

1 Prey encounters and spatial memory influence use of foraging patches in a
2 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 (Global Positioning System) receiver, wet-dry sensor, and pressure
84 sensor, providing geo-referenced summaries of activity and diving patterns via the GSM (Global
85 System for Mobile communications) phone network [39]. Tags also collected tri-axial accelerometer
86 data that were archived onboard, subject to digital storage limitations, but not relayed through the
87 GSM network due to the volume of data from the high sampling frequencies used. Tags from a
88 subset of five individuals were subsequently recovered on the shore after tags detached during the
89 moult, allowing archived tri-axial accelerometer data to be downloaded.

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

104 (b) Identification of ARS behaviour

105 We fitted a total of three HMMs (Table 1) to classify at-sea activities and to build spatial memory
106 maps of searched areas (Model 1), to assess the influence of memory alone on all individuals (Model
107 2), and to assess the simultaneous influence of spatial memory and prey encounters on the subset of
108 five individuals for which accelerometer data were available (Model 3). All models were fitted using
109 the momentuHMM package [42].

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

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

123 Seal activities at sea were classified into two behavioural states using an HMM based on the step
124 length and turning angle between consecutive dive batches. The two states are assumed to
125 represent transit and ARS movement, which are characterised by long directional displacement or
126 short tortuous movement, respectively [41]. We calculated the step length and turning angle
127 between the locations of the first dive of each batch and assumed these observations resulted from
128 state-dependent gamma and wrapped Cauchy distributions [45], respectively. Following the

129 methodology described by Russell *et al.* [46] and Carter *et al.* [47], if any dive batch was not
130 associated with a raw GPS location, the step length and turning angle were set to 'not available' (NA)
131 [36]; thus, the state was assigned solely based on the Markov property (for more details see
132 Appendix B). Finally, we selected the initial values of the parameters using the estimates from the
133 model with the lowest AIC (Akaike Information Criterion) score among 50 iterations with randomly
134 selected initial values. The most likely state sequence given the final model was decoded using the
135 Viterbi algorithm [48].

136 (c) Spatial memory of foraging patches

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

147 As a proxy for spatial memory, we built memory grids using the proportion of dive batches classified
148 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
149 be used in Model 2 and Model 3, respectively (Table 1). We first created a set of spatial memory
150 grids representing the individual's ARS behaviour during the previous month of the data included in
151 Model 2 (Table 1). Then we created a second set of grids representing the areas used during one
152 month prior to data included in Model 3 (Table 1). Due to the differences in accelerometer data

153 availability between individuals (Table S1) the month used to build the spatial memory grid for each
154 of these five individuals varied.

155 (d) Prey encounters

156 We inferred prey encounter events from the accelerometer data while animals were at sea. In
157 coastal waters, harbour seals most frequently dive to the seabed and perform U-shaped dives
158 through all phases of their foraging trips [52, 53]. Therefore, we used accelerometry data to detect
159 prey encounters during the bottom phase of each of these dives [53], characterised as the period
160 when seals were within 20% of the maximum dive depth [54].

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

177 number of prey encounter events in each dive by summing the number of independent attempts
178 detected by either method.

179 (e) Assessing the drivers of ARS behaviour

180 To assess which factors influenced the initiation of ARS behaviour, we ran two separate models
181 Model 2 and Model 3 (Table 1). Model 2 was based on foraging trips occurring in May and included
182 the spatial memory grids of the seals' activities during the month of April as covariates on the
183 transition probabilities between transit and ARS state [58]. In Model 3, we included the spatial
184 memory grid of activities during the month prior to the beginning of the accelerometer data and the
185 mean number of prey encounters per dive in each dive batch as covariates (see 'Identification of ARS
186 behaviour'). Note that although five individuals were represented in both models, the memory grids
187 differed between models (see 'Spatial memory of foraging patches section'). After assessing the
188 correlation between the two covariates, we investigated both their additive effect and the effect of
189 an interaction between the two. To assess the influence of each covariate, we fitted the models
190 including both covariates or each covariate separately and ranked them based on AIC and BIC [59].
191 Covariates were retained in the model if their inclusion reduced the information criteria by at least 2
192 units [59].

193 3. Results

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

200 (a) Memory of foraging patches

201 The first HMM (Model 1) assigned the dive batches into two states: state 1 (step length: 1026.98 m
202 \pm 193.83 m, angle: $\mu = 0$, $\gamma = 0.80$) and state 2 (step length: 587.81 m \pm 172.48 m, angle: $\mu = 0$, $\gamma =$
203 0.027) (Figure S1). Based upon the combination of short step length and low concentration (i.e. high
204 variability) in turning angle, state 2 was assumed to represent ARS behaviour.

205 We were able to compare the areas animals visited in May with those visited in April for 29 seals
206 (two tags stopped recording during May). On average these seals performed 10 (\pm 5.61) foraging
207 trips in each month. We found 5.57 km to be the most appropriate h smoothing value to calculate
208 individual's 50% UD (Figure S2). Individuals were highly consistent in the areas they visited in April
209 and May (Table S3, Figure 2), showing much higher overlap than the null distribution (Figure 2).

210 From the output of Model 1, dive batches classified as state 2 were used to create the spatial
211 memory grids to be used as covariates in Model 2 and Model 3 (e.g. Figure 3B).

212 (b) Detection of prey encounters

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

220 (c) Drivers of ARS behaviour

221 The second model (Model 2) assigned dive batches during foraging trips occurring in May into two
222 behavioural states: (i) the first was characterised by long step length and small turning angle (step:
223 1049.335 m \pm 556.832, angle: $\mu = 0$, $\gamma = 0.826$), which we assumed represents an animal transiting;
224 (ii) the second was characterised by short step length and large turning angle (step: 207.162 m \pm

225 181.983, angle: $\mu = 0$, $\gamma = 0.424$), which we assumed represents ARS behaviour (Figure S5). Both
226 model selection criteria supported the inclusion of spatial memory, based on seal movements in
227 April, as a covariate in the model (Table 2). The proportion of foraging batches spent searching in the
228 same area during the previous month increased an individual's probability of initiating ARS
229 behaviour (Figure 4 – Model 2).

230 Model 3 assigned movement between the dive batches into a Transit state (step: 893.543 m \pm
231 623.451, angle: $\mu = 0$, $\gamma=0.827$) and an ARS state (step: 164.869 m \pm 150.729, angle: $\mu = 0$, $\gamma = 0.397$)
232 (Figure 3C and Figure S6). We found no correlation (*Kendall* $\tau = 0.14$) between the prey encounters
233 detected and the memory maps of the ARS behaviour during the previous month (Figure S7). Based
234 upon the HMM output, the seals spent 27.35% ($\pm 9.22\%$) of the dive batches transiting, and 57.27%
235 ($\pm 21.68\%$) in ARS behaviour, while 15.98% ($\pm 15.72\%$) of the dive batches could not be classified due
236 to a lack of GPS locations. Both model selection criteria suggested that including prey encounter
237 events and a proxy for memory of previous ARS movement (i.e. the proportion of dive batches spent
238 searching in the area) improved the model (Table 2). We found no improvement in the model by
239 including an interaction between the two covariates (Table 2). Model 3 showed that the probability
240 of an individual initiating ARS behaviour was associated with prey encounters and areas where
241 individuals spent time searching before (Figure 4 – Model 3). Finally, the variation we observed in
242 mean prey encounters per batch during times classified as ARS shows that animals spent time
243 actively searching within the foraging patch (Figure S8).

244 4. Discussion

245 Understanding the drivers of animal movement and foraging behaviour remains a central topic in
246 movement ecology [60, 61]. We found that individuals repeatedly used the same areas over time,
247 which supports the reliance on spatial memory by predators to return to previously visited foraging
248 grounds [13]. Therefore, we explored how marine predators use information both within and
249 outside their perceptual ranges to adjust their behaviour and movement, showing that both memory

250 and prey encounters influenced animals' foraging decisions [5, 11]. Specifically, our model shows
251 that encountering prey and having memory of searched areas coincide with an increased probability
252 of an individual initiating ARS behaviour.

253 It is challenging to quantify the distribution and variability of prey encounters at scales that are
254 relevant to marine predators [e.g. 62, 63]. We overcame this challenge by using animal-borne
255 accelerometer data to identify prey catch attempts, which can be used as a proxy for prey
256 encounters [35]. As predators may adapt prey capture strategies according to prey size or type [64,
257 65], we used two previously defined proxies for prey catch attempts. Using either methodology
258 alone would have reduced detections by 60% [55] and 40% [57], respectively. The number of prey
259 encounters showed a positive relationship with the probability of seals initiating searching
260 behaviour. These findings provide support for the hypothesis that predators increase their residence
261 time in foraging patches where encounter success is high [66]. However, individual residence times
262 could increase either due to longer search time between prey encounters or higher prey capture
263 rate and handling time. While we were unable to make inferences about foraging success and
264 handling times from accelerometer data alone, this may be possible in the future using auxiliary
265 sensors [67, 68].

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

275 Many marine central place foragers repeatedly move between and return to terrestrial breeding and
276 resting sites [72, 73] and foraging areas [22, 23, 74]. It is increasingly recognised that individual
277 foraging decisions are modified by the memory of previous experience in different foraging areas
278 [75]. In our results, we showed that the seals displayed a high level of repeatability in the areas they
279 searched for prey in over the span of two months. In contrast, previous research on repeatability in
280 otariids found little overlap of foraging areas between trips within a year [20]. Furthermore, our
281 dataset was not limited to a specific sex or life-history class (e.g. lactating females only as in [20,
282 76]), but included both sexes, as well as pregnant and non-pregnant females. The observed
283 repeatability in this study seems to be a common trait shared across sexes. All seals tagged in this
284 study were adults, for which a higher repeatability is expected compared to young individuals [77].

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

297 Short- and long-term memory of encountered resources can also vary through the lifetime of an
298 individual, with acquisition of new information and memory decay over time [82]. In our study, we
299 compared multiple foraging trips occurring over consecutive months, building upon earlier studies

300 that have investigated the role of memory over a series of dives or paired trips [31, 83]. Our analysis
301 focussed on two months in spring/summer, future research should aim to extend this approach to
302 explore the role of memory over longer temporal scales using movement data across different
303 seasons [78, 80]. For example, seasonal changes in prey distribution might affect the foraging areas
304 targeted by individuals, causing a mismatch between the areas visited in consecutive months and
305 the persistence of memory at longer time scales [79]. Comparison of the movements of individuals
306 during similar time periods in different years would be needed to observe long-term memory-driven
307 behaviour [20, 22]. Spatial and temporal information on prey distribution is also needed to
308 understand how memory of prey patches may vary within or between years.

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

321 In conclusion, this study gives new insights into another driver of ARS behaviour. These findings
322 provide empirical evidence that predators use other information, such as spatial memory, to guide
323 movement decisions and to initiate ARS behaviour. Previous studies showed that predators
324 responded to their recent prey encounters, but this was insufficient to fully explain observed

325 movement patterns [3, 75]. The ability of predators to memorise the distribution of predictable
326 resources has been predicted to have evolved to cope with environmental variability and to
327 maximise their long-term energy intake [18, 19, 88]. These results reinforce the importance of
328 accounting for this ability within movement models [17, 89].

329 Ethics

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

333 Data accessibility

334 All data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.6q573n601>
335 [90] and all processing codes are available in the GitHub Repository
336 (github.com/virginialorio/Drivers-of-seal-ARS-behaviour).

337 Author's contributions

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

343 Competing Interest

344 We declare we have no competing interests.

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587

588 **List of tables**

589 **Table 1.** Overview of the three HMM models, showing the number of individuals included in the
 590 model, the time period for which movement data were used, the covariates that were included in
 591 the model to assess the influence on the transition probabilities and a summary of the objectives
 592 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

593

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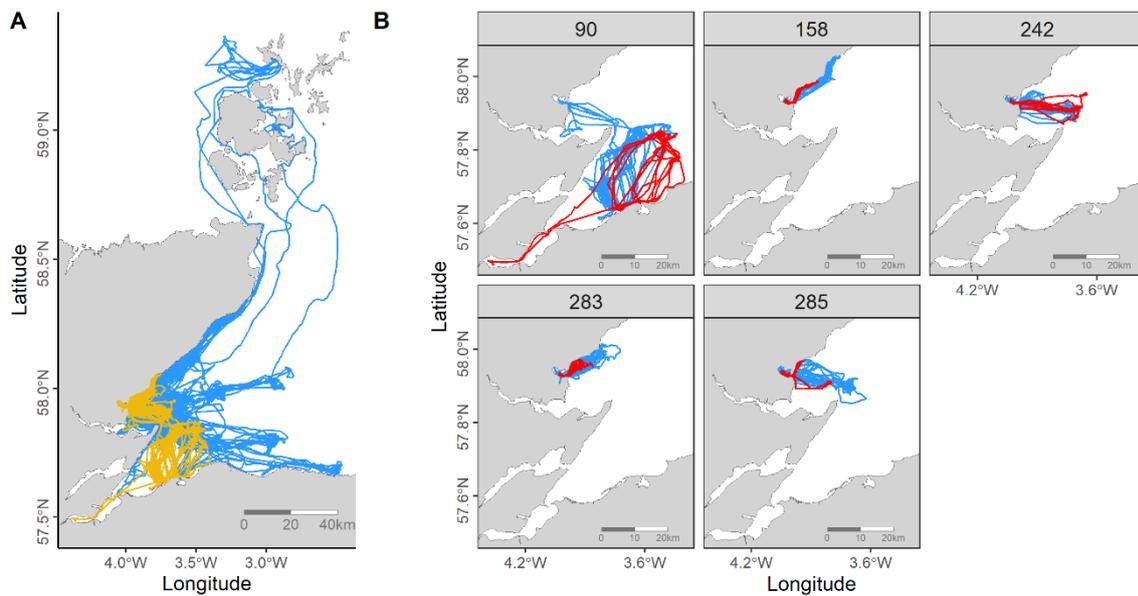
596

597 **Table 2.** Comparison of the models based on AIC and BIC, with covariates and removing one variable
 598 at a time for both Model 2 and Model 3. The memory covariate represents the number of dive
 599 batches spent searching in a grid cell during the previous month, and prey encounters indicates the
 600 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

601

602 **Figures**



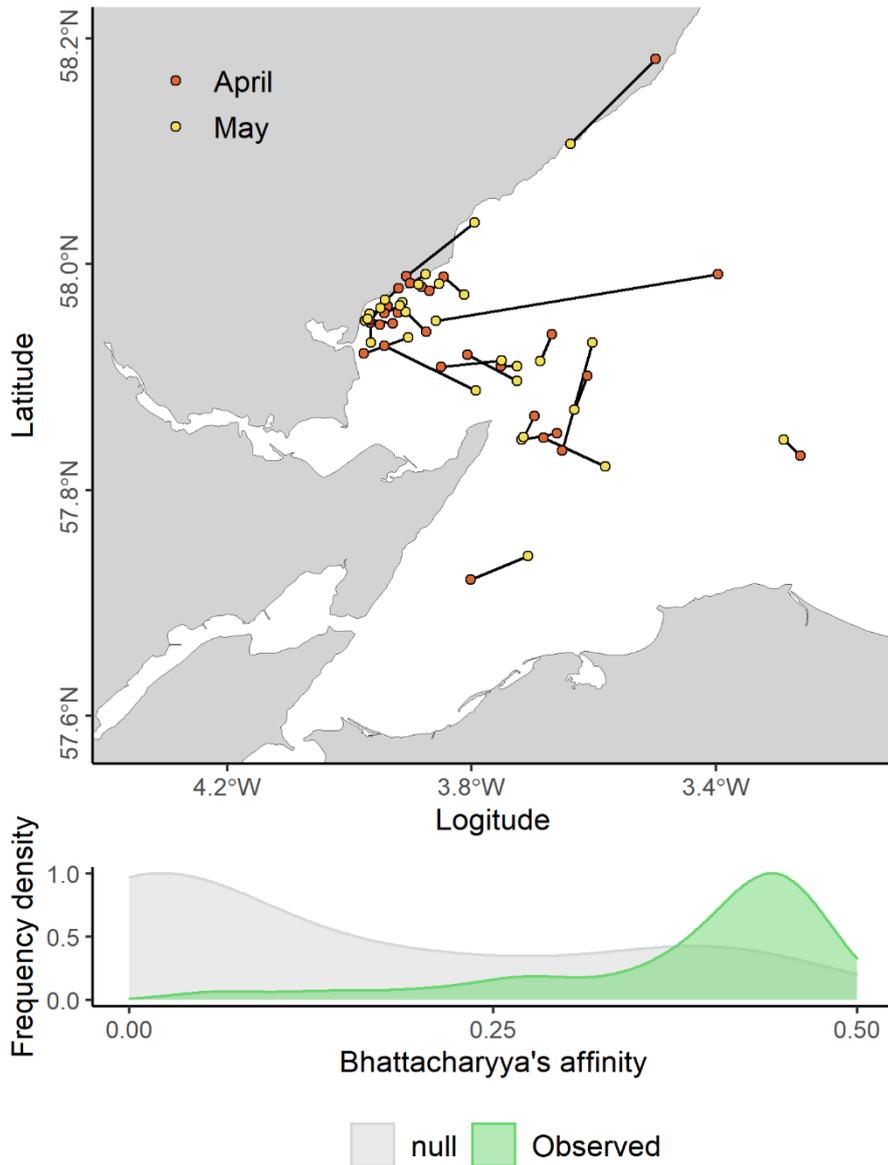
603

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

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

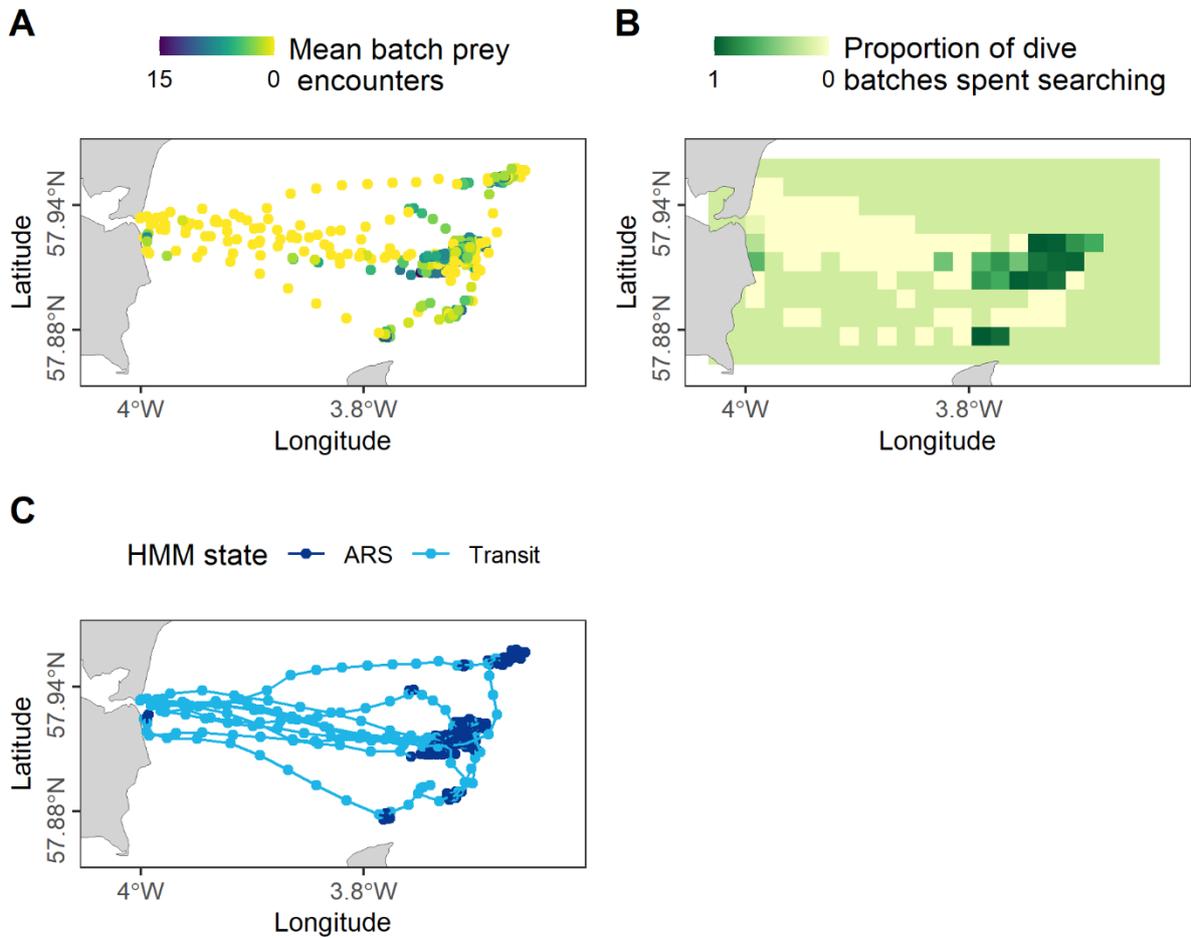
606 tags were recovered. The trips with accelerometer data that were included in the analysis are

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



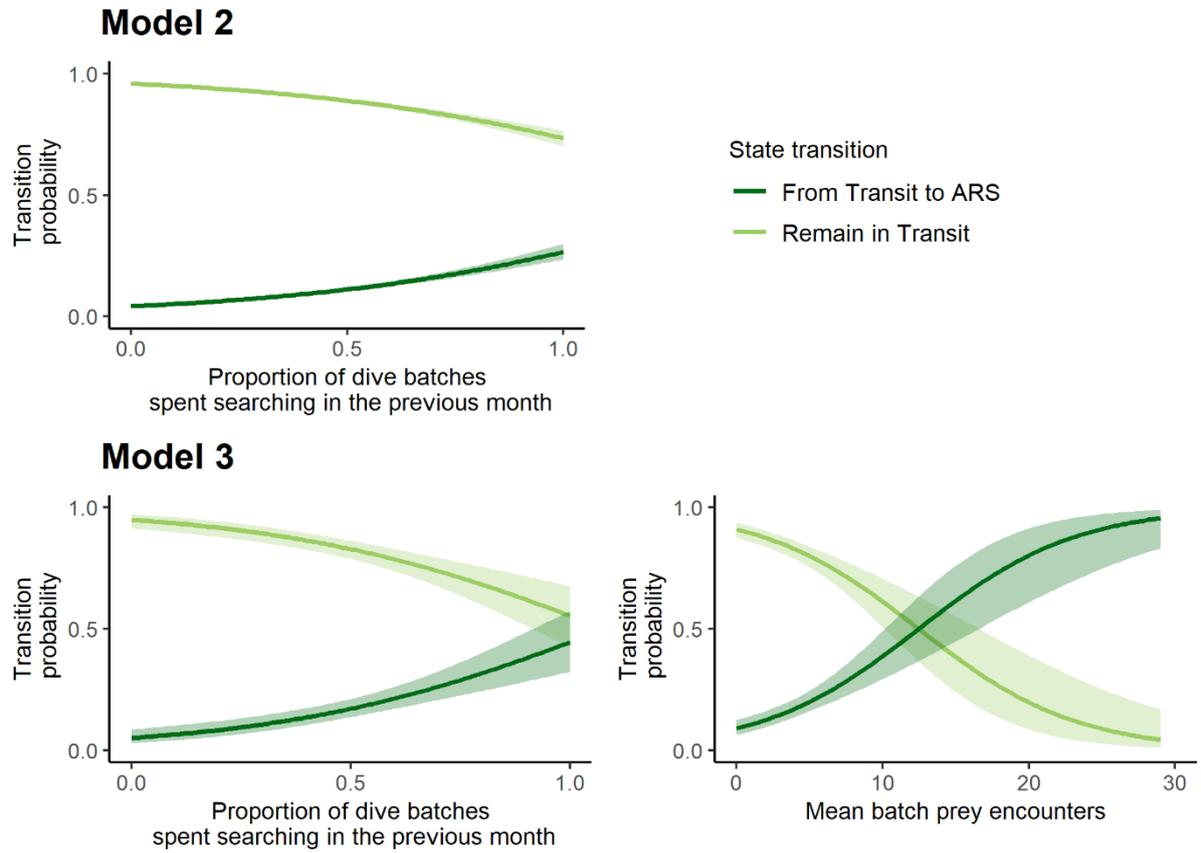
608

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



614

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



622

623 **Figure 4.** Stationary probability (mean and 95% CI) of remaining in a transit state or switching to an
 624 ARS state for the covariates included in Model 2 and Model 3. Model 2: Influence of proportion of
 625 dive batches spent searching in the previous month (proxy for spatial memory) on the 29 individuals
 626 included in Model 2. Model 3: (*left*) Influence of proportion of dive batches spent searching in the
 627 previous month on the five individuals included in Model 3. (*right*) Influence of the mean batch prey
 628 encounters on the five individuals included in Model 3

629