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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 accelerometery 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 Markov Models showed that both spatial memory and prey encounters increased the probability of 28 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 abilities, they are also expected to use other information sources to initiate ARS [3, 11, 12]. 44 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 (*Thalassarche melanophris*) targeted areas of  $< 1 \text{ km}^2$  where they had previously encountered fishing 52 53 vessels, despite these being > 100 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

Harbour seals are central place foragers inhabiting temperate coastal waters [37]. During February
and March 2017, 31 adult harbour seals (11 Males and 20 Females) were captured and tagged in
Loch Fleet, NE Scotland (57.935° N, 4.042° W) (see [13] for background on the study site and
population). Seal capture and handling occurred in accordance with the Home Office Licence issued
to the Sea Mammal Research Unit (Licence No. 192CBD9F) with local licence approval from the
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

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

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

To ensure our analysis focussed on central place foraging trips, we selected round-trips from and to the same haul-out site location, which were a) > 12 hours and b) included locations that were > 2 km from the haul-out site. This avoided the inclusion of shorter periods in the water which typically 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 (± 6.68) minutes, and the 90<sup>th</sup> percentile of the time interval between GPS locations was 25 minutes. Dive locations were estimated by linearly interpolating 117 118 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 between the locations of the first dive of each batch and assumed these observations resulted from 126 127 state-dependent gamma and wrapped Cauchy distributions [45], respectively. Following the methodology described by Russell et al. [46] and Carter et al. [47], if any dive batch was not 128 129 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

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

134 (c) Spatial memory of foraging patches

Searching areas were defined using the locations of dive batches that were classified as ARS by 135 136 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 availability between individuals (Table S1) the month used to build the spatial memory grid for each 151 152 of these five individuals varied.

#### 153 (d) Prey encounters

We inferred prey encounter events from the accelerometer data while animals were at sea. In coastal waters, harbour seals most frequently dive to the seabed and perform U-shaped dives through all phases of their foraging trips [52, 53]. Therefore, we used accelerometery data to detect
prey encounters during the bottom phase of each of these dives [53], characterised as the period
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 activity states, "high" and "low". We assumed an animal made a prey capture attempt, and thus 164 165 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 *q*-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

To assess which factors influenced the initiation of ARS behaviour, we ran two separate models
Model 2 and Model 3 (Table 1). Model 2 was based on foraging trips occurring in May and included
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**

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

#### 198 (a) Memory of foraging patches

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

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

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

#### 210 (b) Detection of prey encounters

Prey encounters were detected in all 51 foraging trips for which we had accelerometer data
(TableS1, Figure 3A). Within each of these trips, 69.45% of dives had at least one prey encounter
identified by one of the two methods. In total, 51,586 encounters were identified from peaks in
acceleration and 78,441 encounters were identified from changes in body pitch angle towards the
seabed (Figure S3). Of these, only 981 events (0.008% of the total attempts identified) overlapped in
time, possibly suggesting that the methods had identified the same event. There was inter-individual
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 ± 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:  $207.162 \text{ m} \pm$ 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 ± 229 623.451, angle:  $\mu = 0$ ,  $\gamma = 0.827$ ) and an ARS state (step: 164.869 m ± 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% (± 9.22%) of the dive batches transiting, and 57.27% 233 (± 21.68%) in ARS behaviour, while 15.98% (± 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).

#### 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.

It is challenging to quantify the distribution and variability of prey encounters at scales that are
relevant to marine predators [e.g. 62, 63]. We overcame this challenge by using animal-borne
accelerometer data to identify prey catch attempts, which can be used as a proxy for prey
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 behaviour [20, 22]. Spatial and temporal information on prey distribution is also needed to
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 accelerometery 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

- All data are available from the Dryad Digital Repository <u>https://doi.org/10.5061/dryad.6q573n601</u>
- 333 [90] and all processing codes are available in the GitHub Repository
- 334 (github.com/virginialorio/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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## 586 List of tables

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

Model Number of **Objective and output** Time Covariates individuals period None • Identification of ARS locations to be used in the repeatability analysis Spatial memory maps with the February -Model 1 31 proportion of dive batches spent June searching for the month of April and a month prior to the beginning of the accelerometer data Spatial memory of ARS Test the influence of memory on the Model 2 29 May behaviour in April. transition probability between ARS and Transit Spatial memory of ARS • Test the influence of memory and ٠ behaviour during the month prey encounters on the transition prior to the beginning of the probability between ARS and Transit April - May -5 Model 3 accelerometer data June Mean number of prey encounters per dive in each dive batch Table 2. Comparison of the models based on AIC and BIC, with covariates and removing one variable at a time for both Model 2 and Model 3. The memory covariate represents the number of dive 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

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# 600 Figures



Figure 1. A) Maps displaying the movements of the 31 tagged harbour seals in the Moray Firth
(Scotland), showing data from the five retrieved tags in yellow. B) Tracks of the five focal seals where
tags were recovered. The trips with accelerometer data that were included in the analysis are
highlighted in red (Model 3), while the time period before and after is shown in blue.







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



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

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