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

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Abstract

Given the patchiness and long-term predictability of marine resources, memory of high-quality foraging grounds is expected to provide fitness advantages for central place foragers. However, it remains challenging to characterise how marine predators integrate memory with recent prey encounters to adjust fine-scale movement and use of foraging patches. Here, we used two months of movement data from harbour seals (*Phoca vitulina*) to quantify the repeatability in foraging patches as a proxy for memory. We then integrated these data into analyses of fine-scale movement and underwater behaviour to test how both spatial memory and prey encounter rates influenced the seals' Area Restricted Search (ARS) behaviour. Specifically, we used one month's GPS data from 29 individuals to build spatial memory maps of searched areas, and archived accelerometery data from a subset of five individuals to detect prey catch attempts, a proxy for prey encounters. 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 seals initiating ARS. These results provide evidence that predators use memory to adjust their fine scale movement and this ability should be accounted for in movement models.

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

1. Introduction

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

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

Previous studies considering both memory and the influence of prey encounters on searching strategies are based either on terrestrial systems [25, 26] or simulations [27-29]. Despite evidence of marine predators returning to foraging grounds [11, 12, 30], it is only recently that advances in biologging and acoustic technologies have provided finer resolution data to empirically test the effect of prey-encounter events on marine mammal and seabird movements [9, 31]. To date, we are aware of no study that has directly explored how marine predators combine longer-term spatial memory and contemporary prey encounters to adjust their fine-scale movements.

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

2. Methods

(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

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

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

(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].

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

Seal activities at sea were classified into two behavioural states using an HMM based on the step length and turning angle between consecutive dive batches. The two states are assumed to represent transit and ARS movement, which are characterised by long directional displacement or 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 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 associated with a raw GPS location, the step length and turning angle were set to 'not available' (NA) [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].

(c) Spatial memory of foraging patches

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

As a proxy for spatial memory, we built memory grids using the proportion of dive batches classified 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 be used in Model 2 and Model 3, respectively (Table 1). We first created a set of spatial memory grids representing the individual's ARS behaviour during the previous month of the data included in Model 2 (Table 1). Then we created a second set of grids representing the areas used during one 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 of these five individuals varied.

(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].

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

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

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).

(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).

(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).

(c) Drivers of ARS behaviour

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

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

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

4. Discussion

Understanding the drivers of animal movement and foraging behaviour remains a central topic in movement ecology [60, 61]. We found that individuals repeatedly used the same areas over time, which supports the reliance on spatial memory by predators to return to previously visited foraging grounds [13]. Therefore, we explored how marine predators use information both within and outside their perceptual ranges to adjust their behaviour and movement, showing that both memory and prey encounters influenced animals' foraging decisions [5, 11]. Specifically, our model shows that encountering prey and having memory of searched areas coincide with an increased probability 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, 65], we used two previously defined proxies for prey catch attempts. Using either methodology alone would have reduced detections by 60% [55] and 40% [57], respectively. The number of prey encounters showed a positive relationship with the probability of seals initiating searching behaviour. These findings provide support for the hypothesis that predators increase their residence time in foraging patches where encounter success is high [66]. However, individual residence times could increase either due to longer search time between prey encounters or higher prey capture rate and handling time. While we were unable to make inferences about foraging success and handling times from accelerometer data alone, this may be possible in the future using auxiliary sensors [67, 68].

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

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

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

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

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

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

Ethics

All research activities were conducted under 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.

Data accessibility

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

Author's contributions

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

Competing Interest

We declare we have no competing interests.

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List of tables

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 individuals	Time period	Covariates	Objective and output
Model 1	31	February – June	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	• Spatial memory of ARS behaviour in April.	• Test the influence of memory on the transition probability between ARS and Transit
Model 3	5	April – May - June	• 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	• Test the influence of memory and prey encounters on the transition probability between ARS and Transit

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 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

Figures

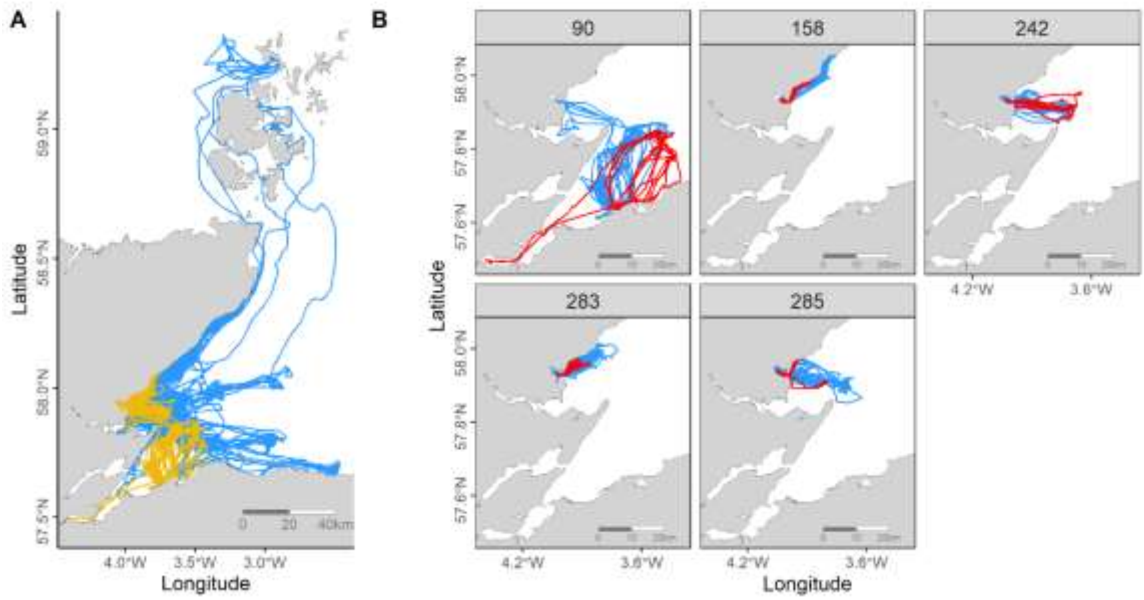

Figure 1. A) Maps displaying the movements of the 31 tagged harbour seals in the Moray Firth (Scotland), showing data from the five retrieved tags in yellow. B) Tracks of the five focal seals where tags were recovered. The trips with accelerometer data that were included in the analysis are highlighted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

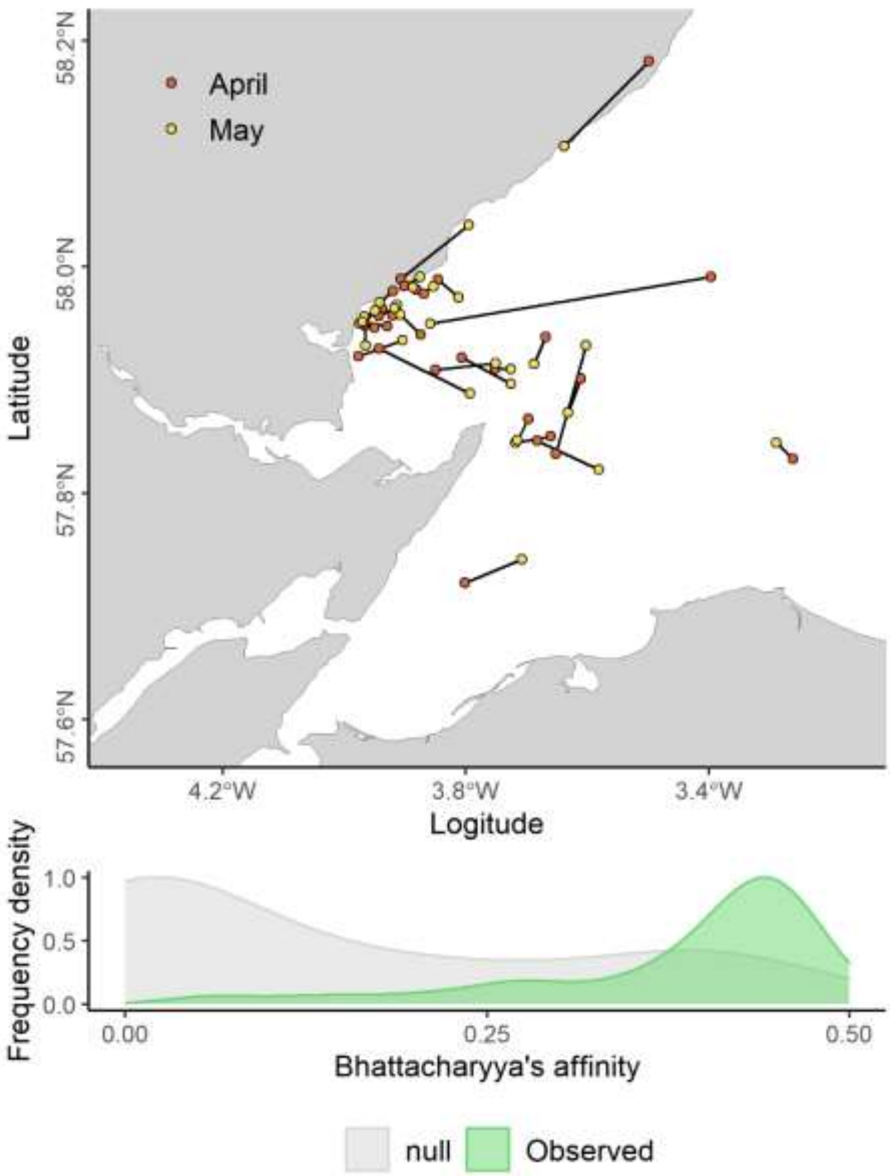

Figure 2. Top: Centroid location of the areas animals searched in April (red) in relation to the centroid location of the ones visited in May (yellow) for 29 individuals. Bottom: Frequency distribution of the observed overlap (green) of an individual's searched areas in consecutive month, estimated using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

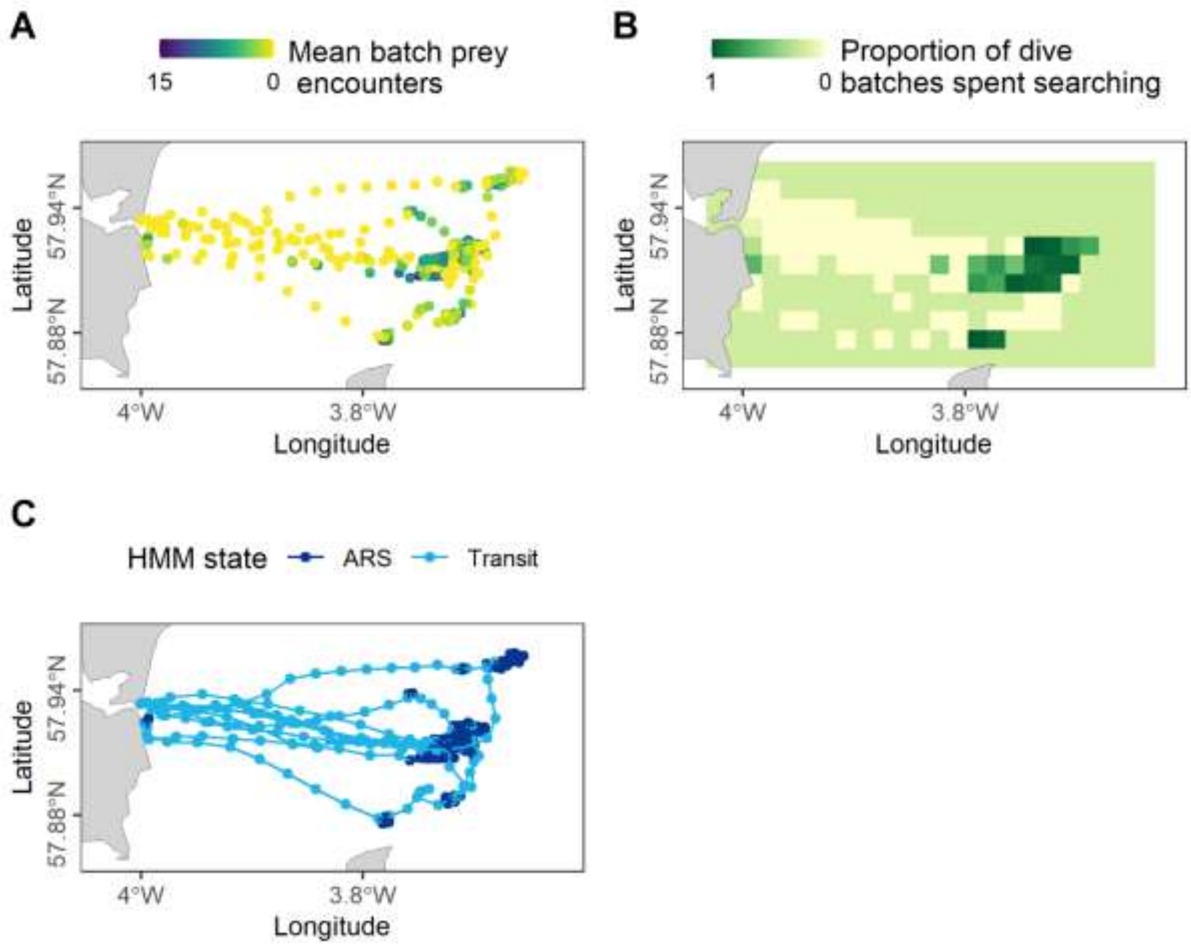

Figure 3. Example of the spatial variation in prey encounters and proxy for spatial memory in relation to the behavioural state classification of Model 3 for the foraging trips of seal 242. A) Locations of dive batches, colour-coded by the mean number of prey encounters per dive batch. B) Memory grid, 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).

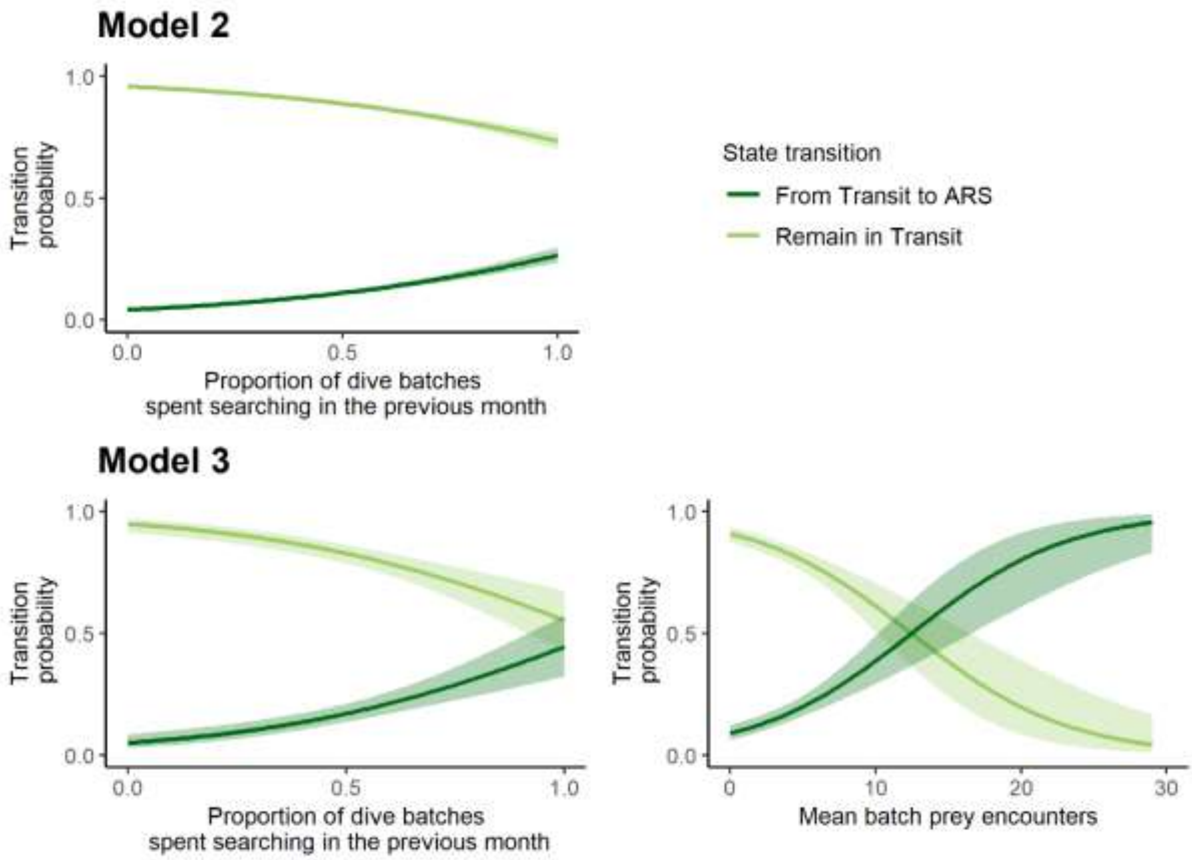

Figure 4. Stationary probability (mean and 95% CI) of occupying either of the two states and transition probability (mean and 95% CI) of remaining in a transit state or switching to an ARS state for the covariates included in Model 2 and Model 3. A) Influence of proportion of dive batches spent searching 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