Experimental evidence of memory-based foraging decisions in a large wild mammal

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Many animals restrict their movements to a characteristic home range. This constrained pattern of space use is thought to result from the foraging benefits of memorizing the locations and quality of heterogeneously distributed resources. However, due to the confounding effects of sensory perception, the role of memory in home-range movement behavior lacks definitive evidence in the wild. Here, we analyze the foraging decisions of a large mammal during a field resource manipulation experiment designed to disentangle the effects of memory and perception. We parametrize a mechanistic model of spatial transitions using experimental data to quantify the cognitive processes underlying animal foraging behavior and to predict how individuals respond to resource heterogeneity in space and time. We demonstrate that roe deer (*Capreolus capreolus*) rely on memory, not perception, to track the spatiotemporal dynamics of resources within their home range. Roe deer foraging decisions were primarily based on recent experience (half-lives of 0.9 and 5.6 d for attribute and spatial memory, respectively), enabling them to adapt to sudden changes in resource availability. The proposed memory-based model was able to both quantify the cognitive processes underlying roe deer behavior and accurately predict how they shifted resource use during the experiment. Our study highlights the fact that animal foraging decisions are based on incomplete information on the locations of available resources, a factor that is critical to developing accurate predictions of animal spatial behavior but is typically not accounted for in analyses of animal movement in the wild.

cognition | foraging behavior | mechanistic modeling | movement model | roe deer

Many animals, both territorial and nonterritorial, constrain their movements to a characteristic home range, an area that is typically much smaller than their movement abilities would allow (1). The ubiquity of this space-use pattern suggests that home ranges are adaptive and that a general mechanism underpins their emergence (2). In particular, home ranges are thought to result from the foraging benefits provided by spatial memory (3)—the process by which animals encode spatial relations (4).

The role of spatial memory is particularly relevant when resources are spatially heterogeneous and temporally dynamic (5), making foraging a complex, spatiotemporal problem. Classic optimal foraging theory (6), as well as resource selection analyses (7), assume that animals have either no knowledge (i.e., a random forager), or perfect knowledge of the spatiotemporal patterns of resources (i.e., an omniscient forager). However, in reality, animal foraging decisions must rely on imperfect information (8) obtained from two sources: direct sensory perception, and memories of previous experiences at locations beyond the individual's current perceptual range (4, 9).

In this context, memory should be adaptive whenever retaining past site-specific information to predict the future occurrence and quality of key resources is more efficient than foraging relying on proximal mechanisms, such as area-restricted search and perception (3). Accordingly, foragers may not only benefit from memorizing spatial locations but also from tracking the profitability of previously-visited resources by means of an attribute memory (4). Such dynamic learning allows the forager to develop an expectation of resource quality from previous experience (10) and implies the discounting of old information (11, 12). In support of this argument, theoretical studies have demonstrated the foraging advantage of memory in spatially heterogeneous, predictable landscapes (13–15).

Empirically, the benefits of memory for resource acquisition have been documented for several kinds of central-place foragers, in particular frugivorous bats (16, 17), hummingbirds (18), food-caching birds (19, 20), and bumblebees (21). Experimental evidence of memory-based foraging decisions in wild mammalian home ranges has been limited. The influence of memory and perception on the movement behavior of mammals has been inferred in several observational studies (22, 23); however, quantifying their respective influences on foraging decisions is challenging because both memory and perception can give rise to long-distance, goal-oriented movements. Field experiments have the potential to address this limitation by providing the level of control required to disentangle the effects of memory and perception (4, 10). In a rare field experiment on mammals, Janson showed that the home-range movements of a brown capuchin (*Cebus apella*) troop deviated from a perception-based movement model (24, 25); however, a mechanistic, quantitative understanding of how memory affects mammalian foraging movements is still lacking.

In this study, we address this gap by formulating a memory-based model of spatial transitions to 1) characterize and quantify

Significance

Understanding how animals respond to changes in resource availability is central to ecological research and to designing effective wildlife conservation and management strategies. To date, little research has been conducted on the cognitive mechanisms—memory or perception—by which large mammals make foraging decisions in nature. By combining a mechanistic cognitive model with a field manipulation of food availability, we show that roe deer rely on memory, not perception, to track the spatial and temporal changes in resource availability in their local environment. Our approach allows us to quantify memory use and to successfully predict how individuals will respond to future changes.

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The authors declare no competing interest.

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the cognitive processes involved in the foraging decisions of a large mammal, and 2) predict the observed patterns of response to a resource manipulation experiment. We performed our experiment on European roe deer (*Capreolus capreolus*). Roe deer are a particularly well-suited species for studying the interplay between cognitive processes and resource dynamics: as browser with limited fat reserves, roe deer exhibit a tight association between movement and resource dynamics (26), particularly during the winter months (i.e., at the time of our experiment) when food scarcity limits foraging performance, and the movements of roe deer are not affected by territoriality. In addition, because roe deer are solitary, their foraging decisions are expected to be primarily based on their individual, personal information (27).

We fitted roe deer with Global Positioning System (GPS) telemetry collars at a site in the Eastern Italian Alps, and followed their movements during a transitory alteration of high-nutritional food accessibility at supplemental feeding sites (FS), located within their home range ($n = 18$ individuals, for a total of 25 animal-years; see *Materials and Methods*). The 6 wk experiment, conducted over 3 y, consisted of three 2 wk phases—pre-closure, closure, and post-closure—and was designed to disentangle the effects of memory and perception. During the closure phase, the food at the most-attended FS of each individual (hereafter referred to as manipulated, M) was rendered inaccessible by installing a physical barrier while maintaining food presence at the site (Fig. 1*B*). This ensured that sensory information on resource availability remained unaltered by the manipulation.

We characterized the temporal dynamics of roe deer foraging patterns during the experiment by quantifying the fraction of time each individual spent in the vicinity of their manipulated FS (M), at alternate FS available within the broader landscape (A), and in natural vegetation (V). We then developed a model describing the transition probabilities between states (M, A, and V) as a function of resource accessibility, resource preference, and cognitive processes, while controlling for environmental cues (illumination patterns and temperature). We evaluated three competing hypotheses concerning the cognitive mechanisms underlying the patterns of movement by roe deer during the experiment (Table 1): 1) Hypothesis 1 is a null hypothesis of omniscience-based movement, in which animals possess complete information on the spatiotemporal dynamics of resources. Under this hypothesis, we predicted that individuals would no longer visit M FS when forage is inaccessible (P1.1) and respond instantaneously to actual changes in resource accessibility (P1.2), irrespective of their previous experience. 2) Hypothesis 2 is a perception-based movement hypothesis in which animals use long-distance sensory cues to guide their foraging decisions. At the spatial scale of this experiment, in which FS are hundreds of meters apart, we assumed that, as in other large herbivores (28), roe deer would primarily rely on olfactory rather than visual perception because the presence of food at FS is not visible from afar. Since the manipulation did not alter the sensory information that can be perceived at long distances, we predicted that, under the perception hypothesis, the rate at which roe deer visited M FS would be constant throughout the experiment (P2.1) and that their foraging decisions should be independent of resource accessibility (P2.2). 3) Hypothesis 3 is a memory-based movement hypothesis in which animals rely on previous experience to guide foraging decisions. We predicted that, under this hypothesis, roe deer would decrease their visits to inaccessible FS (P3.1), conditional on experienced changes in resource accessibility (P3.2). We further predicted that the influence of previously visited FS on roe deer movement would slowly decrease with time since last visit (i.e., slow decay of spatial memory; P3.3) and that the expected value of FS would primarily rely on very recent experience (i.e., fast decay of attribute

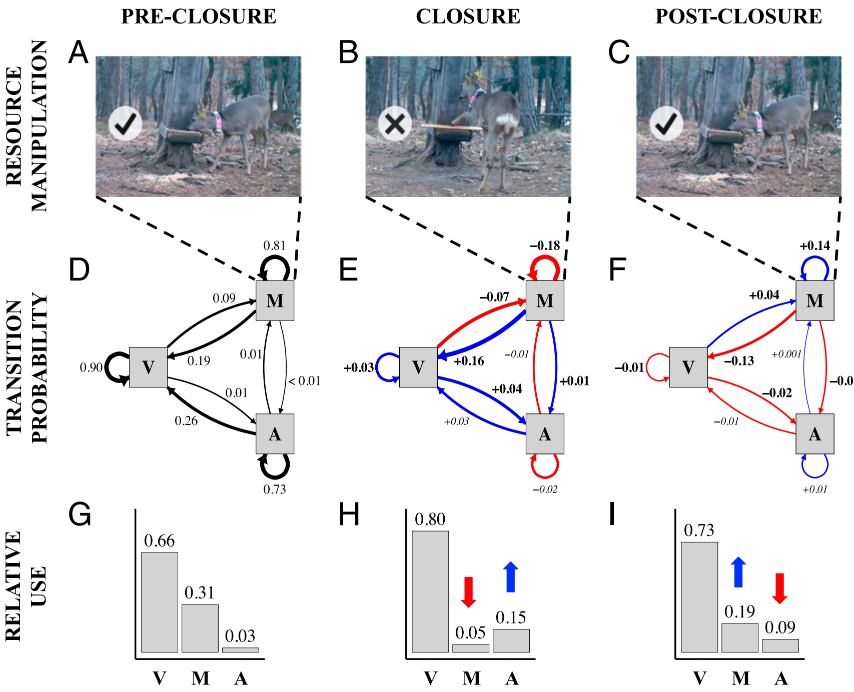

Fig. 1. Transitory changes in resource use patterns during the experiment. (*A*–*C*) Schematic representation of the experiment. High-nutritional food is accessible at M feeding sites (FS) during the pre- and post-closure phases (*A* and *C*, respectively), while it is present but inaccessible during the closure phase (*B*). Supplemental food is also present throughout the experiment at A FS. Roe deer can also access V. (*D*–*F*) Transition probabilities among the three resource types—V, M, and A—for pre-closure (as rates; $n = 9{,}045$ transitions; *D*), closure (as net changes in respect to pre-closure; $n = 9{,}187$; *E*), and post-closure (as net changes in respect to closure; $n = 8{,}417$; *F*). For the net changes, the color of the vertices indicates a decreased (red) or increased (blue) probability (significant changes are in bold). (*G*–*I*) Corresponding relative resource use, with vertical arrows illustrating the compensation pattern observed between the use of M and A.

Table 1. Hypotheses and corresponding predictions

Hypotheses—cognitive mechanism used by animals to guide their foraging decisions	Predictions
Hypothesis 1: omniscience—animals possess complete information on resource availability	P1.1: Roe deer no longer visit M FS when forage is inaccessible. P1.2: Roe deer respond instantaneously to actual changes in resource accessibility.
Hypothesis 2: perception—animals use long-distance sensory cues	P2.1: Roe deer visits to the M FS remain constant throughout the experiment. P2.2: Roe deer foraging decisions are independent of resource accessibility.
Hypothesis 3: memory—animals rely on previous experience	P3.1: Roe deer decrease their visits of the M FS when forage is inaccessible. P3.2: Roe deer respond to the changes in resource accessibility they experience. P3.3: The influence of previously visited FS on roe deer movement slowly decreases with time since last visit. P3.4: The expected value of FS is based on recent experience.

memory; P3.4). To evaluate hypothesis 3, we formulated a bicomponent memory model consisting of two forms of memory: a spatial memory (i.e., recollection of resource locations) and an attribute memory (i.e., recollection of the profitability at previously visited locations; sensu refs. 4 and 23). Further details on the mathematical formulations of the three above hypotheses can be found in the *Materials and Methods*. We fitted the three cognitive models for each individual separately, that is, the scale at which foraging decisions are taken, to evaluate the generality of the cognitive mechanisms used by roe deer (*Results*); we also fitted population-level models to summarize the relative importance of the underlying drivers (*SI Appendix*, section 5).

Results

Transitory Changes in Resource Use Patterns. The experiment led to significant changes in movement rates between the three resource types. Prior to closure, roe deer, when in vegetation (V), had a 0.9 probability (per unit time) of remaining, a 0.09 probability of visiting the manipulated feeding sites (M FS), and a low (0.01) probability of visiting alternate feeding sites (A FS; Fig. 1*D*). Closure of M led to decreases in the probability of individuals remaining at their respective M (−0.18) and decreases in transitions from V to M (−0.07) (Fig. 1*E*)—responses that are consistent with P1.1 and P3.1 but inconsistent with P2.1. Roe deer compensated for the loss of M by increasing their movements from V toward A (+0.04) (Fig. 1*E*). Reopening of the M sites led to a recovery of pre-closure patterns of transition probabilities with, in particular, increases in probabilities of residence at M (+0.14), and transitions from V to M (+0.04), and a decrease in transition probability from V to A (−0.02) (Fig. 1*F*).

As a result of these movement responses, resource use shifted dramatically between the different phases of the experiment. During pre-closure, roe deer primarily used V (66%), followed by M (31%), and rarely A (3%; Fig. 1*G*). Following closure, roe deer use of M dropped to 5% and use of A increased to 15% (Fig. 1*H*). Following reopening, roe deer use of M recovered to 19% and use of A declined to 9% (Fig. 1*I*). While less marked, the temporal changes in use of V mirrored those of A, increasing from 66% (Fig. 1*G*) to 80% during closure (Fig. 1*H*) and then declining to 73% during post-closure (Fig. 1*I*).

Evidence for Memory-Based Foraging Decisions. Memory use was widespread across our monitored roe deer population: the memory-based model (Hypothesis 3) had significantly stronger support than alternate cognitive mechanisms for 24 out of the 25 animal-years (see Fig. 2 and reference *SI Appendix*, Table S1 for the Akaike Information Criterion values of each individual-level model). The omniscience-based model (Hypothesis 1) was marginally supported for one animal in 1 y, and the perception (Hypothesis 2) was the least supported cognitive mechanism for all animals in all years. Overall, the estimates and confidence intervals of the parameters shared among the three models (within-state resource accessibility, preference for M, and minimum daily temperature and illumination) were highly consistent (Fig. 3), suggesting that the differences in model support result from the differences in the underlying cognitive formulations rather than spurious correlation with other covariates affecting the probability of movement.

Fig. 4 illustrates the predictive capabilities of the individual-level memory-, omniscience-, and perception-based movement models by showing the temporal trends in the probability of moving from V to either the M FS (i.e., V to M transition, black lines) or A FS (i.e., V to A transition; red lines). The predictions of the memory-based model more accurately capture the patterns of FS use by roe deer than either the omniscience-based or perception-based models (mean squared errors of 2.4×10^{-4}, 8.7×10^{-4}, and 14.0×10^{-4}, respectively). In particular, the memory-based model captures both the sudden drop in the

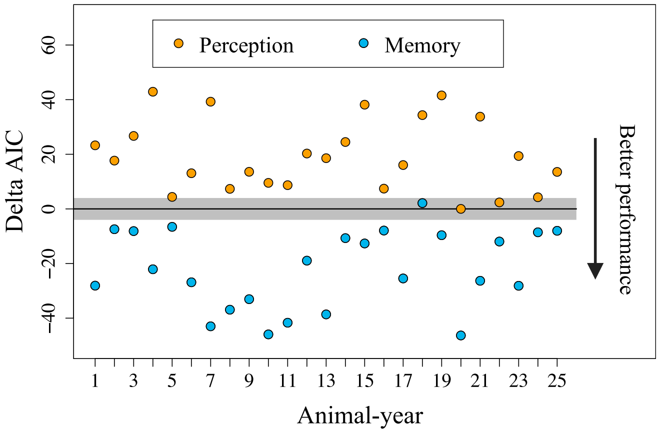

Fig. 2. Evidence for the generality of memory use in the roe deer population. The relative support for the perception-based (orange) and memory-based (blue) models are shown as the delta Akaike Information Criterion (AIC) relative to the omniscience-based model (null hypothesis; horizontal black line), with smaller values indicating better performing models (reference *SI Appendix*, Table S1 for the AIC values of each model). Values in the gray area are not statistically different from the omniscience model (±4 AIC values).

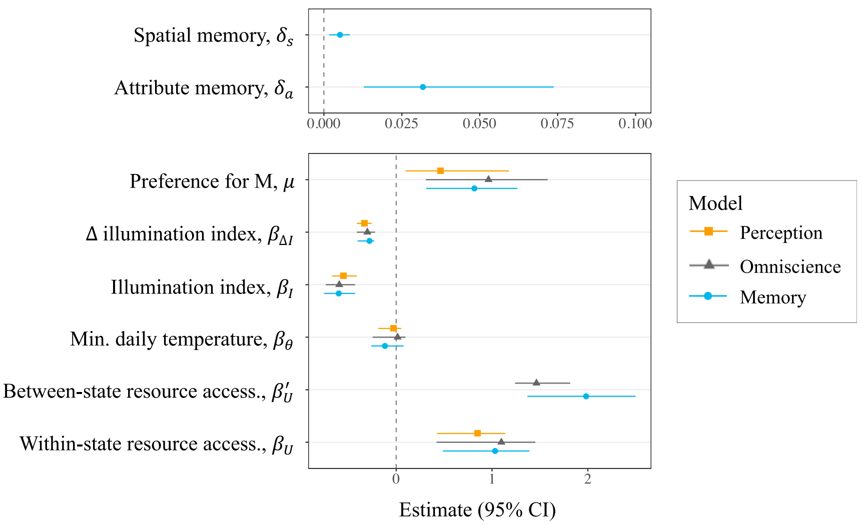

Fig. 3. Parameter estimates. The median of the individual-level estimates for the perception-based (orange square), omniscience-based (gray triangle), and memory-based (blue circle) models are plotted with the bootstrapped 95% CI. Memory parameters are presented separately for readability (different magnitudes).

visiting probability of the M FS following experimental closure (Fig. 4*A*, black line) and the respective compensatory increase in the visitation of A FS (Fig. 4*A*, red line). The omniscience-based model also predicts a decline in V to M transitions following closure (Fig. 4*B*, black line); however, it fails to capture the compensatory increase in V to A transitions following closure, and the respective upward and downward temporal trends in the probabilities of V to A and V to M transitions during the closure phase that are captured by the memory-based model (compare red and black lines in Fig. 4 *A* and *B* during the closure period). Similarly, the memory-based model is the only model that captures the downward and upward temporal trends in the probabilities of V to A and V to M transitions during the post-closure period (compare red and black lines in Fig. 4 *A* and *B* during the post-closure period). Finally, the perception-based model fails to capture any of the temporal shifts in foraging behavior that occur during the experiment (Fig. 4*C*).

The results of the population-level model were highly consistent with those of the individual-level model (*SI Appendix*, section 5). The population-level model conveniently summarizes the overall importance of variables across individuals (*SI Appendix*, Table S2); spatial memory was the most important variable influencing roe deer selection of distant resources (δ_s; ΔAIC = +500 at the population level when spatial memory was removed) and the main driver underlying the higher support of the memory- over omniscience-based movement models. Roe deer favored recently visited resources (P3.3); spatial memory decreased exponentially with time since last visit with a half-life ($t_{1/2}$) of 5.6 d ($\delta_s = 5.2 \times 10^{-3}$ h^{-1}; Fig. 5; at the population level: $t_{1/2}$ = 3.4 d, $\delta_s = 8.5 \times 10^{-3}$ h^{-1}).

When evaluating the profitability of distant resources (i.e., between-state), roe deer strongly selected for accessible FS (β'_U; Fig. 3), consistent with either omniscience or memory but contradicting the perception hypothesis (P2.2 not supported). In addition, roe deer foraging decisions were consistent with a selection for expected, rather than actual, resource accessibility ($\tilde{U}$), thereby supporting the memory hypothesis over the omniscience hypothesis (i.e., P3.2 supported; P1.2 not supported). The rapid rate of attribute memory decay—half-life of 0.9 d ($\delta_a = 3.2 \times 10^{-2}$ h^{-1}; Fig. 5; at the population level: $t_{1/2}$ = 0.6 d, $\delta_s = 4.8 \times 10^{-2}$ h^{-1})—indicates that roe deer expectations of resource profitability primarily relied on recent experience of FS accessibility (P3.4), that is, time averaging over short periods. Support for time averaging of previous experiences, as opposed to reliance on the last experience, was relatively weak (ΔAIC = +5 at the population level when attribute memory decayed instantly, i.e., $\delta_a = 1$; *SI Appendix*, Table S2).

Roe deer residence time at FS (as indicated by the probability of remaining at a given site per unit time, i.e., within-state) was also influenced by resource accessibility, with deer attending FS for significantly shorter durations when food was inaccessible (β_U; Fig. 3). When resources were equally accessible, roe deer preferred the M FS over A FS ($\mu > 0$; Fig. 3), leading to a higher probability of transitions from V to M compared to transitions to A (*SI Appendix*, Fig. S7) and to a higher residence time at M.

Environmental conditions also influenced roe deer foraging behavior during the experiment. In particular, roe deer use of FS was markedly affected by illumination with peak visitation rates at dusk and a higher probability of visitation at night than during the day (*SI Appendix*, Fig. S7), as indicated by the significant effects of illumination index and its rate of change (β_I and $\beta_{\Delta I}$; Fig. 3). Instead, the absolute rate of change of the illumination index had a negligible effect ($\beta_{|\Delta I|}$; *SI Appendix*, Table S2 and Fig. S4) and, therefore, was not retained in the final models. There was also an effect of minimum daily temperature, with a tendency for roe deer to attend FS more intensely on colder days (β_θ; Fig. 3).

Discussion

Developing a unified theory of animal space use requires a mechanistic understanding of the cognitive processes underlying animal movement decisions and their fitness consequences in nature (2, 3, 29). In this study, we disentangled the respective influences of perception and memory on the foraging behavior of a large mammal by assessing the abilities of perception-, memory-, and omniscience-based movement models to capture individual roe deer responses with data from an in situ resource manipulation experiment. As seen in Fig. 4, combining a dynamic, bicomponent memory model (Hypothesis 3) with environmental cues allowed us to accurately predict how roe deer shifted resource use in response to the experimentally imposed shifts in resource accessibility. Instead, the mismatch between the predictions of a corresponding perception-based model (Hypothesis 2) and the

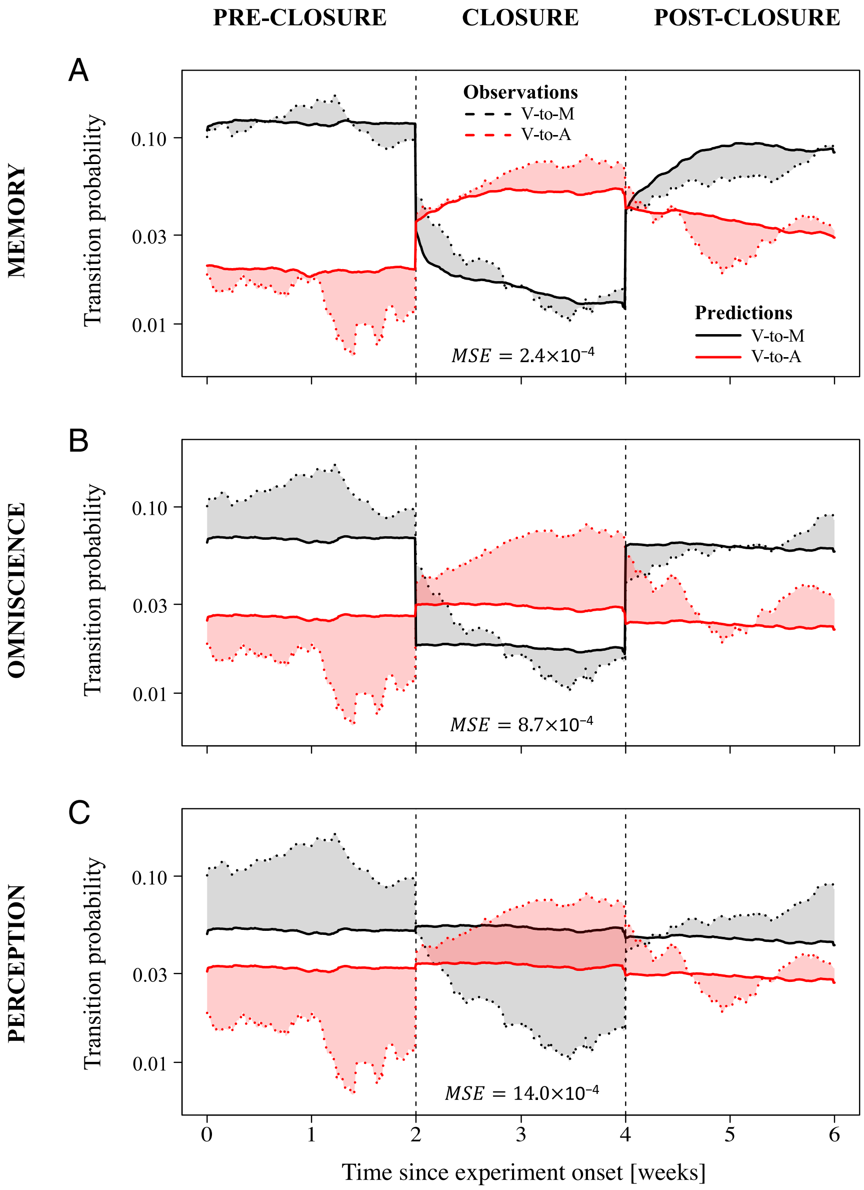

Fig. 4. Predictions from the three competing cognitive models. Predictions are shown for memory-based (*A*), omniscience-based (*B*), and perception-based models (*C*), calculated from the individual-level median estimates. The predicted (solid lines) and observed (dotted lines) transition probabilities from V to either M feeding sites (V to M transition; black lines) or A feeding sites (V to A; red lines) during the three experimental phases are plotted as running 4 d means across all animal-years on a log scale. Transition probabilities were calculated from 5,941 transitions (from V to either V, M, or A) during pre-closure, 7,336 during closure, and 6,107 during post-closure. The red and gray shadings in each panel indicate the difference between the predicted and observed probabilities of V to M and V to A transitions, respectively. The mean squared error (MSE) between predictions and observations are reported for each model.

observations indicates that the foraging decisions of roe deer during the experiment were not caused by long-distance sensory cues of resource presence. The ability of roe deer to perceive the smell of supplemental food from afar is largely unknown. It could be that roe deer are not able to perceive food presence through olfaction from afar (i.e., memory is their only source of information). Alternatively, the information encoded in their memory about a resource's accessibility overrode sensory cues. Such hierarchical processing of information has been shown for wild capuchin monkeys (*Cebus capucinus*), which primarily used memory, overriding conflicting perceptual cues, when resource locations were predictable (10).

In addition, by accounting for the temporal lags in the movement behavior of individuals around experimental manipulations, the predictions of the memory-based model (Hypothesis 3) provide a much better fit to the observations than our omniscience-based model (null; Hypothesis 1) that assumes perfect knowledge of the changing resource dynamics by roe deer (Fig. 4). This key result highlights the fact that animal foraging decisions are indeed based on incomplete information on the location and quality of available resources (8), a factor that is typically not accounted for in analyses of animal movement in the wild.

In previous observational studies, memory effects have been inferred either from the revisitation of geographic locations (30) or from the discrepancy between observations and either random or perception-based movement models (25). Our findings build upon these results in two important ways. First, in contrast to studies of geographic revisitation (30), the findings of our experimental study rule out the possibility that the observed movement

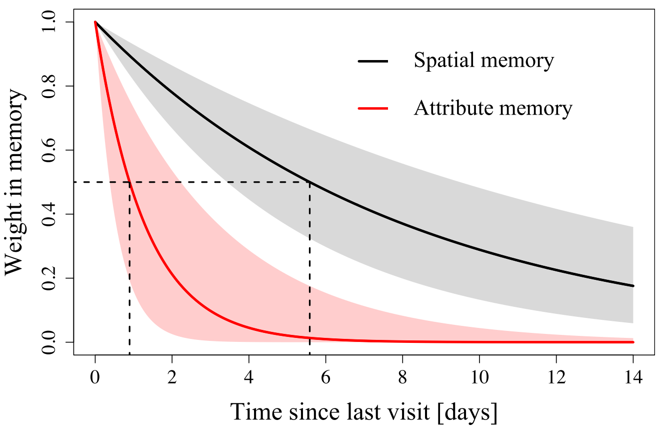

Fig. 5. Decay of spatial and attribute memory with time since last visit. Shaded areas indicate the 95% confidence intervals (CI) around the median of the individual-level estimates, and dashed lines represent the corresponding half-life values ($t_{1/2}$). Spatial memory decreased exponentially with time since last visit at rate 5.2×10^{-3} h^{-1} (95% CI: $3.0–8.4 \times 10^{-3}$; $t_{1/2} = 5.6$ d), and attribute memory decayed at rate 3.2×10^{-2} h^{-1} (CI: $1.3–7.4 \times 10^{-2}$; $t_{1/2} = 0.9$ d).

patterns are caused by perception rather than memory—two mechanisms that are often confounded in observational studies of animal movement (10). Moreover, our results show that the impacts of memory on movement behavior are dynamic and conditional on resulting performance—in this case, the effects of memory are mediated by the impacts on the resulting foraging success of individuals. Second, rather than merely inferring the influence of memory from discrepancies with random or perception-based movement behavior (25), we explicitly formulated a memory process and showed that it had higher support and predictive ability than corresponding perception- and omniscience-based movement models.

When resources are heterogeneously distributed and spatiotemporally predictable, a forager's past experience is informative on resource availability dynamics. In such situations, relying on memory is therefore predicted to be more advantageous than perception-based foraging (3–5, 8, 31). In our experimental system, in which resources are characterized by a high spatial heterogeneity and short-term predictability (ad libitum, highly nutritious food concentrated at distinct feeding sites), we show that roe deer foraging decisions rely on memory. This finding is consistent with both theoretical predictions on the benefits of memory in heterogeneous, predictable landscapes and previous enclosure-based experiments showing that large herbivores are capable of memorizing the location of available food resources (32, 33). The probability that roe deer visited particular resource patches decreased exponentially with time since last visit with a corresponding half-life for spatial memory of 5.6 d (Fig. 5). This finding contrasts with two recent studies showing that the movements of bison (*Bison bison*) (23) and caribou (*Rangifer tarandus*) (22) are influenced by long-term spatial information, that is, negligible or no decay of spatial memory over a period of 6 mo. The relatively rapid decay of spatial memory estimated in this study has to be interpreted in the context of the species revisitation rate of locations and resources within their home range. Given the average movement rate with respect to the home-range size in the monitored population (63 m · h^{-1}, 28 ha · biweek^{-1}; see ref. 26), roe deer typically visit much of their home range in just a few days (as opposed to caribou and bison). As a consequence of this high revisitation rate, and despite the relatively high estimated decay, roe deer spatial memory rarely (if ever) dropped to zero, that is, feeding sites were never totally forgotten. The rapid decrease in memory with elapsed time since last visit allows roe deer to rapidly shift away from less profitable resources, and hence enable them to quickly adapt to spatiotemporal changes in resource availability, as seen in this experiment.

As time increases, old information about resource quality becomes increasingly unreliable over more-recent experiences (11, 12), and therefore should be discounted at a rate commensurate with the temporal scale of environmental change (8). Our finding of a rapid decay in attribute memory (half-life of 0.9 d, Fig. 5) implies that roe deer primarily rely on their last experience to evaluate feeding site quality. This result is consistent with enclosure-based experiments in least chipmunks (*Tamias minimus*) and golden-mantled ground squirrels (*Spermophilus lateralis*), which suggest that individuals increasingly rely on recent experience when resource dynamics are slow (34). In contrast, in a recent study of bison, Merkle et al. (23) showed that individuals appear to rely on long-term memory of profitability to inform their selection of grazing meadows (slow decay of attribute memory in summer: half-life of 10.4 d; negligible decay in winter). In our system, the movement transitions between resources occur over a few hundred meters (i.e., over relatively short distances compared to roe deer movement rates). Information about the profitability of resource locations can therefore be reestablished in a short period of time and with marginal acquisition cost (as opposed to the situations such as the aforementioned study of bison). Such a rapid decay of past experiences is likely to be adaptive in dynamic landscapes akin to the one that roe deer experienced in this study, as it allows animals to stay in tune with the spatiotemporal dynamics of their environment (35), while reducing the physiological cost of memory storage and processing (36, 37). An alternative explanation for the differing timescales of attribute memory between this study and Merkle et al. (23) study of bison is that animals may use very recent information of a given patch profitability to determine its future quality (i.e., fast decay of the within-patch attribute memory; this study), but integrate information over longer temporal scales to assess the relative profitability of competing patch alternatives (i.e., slow decay of the between-patch attribute memory; ref. 23).

Site familiarity is thought to provide fitness benefits in relation to foraging efficiency (38) or predation avoidance (39) and to emerge from the revisitation of known areas through spatial memory (13). In large herbivores, observational studies have shown that animals select for previously visited locations (22, 23, 30, 40). Here, we found that roe deer strongly preferred their most familiar feeding sites (i.e., the manipulated feeding site, M, by definition; see *Materials and Methods*) even after individuals had knowledge of equally profitable, alternate feeding sites (A; see Fig. 3 and *SI Appendix*, Fig. S7). The restoration of predisturbance patterns of resource use observed in this experiment cannot be explained by optimal foraging theory alone and instead supports the existence of site familiarity effects (26).

Our analysis also revealed how environmental cues influenced roe deer foraging. Specifically, we found that roe deer visits to feeding sites were strongly influenced by patterns of illumination (nocturnal and crepuscular attendance; *SI Appendix*, Fig. S7), in accordance with the species' diel activity and movement patterns (41–43), and increased at low temperatures, consistent with the higher energetic demand of thermoregulation (44). In the present study, the parameters associated with the environmental drivers of resource selection were highly conserved across the three cognitive hypotheses evaluated (Fig. 3), that is, relatively independent of the underlying cognitive mechanisms. Instead, long-distance (between-states) response to feeding site accessibility and the preference for the manipulated (M; i.e., most familiar) feeding sites varied considerably with the cognitive hypothesis considered.

Because foraging can be linked to fitness (45, 46), resource acquisition is considered to be a primary driver of animal movement (5). Although resource selection analysis has become a major tool in animal ecology (7) that is used to inform conservation strategies (47), the actual mechanisms through which wild animals interact with their surrounding landscape have not been elucidated. Identifying and quantifying the cognitive mechanisms used by animals is required to move from a physical and structural description (i.e., the researcher's perspective) to a functional characterization [i.e., the animal's perspective; the umwelt (48)] of resources, and therefore to study resource selection as a behavioral process (49). Developing a mechanistic understanding of resource selection, based on explicit consideration of animal cognition, is crucial to predicting how animals will respond to changing environmental conditions and ultimately designing effective conservation strategies (49, 50). Here, we have shown that memory-based movement models (specifically, a memory-based model of spatial transitions) parametrized using experimental data can successfully be used to quantify cognitive processes and to predict how animals respond to resource heterogeneity in space and time. The resource-manipulation experiment approach adopted here could be adapted to empirically quantify the foraging benefits (e.g., resource acquisition) of memory (18) and test their dependence on the spatiotemporal patterns of resources (density, quality, spatiotemporal heterogeneity, and predictability) (3, 4, 31). In this context, the spatially implicit modeling framework proposed in this study represents an important stepping stone toward spatially explicit, mechanistic models of animal movement (51) and their parametrization using empirical data (40). By characterizing the spatial dimension of the interplay between memory and resource selection, such models would have the potential to shed light on the biological processes underlying home ranges in nature.

Materials and Methods

Study Area. The study area, located in the north-eastern Italian Alps (ca. 16 km^2; Autonomous Province of Trento), ranges between 600 and 1,000 m above sea level and is dominated by mixed forest (>80%). The climate is continental (mean daily temperature in January: 1.0 °C; in July: 21.0 °C; mean annual rainfall: 966 mm) with occasional snow cover. Roe deer is the most prevalent ungulate in the area (7 to 8 individuals km^{-2}; reference values from Autonomous Province of Trento Wildlife Office) and is selectively hunted between September and December. Supplemental feeding of roe deer is conducted year-round by private hunters at >50 distinct feeding sites (FS; *SI Appendix*, Fig. S1), typically shaped as hopper dispensers where corn can be accessed through a tray (Fig. 1 *A*–*C*).

Roe Deer Captures and Collaring. Roe deer were captured using baited box traps near FS in winter ($n = 15$) and net drives in spring and fall ($n = 3$) and were fitted with GPS-GSM radio collars scheduled to acquire hourly GPS locations for a year, after which they were released via a drop-off mechanism. GPS acquisition success was extremely high (99.57% during the experiment), and hence we did not interpolate missing fixes in the collected data. We collected data on 18 roe deer: 11 had collars for a single winter; 2 had collars that spanned two winters; and 5 were recaptured and recollared for a second year, leading to a total of 25 animal-years (21 adults: 15 females, 6 males; 4 yearlings: 2 females, 2 males; reference *SI Appendix*, section 1 for details) in 3 consecutive years ($n = 4$ in 2017, $n = 11$ in 2018, and $n = 10$ in 2019).

Experimental Design. Taking advantage of roe deer use of a focal, identifiable resource—the supplemental FS—we designed an in situ manipulation of resource accessibility for evaluating competing hypotheses pertaining to the processes governing roe deer foraging decisions. We created three successive experimental phases—pre-closure, closure, and post-closure—by physically managing the accessibility of food at the FS. During the closure phase, we transitorily restricted the access of forage at manipulated (M) FS by placing wooden boards obstructing the tray (Fig. 1). Forage presence was maintained constantly throughout the experiment at all FS. In the immediate proximity to FS, roe deer may assess the accessibility of corn through either visual or tactile cues. Over longer distances, perceptual cues (most likely, olfaction) may be used by roe deer to evaluate food presence; in the experiment, food presence was held constant, and food accessibility was the quantity that was manipulated.

During the pre-closure phase, we used roe deer movement data to identify M, defined as the most attended FS (hence, the most familiar) for each animal-year (see ref. 26 for details). During the closure phase, we made corn at M inaccessible for a duration of about 15 d (minimum = 14.0 d, maximum = 18.1 d, and mean = 15.5 d), depending on fieldwork constraints. We initiated the post-closure phase by restoring the accessibility of corn at M. During both pre- and post-closure phases, corn was available ad libitum to roe deer at M. All alternate (A) managed FS (i.e., supplied at least once in the month prior to the experiment) had corn available ad libitum throughout the experiment. Roe deer tended to concentrate their use at a single FS (M accounted for 94% of all FS use during the pre-closure, and each individual's most used A accounted for 91% of all FS use during the closure phase). Each manipulated roe deer had access to at least one A FS (within its annual home range) where it could shift its dominant use away from the M FS during the closure phase.

The experiment was conducted in winter, when vegetation resources are least abundant (and most homogeneous), and therefore when roe deer use of supplemental feeding is the most intense (44, 52). Animals were considered for the experiment after they revisited their capture location, used as an indicator for the end of the postcapture response behavior. We ensured that cooccurring manipulations took place in separate areas to avoid potential interference. Specifically, we delayed the closure of a given M site until all roe deer likely to use it as an A site completed the experiment (susceptibility was evaluated based on previous FS visit history and home-range boundaries); this ensured that during the course of the experiment no roe deer experienced an inaccessible FS other than the one identified as its M site, during the 2 wk closure phase.

To ensure that food was available ad libitum, FS were visited and replenished every third day. All FS (M or A) were visited during daylight hours, when diel activity levels of roe deer are lowest (41), to minimize human interference, and on the same day to ensure a constant between-site exposure to human presence. We defined animal-year (see above) as our sampling unit, on the assumption that the same individual may show an independent response to experimental manipulations in subsequent years as a consequence to varying internal (e.g., life history) or external conditions.

Spatial-Transition Model. We developed a mechanistic spatial-transition model to characterize the movements of roe deer between three distinct resource types, hereafter referenced to as states: M, A, and V. We then characterized the movements of the roe deer between these states from their GPS locations. For M and A, we converted the FS point locations into areas by applying a buffer equal to the mean hourly step length of roe deer in our study area (i.e., 61.2 m). Previous exploration showed that the results of the analysis are not strongly affected by the choice of buffer size (26).

We derived the probability of moving to state $\mathbf{x}^i(t) \in (M, A, V)$ from the attraction weight of state $\mathbf{x}$ in the previous hour, $w^i(\mathbf{x}, t-1)$:

$$\underbrace{p^i(\mathbf{x}, t)}_{\textit{movement probability to state x}} = \underbrace{\frac{w^i(\mathbf{x}, t-1)}{w^i(M, t-1) + w^i(A, t-1) + w^i(V, t-1)}}_{\textit{relative attraction weight of state x}}, \qquad [1]$$

where $p^i(\mathbf{x}, t)$ is the probability of moving at time t for a given animal-year i ($i = 1 \ldots N$, where N is the number of animal-years). Because the movement probabilities were derived from relative attraction weights, we could simplify the model into an estimation of $w^i(M, t-1)$ and $w^i(A, t-1)$ by setting $w^i(V, t-1) = 1$.

Unlike other mechanistic models of resource selection (13, 23), our model formulation does not only account for state-to-state movements (or patch-to-patch, e.g., transition from V to M) but is generalized to within-state movements as well (or residence, e.g., transition from V to V). This is achieved by defining the attraction weight of M and A as conditional on the state occupied by the animal at time t, $\mathbf{x}^i(t)$.

Within-State Attraction. We defined within-state attraction as a function of the actual resource accessibility at M ($U(M, t) = 1$ in pre- and post-closure and $U(M, t) = 0$ during closure) or A ($U(A, t) = 1$ throughout the experiment), environmental covariates of FS use, $E(t)$, and a population-level preference for M over A, μ:

$$\underbrace{w^{i}(M,t)}_{\text{attraction of state } M} = exp\left(\beta_0 + \underbrace{\beta_U U(M,t)}_{\text{actual res. access.}} + \underbrace{E(t)}_{\text{env. covariates}} + \underbrace{\mu}_{\text{pref. for } M}\right), \quad \underbrace{\mathbf{x}^{i}(t) = M.}_{\text{when at } M} \tag{2}$$

$$\underbrace{w^{i}(A,t)}_{\text{attraction of state } A} = exp(\beta_0 + \beta_U U(A,t) + E(t)), \quad \underbrace{\mathbf{x}^{i}(t) = A}_{\text{when at } A} \; . \tag{3}$$

Environmental covariates, $E(t)$: in ungulates, and roe deer in particular, FS use is correlated with winter severity (44, 52), whose effect we approximated by using minimum daily temperature, $\theta(t)$. At shorter temporal scales, roe deer exhibit a strong diel pattern in activity and movement behavior (41), and in particular, in their use of FS. For this purpose, we developed an illumination index derived from solar elevation, $I(t)$, which approximates the sigmoidal shape of the log-transformed daily irradiance (reference *SI Appendix*, section 2 for details). Because roe deer activity typically peaks during twilight and may differ between dawn and dusk, we included the rate of change of illumination, $\mathrm{I}_{\Delta}(t)$, and its absolute value,$\mathrm{I}_{|\Delta|}(t)$. The influence of environmental covariates on FS is given by the following:

$$\underbrace{E(t)}_{\text{environmental covariates}} = \underbrace{\beta_\theta \theta(t)}_{\text{temperature}} \underbrace{+ \beta_I I(t) + \beta_{\Delta I} \mathrm{I}_{\Delta}(t) + \beta_{|\Delta I|} \mathrm{I}_{|\Delta|}(t)}_{\text{circadian illumination pattern}} \; . \tag{4}$$

Cognitive Dependence of between-State Attraction. By contrast to within-patch attractions, the formulation of between-patch attraction in our model depends on which cognitive mechanisms roe deer use to evaluate the quality of distant resources (i.e., beyond current state). We formulated three competing cognitive hypotheses—omniscience, perception, and memory—whose equations are detailed below. Because the equations characterizing the attraction of M and A only differ by the preference of M over A (μ, see Eq. **2**), we present only the formulations for $w^{i}(M,t)$.

If the roe deer possess a full knowledge of spatiotemporal resource dynamics, that is, omniscience (Hypothesis 1), between-state attraction depends on actual resource accessibility at M, $U(M,t)$:

$$w^{i}(M,t) = exp\left(\beta'_0 + \underbrace{\beta'_U U(M,t)}_{\text{actual res. access}} + E(t) + \mu\right), \quad \mathbf{x}^{i}(t) \neq M. \tag{5}$$

The above equation posits that the between-state attraction of M, independently of any covariates (i.e., the intercept), may differ from that of within-state attraction ($\beta'_0 \neq \beta_0$). This conditionality on state occupancy, $\mathbf{x}^{i}(t)$, allows accounting for the high probability to remain within the currently occupied state (i.e., $\beta_0 > \beta'_0$), as indicated by the observed high serial correlation in the state time series (see ref. 26 for details). In addition, this formulation considers that roe deer response to changes in resource accessibility may affect movement (i.e., between-state transitions) and residence time (i.e., within-state transitions) differently such that $\beta'_U \neq \beta_U$.

If roe deer rely on perception alone (Hypothesis 2), they possess information (e.g., via olfaction) on resource presence at FS (constant at M throughout the experiment) but not on resource accessibility, which is manipulated (i.e., temporally variable) at M. As a result, the between-state attraction equation for the perception model is not a function of $U(M,t)$:

$$\underbrace{w^{i}(M,t)}_{\text{attraction of state } M} = exp(\beta'_0 + E(t) + \mu), \quad \underbrace{\mathbf{x}^{i}(t) \neq M.}_{\text{when not at } M} \tag{6}$$

Alternatively, roe deer may rely on previous experience, that is, their memory, to guide foraging decisions (Hypothesis 3). Two different memory streams may be involved in decision-making: an attribute memory integrating previous experiences of resource quality to define the expected value of resource locations and a spatial memory encoding the spatial locations of resources (4). Accordingly, roe deer movements should be influenced by expected resource accessibility—$\tilde{U}^{i}(M,t)$ and $\tilde{U}^{i}(A,t)$—instead of the actual resource accessibility—$U(M,t)$ and $U(A,t)$. We defined the expected resource accessibility as a temporally weighted devaluation function of previous experience (34). This formulation extends the exponentially weighted moving average of past experience (8, 12), derived from the linear-operator model (11), by accounting for the time interval between subsequent experiences and not only the serial order of experiences. We quantified the expected resource accessibility at M, $\tilde{U}^{i}(M,t)$, as the sum of experienced accessibility, $U(M,t_j)$, during all visits $\boldsymbol{v}(j = 1 \dots \mathrm{Y})$ at M that have occurred up to the current time t, and their associated times t_j, weighted by their respective attribute memory, $m_a^{i,j}(M,t) \in [0,1]$:

$$\underbrace{\tilde{U}^{i}(M,t)}_{\text{expected res. access.}} = \left(\sum_{j=1}^{\mathrm{Y}} \underbrace{m_a^{i,j}(M,t)}_{\text{attribute memory}} \times \underbrace{U(M,t_j)}_{\text{experienced res. access.}}\right) \times \underbrace{\left(\sum_{j=1}^{\mathrm{Y}} m_a^{i,j}(M,t)\right)^{-1}}_{\text{normalization}} \tag{7}$$

(see ref. 23 for a similar formulation). The expected accessibility is updated at the end of each visit j such that, t_j satisfies $\mathbf{x}^{i}(t_j) = M$ and $\mathbf{x}^{i}(t_j + 1) \neq M$. We modeled the attribute memory as an exponential decay function whose rate $(0 \leq \delta_a \leq 1)$ governs the devaluation of old experiences:

$$\underbrace{m_a^{i,j}(M,t)}_{\text{attribute memory}} = (1 - \delta_a)^{(t - t_j)} \; . \tag{8}$$

However, roe deer foraging decisions should not only rely on their capacity to integrate past experience of resource quality (attribute memory) but also on the ability to encode and retrieve spatial locations. To account for this process, we scaled FS attraction by a spatial memory weight, $m_s^{i}(M,t)$:

$$w^{i}(M,t) = exp\left(\beta'_0 + \underbrace{\beta'_U \tilde{U}^{i}(M,t)}_{\text{expected res. access.}} + E(t) + \mu\right) \times \underbrace{m_s^{i}(M,t)}_{\text{spatial memory}}, \quad \mathbf{x}^{i}(t) \neq M. \tag{9}$$

The spatial memory is maximum upon visit of the FS and then decays exponentially with time since last visit $(t - t_{\mathrm{Y}})$, at rate δ_s $(0 \leq \delta_s \leq 1)$:

$$\underbrace{m_s^{i}(M,t)}_{\text{spatial memory}} = (1 - \delta_s)^{(t - t_{\mathrm{Y}})}. \tag{10}$$

We chose to represent the temporal decay of attribute and spatial memory by negative (discrete) exponentials as this functional form of forgetting is supported by substantial empirical evidence (53) and theoretical grounds (54).

The spatial memory and expected resource accessibility values were initialized using the last encounter of M and A before the experiment onset (i.e., $\boldsymbol{v}(j = 0)$). For one individual, F4-2017, we did not have any recorded visit of A before the experiment and used the collaring date as visit event instead.

Model Parametrization and Predictive Ability. We fitted both 1) population-level models to select the model structure and evaluate the contribution of each covariate to the performance of the memory-based model (i.e., variable importance) and 2) individual-level models to each animal-year separately to evaluate their consistency and predict roe deer responses to the resource manipulation. For the sake of brevity, we present here the procedure and the results associated with the individual-level models; the details on the population-level models can instead be found in *SI Appendix*, section 5.

We estimated the model parameters through maximum likelihood; the likelihood for the individual-level parameter set $\boldsymbol{\omega}_i = (\beta_{0,i}, \beta'_{0,i}, \beta_{U,i}, \beta'_{U,i}, \beta_{\theta,i}, \beta_{I,i}, \beta_{\Delta I,i}, \mu_i, \delta_{s,i}, \delta_{a,i})$ is given as

$$L(\boldsymbol{\omega}_i) = \prod_{t=1}^{T_i} p\left(\mathbf{x}^{i}(t) \middle| \mathbf{x}^{i}(t-1), \boldsymbol{\omega}_i\right) , \tag{11}$$

where T_i is the number of observations for a given animal-year i $(i = 1 \dots N$, where N is the number of animal-years, i.e., 25). The parameter $\beta_{|\Delta I|}$ was not retained in the best model (*SI Appendix*, section 5) and was therefore not included in $\boldsymbol{\omega}_i$. Missing GPS locations were omitted from the likelihood function. We used the particle swarm optimization algorithm (PSO; reference *SI Appendix*, section 3), a nonlinear heuristic solver, to estimate the global minima of the log-likelihood function [$ln(L(\boldsymbol{\omega}_i))$; that is, the objective function]. For each parameter, we calculated the median of the individual-level estimates ($n = 25$) and calculated the corresponding 95% CI via bootstrapping: for each parameter, we generated 10,000 resamples (drawn randomly with replacement) of the 25 individual-level estimates and calculated the associated CI via the bias-corrected and accelerated method (55).

To evaluate the ability of the fitted mechanistic models to predict the movement behavior of roe deer during the experiment, we investigated whether they could capture the temporal dynamics in the rates of FS visit (V to M and V to A transitions), which summarize the general behavior of the system (Fig. 1). To this end, we compared the observed FS visit probabilities during the experiment, that is, the transition probability matrix reporting $p(M(t)|V(t-1))$ and $p(A(t)|V(t-1))$, to the predictions of the mechanistic models, parametrized with the median of the individual-level estimates. We obtained a temporal trend in transition probabilities from observed (discrete) transitions by calculating a running 4 d mean and computed the corresponding mean squared errors.

Eqs. **1**–**11** were solved numerically in C++ and the parameters estimated using the PSO algorithm in MATLAB R2017b (MathWorks) using the Global Optimization Toolbox. The optimization ran on a computer cluster using the MATLAB Distributed Computer Server. We calculated the illumination index ["GeoLight" package (56)], the bootstrapped CIs ["boot" package (57)], and produced effect size plots in R (58).

Data Availability. Data and code are available from the Zenodo Digital Repository (http://doi.org/10.5281/zenodo.4609649) (59).

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