

Title	Prey encounters and spatial memory influence use of foraging patches in a marine central place forager
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16 Abstract

17 Given the patchiness and long-term predictability of marine resources, memory of high-quality
18 foraging grounds is expected to provide fitness advantages for central place foragers. However, it
19 remains challenging to characterise how marine predators integrate memory with recent prey
20 encounters to adjust fine-scale movement and use of foraging patches. Here, we used two months
21 of movement data from harbour seals (*Phoca vitulina*) to quantify the repeatability in foraging
22 patches as a proxy for memory. We then integrated these data into analyses of fine-scale movement
23 and underwater behaviour to test how both spatial memory and prey encounter rates influenced
24 the seals' Area Restricted Search (ARS) behaviour. Specifically, we used one month's GPS data from
25 29 individuals to build spatial memory maps of searched areas, and archived accelerometry data
26 from a subset of five individuals to detect prey catch attempts, a proxy for prey encounters.
27 Individuals were highly consistent in the areas they visited over two consecutive month. Hidden
28 Markov Models showed that both spatial memory and prey encounters increased the probability of
29 seals initiating ARS. These results provide evidence that predators use memory to adjust their fine
30 scale movement and this ability should be accounted for in movement models.

31 **Keywords:** ARS; spatial memory; Hidden Markov Model; accelerometer; harbour seals; repeatability

32 1. Introduction

33 Whilst key aspects of predator movements can be explained by theoretical search strategies [1], it is
34 recognised that factors such as cognitive and perceptual abilities may also influence movement
35 patterns [1-3]. Predator movements can be characterised into different modes (e.g. oriented vs.
36 non-oriented, exploratory vs. area-restricted search), with switches between these modes
37 characterising temporal and spatial variation in foraging effort [4]. Area Restricted Search (ARS)
38 movement is widely recognised as a strategy by which predators concentrate their search activity in
39 areas rich in resources [5, 6]. Specifically, predators are expected to decrease their speed and
40 increase turning angles upon encountering prey, thereby increasing time spent in areas where the
41 probability of encountering further prey items is high [5, 7, 8]. Thus, an increase in prey encounters
42 has been hypothesised to drive the initiation of ARS behaviour [9, 10]. However, prey encounters are
43 often highly stochastic, and since most predators have well-developed cognitive and sensory
44 abilities, they are also expected to use other information sources to initiate ARS [3, 11, 12].

45 Many terrestrial and marine species display site fidelity to foraging and breeding locations,
46 supporting their ability to store information on habitat quality [13-15]. Furthermore, mechanistic
47 movement models that include spatial memory can successfully replicate observed patterns of site
48 fidelity [16, 17]. Given the patchiness and high spatio-temporal predictability of marine resources,
49 site fidelity and memory of foraging grounds is hypothesised to provide fitness advantages over an
50 individual's lifespan [18-20]. In particular, animals may use spatial memory to target patches of
51 resources outside their perceptual ranges [2, 21, 22]. For example, black-browed albatrosses
52 (*Thalassarche melanophris*) targeted areas of $< 1 \text{ km}^2$ where they had previously encountered fishing
53 vessels, despite these being $> 100 \text{ km}$ from their colony [23]. Predators may thus use spatial memory
54 to identify foraging areas, within which they then focus searching activity using ARS movement [24].

55 Previous studies considering both memory and the influence of prey encounters on searching
56 strategies are based either on terrestrial systems [25, 26] or simulations [27-29]. Despite evidence of

57 marine predators returning to foraging grounds [11, 12, 30], it is only recently that advances in
58 biologging and acoustic technologies have provided finer resolution data to empirically test the
59 effect of prey-encounter events on marine mammal and seabird movements [9, 31]. To date, we are
60 aware of no study that has directly explored how marine predators combine longer-term spatial
61 memory and contemporary prey encounters to adjust their fine-scale movements.

62 Here, we used movement data from biologgers deployed on coastal harbour seals (*Phoca vitulina*) to
63 test the influence of both spatial memory and prey encounters, and their interaction, on ARS
64 behaviour in this central place forager [32]. First, movement data were used to classify seal activities
65 at sea [33]. To provide initial support that seals have memory of foraging areas, we explored
66 individual repeatability of foraging patches over two consecutive months. As a proxy for memory,
67 data on the seal's activities were used to build spatial memory maps representing the areas in which
68 seals concentrated their searching effort over a one month period. For a subset of animals, we then
69 used fine-scale accelerometer data [34, 35], to infer prey encounter events while the animal was
70 diving. Finally, we fitted two Hidden Markov Models (HMM) [36] to test whether spatial memory
71 alone, or in combination with prey encounters, increased the probability of an animal initiating ARS
72 behaviour during a foraging trip.

73 2. Methods

74 (a) Case study species and data collection

75 Harbour seals are central place foragers inhabiting temperate coastal waters [37]. During February
76 and March 2017, 31 adult harbour seals (11 Males and 20 Females) were captured and tagged in
77 Loch Fleet, NE Scotland (57.935° N, 4.042° W) (see [13] for background on the study site and
78 population). Seal capture and handling occurred in accordance with the Home Office Licence issued
79 to the Sea Mammal Research Unit (Licence No. 192CBD9F) with local licence approval from the
80 University of St Andrews Animal Welfare and Ethics Committee. Fastloc GPS-GSM phone tags (Sea

81 Mammal Research Unit Instrumentation, University of St Andrews, UK) were attached to the pelage
82 at the back of the neck, using the capture and handling methods detailed in Russell *et al.* [38]. Tags
83 were equipped with a GPS receiver, wet-dry sensor, and pressure sensor, providing geo-referenced
84 summaries of activity and diving patterns via the GSM phone network [39]. Tags also collected tri-
85 axial accelerometer data that were archived onboard, subject to digital storage limitations, but not
86 relayed through the GSM network due to the volume of data from the high sampling frequencies
87 used. Tags from a subset of five individuals were subsequently recovered on the shore after tags
88 detached during the moult, allowing archived tri-axial accelerometer data to be downloaded.

89 Tags were programmed to record GPS information every time a seal surfaced. However, due to
90 variation in satellite availability, this resulted in an irregular time series. On average, locations were
91 recorded every 15 minutes. When the wet-dry sensor determined that the animal was at sea, the
92 pressure sensor also recorded depth. Below a depth threshold of 1.5 m, time-depth data were
93 recorded every 4 seconds and stored in the tags. Dives were summarised using depth bins at 23
94 equally spaced time points throughout the dives. For each dive, the maximum diving depth,
95 duration, and time-depth summary were transmitted through the GSM network. The tri-axial
96 accelerometer measured the g -force at a frequency of 12.5 Hz. Because the accelerometers were
97 not calibrated prior to release, a post-hoc calibration was applied to the data, described in detail in
98 Appendix A. Next, a box-moving average (window width of 12 Hz) of each of the three axes was
99 calculated. These smoothed values represent an approximation for the gravitational component,
100 which can be used to derive the pitch angle. Finally, these smoothed estimates were subtracted
101 from the measured raw g -forces to obtain the dynamic or specific acceleration, which can be used to
102 determine prey capture attempts [40].

103 (b) Identification of ARS behaviour

104 We fitted a total of three HMMs (Table 1) to classify at-sea activities and to build spatial memory
105 maps of searched areas (Model 1), to assess the influence of memory alone on all individuals (Model

106 2), and to assess the simultaneous influence of spatial memory and prey encounters on the subset of
107 five individuals for which accelerometer data were available (Model 3). All models were fitted using
108 the momentuHMM package [42].

109 To ensure our analysis focussed on central place foraging trips, we selected round-trips from and to
110 the same haul-out site location, which were a) > 12 hours and b) included locations that were > 2 km
111 from the haul-out site. This avoided the inclusion of shorter periods in the water which typically
112 represent resting near intertidal haul-out sites [13, 43].

113 We used batches of five dives as the unit of analysis to avoid potential numerical problems in
114 estimating the maximum likelihood and extreme residual autocorrelation associated with a dive-by-
115 dive analysis [44]. The mean dive cycle (i.e. dive and subsequent period at surface, a dive being the
116 time spent below 1.5 m depth) was 4.46 (\pm 6.68) minutes, and the 90th percentile of the time interval
117 between GPS locations was 25 minutes. Dive locations were estimated by linearly interpolating
118 between the GPS positions using the manufacturer software. However, due to gaps in the GPS
119 datasets there might be uncertainty around some dive locations (Appendix B - Figure B1). Therefore,
120 in the analyses we only used batches of five dives that were associated with at least one raw GPS
121 location (for more details see Appendix B).

122 Seal activities at sea were classified into two behavioural states using an HMM based on the step
123 length and turning angle between consecutive dive batches. The two states are assumed to
124 represent transit and ARS movement, which are characterised by long directional displacement or
125 short tortuous movement, respectively [41]. We calculated the step length and turning angle
126 between the locations of the first dive of each batch and assumed these observations resulted from
127 state-dependent gamma and wrapped Cauchy distributions [45], respectively. Following the
128 methodology described by Russell *et al.* [46] and Carter *et al.* [47], if any dive batch was not
129 associated with a raw GPS location, the step length and turning angle were set to 'not available' (NA)
130 [36]; thus, the state was assigned solely based on the Markov property (for more details see

131 Appendix B). Finally, we selected the initial values of the parameters using the estimates from the
132 model with the lowest AIC score among 50 iterations with randomly selected initial values. The most
133 likely state sequence given the final model was decoded using the Viterbi algorithm [48].

134 (c) Spatial memory of foraging patches

135 Searching areas were defined using the locations of dive batches that were classified as ARS by
136 Model 1. To quantify how consistently seals visited the same areas over time, we calculated the
137 spatial overlap between searched areas visited during two consecutive months [20]; here, April and
138 May. Kernel distributions (UD) for each of the two months were calculated using the *adehabitatHR*
139 package [49] using a grid size of 500 m by 500 m. The most appropriate kernel bandwidth was
140 estimated using the First-Passage-Time method described in Lascelles *et al.* [50]. Overlap between
141 50% UD was estimated using the Bhattacharyya's affinity (BA) index [51], where 0 indicates no
142 overlap and 1 identical distributions. To compare the observed overlap with a null distribution of BA
143 values, we used a pairwise comparison to calculate the overlap between a seal's UD in May with the
144 UD in April of another randomly selected individual.

145 As a proxy for spatial memory, we built memory grids using the proportion of dive batches classified
146 as ARS by Model 1, in a 1 km x 1 km grid over the study area. Two sets of memory grids were built to
147 be used in Model 2 and Model 3, respectively (Table 1). We first created a set of spatial memory
148 grids representing the individual's ARS behaviour during the previous month of the data included in
149 Model 2 (Table 1). Then we created a second set of grids representing the areas used during one
150 month prior to data included in Model 3 (Table 1). Due to the differences in accelerometer data
151 availability between individuals (Table S1) the month used to build the spatial memory grid for each
152 of these five individuals varied.

153 (d) Prey encounters

154 We inferred prey encounter events from the accelerometer data while animals were at sea. In
155 coastal waters, harbour seals most frequently dive to the seabed and perform U-shaped dives

156 through all phases of their foraging trips [52, 53]. Therefore, we used accelerometry data to detect
157 prey encounters during the bottom phase of each of these dives [53], characterised as the period
158 when seals were within 20% of the maximum dive depth [54].

159 We used two different methodologies to detect prey encounters. First, we identified sudden peaks
160 in dynamic acceleration resulting from rapid head and body movements [34, 55, 56]. This method
161 has been validated with captive harbour seals and was able to identify prey capture attempts [34,
162 35]. We calculated the standard deviation in dynamic acceleration over a moving window of 1.5 s for
163 each axis and used a k-means cluster analysis to group the standard deviation values into two
164 activity states, “high” and “low”. We assumed an animal made a prey capture attempt, and thus
165 encountered a prey item, when its activity was determined to be “high” on all three axes [34, 55,
166 56]. Second, we identified changes in body pitch angle, which have been used as indicators of the
167 more subtle movements that harbour seals may use to catch benthic prey in shallow coastal waters
168 [57]. The pitch angle was calculated based on the estimated gravitational component of the
169 measured *g*-forces [34]. We calculated the differences between peaks and troughs in the time series
170 of body pitch angle during each dive. Prey capture attempts were identified when a change in pitch
171 angle greater than 20° occurred within a window of 5 seconds [57]. As these two methodologies
172 have not previously been used together, we assessed whether the identified foraging attempts
173 derived from the two methods (i.e. bursts in dynamic acceleration and drops in body pitch angle)
174 occurred at the same time. To avoid counting the same event twice, we then calculated the total
175 number of prey encounter events in each dive by summing the number of independent attempts
176 detected by either method.

177 (e) Assessing the drivers of ARS behaviour

178 To assess which factors influenced the initiation of ARS behaviour, we ran two separate models
179 Model 2 and Model 3 (Table 1). Model 2 was based on foraging trips occurring in May and included
180 the spatial memory grids of the seals’ activities during the month of April as covariates on the

181 transition probabilities between transit and ARS state [58]. In Model 3, we included the spatial
182 memory grid of activities during the month prior to the beginning of the accelerometer data and the
183 mean number of prey encounters per dive in each dive batch as covariates (see 'Identification of ARS
184 behaviour'). Note that although five individuals were represented in both models, the memory grids
185 differed between models (see 'Spatial memory of foraging patches section'). After assessing the
186 correlation between the two covariates, we investigated both their additive effect and the effect of
187 an interaction between the two. To assess the influence of each covariate, we fitted the models
188 including both covariates or each covariate separately and ranked them based on AIC and BIC [59].
189 Covariates were retained in the model if their inclusion reduced the information criteria by at least 2
190 units [59].

191 3. Results

192 Between February and July 2017, each of the 31 tagged seals performed on average 44 foraging
193 trips, which extended across the NE of Scotland (Figure 1A). Foraging trips lasted on average 38.65
194 hours (± 34.79 hours), with the longest trip performed by a male lasting 6.36 days. There was large
195 inter-individual variation in at-sea distribution (Figure 1A). However, the ranging patterns and
196 characteristics of the trips of the five individuals for which accelerometer data were available fell
197 within the range of all tagged individuals (Figure 1B, Table S2).

198 (a) Memory of foraging patches

199 The first HMM (Model 1) assigned the dive batches into two states: state 1 (step length: 1026.98 m
200 ± 193.83 m, angle: $\mu = 0$, $\gamma = 0.80$) and state 2 (step length: 587.81 m ± 172.48 m, angle: $\mu = 0$, $\gamma =$
201 0.027) (Figure S1). Based upon the combination of short step length and low concentration (i.e. high
202 variability) in turning angle, state 2 was assumed to represent ARS behaviour.

203 We were able to compare the areas animals visited in May with those visited in April for 29 seals
204 (two tags stopped recording during May). On average these seals performed 10 (± 5.61) foraging

205 trips in each month. We found 5.57 km to be the most appropriate h smoothing value to calculate
206 individual's 50% UD (Figure S2). Individuals were highly consistent in the areas they visited in April
207 and May (Table S3, Figure 2), showing much higher overlap than the null distribution (Figure 2).
208 From the output of Model 1, dive batches classified as state 2 were used to create the spatial
209 memory grids to be used as covariates in Model 2 and Model 3 (e.g. Figure 3B).

210 (b) Detection of prey encounters

211 Prey encounters were detected in all 51 foraging trips for which we had accelerometer data
212 (Table S1, Figure 3A). Within each of these trips, 69.45% of dives had at least one prey encounter
213 identified by one of the two methods. In total, 51,586 encounters were identified from peaks in
214 acceleration and 78,441 encounters were identified from changes in body pitch angle towards the
215 seabed (Figure S3). Of these, only 981 events (0.008% of the total attempts identified) overlapped in
216 time, possibly suggesting that the methods had identified the same event. There was inter-individual
217 variability in the detection of prey encounters by the two methods (Figure S4).

218 (c) Drivers of ARS behaviour

219 The second model (Model 2) assigned dive batches during foraging trips occurring in May into two
220 behavioural states: (i) the first was characterised by long step length and small turning angle (step:
221 1049.335 m \pm 556.832, angle: $\mu = 0$, $\gamma = 0.826$), which we assumed represents an animal transiting;
222 (ii) the second was characterised by short step length and large turning angle (step: 207.162 m \pm
223 181.983, angle: $\mu = 0$, $\gamma = 0.424$), which we assumed represents ARS behaviour (Figure S5). Both
224 model selection criteria supported the inclusion of spatial memory, based on seal movements in
225 April, as a covariate in the model (Table 2). The proportion of foraging batches spent searching in the
226 same area during the previous month increased an individual's probability of initiating ARS
227 behaviour (Figure 4 – Model 2).

228 Model 3 assigned movement between the dive batches into a Transit state (step: 893.543 m \pm
229 623.451, angle: $\mu = 0$, $\gamma = 0.827$) and an ARS state (step: 164.869 m \pm 150.729, angle: $\mu = 0$, $\gamma = 0.397$)

230 (Figure 3C and Figure S6). We found no correlation (*Kendall* $\tau = 0.14$) between the prey encounters
231 detected and the memory maps of the ARS behaviour during the previous month (Figure S7). Based
232 upon the HMM output, the seals spent 27.35% ($\pm 9.22\%$) of the dive batches transiting, and 57.27%
233 ($\pm 21.68\%$) in ARS behaviour, while 15.98% ($\pm 15.72\%$) of the dive batches could not be classified due
234 to a lack of GPS locations. Both model selection criteria suggested that including prey encounter
235 events and a proxy for memory of previous ARS movement (i.e. the proportion of dive batches spent
236 searching in the area) improved the model (Table 2). We found no improvement in the model by
237 including an interaction between the two covariates (Table 2). Model 3 showed that the probability
238 of an individual initiating ARS behaviour was associated with prey encounters and areas where
239 individuals spent time searching before (Figure 4 – Model 3). Finally, the variation we observed in
240 mean prey encounters per batch during times classified as ARS shows that animals spent time
241 actively searching within the foraging patch (Figure S8).

242 4. Discussion

243 Understanding the drivers of animal movement and foraging behaviour remains a central topic in
244 movement ecology [60, 61]. We found that individuals repeatedly used the same areas over time,
245 which supports the reliance on spatial memory by predators to return to previously visited foraging
246 grounds [13]. Therefore, we explored how marine predators use information both within and
247 outside their perceptual ranges to adjust their behaviour and movement, showing that both memory
248 and prey encounters influenced animals' foraging decisions [5, 11]. Specifically, our model shows
249 that encountering prey and having memory of searched areas coincide with an increased probability
250 of an individual initiating ARS behaviour.

251 It is challenging to quantify the distribution and variability of prey encounters at scales that are
252 relevant to marine predators [e.g. 62, 63]. We overcame this challenge by using animal-borne
253 accelerometer data to identify prey catch attempts, which can be used as a proxy for prey
254 encounters [35]. As predators may adapt prey capture strategies according to prey size or type [64,

255 65], we used two previously defined proxies for prey catch attempts. Using either methodology
256 alone would have reduced detections by 60% [55] and 40% [57], respectively. The number of prey
257 encounters showed a positive relationship with the probability of seals initiating searching
258 behaviour. These findings provide support for the hypothesis that predators increase their residence
259 time in foraging patches where encounter success is high [66]. However, individual residence times
260 could increase either due to longer search time between prey encounters or higher prey capture
261 rate and handling time. While we were unable to make inferences about foraging success and
262 handling times from accelerometer data alone, this may be possible in the future using auxiliary
263 sensors [67, 68].

264 Previous studies have also found that predators adjust their foraging behaviour to the density of
265 resources encountered [69]. For example, prey capture rate of double-crested cormorant
266 (*Phalacrocorax auritus*) was a good indicator of prey density [70]. Similarly, blue whales
267 (*Balaenoptera musculus*) adjusted the number of feeding lunges per dive to krill density [71]. The
268 results of our study show a similar positive relationship, with a higher probability of transitioning to
269 ARS when more prey encounters occurred. This further suggests that predators might be using the
270 number of prey encounters to assess the profitability of the foraging patch. Therefore, we can
271 hypothesise that the probability of initiating ARS behaviour is indeed indicative of the quality of the
272 foraging site.

273 Many marine central place foragers repeatedly move between and return to terrestrial breeding and
274 resting sites [72, 73] and foraging areas [22, 23, 74]. It is increasingly recognised that individual
275 foraging decisions are modified by the memory of previous experience in different foraging areas
276 [75]. In our results, we showed that the seals displayed a high level of repeatability in the areas they
277 searched for prey in over the span of two months. In contrast, previous research on repeatability in
278 otariids found little overlap of foraging areas between trips within a year [20]. Furthermore, our
279 dataset was not limited to a specific sex or life-history class (e.g. lactating females only as in [20,

280 76]), but included both sexes, as well as pregnant and non-pregnant females. The observed
281 repeatability in this study seems to be a common trait shared across sexes. All seals tagged in this
282 study were adults, for which a higher repeatability is expected compared to young individuals [77].
283 Given that individuals in this population showed high repeatability of searched areas, we tested
284 whether memory influenced fine-scale movement decisions by including spatial memory in the
285 Hidden Markov Model. We found that the probability of initiating ARS behaviour was linked with
286 individuals' spatial memory. Similarly, Thums *et al.* [11] found that southern elephant seals
287 (*Mirounga leonina*) had a high probability of engaging in ARS behaviour along the shelf edge,
288 independent of prey capture attempts recorded while diving. In our study, individuals changed their
289 behaviour in anticipation of profitable foraging areas. The differences observed between Model 2
290 (with data from 31 individuals) and Model 3 (with data from 5 just individuals) could indicate di
291 individual differences in the importance of memory which should be investigated further. Our
292 analysis assessed the influence of spatial memory associated with a 1 km x1 km grid without making
293 any assumptions about what features the animals might be using to recognize the areas [11] or
294 which cues they might be following to return to these areas [81].

295 Short- and long-term memory of encountered resources can also vary through the lifetime of an
296 individual, with acquisition of new information and memory decay over time [82]. In our study, we
297 compared multiple foraging trips occurring over consecutive months, building upon earlier studies
298 that have investigated the role of memory over a series of dives or paired trips [31, 83]. Our analysis
299 focussed on two months in spring/summer, future research should aim to extend this approach to
300 explore the role of memory over longer temporal scales using movement data across different
301 seasons [78, 80]. For example, seasonal changes in prey distribution might affect the foraging areas
302 targeted by individuals, causing a mismatch between the areas visited in consecutive months and
303 the persistence of memory at longer time scales [79]. Comparison of the movements of individuals
304 during similar time periods in different years would be needed to observe long-term memory-driven

305 behaviour [20, 22]. Spatial and temporal information on prey distribution is also needed to
306 understand how memory of prey patches may vary within or between years.

307 Having prior knowledge on prey distribution can be particularly useful for predators that feed on
308 cryptic prey species with low encounter rates. In this case, predators should adopt a Bayesian
309 foraging strategy, whereby historic prey encounters are used as prior information that is updated
310 while encountering prey [84, 85]. In our study predators appeared to adjust their movement in
311 response to both prior knowledge and current experience to initiate ARS. However, the same drivers
312 could also influence predators patch departure [86]; the Marginal Value Theorem predicts that
313 foragers should only leave a patch and switch back to transit movement when intake rate drops
314 below the average intake rate of the entire area [87]. Here, we were only able to incorporate
315 archival accelerometry data from the subset of tags that were recovered. However, with
316 improvements in on-board processing [34], data on prey encounters can now be accessed in near
317 real-time with the associated GPS data, allowing these models to be tested over ecologically relevant
318 spatial and temporal scales.

319 In conclusion, this study gives new insights into another driver of ARS behaviour. These findings
320 provide empirical evidence that predators use other information, such as spatial memory, to guide
321 movement decisions and to initiate ARS behaviour. Previous studies showed that predators
322 responded to their recent prey encounters, but this was insufficient to fully explain observed
323 movement patterns [3, 75]. The ability of predators to memorise the distribution of predictable
324 resources has been predicted to have evolved to cope with environmental variability and to
325 maximise their long-term energy intake [18, 19, 88]. These results reinforce the importance of
326 accounting for this ability within movement models [17, 89].

327 Ethics

328 All research activities were conducted under the Home Office Licence issued to the Sea Mammal
329 Research Unit (Licence No. 192CBD9F) with local licence approval from the University of St Andrews
330 Animal Welfare and Ethics Committee.

331 Data accessibility

332 All data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.6q573n601>
333 [90] and all processing codes are available in the GitHub Repository
334 (github.com/virginalorio/Drivers-of-seal-ARS-behaviour).

335 Author's contributions

336 V.I-M.: conceptualization, methodology, formal analysis, writing – original draft, visualization.
337 I.M.G.: conceptualization, writing – review and editing, supervision, investigation, data curation.
338 R.C.H.: investigation. G.A.: methodology, writing – review and editing. E.P.: methodology, formal
339 analysis, writing – review and editing. G.D.H.: investigation, writing – review and editing. P.M.T.:
340 conceptualization, writing – review and editing, supervision, project administration, funding.

341 Competing Interest

342 We declare we have no competing interests.

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585

586 **List of tables**

587 **Table 1.** Overview of the three HMM models, showing the number of individuals included in the
 588 model, the time period for which movement data were used, the covariates that were included in
 589 the model to assess the influence on the transition probabilities and a summary of the objectives
 590 and what was the output used for.

Model	Number of individuals	Time period	Covariates	Objective and output
Model 1	31	February – June	None	<ul style="list-style-type: none"> • Identification of ARS locations to be used in the repeatability analysis • Spatial memory maps with the proportion of dive batches spent searching for the month of April and a month prior to the beginning of the accelerometer data
Model 2	29	May	<ul style="list-style-type: none"> • Spatial memory of ARS behaviour in April. 	<ul style="list-style-type: none"> • Test the influence of memory on the transition probability between ARS and Transit
Model 3	5	April – May - June	<ul style="list-style-type: none"> • Spatial memory of ARS behaviour during the month prior to the beginning of the accelerometer data • Mean number of prey encounters per dive in each dive batch 	<ul style="list-style-type: none"> • Test the influence of memory and prey encounters on the transition probability between ARS and Transit

591

592

593

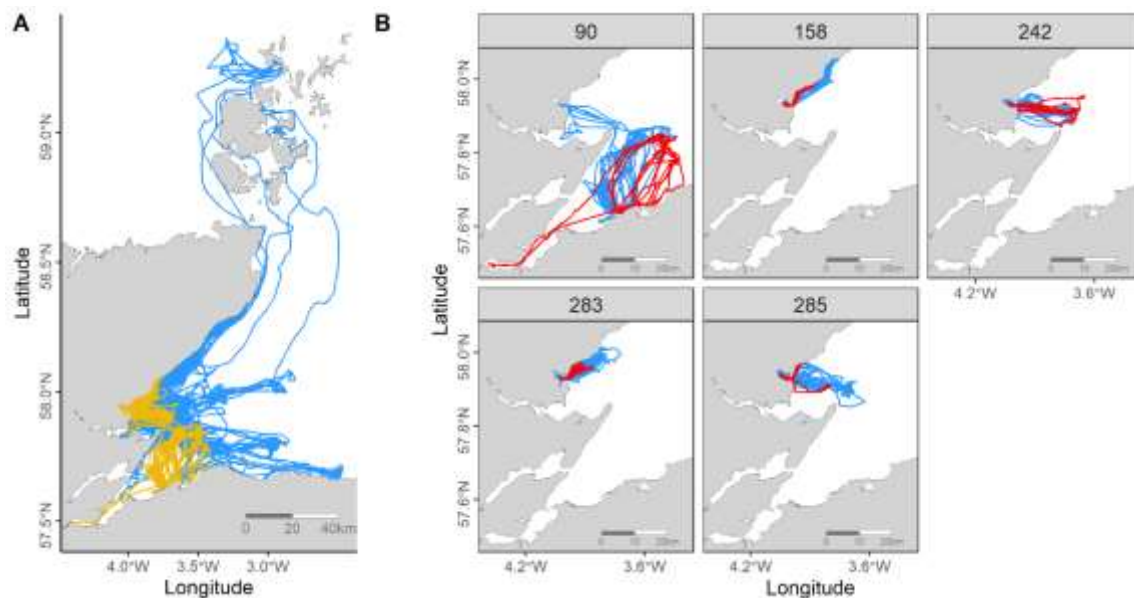
594

595 **Table 2.** Comparison of the models based on AIC and BIC, with covariates and removing one variable
 596 at a time for both Model 2 and Model 3. The memory covariate represents the number of dive
 597 batches spent searching in a grid cell during the previous month, and prey encounters indicates the
 598 mean number of catch attempts per dive for each batch.

Model 2	Log-Likelihood	AIC	BIC	Δ AIC	Δ BIC
With memory	-164,875	329,759	329,848	0	0
Without memory	-165,000	330,017	330,090	258	242
Model 3	Log-Likelihood	AIC	BIC	Δ AIC	Δ BIC
Memory + Prey encounters	-26,816	53,657	53,739	0	0
Memory * Prey encounters	-26,814	53,657	53,751	0	12
- Memory	-26,845	53,780	53,781	54	41
- Prey encounters	-26,882	53,909	53,910	129	116

599

600 Figures



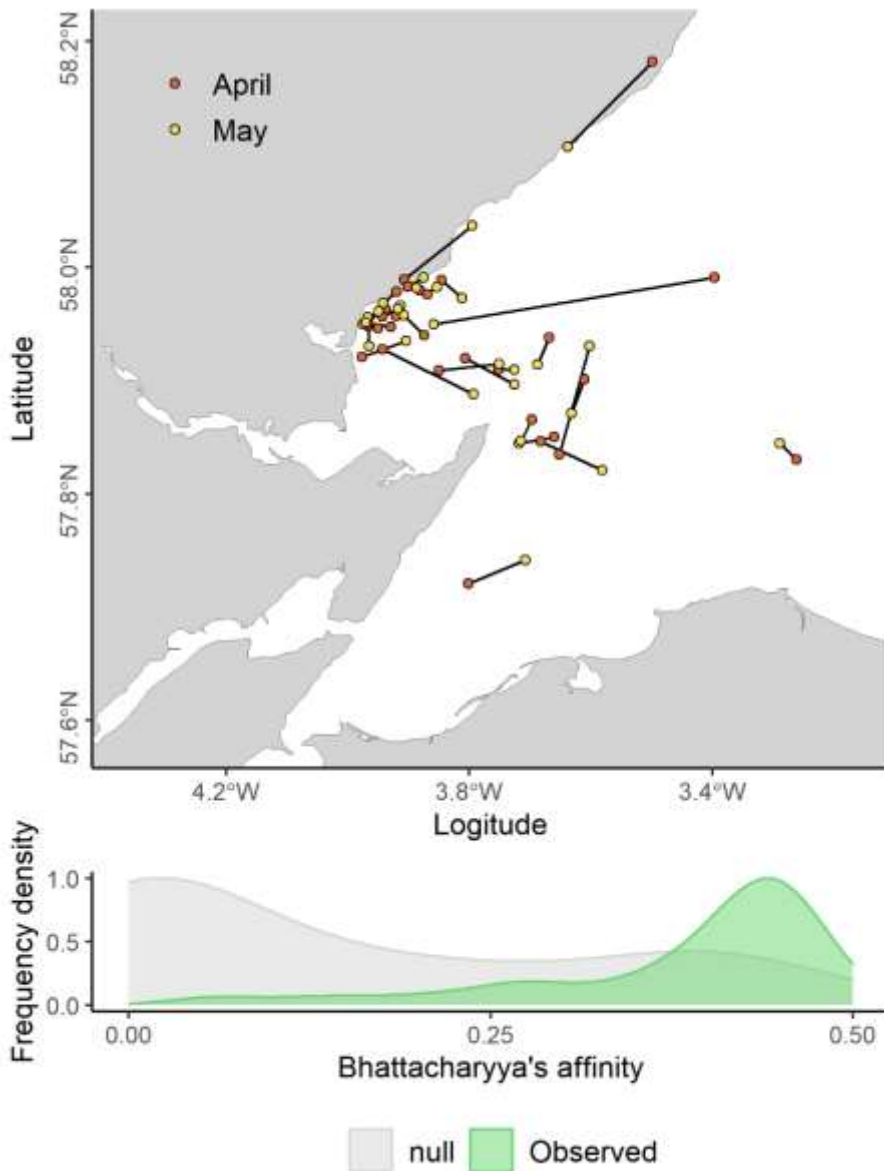
601

602 **Figure 1.** A) Maps displaying the movements of the 31 tagged harbour seals in the Moray Firth

603 (Scotland), showing data from the five retrieved tags in yellow. B) Tracks of the five focal seals where

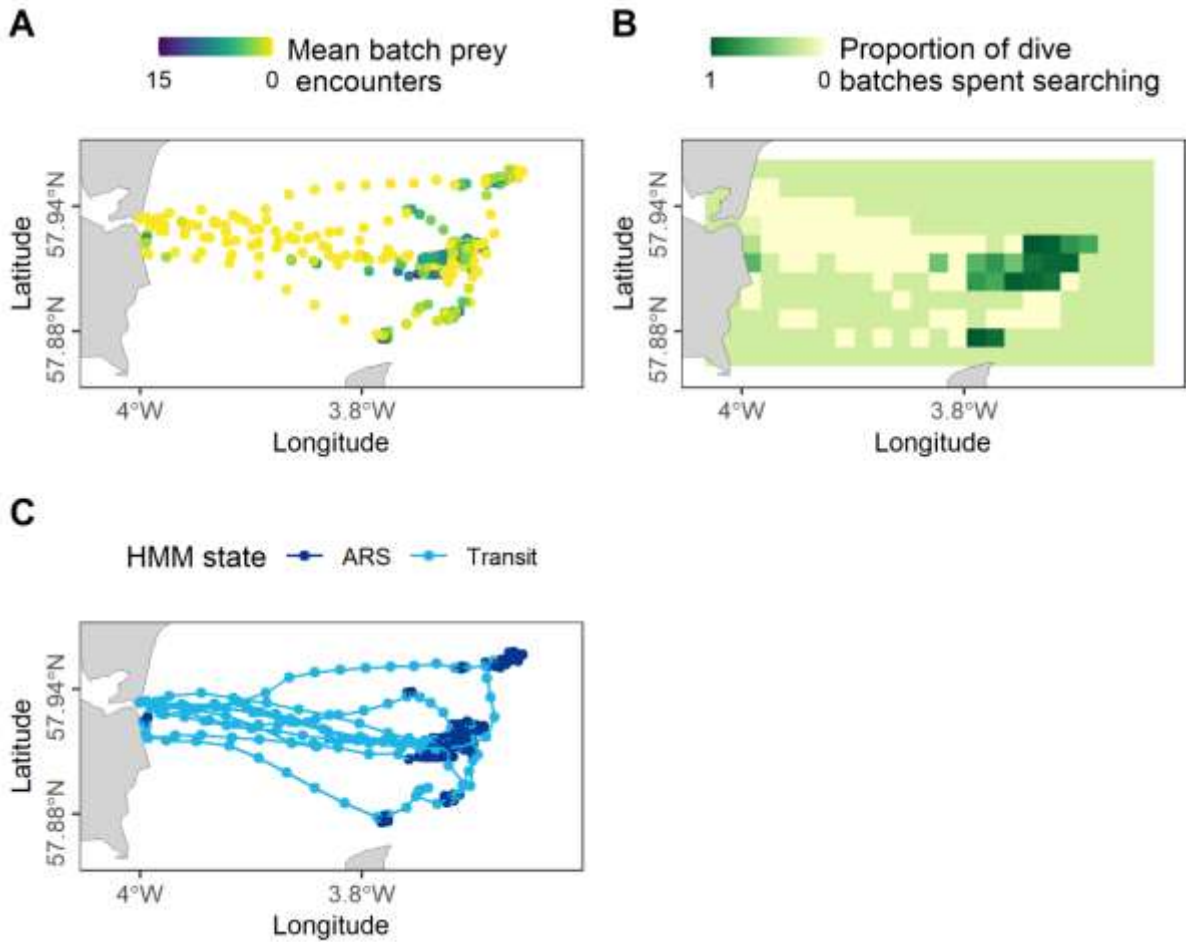
604 tags were recovered. The trips with accelerometer data that were included in the analysis are

605 highlighted in red (Model 3), while the time period before and after is shown in blue.



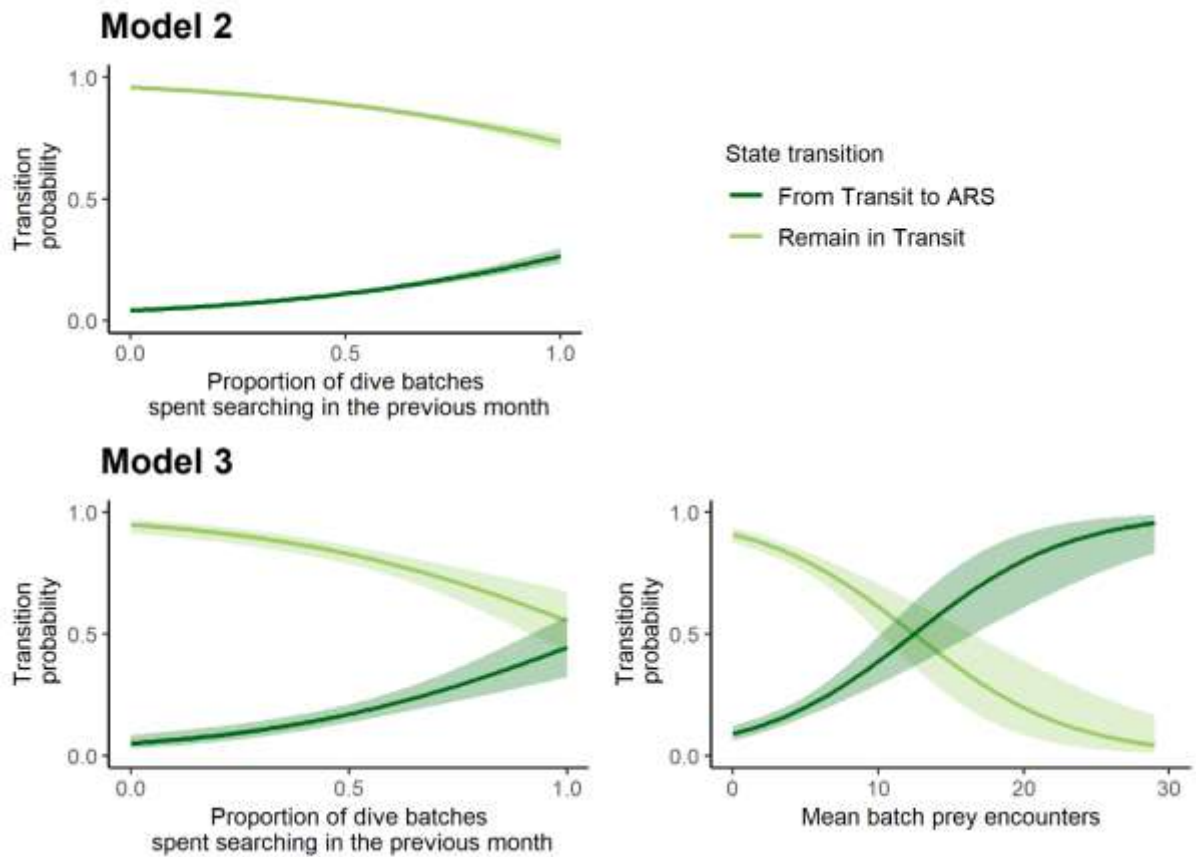
606

607 **Figure 2.** Top: Centroid location of the areas animals searched in April (red) in relation to the
 608 centroid location of the ones visited in May (yellow) for 29 individuals. Bottom: Frequency
 609 distribution of the observed overlap (green) of an individual's searched areas in consecutive month,
 610 estimated using Bhattacharyya's affinity index, and the null distribution of Bhattacharyya's affinity
 611 values from the overlap with the areas searched by another randomly selected individual.



612

613 **Figure 3.** Example of the spatial variation in prey encounters and proxy for spatial memory in
 614 relation to the behavioural state classification of Model 3 for the foraging trips of seal 242. A)
 615 Locations of dive batches, colour-coded by the mean number of prey encounters per dive batch. B)
 616 Memory grid, showing the proportion of dive batches classified as ARS by Model 1 in each grid cell
 617 during the month prior to the trips in Model 3. C) Tracks of the trips used in Model 3, colour-coded
 618 by the decoded HMM state. Missing parts of the tracks are due to unreliable dive batches (see
 619 Appendix B).



620

621 **Figure 4.** Stationary probability (mean and 95% CI) of occupying either of the two states and
 622 transition probability (mean and 95% CI) of remaining in a transit state or switching to an ARS state
 623 for the covariates included in Model 2 and Model 3. A) Influence of proportion of dive batches spent
 624 searching in the previous month (proxy for spatial memory) on the 29 individuals included in Model
 625 2. B) Influence of proportion of dive batches spent searching in the previous month on the five
 626 individuals included in Model 3. C) Influence of the mean batch prey encounters on the five
 627 individuals included in Model 3

628