austria. Retrieved from http://www.r-project.org

532  Shields, W. M., Cook, J. R., Hebblethwaite, M. L., & Wiles-Ehmann, S. S. (1988). Ideal free

533      coloniality in the swallows. In C. N. Slobodchikolf (Ed.), *The Ecology of Social*

534      *Behavior* (pp. 189–228). San Diego: Academic Press.

535  Simmons, S. E. (2008). *Environmental and individual effects on the foraging success of an*

536      *apex predator, the northern elephant seal (Mirounga angustirostris)*. Ph.D. thesis,

537      University of California, Santa Cruz.

538  Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional

539      kernel utilization distributions improve estimates of space use in aquatic animals.

540      *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 565–572. doi:10.1139/F2011-

541      179

542  Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Kramer-Schadt, S. (2015). When

543      top predators become prey: Black bears alter movement behaviour in response to

544      hunting pressure. *Behavioural Processes*, *120*, 30–39. doi:10.1016/j.beproc.2015.08.003

545  Swart, S., & Speich, J. (2010). An altimetry-based gravest empirical mode south of Africa: 2.

546      Dynamic nature of the Antarctic Circumpolar Current fronts. *Journal of Geophysical*

547      *Research*, *115*.

548  Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary*

549      *Ecology*, *7*, 533–555.

550  Tosh, C. A., de Bruyn, P. J. N., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B. S., …

551      Bester, M. N. (2015). The importance of seasonal sea surface height anomalies for

552    foraging juvenile southern elephant seals. *Marine Biology*, *162*(10), 2131–2140.

553    doi:10.1007/s00227-015-2743-4

554  Tosh, C. A., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B., Plötz, J., & Bester, M.

555    (2012). Marine habitats of juvenile southern elephant seals from Marion Island. *Aquatic*

556    *Biology*, *17*(1), 71–79. doi:10.3354/ab00463

557  Tracey, J. A., Sheppard, J., Zhu, J., Wei, F., Swaisgood, R. R., & Fisher, R. N. (2014).

558    Movement-Based estimation and visualization of space use in 3D for wildlife ecology

559    and conservation. *PLoS ONE*, *9*(7), e101205. doi:10.1371/journal.pone.0101205

560  Vander Zanden, H. B., Bolten, A. B., Tucker, A. D., Hart, K. M., Lamont, M. M., Fujisaki, I.,

561    … Bjorndal, K. A. (2016). Biomarkers reveal sea turtles remained in oiled areas

562    following the Deepwater Horizon oil spill. *Ecological Applications*, *26*(7), 2145–2155.

563    doi:10.1002/eap.1366

564  Vardanis, Y., Nilsson, J.-Å., Klaassen, R. H. G., Strandberg, R. & Alerstam, T. (2016)

565    Consistency in long-distance bird migration: contrasting patterns in time and space for

566    two raptors. *Animal Behaviour*, *113*, 177-187.

567  Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D., Failla, M., Intrieri, E., & Bräger,

568    S. (2016). Site-fidelity and movement patterns of bottlenose dolphins ( Tursiops

569    truncatus ) in central Argentina : essential information for effective conservation.

570    *Aquatic Conservation: Marine and Freshwater Ecosystems*, (January 2015).

571    doi:10.1002/aqc.2618

572  Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., …

573    Hamer, K. C. (2015). Long-term individual foraging site fidelity — why some gannets

574    don' t change their spots. *Ecology*, *96*(11), 3058–3074.

575  Ward, J. H. J. (1963). Hierarchical grouping to optimize an objective function. *Journal of the*

576    *American Statistical Association*, *58*(301), 236–244.

577    Weber, N., Duengkae, P., Fahr, J., Dechmann, D. K. N., Phengsakul, P., Khumbucha, W., …

578        Newman, S. (2015). High-resolution GPS tracking of Lyle's flying fox between temples

579        and orchards in central Thailand. *The Journal of Wildlife Management*, *79*(6), 957–968.

580        doi:10.1002/jwmg.904

581    Wege, M., Tosh, C. A., de Bruyn, P. J. N., & Bester, M. N. (2016). Cross-seasonal foraging

582        site fidelity of subantarctic fur seals: implications for marine conservation areas. *Marine*

583        *Ecology Progress Series*, *554*, 225–239. doi:10.3354/meps11798

584    Whisson, D. A., Dixon, V., Taylor, M. L., & Melzer, A. (2016). Failure to respond to food

585        resource decline has catastrophic consequences for koalas in a high-density population

586        in southern Australia. *PLoS ONE*, *11*(1), 1–12. doi:10.1371/journal.pone.0144348

587    Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating

588        repeatability. *Methods in Ecology and Evolution*, *3*, 129–137. doi:10.1111/j.2041-

589        210X.2011.00125.x

590

591

592 **Tables**

593 <mark>**Table 1:**</mark> Elephant seals tracked over multiple migrations.

| Tag | Sex | <mark>*N*</mark> | 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 <mark>Mean (± SD) overlap in inter-annual utilization distributions, as well as mean (± SD) overlap</mark>

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

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

597

598 **Table 2:** <mark>Inter-annual and multi-year overlap in 95% and 50% three-dimensional utilization</mark>

599 <mark>distributions (3D-UDs) for southern elephant seals.</mark>

| | | *95% 3D-UD* | | | |
|---|---|---|---|---|---|
| | | **Inter-annual** | | **Multi-year** | |
| *Tag* | <mark>*N*</mark> | *Day* | *Night* | *Day* | *Night* |
| **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** |
| | | *50% 3D-UD* | | | |
| **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

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

| Parameter | Repeatability (r) |
|---|---|
| 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

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

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

**Figure 3:** Hierarchical cluster analysis of migration strategies of southern elephant seals tracked over multiple post-moult migrations, illustrating the three identified behavioural clusters (C1-C3). Locations of migrations identified in each of the clusters are presented in the three maps. Positions of all track locations not within a particular cluster are illustrated in light grey. PO225 is represented in only one migration, due to a comparatively low number of recorded daytime dive depths in 2007. STF = Subtropical Front, SAF = Subantarctic Front, 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 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).

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 UDs 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 UDs 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 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% UDs 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 ±

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 ±

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% UDs, 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 at 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 UDs, compared to their 3-D UDs (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

354 **References**

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

356     (2015). Return customers: foraging site fidelity and the effect of environmental

357     variability in wide-ranging Antarctic fur seals. *Plos One*, *10*, e0120888.

358     doi:10.1371/journal.pone.0120888

359 ATCM (2011) SCAR's Code of Conduct for the Use of Animals for Scientific Purposes in

360     Antarctica. IP53, Agenda Item CEP 8c, presented by SCAR during XXXIV Antarctic

361     Treaty Consultative Meeting, Buenos Aires, Argentina, 20 June - 21 July 2011, 4pp.

362     http://www.scar.org/scar_media/documents/science/atcm34_ip053_CofC_Animals.pdf

363 Augé, A. A., Chilvers, B. L., Moore, A. B., & Davis, L. S. (2014). Importance of studying

364     foraging site fidelity for spatial conservation measures in a mobile predator. *Animal*

365     *Conservation*, *17*, 61–71. doi:10.1111/acv.12056

366 Authier, M., Bentaleb, I., Ponchon, A., Martin, C., & Guinet, C. (2012). Foraging fidelity as a

367     recipe for a long life: foraging strategy and longevity in male southern elephant seals.

368     *PloS One*, *7*(4), e32026. doi:10.1371/journal.pone.0032026

369 Bailleul, F., Lesage, V., & Hammill, M. O. (2010). Spherical First Passage Time: A tool to

370     investigate area-restricted search in three-dimensional movements. *Ecological*

371     *Modelling*, *221*, 1665–1673.

372 Baylis, A. M. M., Orben, R. A., Arnould, J. P. Y., Peters, K., Knox, T., Costa, D. P., &

373     Staniland, I. J. (2015). Diving deeper into individual foraging specializations of a large

374     marine predator , the southern sea lion. *Oecologia*, *179*(4), 1053–1065.

375     doi:10.1007/s00442-015-3421-4

376 Baylis, A. M. M., Orben, R. A., Pistorius, P., Brickle, P., Staniland, I., & Ratcliffe, N. (2015).

377     Winter foraging site fidelity of king penguins breeding at the Falkland Islands. *Marine*

378     *Biology*, *162*, 99–110. doi:10.1007/s00227-014-2561-0

379      Bennett, K. A., McConnell, B. J., & Fedak, M. (2001). Diurnal and seasonal variations in the

380          duration and depth of the longest dives in southern elephant seals (Mirounga leonina):

381          possible physiological and behavioural constraints. *Journal of Experimental Biology*,

382          *204*, 649–662.

383      Berthold, P., v. d. Bossche, W., Jakubiec, Z., Kaatz, C., Kaatz, M. & Querner, U. (2002).

384          Long-term satellite tracking sheds light upon variable migration strategies of White

385          Storks (*Ciconia ciconia*). *Journal of Ornithology*, *143*, 489-495.

386      Bester, M. N. (1988). Marking and monitoring studies of the Kerguelen stock of southern

387          elephant seals Mirounga leonina and their bearing on biological research in the Vestfold

388          Hills. *Hydrobiologia*, *165*, 269–277.

389      Bester, M. N., Bornemann, H., & McIntyre, T. (n.d.). Antarctic marine mammals and sea ice.

390          In D. N. Thomas & G. S. Dieckman (Eds.), *Sea Ice* (3rd ed.). Oxford: Wiley-Blackwell.

391      Biuw, M., Nøst, O. A., Stien, A., Zhou, Q., Lydersen, C., & Kovacs, K. M. (2010). Effects of

392          hydrographic variability on the spatial, seasonal and diel diving patterns of southern

393          elephant seals in the eastern Weddell Sea. *PLoS ONE*, *5*(11), e13816.

394          doi:10.1371/journal.pone.0013816

395      Boehme, L., Lovell, P., Biuw, M., Roquet, F., Nicholson, J., Thorpe, S. E., … Fedak, M.

396          (2009). Technical Note: Animal-borne CTD-Satellite Relay Data Loggers for real-time

397          oceanographic data collection. *Ocean Science*, *5*, 685–695.

398      Bolnick, D. I., Amarasekare, P., Araujo, M. S., R, B., Levine, J. M., Novak, M., … Vasseur,

399          D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in*

400          *Ecology and Evolution*, *26*(4), 183–192. doi:10.1016/j.tree.2011.01.009

401      Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., &

402          Forister, M. L. (2003). The ecology of individuals: incidence and implications of

403          individual specialization. *The American Naturalist*, *161*(1), 1–28.

404    Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays:

405        potential life history consequences of fidelity to marine foraging regions by southern

406        elephant seals. *Animal Behaviour*, *68*, 1349–1360.

407    Braham, M., Miller, T., Duerr, A. E., Lanzone, M., Fesnock, A., LaPre, L., … Katzner, T.

408        (2015). Home in the heat: Dramatic seasonal variation in home range of desert golden

409        eagles informs management for renewable energy development. *Biological*

410        *Conservation*, *186*, 225–232. doi:10.1016/j.biocon.2015.03.020

411    Calenge, C. (2015). Home Range Estimation in R : the adehabitatHR Package. Retrieved

412        from https://cran.r-project.org/web/packages/adehabitatHR/index.html

413    Carman, V. G., Bruno, I., Maxwell, S., Álvarez, K., Albareda, D., Acha, E. M., & Campagna,

414        C. (2016). Habitat use, site fidelity and conservation opportunities for juvenile

415        loggerhead sea turtles in the Río de la Plata, Argentina. *Marine Biology*, *163*.

416        doi:10.1007/s00227-015-2795-5

417    Clarke, M. F., da Silva, K. B., Lair, H., Pocklington, R., Kramer, D. L., & McLaughlin, R. L.

418        (1993). Site familiarity affects escape behaviour of the eastern chipmunk, Tamias

419        striatus. *Oikos*, *66*(3), 533–537.

420    Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes,

421        D. K. A., … Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I : how

422        changes in physical habitats directly affect marine biota. *Global Change Biology*.

423        doi:10.1111/gcb.12623

424    Cooper, N. W., Sherry, T. W., & Marra, P. P. (2014). Modeling three-dimensional space use

425        and overlap in birds. *Auk*, *131*, 681–693. doi:10.1642/AUK-14-17.1

426    Costa, D. P., Breed, G. A., & Robinson, P. W. (2012). New insights into pelagic migrations :

427        implications for ecology and conservation. *Annual Review of Ecology, Evolution, and*

428        *Systematics*, *43*, 73–96. doi:10.1146/annurev-ecolsys-102710-145045

429    Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary

430         ecology of individual differences. *Ecology Letters*, *15*, 1189–1198. doi:10.1111/j.1461-

431         0248.2012.01846.x

432    de Bruyn, P. J. N., Tosh, C. A., Oosthuizen, W. C., Phalanndwa, M. V, & Bester, M. N.

433         (2008). Temporary marking of unweaned southern elephant seal (Mirounga leonina L.)

434         pups. *South African Journal of Wildlife Research*, *38*(2), 133–137.

435    Duong, T. (2016). Package "ks". Retrieved from https://cran.r-

436         project.org/web/packages/ks/index.html

437    Duong, T., & Hazelton, M. (2003). Plug-in bandwidth matrices for bivariate kernel density

438         estimation. *Journal of Nonparametric Statistics*, *15*(1), 17–30.

439         doi:10.1080/10485250306039

440    Farnsworth, M. L., Dickson, B. G., Zachmann, L. J., Hegeman, E. E., Cangelosi, A. R.,

441         Jackson, T. G. J., & Scheib, A. F. (2015). Short-term space-use patterns of translocated

442         Mojave desert tortoise in southern California. *PLoS ONE*, *10*(9), e0134250.

443         doi:10.1371/journal.pone.0134250

444    Field, I. C., Harcourt, R. G., Boehme, L., Bruyn, P. J. N. De, Charrassin, J.-B., McMahon, C.

445         R., … Hindell, M. a. (2012). Refining instrument attachment on phocid seals. *Marine*

446         *Mammal Science*, *28*(3), E325–E332. doi:10.1111/j.1748-7692.2011.00519.x

447    Forrester, T. D., Casady, D. S., & Wittmer, H. U. (2015). Home sweet home: fitness

448         consequences of site familiarity in female black-tailed deer. *Behavioral Ecology and*

449         *Sociobiology*, *69*, 603–612. doi:10.1007/s00265-014-1871-z

450    Freitas, C., Lydersen, C., Fedak, M., & Kovacs, K. M. (2008). A simple new algorithm to

451         filter marine mammal Argos locations. *Marine Mammal Science*, *24*(2), 315–325.

452    Gannon, R., Payne, N. L., Suthers, I. M., Gray, C. A., Meulen, D. E. Van Der, & Taylor, M.

453         D. (2015). Fine-scale movements , site fidelity and habitat use of an estuarine dependent

454     sparid. *Environmental Biology of Fishes*, *98*, 1599–1608. doi:10.1007/s10641-015-0385-

455     5

456     Greenwood, B. Y. P. J. (1980). Mating systems, philopatry and dispersal in birds and

457     mammals. *Animal Behaviour*, *28*, 1140–1162.

458     Grundling, A. (2014). *Ontogeny of southern elephant seal ( Mirounga leonina ) dive*

459     *behaviour*. B.Sc. hons. thesis, University of Pretoria.

460     Guinet, C., Vacquié-garcia, J., Picard, B., Bessigneul, G., Lebras, Y., Dragon, A. C., …

461     Bailleul, F. (2014). Southern elephant seal foraging success in relation to temperature

462     and light conditions : insight into prey distribution. *Marine Ecology Progress Series*,

463     *499*, 285–301. doi:10.3354/meps10660

464     Hindell, M. A., McMahon, C. R., Bester, M. N., Boehme, L., Costa, D., Fedak, M. A., …

465     Charrassin, J.-B. (2016). Circumpolar habitat use in the southern elephant seal:

466     implications for foraging success and population trajectories. *Ecosphers*, *7*(May),

467     e01213. doi:10.1002/ ecs2.1213

468     Hipfner, J. M. (2008). Matches and mismatches: ocean climate, prey phenology and breeding

469     success in a zooplanktivorous seabird. *Marine Ecology Progress Series*, *368*, 295–304.

470     doi:10.3354/meps07603

471     Hofmeyr, G. J. G., Kirkman, S. P., Pistorius, P. A., & Bester, M. N. (2012). Natal site fidelity

472     by breeding female southern elephant seals in relation to their history of participation in

473     the winter haulout. *African Journal of Marine Science*, *34*(3), 373–382.

474     Hückstädt, L. A., Koch, P. L., McDonald, B. I., Goebel, M. E., Crocker, D. E., & Costa, D. P.

475     (2012). Stable isotope analyses reveal individual variability in the trophic ecology of a

476     top marine predator, the southern elephant seal. *Oecologia*, *169*(2), 395–406.

477     doi:10.1007/s00442-011-2202-y

478     Jabour, J., Lea, M.-A., Goldsworthy, S. D., Melcher, G., Sykes, K., & Hindell, M. A. (2016).

479          Marine telemetry and the conservation and management of risk to seal species in Canada

480          and Australia. *Ocean Development & International Law*, *47*(3), 255–271.

481          doi:10.1080/00908320.2016.1194094

482     Kamil, A. C. (1983). Optimal foraging theory and the psychology of learning. *American*

483          *Zoologist*, *23*(2), 291–302.

484     Krebs, J. R. (1971). Territory and breeding density in the Great Tit, Parus Major L. *Ecology*,

485          *52*(1), 2–22.

486     Le Boeuf, B. J., & Laws, R. M. (1994). *Elephant Seals: Population Ecology, Behavior, and*

487          *Physiology*. Berkeley: University of California Press.

488          doi:http://ark.cdlib.org/ark:/13030/ft7b69p131/

489     López-López, P., García-Ripollés, C. & Urios, V. (2014). Individual repeatability in timing

490          and spatial flexibility of migration routes of trans-Saharan migratory raptors. *Current*

491          *Zoology*, *60*(5), 642-652.

492     Massie, P. P., McIntyre, T., Ryan, P. G., Bester, M. N., Bornemann, H., & Ansorge, I. J.

493          (2016). The role of eddies in the diving behaviour of female southern elephant seals.

494          *Polar Biology*, *39*, 297–307. doi:10.1007/s00300-015-1782-0

495     Mazor, T., Beger, M., Mcgowan, J., Possingham, H. P., & Kark, S. (2016). The value of

496          migration information for conservation prioritization of sea turtles in the Mediterranean.

497          *Global Ecology and Biogeography*, *25*, 540–552. doi:10.1111/geb.12434

498     McFarlane Tranquilla, L. A., Montevecchi, W. A., Fifield, D. A., Hedd, A., Gaston, A. J.,

499          Robertson, G. J., & Phillips, R. A. (2014). Individual winter movement strategies in two

500          species of Murre (Uria spp.) in the Northwest Atlantic. *PLoS ONE*, *9*(4).

501          doi:10.1371/journal.pone.0090583

502    McIntyre, T., Ansorge, I. J., Bornemann, H., Plötz, J., Tosh, C. A., & Bester, M. N. (2011).

503        Elephant seal dive behaviour is influenced by ocean temperature: implications for

504        climate change impacts on an ocean predator. *Marine Ecology Progress Series*, *441*,

505        257–272. doi:10.3354/meps09383

506    McIntyre, T., Bornemann, H., Plötz, J., Tosh, C. A., & Bester, M. N. (2011). Water column

507        use and forage strategies of female southern elephant seals from Marion Island. *Marine*

508        *Biology*, *158*(9), 2125–2139. doi:10.1007/s00227-011-1719-2

509    McMahon, C. R., Field, I. C., Bradshaw, C. J. A., White, G. C., & Hindell, M. A. (2008).

510        Tracking and data–logging devices attached to elephant seals do not affect individual

511        mass gain or survival. *Journal of Experimental Marine Biology and Ecology*, *360*, 71–

512        77.

513    Merkle, J. A., Cherry, S. G., & Fortin, D. (2015). Bison distribution under conflicting

514        foraging strategies: site fidelity vs. energy maximization. *Ecology*, *96*(7), 1793–1801.

515    Mingozzi, T., Mencacci, R., Cerritelli, G., Giunchi, D., & Luschi, P. (2016). Living between

516        widely separated areas: Long-term monitoring of Mediterranean loggerhead turtles

517        sheds light on cryptic aspects of females spatial ecology. *Journal of Experimental*

518        *Marine Biology and Ecology*, *485*, 8–17. doi:10.1016/j.jembe.2016.08.007

519    Newell, G. R. (1999). Responses of Lumholtz's tree-kangaroo ( Dendrolagus lumholtzi ) to

520        loss of habitat within a tropical rainforest fragment. *Biological Conservation*, *91*, 181–

521        189.

522    Oosthuizen, W. C., Bester, M. N., Altwegg, R., McIntyre, T., & de Bruyn, P. J. N. (2015).

523        Decomposing the variance in southern elephant seal weaning mass: partitioning

524        environmental signals and maternal effects. *Ecosphere*, *6*(August), 1–22.

525    Piper, W. H. (2011). Making habitat selection more "familiar" : a review. *Behavioral Ecology*

526        *and Sociobiology*, *65*, 1329–1351. doi:10.1007/s00265-011-1195-1

527    Postma, M., Bester, M. N., & De Bruyn, P. J. N. (2013). Spatial variation in female southern

528        elephant seal mass change assessed by an accurate non-invasive photogrammetry

529        method. *Antarctic Science*, *25*(6), 731–740. doi:10.1017/S0954102013000059

530    R Core Team (2016). R: A language and environment for statistical computing. R Foundation

531        for Statistical Computing, Vienna, Austria. Retrieved from http://www.r-project.org

532    Shields, W. M., Cook, J. R., Hebblethwaite, M. L., & Wiles-Ehmann, S. S. (1988). Ideal free

533        coloniality in the swallows. In C. N. Slobodchikolf (Ed.), *The Ecology of Social*

534        *Behavior* (pp. 189–228). San Diego: Academic Press.

535    Simmons, S. E. (2008). *Environmental and individual effects on the foraging success of an*

536        *apex predator, the northern elephant seal (Mirounga angustirostris)*. Ph.D. thesis,

537        University of California, Santa Cruz.

538    Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional

539        kernel utilization distributions improve estimates of space use in aquatic animals.

540        *Canadian Journal of Fisheries and Aquatic Sciences*, *69*, 565–572. doi:10.1139/F2011-

541        179

542    Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Kramer-Schadt, S. (2015). When

543        top predators become prey: Black bears alter movement behaviour in response to

544        hunting pressure. *Behavioural Processes*, *120*, 30–39. doi:10.1016/j.beproc.2015.08.003

545    Swart, S., & Speich, J. (2010). An altimetry-based gravest empirical mode south of Africa: 2.

546        Dynamic nature of the Antarctic Circumpolar Current fronts. *Journal of Geophysical*

547        *Research*, *115*.

548    Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary*

549        *Ecology*, *7*, 533–555.

550    Tosh, C. A., de Bruyn, P. J. N., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B. S., …

551        Bester, M. N. (2015). The importance of seasonal sea surface height anomalies for

552    foraging juvenile southern elephant seals. *Marine Biology*, *162*(10), 2131–2140.

553    doi:10.1007/s00227-015-2743-4

554    Tosh, C. A., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B., Plötz, J., & Bester, M.

555    (2012). Marine habitats of juvenile southern elephant seals from Marion Island. *Aquatic*

556    *Biology*, *17*(1), 71–79. doi:10.3354/ab00463

557    Tracey, J. A., Sheppard, J., Zhu, J., Wei, F., Swaisgood, R. R., & Fisher, R. N. (2014).

558    Movement-Based estimation and visualization of space use in 3D for wildlife ecology

559    and conservation. *PLoS ONE*, *9*(7), e101205. doi:10.1371/journal.pone.0101205

560    Vander Zanden, H. B., Bolten, A. B., Tucker, A. D., Hart, K. M., Lamont, M. M., Fujisaki, I.,

561    … Bjorndal, K. A. (2016). Biomarkers reveal sea turtles remained in oiled areas

562    following the Deepwater Horizon oil spill. *Ecological Applications*, *26*(7), 2145–2155.

563    doi:10.1002/eap.1366

564    Vardanis, Y., Nilsson, J.-Å., Klaassen, R. H. G., Strandberg, R. & Alerstam, T. (2016)

565    Consistency in long-distance bird migration: contrasting patterns in time and space for

566    two raptors. *Animal Behaviour*, *113*, 177-187.

567    Vermeulen, E., Balbiano, A., Belenguer, F., Colombil, D., Failla, M., Intrieri, E., & Bräger,

568    S. (2016). Site-fidelity and movement patterns of bottlenose dolphins ( Tursiops

569    truncatus ) in central Argentina : essential information for effective conservation.

570    *Aquatic Conservation: Marine and Freshwater Ecosystems*, (January 2015).

571    doi:10.1002/aqc.2618

572    Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., …

573    Hamer, K. C. (2015). Long-term individual foraging site fidelity — why some gannets

574    don' t change their spots. *Ecology*, *96*(11), 3058–3074.

575    Ward, J. H. J. (1963). Hierarchical grouping to optimize an objective function. *Journal of the*

576    *American Statistical Association*, *58*(301), 236–244.

577    Weber, N., Duengkae, P., Fahr, J., Dechmann, D. K. N., Phengsakul, P., Khumbucha, W., …

578        Newman, S. (2015). High-resolution GPS tracking of Lyle's flying fox between temples

579        and orchards in central Thailand. *The Journal of Wildlife Management*, *79*(6), 957–968.

580        doi:10.1002/jwmg.904

581    Wege, M., Tosh, C. A., de Bruyn, P. J. N., & Bester, M. N. (2016). Cross-seasonal foraging

582        site fidelity of subantarctic fur seals: implications for marine conservation areas. *Marine*

583        *Ecology Progress Series*, *554*, 225–239. doi:10.3354/meps11798

584    Whisson, D. A., Dixon, V., Taylor, M. L., & Melzer, A. (2016). Failure to respond to food

585        resource decline has catastrophic consequences for koalas in a high-density population

586        in southern Australia. *PLoS ONE*, *11*(1), 1–12. doi:10.1371/journal.pone.0144348

587    Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating

588        repeatability. *Methods in Ecology and Evolution*, *3*, 129–137. doi:10.1111/j.2041-

589        210X.2011.00125.x

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 (± 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    **Table 2:** Inter-annual and multi-year overlap in 95% and 50% three-dimensional utilization

598    distributions (3D-UDs) for southern elephant seals.

| | | 95% 3D-UD | | | |
| | | Inter-annual | | Multi-year | |
| *Tag* | *N* | *Day* | *Night* | *Day* | *Night* |
| **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** |
| | | 50% 3D-UD | | | |
| **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** |

599

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

| Parameter | Repeatability (r) |
|---|---|
| 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

**Figure 2**
**Click here to download high resolution image**
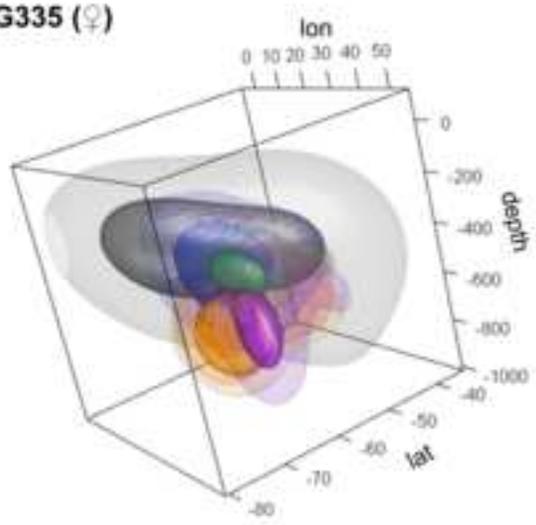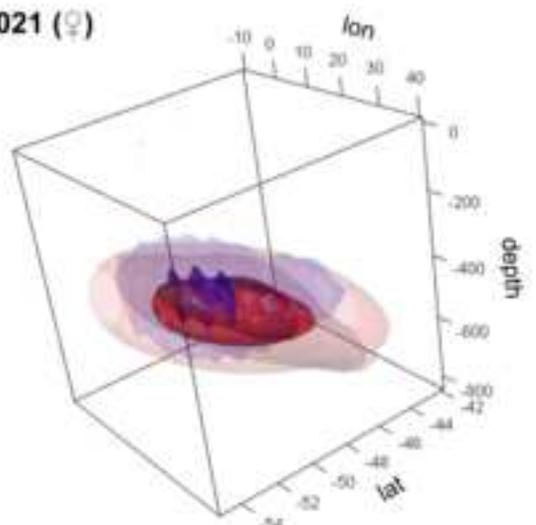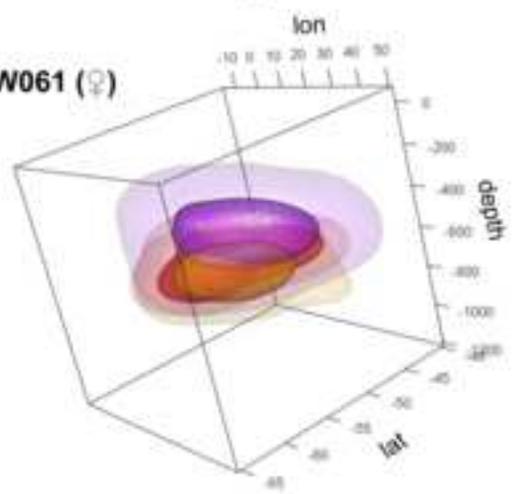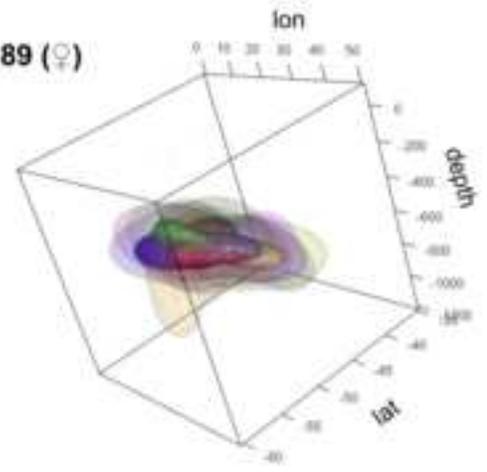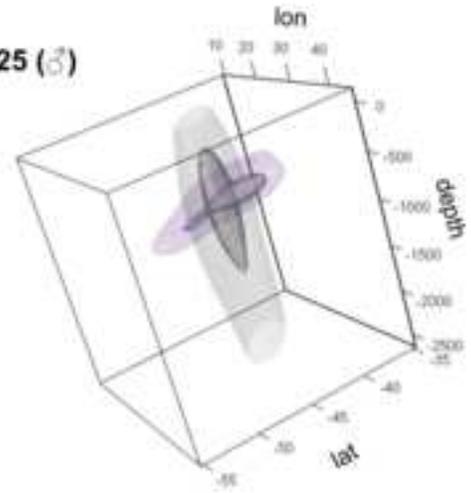
**Figure 3**
**Click here to download high resolution image**