ECOLOGY LETTERS

Ecology Letters, (2013) **16**: 1316–1329 doi: 10.1111/ele.12165

REVIEW AND SYNTHESIS

Spatial memory and animal movement

William F. Fagan,[1]*† Mark A. Lewis,[2,3†] Marie Auger-Méthé,[3] Tal Avgar,[4] Simon Benhamou,[5] Greg Breed,[3] Lara LaDage,[6] Ulrike E. Schlägel,[2] Wen-wu Tang,[7] Yannis P. Papastamatiou,[8] James Forester[9] and Thomas Mueller[1,10]

Abstract

Memory is critical to understanding animal movement but has proven challenging to study. Advances in animal tracking technology, theoretical movement models and cognitive sciences have facilitated research in each of these fields, but also created a need for synthetic examination of the linkages between memory and animal movement. Here, we draw together research from several disciplines to understand the relationship between animal memory and movement processes. First, we frame the problem in terms of the characteristics, costs and benefits of memory as outlined in psychology and neuroscience. Next, we provide an overview of the theories and conceptual frameworks that have emerged from behavioural ecology and animal cognition. Third, we turn to movement ecology and summarise recent, rapid developments in the types and quantities of available movement data, and in the statistical measures applicable to such data. Fourth, we discuss the advantages and interrelationships of diverse modelling approaches that have been used to explore the memory–movement interface. Finally, we outline key research challenges for the memory and movement communities, focusing on data needs and mathematical and computational challenges. We conclude with a roadmap for future work in this area, outlining axes along which focused research should yield rapid progress.

Keywords

Animal spatial cognition, attribute memory, cognitive maps, movement ecology, orientation tasks, return points, spatial memory, systematic searches.

Ecology Letters (2013) **16**: 1316–1329

INTRODUCTION

Animal movements and their underlying mechanistic basis have intrigued biologists for generations. Key studies established the link between spatial learning and movement (e.g. Von Frisch 1967; Sutherland & Gass 1995), while optimal foraging theory (Charnov 1976), search theory (Rosenzweig 1981) and home range behaviour (Moorcroft & Lewis 2006; Börger *et al.* 2008) have identified fundamental issues surrounding animal movement in heterogeneous landscapes. Navigation studies, particularly those drawing upon geographic perspectives of navigation (Golledge 1998; Kitchin & Blades 2002) and animal spatial cognition (e.g. O'Keefe & Nadel 1978; Thinus Blanc 1996), highlight just how sophisticated animal movements can be.

Recently, the link between memory and movement received much theoretical attention in the context of home range behaviour because attraction towards memorised localities will generate bounded, reoccurring space use patterns (e.g. biased random walks where the bias is towards previously visited localities; Börger *et al.* 2008; Van Moorter *et al.* 2009). However, home range behaviour is only one aspect of the eco-evolutionary interface between memory and movement. Other aspects include the co-evolution of cognitive and movement capacities, the inference of memory use from movement patterns and the role of movement behaviour in shaping memory. With this review, we aim to provide a broad perspective of the memory–movement interface.

Overall, an animal's navigation and motion capacity determine how an individual will move relative to external forcing factors and internal states (Nathan *et al.* 2008). Among navigation mechanisms, random search behaviours and perceptual cues have been extensively studied (summarised in Mueller *et al.* 2011a; Hein & McKinley 2012), whereas the important role that memory plays in driving animal movement remains a major challenge. Better understanding of the role of memory will provide a deeper understanding of complex, emergent movement phenomena, such as migration, nomadism and home range behaviour (Mueller & Fagan 2008). Explicit focus on

---

[1] *Department of Biology, University of Maryland, College Park, MD, 20742, USA*

[2] *Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, AB, Canada T6G 2G1,*

[3] *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9,*

[4] *Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1,*

[5] *Centre d'Ecologie Fonctionnelle et Evolutive, CNRS UMR5175, 34000, Montpellier, France*

[6] *Department of Biology, ms 314, University of Nevada, Reno, Reno, NV, 89557, USA*

[7] *Department of Geography and Earth Sciences, Center for Applied Geographic Information Science, University of North Carolina at Charlotte, Charlotte, NC, 28223, USA*

[8] *Florida Museum of Natural History, University of Florida, Gainesville, FL, 32611, USA*

[9] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Saint Paul, MN, 55108, USA*

[10] *Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325, Frankfurt (Main), Germany*

**Correspondence: E-mail: bfagan@umd.edu*

†Joint first authors.

behavioural mechanisms integrating information acquisition (learning) and retention (memory) is essential for developing a robust portrait of where and when particular movement behaviours are likely to emerge as adaptive solutions and give rise to different movement patterns (Table 1).

Many early investigations of animal movement and memory relied on manipulative experiments in fixed arenas (reviewed in Paul *et al.* 2009). Increasingly, such studies are complemented by large data sets of animal tracking data made possible by advances in technology and miniaturisation (e.g. Collins *et al.* 2006). Indeed, recent, dramatic increases in data availability have spurred great attention to movement ecology (Nathan *et al.* 2008). However, developments in this field remain heavily driven by technology and the rapid accumulation of new data. Efforts to use these data to understand the mechanisms underlying movements and the role of memory have proven difficult, although researchers are tackling the new data sets with increasingly sophisticated modelling techniques (e.g. Gautestad *et al.* 2013).

However, tracking technologies can not only provide highly resolved movement data but additionally also collect data with accelerometers and physiological sensors to yield extensive data sets for individual animals. These new technologies allow researchers to quantify specific behaviours (e.g. feeding) or physiological states (e.g. pregnancy) during the track, providing much greater insight into the factors responsible for the observed movement decisions. Cognitive processes, such as sensory perception and memory, are fundamental to the behaviour–environment interface. Full understanding of how cognitive processes are influenced by, and give rise to movement patterns will require better remote sensing data of the environment animals move in to complement tracking data, novel perspectives on data analysis and new approaches for mathematical and computational modelling. Ultimately, understanding the links between cognitive processes and movement patterns will also require coupling tracking data with carefully controlled behavioural experiments and improved linkages with theoretical frameworks for spatial memory emerging from psychology, neuroscience and animal cognition will improve understanding of how memory influences movement (Fig. 1).

To achieve this synthesis, we first define different types of memory and characterise the costs and benefits of memory by drawing upon the literatures in psychology and neuroscience. We then turn to the fields of behavioural ecology and animal cognition where we review the dominant theories and conceptual frameworks that link memory with movement. Third, we turn to movement ecology and summarise recent, rapid developments in the types and quantities of available movement data, and the suite of statistical measures applicable to such data. Fourth, we discuss the advantages and interrelationships of diverse modelling approaches that have been used to explore the memory–movement interface. We conclude by outlining key data, computational and modelling challenges for the memory–movement community. We identify several axes along which focused research should yield rapid progress and offer a road map for future research.

PSYCHOLOGICAL PERSPECTIVES: SPATIAL VS. ATTRIBUTE MEMORY

Memory may be defined many ways (Tulving 2000), but here we restrict the definition to the acquisition, encoding, storage and retrieval of information (Baddeley 2004). Acquisition of a particular memory may be genetic (e.g. inherited genetic triggers for migration, inherited avoidance of a predator) or obtained within an individual's lifetime via direct experience or social communication. Encoding and storage refer to the processing of acquired information, often involving reduction and consolidation (Craik & Lockhart 1972). Retrieval is the context-dependent use of memorised information (i.e. using past experiences to inform decision making and affect subsequent behaviours).

Memory is one of many cognitive and information-use processes that may affect movement and navigation. However, differentiating between memory and other such processes (e.g. following marked trails, goal-oriented movement driven by perception) is extremely challenging (Table 1), and there exists a general need for a theoretical framework that can formally disentangle the different cognitive and information-use processes that might influence movement.

Further complicating the matter is that multiple cognitive processes are associated with memory. For example, information memorised can be used for inference, such as when an animal infers the current state of a (potentially unvisited) location based on information remembered from visits to neighbouring locations (e.g. Fronhofer *et al.* 2011). Also connected here is the decision-making concept of the 'Bayesian forager' (Klaassen *et al.* 2006; Van Gils 2010) in which information an animal gained while visiting a patch (e.g. prey density, proximity of resources) influences the decision of whether to stay or not in the next patch.

Many typologies of memory exist (e.g. Schacter 1992). Here, we distinguish two types of memory that are particularly germane to animal movement, acting on different kinds of information: *spatial memory* encodes spatial relationships or configurations, whereas *attribute memory* encodes the attributes of local features. Both can act together and strongly influence movement.

Spatial information allows an animal to reduce uncertainty with regard to its position with respect (e.g. distance and direction) to geographical objects/locations (Table 2). Spatial information may include some sensory characteristics of a specific location (e.g. the geomagnetic field intensity, or the local landscape view) but may also include the speed and direction of current and past movement bouts (Table 2).

Attribute information, in contrast, allows animals to reduce uncertainty with regard to location-independent characteristics of objects or object classes. Information in attribute memory may be as simple as abundance or types of food, and can be linked to spatial information, so that, for example, food patch quality can be spatially encoded: the location of a patch is spatial information and patch quality is an attribute. Memorisation of resource quality or abundance allows animals to choose among alternative pathways, as occurs in bumblebees (Lihoreau *et al.* 2011). The same attribute, however, may be encoded for many locations or may be spatially independent (e.g. Clark & Gronlund 1996). In the context of movement behaviour, the time passed since a location was last visited is another aspect of attribute memory, and it is especially useful in avoiding recently explored areas (Van Moorter *et al.* 2009). Moreover, other attributes, such as food quality, can also be time-dependent, yielding time-dependent effects on movement (e.g. perishability of resources: Clayton & Dickinson 1998; seasonal or weather-dependent visitation of fruit-bearing trees: Janmaat *et al.* 2006). Values associated with attribute memory may also affect the accuracy, precision and persistence of the associated spatial memory. For example, a valuable resource, or a dangerous area, may be retained in the animal's memory with higher resolution and for longer periods than will locations with more neutral attributes (e.g. Milinski 1994; Wolf *et al.* 2009). In the following sections,

Table 1 Examples of well-demonstrated memory-driven movement behaviours and memory mechanisms that have been ascribed to those behaviours

Movement behaviour	Typical movement pattern	Rarity and taxonomic breadth	Examples[†]	Causal memory mechanisms (listed in order of behavioural complexity)	Confounding sensory mechanisms
Central place foraging	Foray loops with regular return to a central location	*Common* Numerous taxa	Bell (1990)	Path integration; cognitive map of central place and nearby foraging areas	*None* – Central place patterns are unlikely without memory
Migration; Philopatry	Seasonal or longer movement between two distant habitats	*Common* Numerous taxa	van Schaik (2010), Kitchin & Blades (2002)	Cultural transmission of movement patterns, cognitive map, genetic memory, natal homing, episodic-like memory.	Innate directional bias, sensory gradient following.
Trapline nectaring	Regular routes visiting flowers in a precise repeated order	*Rare* Bees, hummingbirds	Osborne & Clark (2001), Gill (1988)	Precise episodic-like memory of nectar refilling times and cognitive map of flower locations	*None* – Memory is sufficient to perform this behaviour
Caching	Deposition and retrieval of food items at hidden locations	*Rare* Mammals, birds, some reptiles	Gould *et al.* (2010), LaDage *et al.* (2009)	Precise spatial memory of cache locations combined with episodic-like memory of storage and retrieval events	*None* – Memory is sufficient to perform this behaviour
Territoriality	Remaining within and defending a small, bounded area	*Common* Numerous taxa	van Schaik (2010), Moorcroft *et al.* (2006)	Cognitive map, episodic-like memory	Emergent from reactive conspecific interactions
Home ranging	Remaining in a bounded area	*Common* Numerous taxa	Moorcroft & Lewis (2006), Van Moorter *et al.* (2009),	Cognitive map, episodic-like memory	Emergent from interactions with habitats and edges
Predator avoidance	Aversion from areas of high predator density	*Common* Numerous taxa	Moorcroft & Lewis (2006), Laundré *et al.* (2001)	Cognitive map (sensu 'landscapes of fear')	Emergent from reactive predator–prey interactions
Memory-informed searches	No typical pattern, in some rare cases systematic search patterns such as spirals possible	*Likely common but demonstration difficult*	Moorcroft & Lewis (2006), Mueller & Fagan (2008)	Attribute and associational memory; cognitive map, episodic-like memory	Difficult to distinguish memory-informed searches from sensory-driven searches
Patrolling	Repeated loops or back-and-forth routes to defend resources from conspecifics	*Uncommon* Mammalian predators, insects	Scott (1974), Kolowski *et al.* (2007)	Cognitive map of beacons and landmarks, episodic-like memory of previous visits and past locations of conspecifics	Emergent from reactive conspecific interactions

As noted in the rightmost column, some movement processes may not require memory: sensory processes often confound with memory-driven behaviours, making some memory-driven movement processes difficult to distinguish from reactive sensory-driven movement behaviours. We use the term cognitive map to indicate any of the range of neurological or psychological mechanisms that store relational spatial information in animal memory. [†]References cited in this table appear in the Supporting Information (see Appendix A).

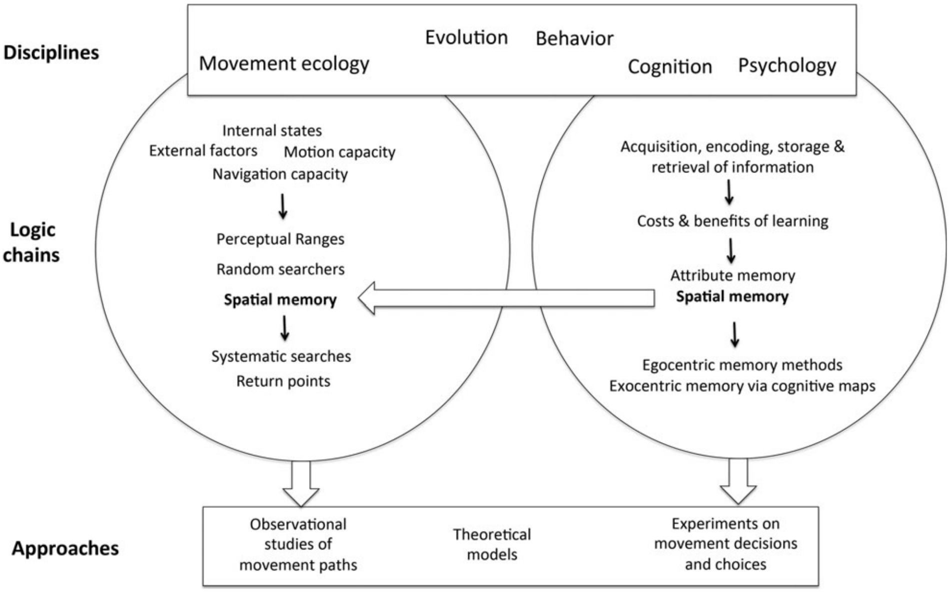

Figure 1 Schematic outlining the contributions of movement ecology and other disciplines to research at the interface of animal movement and memory. Discipline-specific logic chains lead to complementary approaches for studying memory-driven movement. However, spatial memory is central to both frameworks, providing a nexus for synthesis.

Table 2 Basic orientation tasks, providing a comprehensive classification of the functionalities of spatial memory, listed from simplest to most complex

Task ID	Orientation task	Required spatial memory (genetic or learned)
1	Move towards a peak or valley in a perceived gradient field	At minimum, none. However, memorising the slope of the field increases efficiency, allowing the estimation of the extent to which the current movement direction is the correct one
2	Determine whether an animal is currently at the goal location	Unique site identifier (to match against the sensory input)
3	Move towards a specific goal along a perceived gradient field in one dimension (*n* fields in *n* dimensions)	At minimum, the gradient field's value(s) at the goal. This allows calculation of the absolute difference between the memorised and perceived values so that the task in identical to that of row 1. Improved efficiency is achieved by memorising of the slopes of the fields and their orientation with respect to a compass
4	Move back towards a previously visited goal based on path integration	Bearing and distance to the goal. A computation based only on directions (i.e. without distance weighting) can provide accurate approximations in some cases, but usually leads to large errors in homing direction
5	Move towards a goal based on a series of sequentially perceptible beacons (i.e. 'signposts', that are not necessarily visual)	Unique site identifiers for each of the beacons
6	Move towards a goal based on a series of perceptually disconnected beacons	If the beacons are identifiable as localities along a gradient field, this task is a more complex version of task 3, requiring, at minimum, remembering the field value at each beacon. Otherwise, this task requires a series of unique site identifiers for each of the beacons, each coupled with a bearing to the next beacon
7	Move towards a goal based on a set of landmarks that are simultaneously perceptible from both the current and goal locations (i.e. the same landmark-based system of reference can be used at both places)	At minimum, memorisation of the goal location in the landmark-based system of reference. The navigation task itself can be performed using gradient fields

Execution of these tasks depends not only on memory capacities but on the required level of computational sophistication. Each task may be motivated by attribute memories with or without explicit spatial links. Notice that a single movement phase (e.g. bird migration) may encompass multiple tasks (e.g. gradient following complemented by goal identification).

unless specifically mentioning attribute memory, all references to memory refer to spatial memory.

EVOLUTIONARY PERSPECTIVES: COSTS, BENEFITS AND TRADE-OFFS INVOLVING SPATIAL MEMORY

Spatial memory provides animals with many advantages. At local scales, these benefits include improved choice of critical locations, such as food caches, nesting locations or hiding sites for dependent young. At larger scales, spatial memory aids navigation in landscapes that feature complex spatial structure, rare but essential sites that must be relocated (e.g. calving grounds, nesting beaches), or resources that are only available periodically (e.g. Bingman & Cheng 2005; Janmaat *et al.* 2006; Papastamatiou *et al.* 2013).

However, memory is not physiologically free. Both memory storage capacity (metabolic overhead of bigger brains) and the process of encoding and retrieving memories (brain activity) incur energetic and material costs (Dukas 1999; Burns *et al.* 2011). For example, memory formation and maintenance involves DNA methylation, a type of DNA modification that alters patterns of gene expression (Day & Sweatt 2010). In addition, accurate memory may require redundancy, encoding information across many neuronal pathways so that if one is inaccessible, the memory is not lost (Dukas 1999). More deeply engrained memories are expected to require more brain tissue and incur higher metabolic overhead.

Unfortunately, current frameworks for modelling memory-based movement generally do not consider, even in an elementary fashion, physiological costs and time demands for learning that could constrain movement. For example, studies that compare the efficiency of different movement strategies involving spatial memory typically do not incorporate the costs of memory, such as the cost of information acquisition and/or retention (Mueller *et al.* 2011a; Fronhofer *et al.* 2013). Linking fitness to increased spatial memory is a difficult empirical problem, but it provides interesting modelling opportunities. Even if memory affords only small increases in movement efficiency on a per step basis, such effects would compound across the lifetime of animals, and in a modelling context such benefits could be explored in detail. In parallel, biologging sensors can be used to quantify energy expenditure in free-ranging animals, making it possible for future studies to actually measure the costs of animal search patterns and memory in habitats of varying complexity (e.g. Gleiss *et al.* 2011).

A less obvious cost is memory interference. As memory capacity increases, the likelihood that two memories will interact or confound also increases. Interference can occur as new memories degrade the accuracy of old memories (known as retroactive interference) or old memories prevent the accurate acquisition of new memories (known as proactive interference) (Bouton 1993). Depending in part on whether memories are closely related in context, memory interference can lead to mistaken recollections (Bouton 1993). Such mistakes could produce costly errors in navigation, foraging or risk assessment. Thus, animals need mechanisms for prioritising information storage based on the importance of the memory to their life history and the reliability of the information (Dukas 1999; Burns *et al.* 2011). Interference costs and mechanisms for prioritising information have been little studied with regard to movements; including these aspects in future studies on movement strategies may provide a more complete picture of memory processes in animal movements.

Larger memory and cognitive capacity also require prolonged sleep. Sleep is needed for the consolidation of long-term memory (e.g. Stickgold 2005), and the need increases with brain size (e.g. Lesku *et al.* 2006). The costs of sleep include lost foraging opportunities, decreased use of energy-conserving mechanisms such as torpor, and increased risks of predation because vigilance necessarily decreases during sleep (Lima *et al.* 2005; Roth *et al.* 2010). Memory-based movement models currently neglect these costs, but they could be incorporated via explicit consideration of distinct behavioural phases (Morales *et al.* 2004; McClintock *et al.* 2012) in models, facilitating consideration of the interplay between movement exploration and the amount of sleep within an individual's overall behavioural budget.

Finally, encoding extensive sets of interrelated memories may require a protracted and potentially costly learning period. Juvenile periods, when inexperienced individuals are learning to forage and avoid predators, are associated with low foraging success and high mortality rates (Dukas 2009). Parental care can reduce these costs to juveniles, but only through direct costs to parental energy and time, which can reduce adult survival, mating opportunities, and can delay production of future offspring (Alonso-Alvarez & Velando 2012). Learning also occurs laterally via social or cultural transmission, but even those types of learning will involve costs, such as the risks of learning false information (van Schaik 2010). Moreover, acquiring useful information about the environment may involve exploratory movements, which can increase energy costs and predation risks (Sih & Del Giudice 2012).

Considering these several costs of memory, we can make several predictions. First, due to the temporal costs of learning, memory may be less useful in short lived animals where instinctive genetically coded behaviours will be favoured. Likewise, after completion of their learning phase, species with long learning periods might be expected to exhibit different (e.g. more 'refined' or systematic) spatial patterns than those with short-learning periods. Lastly, if early learning and memorisation of the landscape are indeed costly, among-individual differences in initial conditions (e.g. physiological states, pedigrees, natal sites) should impact how animals use space after the conclusion of their learning periods.

Costs and benefits of memory as a series of adaptive trade-offs

Animals have limited capacities for processing and storing information accurately over the long term, creating possible trade-offs with the benefits of memory. For example, the benefits of memory may trade-off against sensory capacity for information collection, which lessens the need to rely on memory. Another key trade-off exists between the quantity and quality of memories, meaning that only some memories will be encoded in detail. Mechanisms for prioritising long-term memory based on importance and reliability are needed to prevent memory interference (e.g. Anderson 2000). Forgetting is the major mechanism for mitigating interference, and memory that does not lose irrelevant or unimportant information does not function properly.

Yet, another trade-off involves the capacity, duration and precision of memory because memories will decay unless reinforced and maintained (Fig. 2). Decay in the intensity or precision of spatial memories could strongly affect how animals move through a landscape, lessening fidelity to favoured areas (Avgar *et al.* 2013a). Moreover, partially decayed memories may produce mismatches between perceived and encoded information, which could introduce error in movement or navigation decision-making processes. Likewise, heavy reliance on memory when moving in dynamic landscapes may not allow an animal to update memorised landscape information with current environmental conditions (Boyer & Walsh 2010). The series of constraints and trade-offs outlined above help establish when, and in what kinds of landscapes, memory will be most useful for animal movement. For example, memory would be of little benefit in spatially homogeneous, temporally stable landscapes or in landscapes featuring temporal dynamics that are rapid and/or unpredictable (McNamara & Houston 1987). In contrast, memory should be particularly valuable in landscapes of intermediate complexity (with predictable spatiotemporal dependency) where remembering several locations and their attributes would be sufficient to accrue fitness benefits through efficient navigation or timely returns (Fig. 3).

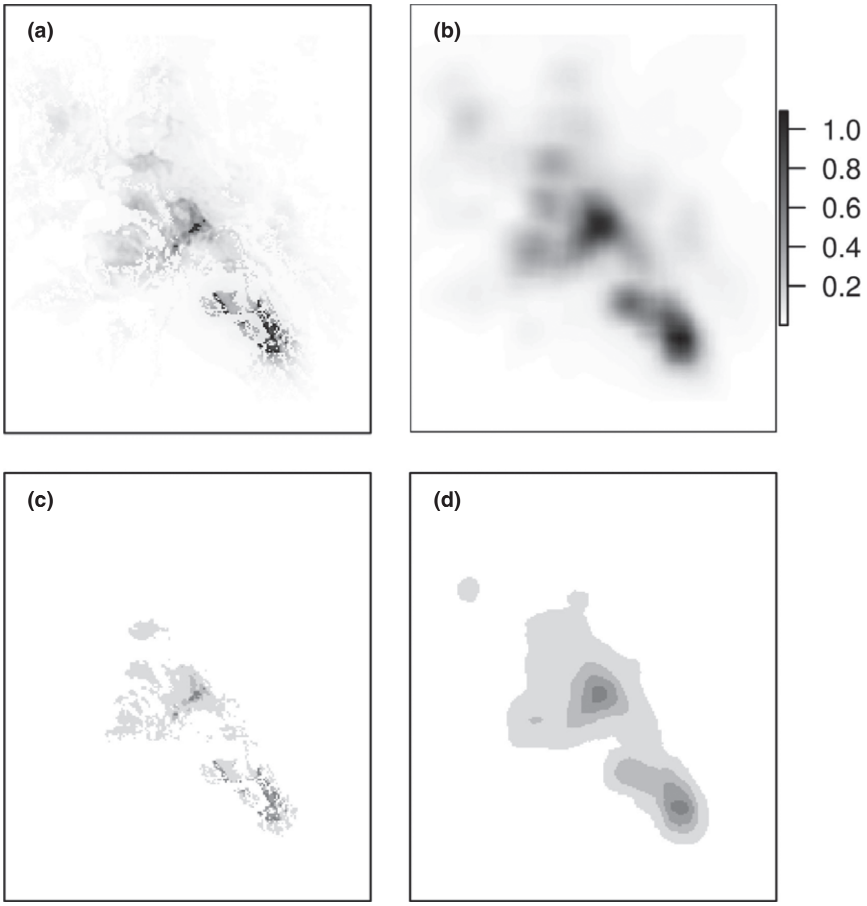

Figure 2 Spatial memories decay with time, and these decays may include decreases in intensity (black to grey transition from a–c) and spatial precision (expansion of shaded cells from a to b) or both (from a–d). These figures show the interaction between resource selection and memory when memory is summarised within fine (a and c) and coarse (b and d) grids. Panels (c and d) represent cases where the decay of memory is more rapid leading to a lower overall intensity of memory and reduced contrast between high and low memory areas. Time-dependent changes in the intensity and precision of spatial memories could be included in mechanistic movement models through their influences on, respectively, the strength and directionality of movement vectors.

COGNITIVE PERSPECTIVES: COGNITIVE MAPPING AND OTHER NAVIGATING PROCESSES

Cognitive mapping

Cognitive mapping is a series of psychological transformations for acquiring, coding, storing, recalling and decoding spatial information and attribute information in memory. Although memory-based behaviours may rest on simpler processes such as path integration, there is clear evidence that animals can also form complex representations of their worlds (Bingman & Cheng 2005). More recently, the debate has shifted from whether cognitive maps exist to the form that such maps actually take (e.g. Euclidean vs. topological maps; Asensio *et al.* 2011; Normand & Boesch 2009).

Cognitive representations of spatial information may be of either egocentric (i.e. structured relative to one's own position) or exocentric (i.e. structured relative to landscape features) formats (Klatzky 1998). Some research communities use autocentric vs. allocentric instead of egocentric versus exocentric, but the dichotomies convey the same meaning. Exocentric storage may be analogous to the way a human might understand a folding road map where information is stored completely independent of the self (Slocum *et al.* 2009). A key question is the extent of the system of reference used (Benhamou 1997, 2010): is it universal (as for a road map) so that a single one can cover the life-time home range of an animal or is it only effective over a restricted range, so that any important distant place requires its own local system of reference?

Evidence remains elusive that animals navigate by universal exocentric mapping alone. Furthermore, animals that appear to use exocentric representations might actually navigate by a mixture of egocentric and local exocentric methods that connect the animal's current position to other locations with the help of trails, external sensory fields, path integration and related approaches (Benhamou 1997, 2010). For many species, this mix could provide a functional navigation system that closely approximates the benefits of universal exocentric mapping.

Current consensus is that, in young animals, or older animals exposed to a novel landscape, spatial information is first used to encode egocentric spatial memory, but tends later to be involved in exocentric encoding. As spatial information becomes more complete, egocentric memories are gradually connected, leading to the emergence of effective exocentric representations (e.g. Benhamou 1997; Aznar-Casanova *et al.* 2008). Modelling the role of this learning process in memory presents many exciting opportunities for theoreticians.

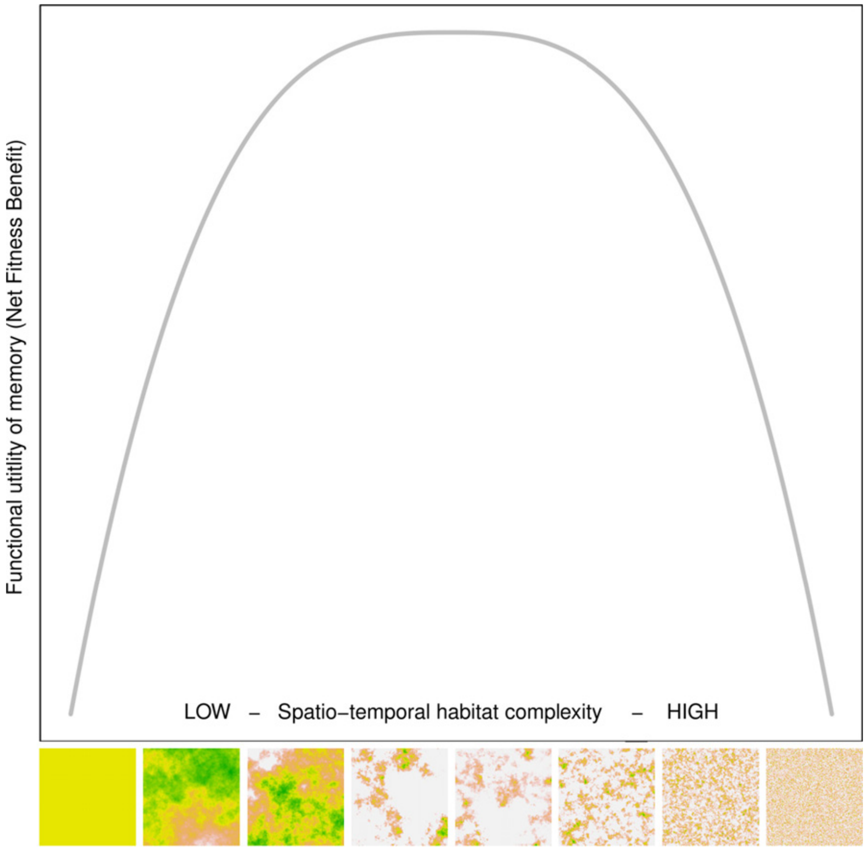

Figure 3 Heuristic representation of the functional utility of memory for animal movement in heterogeneous landscapes. Memory is most valuable (i.e. provides the greatest fitness benefit) in landscapes with moderate levels of spatio-temporal complexity. In contrast, highly homogeneous landscapes do not feature enough distinguishing features to aid navigation based on memory, and highly heterogeneous landscapes are so complex that memorising information sufficient for navigation would incur extensive costs.

Landscape features and navigating processes

Animals use three basic memory-driven mechanisms (which can be combined or used in parallel) to move towards a specific goal: beacon/gradient-based navigation and location-based navigation (both of which depend on landscape features), and landscape-independent route-based navigation.

In beacon-based navigation (Table 2, tasks 2, 4 and 6), animals memorise the perceptual (e.g. olfactory) signature of one or more beacons (i.e. conspicuous objects that are closely associated to the final goal or to intermediate goals along the route leading to the final goal). The animal thus reaches the final goal by moving from one beacon to the next, each time moving up the local gradient of perceptual information provided by the beacon's relative size in its field of view. Gradient-based navigation (Table 2, tasks 1 and 3) is conceptually similar to beacon-based navigation, but the goal location is memorised with respect to stimuli continuously varying in space (gradient fields) rather than discrete objects (beacons).

Location-based (or eidetic) navigation (Table 2, task 7) rests on goal memories defined by the spatial relationships between the location of the goal location and those of surrounding nearby objects, called landmarks, forming an exocentric frame of reference. This form of navigation may involve spatial memory restricted to a simple snap-shot of the set of landmarks as perceived from the goal, or much more complex forms of spatial memory involving complex exocentric cognitive mapping (Benhamou 2010).

In route-based navigation (Table 2, task 5), an animal memorises its position relative to its starting point to which it is seeking to return using path integration. This animal equivalent of dead reckoning, which has been demonstrated in a number of central place foraging hymenopteran species (e.g. Wehner *et al.* 1996), requires little memorization. As currently understood, the animal continuously updates its position with respect to the starting location by combining translational and rotational information collected en-route. Hence, the only piece of information that must be committed to memory at any given time is the current homing vector (Table 2). Using route-based navigation requires an ability to estimate the direction of movement. Such ability can be compass-based, relying on the earth's magnetic field or the positions of the sun or stars. Precise solar navigation can be achieved using a time-compensated sun compass (e.g. Perez *et al.* 1997).

ECOLOGICAL PERSPECTIVES: DETECTION OF MEMORY PROCESSES IN ANIMAL MOVEMENT DATA

Return points and recursion distributions help identify memory-driven movements

Analyses of movement recursions, in which animals repeatedly return to particular locations (called return points), can help identify memory-driven movement processes (Table 1). Movement recursions exist at different scales. For example, at landscape and continental scales, migratory animals return to breeding and overwintering grounds year after year. Within landscapes, animals may repeatedly visit locations in their home ranges, such as reproductive sites, resting sites or resource locations (e.g. water holes, kill sites). At the finest scales, movement recursions may constitute an efficient foraging of trap-lines or means of performing area-restricted searches to locate resources or specific targets (Benhamou 1994).

However, the existence of movement recursions is not a reliable indicator of memory. At fine scales, recursive movements may stem from reactive response to a stimulus or perception of targets (e.g. moths circling a light bulb at night). At larger scales, where it is more likely that movement recursions are memory-driven because re-visited areas are beyond an animal's perceptual range, analyses of movement data can help identify return points and gauge the importance of memory (Benhamou & Riotte-Lambert 2012). Measures of site fidelity, such as those from the breeding site literature (Haas 1998), may be particularly useful for identifying memory-related recurrent movements. Likewise, high movement precision and low navigational variance may also be strong indicators of memory-guided movement processes, such as homing (Hagstrom 2013).

Analyses of return delays may be particularly useful indicators of how memory influences movement decisions. Consider three scenarios in which an animal searches for resources in the vicinity of a memorised site such as a water hole or nest. In the first, an animal searches using an unconstrained biased correlated random walk (Benhamou 1994), in which case we would expect return delays to a memorised site to be exponentially distributed. Alternatively, if some physiological factor (e.g. thirst, nestling hunger) constrains the animal to return to the memorised site, this constraint should increase regularity of return delays. Such regularity would manifest as a distribution of return delays in which the mode, median and mean are closer together, and of smaller variance than an exponential distribution with the same mean, and the duration of consecutive return delays should be independent (i.e. not correlated) of each other. Finally, animals whose visits to the memorised site follow some external periodic driver (e.g. predation risk tied to solar or lunar cycles) should feature return delays with reduced variation but autocorrelation between delays. For example, if an animal frequents a water hole on a daily schedule, an early visit to the water hole one day, with a corresponding intervisit period of less than 24 h, will likely be followed by an intervisit period of more than 24 h as the animal regains its schedule. This periodicity is reinforced, generating negative autocorrelation in return periods, because temporarily ignoring the internal driver of the visit (e.g. thirst) is far less dangerous than ignoring the diurnal cycle of the external driver (e.g. predation risk).

Fourier analyses can efficiently highlight the types of periodic return behaviours expected when memory drives movement (Bar-David *et al.* 2009; Li *et al.* 2012; Riotte-Lambert *et al.* 2013). As a complementary tool, wavelet analyses can identify of episodes during which periodic behaviour is expressed. For example, if an animal alternates episodes of periodic behaviour with longer episodes of aperiodic behaviour, Fourier analyses will detect the existence of periodicity but will not characterise whether that periodicity occurs uniformly through the data set. In contrast, wavelet analyses make it possible to show when the periodic behaviour is expressed in a long-term movement data set (March *et al.* 2010; Riotte-Lambert *et al.* 2013).

In some contexts, such as marine systems, return points can be difficult to detect directly. We are then challenged with the task of identifying goal-oriented movements without knowing what the goal is, or if it has been reached. In such cases, we can sometimes use the structure of an animal's movements to identify goal-oriented movements. An animal's net displacement might be compared to the predictions of a random walk at multiple spatial scales and used to identify the spatial scales over which orientation occurs (Benhamou 2006). Alternatively, a more mechanistic approach may enable identification of local attractors based on a model of multistate random walks (McClintock *et al.* 2012). When memory is at play, we anticipate that oriented movements can operate at spatial scales beyond the perceptual range of the animal (Mueller & Fagan 2008). While long distance goal-oriented movements do not necessarily require memory (e.g. tuna in open ocean may be able to hear sounds 10s or 100s of kilometres away; Girard *et al.* 2004), in cases where the scale of orientation are demonstrably much greater than the perceptual range of the animal (e.g. Brooks & Harris 2008; Papastamatiou *et al.* 2011), memory effects are more likely.

Once return points and return delays have been identified, an individual's behaviour can be analysed in a time-dependent fashion (Fig. 4). For example, memory may be statistically identified by the prevalence of least-cost paths between return points beyond sensory range (Asensio *et al.* 2011). Similarly, memory may be expressed as biases towards return points, which can be detected by fitting biased correlated random walks to data from movement paths (McClintock *et al.* 2012). For example, paths between key landscape features that become increasingly direct as an animal gains experience provide strong evidence of memory in movement processes (e.g. Papastamatiou *et al.* 2011). Given the difficulty of observing animals through long-learning periods, relocating animals to novel environments may prove exceptionally helpful in the identification and characterization of movement processes.

Systematic searches as memory-driven movement without return points

One qualitatively different manifestation of memory is the emergence of 'systematic' searches in movement pathways (Table 1). For example, an animal relying on systematic searches can adjust its search radius based on previous information of the spatial location of a movement target. In addition, memories gained during previous foraging events would give rise to movement strategies that maximise, or at least increase, encounters with patches of similar size and dispersion (Mueller *et al.* 2011a). As such, it would be worth investigating whether one statistical indicator of memory could be an improved match between the scale of searches and the scale of resources as an animal gains experience. However, perceptual ranges and habitat patterns need to be considered to exclude the possibility that movements are simply a response to environmental stimuli rather than memory (Brooks & Harris 2008).

Exhaustive systematic searches also require memory because animals must remember and avoid searching in previously visited areas (e.g. Fronhofer *et al.* 2013). Thus, a nother good indicator of memory-driven movement is systematic avoidance of certain areas due to perceived risks or delays in resource renewal. However, such avoidance may be accomplished by marking behaviour, in which case avoidance is not necessarily a memory-based process (e.g. Reid *et al.* 2012). Detecting systematic avoidance is the logical inverse of

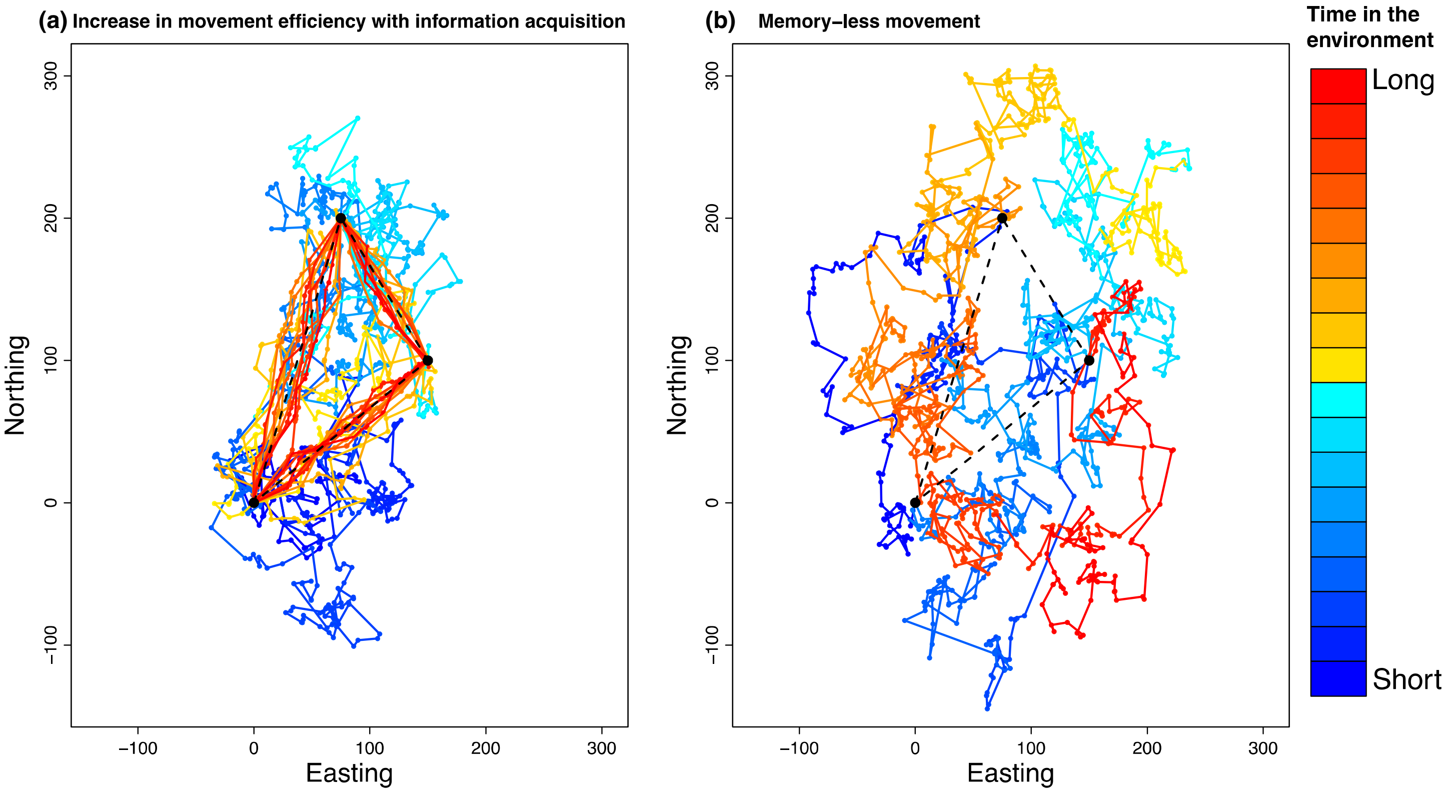

Figure 4 Analysis of movement in a time-dependent fashion, and especially for individuals newly introduced in an environment, can help identify the use of memory. Scenarios with (panel a) and without (panel b) memory-based movement are illustrated. Panel (a) represents an increase in efficiency of the movement between return points (black dots) with increased knowledge of the environment. Straight lines represent the most efficient movement (dashed lines). In complex environments, the most efficient movement between return points may not be straight and could be better represented by least-cost paths.

the recursion analyses discussed above, and presents a challenging analytical task.

THEORETICAL PERSPECTIVES: MODELLING AT THE MEMORY–MOVEMENT INTERFACE

Insights from a diversity of modelling approaches

Recent research has demonstrated a variety of promising modelling approaches for the connection of movement and memory (Table S1). Roughly speaking, those modelling approaches can be differentiated as having heuristic, mechanistic and phenomenological dimensions. Often, models do not purely belong to one of these three types, but mix different elements (Fig. 5).

Heuristic (or conceptual) studies help to describe broad causal relationships that are independent of particular mechanisms. This approach has been employed, e.g. to define a general paradigm for movement ecology (Nathan *et al.* 2008) and to classify differences in population-level spatial distributions in relation to individual movement behaviours and resource dynamics (Mueller & Fagan 2008; Mueller *et al.* 2011b).

Mechanistic models are routinely used to investigate the specific manners in which memory processes and movement are linked. Agent-based models have proven particularly useful for the incorporation of memory-based movement decisions. Examples include studies of the connections between cognitive abilities and foraging success (e.g. Boyer & Walsh 2010), investigations of the emergence of home ranges via familiarity and memory effects (Börger *et al.* 2008; Van Moorter *et al.* 2009; Berger-Tal & Avgar 2012), and the potential to infer individual memory capacities based on observed movement and environmental data (Avgar *et al.* 2013a). Even more intricate system simulations provide a tool for studying the contributions of memory to complex movement phenomena such as animal migration (Tang & Bennett 2010). An alternative mechanistic approach replaces agent-based and system simulations with an Eulerian description of animal movement. Rather than following many realizations of a stochastic process that describe possible movement paths of individuals, the Eulerian approach provides an approximate solution via a deterministic system of equations that describe a density function for the expected space use of individuals over time. Such deterministic models are expressed as advection-diffusion or integrodifferential equations that approximate a system of coupled master equations. While the inclusion of memory in such an approach would be new, the underlying mathematical structure of such Eulerian modelling approaches is well established (see, for example Moorcroft & Lewis 2006). One promising area for further development may be to include memory into Eulerian models via analysis of 'step selection functions,' which are mathematical expressions for the behavioural choices involved in movement decision making as influenced by environmental covariates (Fortin *et al.* 2005) (Table S1).

Phenomenological models, which are effectively statistical in nature, seek to summarise observed movement patterns and to establish associations between variables without necessarily testing causal relations. For example, such models have been used to detect cor-

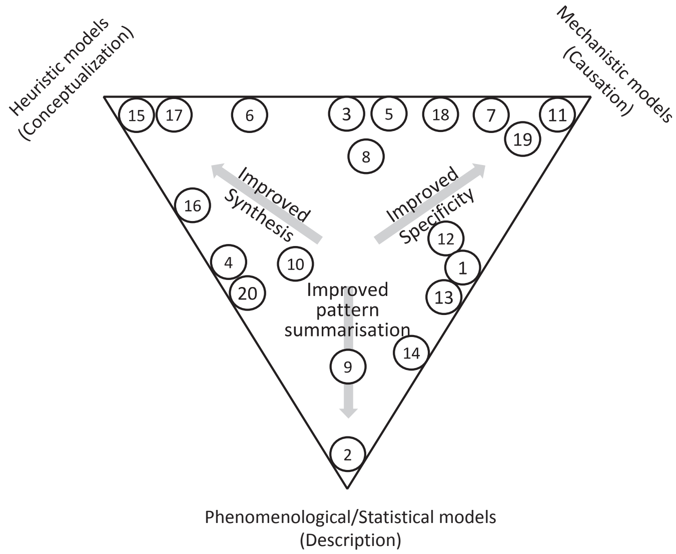

Figure 5 Triangular schematic representation of the relationships among heuristic, mechanistic and phenomenological/statistical modelling approaches for the study of spatial memory in ecology. Several relevant articles are positioned in the triangle, illustrating the extent to which they include elements of the three modelling approaches. References cited in this figure appear in the Supporting Information (see Appendix A): 1: Avgar *et al.* (2013a); 2: Bar-David *et al.* (2009); 3: Benhamou (1994); 4: Benhamou & Riotte-Lambert (2012); 5: Bennett & Tang (2006); 6: Berbert & Fagan (2012); 7: Berger-Tal & Avgar (2012); 8: Boyer & Walsh (2010); 9: Breed *et al.* (2012); 10: Dalziel *et al.* (2008); 11: Fronhofer *et al.* (2013) ; 12: Gautestad & Mysterud (2010); 13: McClintock *et al.* (2012); 14: Mills-Flemming *et al.* (2010); 15: Mueller & Fagan (2008); 16: Mueller *et al.* (2011b); 17: Nathan *et al.* (2008); 18: Shaw & Couzin (2013); 19: Van Moorter *et al.* (2009); 20: Wolf *et al.* (2009).

relations between space use and environmental variables (Fortin *et al.* 2005; Barraquand & Benhamou 2008; Avgar *et al.* 2013b; Bestley *et al.* 2013). Inferring memory usage is more challenging, however, because memory processes interact dynamically with movement and can never be observed directly. The application of such statistical models to the study of memory and movement requires first identifying pattern-based indicators of memory effects (e.g. recursions – see previous sections) and, depending on the reliability of those indicators, using their occurrence and intensity to gain statistical inference regarding memory usage.

Recent models at the memory–movement interface involve various combinations of heuristic, mechanistic and statistical models (Fig. 5). For example, mechanistic and statistical approaches can be used together to test whether memory partly explains observed movement paths (e.g. Avgar *et al.* 2013a; Gautestad *et al.* 2013) or to segment heterogeneous movement data into different, internally homogeneous activity periods (e.g. resting, moving, foraging) that can be more easily analysed (e.g. Morales *et al.* 2004). Hierarchical modelling approaches, which account for observed patterns generated by putative hidden processes changing in space and time (Patterson *et al.* 2008), could also be used here. For example, hidden Markov models segment paths by mixing mechanistic modelling of the movement process (as biased and/or correlated random walks) with a statistical procedure for distinguishing and clustering the component walks (Morales *et al.* 2004; McClintock *et al.* 2012). An alternative segmentation can be accomplished using models that mix heuristic and phenomenological perspectives to explore data on residence time (i.e. the time spent by an animal in the neighbourhood of a location; Barraquand & Benhamou 2008). Movement bouts so identified must be regrouped categorically based on residence time prior to analysis using mechanistic movement models.

Biological memory is an extremely complex and often poorly understood phenomenon. Consequently, quantitative models must abstract and simplify memory processes, leading to useful approximations of the underlying biology. These approximations will improve as these modelling approaches mature.

Advantages of particular modelling tools and techniques

Several modelling techniques show particular promise for use at the memory–movement interface (Table 1, Table S1). For example, machine-learning algorithms, such as artificial neural networks and reinforcement learning, can be used to formulate decision processes of animals faced with many internal and external cues (Dalziel *et al.* 2008; Tang & Bennett 2010). Such approaches have provided insight into both the tension between long- and intermediate-term memory and discussions about conditions under which spatial cognition may emerge (e.g. Anderson 2000).

Hidden Markov and state-space models provide flexible frameworks for accommodating the hierarchical structures necessarily involved in modelling memory-driven movement (Table S1). Examples of such hierarchical considerations are the need to infer information about unobserved processes from observed patterns (Patterson *et al.* 2008) and the need to consider competing objectives that may lead to switching among alternative behavioural states (McClintock *et al.* 2012).

Experimental psychologists and neurobiologists have long considered Bayesian decision making as a plausible mechanism for the integration of hierarchical sources of information with varying levels of uncertainty (Körding 2007). Under some circumstances, simple linear approximations, reminiscent of linear operators, may perform as well as the more computationally demanding Bayesian processes (Dukas & Lange 2009). A different approach requires explicit assumptions about the spatiotemporal dependence of information resolution (Farnsworth & Beecham 1999). Regardless of the modelling formulation, explicit consideration of the hierarchical structure of information is needed to successfully combine movement and memory.

The above issues highlight in broad terms the types of complexities that characterise memory and its inclusion in movement models. More specifically, these complexities may be decomposed based on the definitions of memory provided above and in Table 2. At the simplest level, spatial memory may be used to answer the question 'have I been here before?' (e.g. Dalziel *et al.* 2008). When this memory is coupled with a time stamp (i.e. a temporal attribute memory), a substantially more complex question can be answered: 'when was I last at a given location that is not my current location?' Answering this question requires memorization of the spatial and temporal relations between the individual and multiple goals (e.g. Van Moorter *et al.* 2009). Spatially independent attribute memory may be used to compare the expected utility of different possible movements to the currently experienced value; this is a component of many optimal foraging models but is readily expandable to memory-driven movement (e.g. Berger-Tal & Avgar 2012). In contrast, spatially linked attribute memory can be used to answer questions ranging in complexity from 'what do I remember about my current location?' to 'which is the least-cost path between multiple variable food patches?' To date, models of memory-based movement rely on and implement many different aspects of memory. In future efforts, much progress and clarity could be gained by explicitly acknowledging the complexity and functionality of the modelled memory mechanism, leading to tests of whether a specific mechanism is both necessary and sufficient to account for a particular movement pattern.

CURRENT CHALLENGES: DATA NEEDS AND QUANTITATIVE OPPORTUNITIES

Specific data sets could accelerate research on memory-based movement

When investigating the role of memory in animal movement, a key challenge is that researchers have incomplete knowledge about the individual's information status at the beginning of the observation period. Improved data sets may be obtained via at least three experimental strategies. The first is to translocate individuals into novel environments where they have no previous knowledge. While this can be logistically challenging, researchers could take advantage of conservation programs, such as reintroduction and translocation programmes to establish new populations or displace problem animals (e.g. Fryxell *et al.* 2008; Wolf *et al.* 2009). A second approach would leverage experimental manipulations undertaken in areas undergoing rapid environmental change. Experimental addition or removal of resources or movement barriers could provide useful insights into animals' use of memory. Third, researchers could tag juveniles and monitor them as they develop (and, perhaps, return to their natal site to reproduce), thus obtaining extensive data on animals' movement histories (Hazen *et al.* 2012). This approach, in combination with genetic identification and parentage analysis, affords additional advantages including tracking of site fidelity throughout ontogeny.

In addition to historical space-use data, ancillary data on animal physiology and environmental properties may also provide insights into how memory influences movement. Environmental data can be important because it allows researchers to identify animals' use of landmarks, whereas physiological data can identify successful foraging events that may prompt recursive movements (e.g. Weimerskirch *et al.* 2007) or hazardous encounters that prompt future avoidance. Such ancillary data would be most useful for the study of memory-based movement if their temporal and spatial scales match those of the movement observations (Avgar *et al.* 2013a), but aligning these scales of observation is not always simple. While there has been great progress in the remote sensing of landscape data (e.g. chlorophyll, snow cover), the temporal and spatial resolution of environmental data remains coarse relative to the scale of movement data (Bestley *et al.* 2013; Papastamatiou *et al.* 2013).

Research designs must consider spatial error in location estimates and the spatial and temporal resolution of important covariates. For example, coarser spatio-temporal resolution may be satisfactory for satellite tracking of animals on landscape scales, allowing for longer time records on a given battery. In contrast, other research questions, such as those focusing on the interplay between memory and motivation, may require such fine scale data that only the smallest relocation errors could be tolerated. Experimental studies of memory and movement, such as those used in bumblebees or hummingbirds (e.g. Osborne & Clark 2001), will be critical for disentangling memory from oriented movement behaviours constrained by individuals' perceptual range.

Memory-driven movement affords complex mathematical and computational challenges

Because memory is a complex cognitive process and the patterns it affects are represented by multidimensional time-series data, accurate representations of movement processes may require considerable computational power, especially in agent-based models. Often, animal movement problems are decomposed into many sub-problems that can be concurrently handled by high-performance and parallel computing resources (e.g. Tang & Wang 2009). The degree of parallelization required depends on problem size, characterised by factors such as spatio-temporal configuration, the number of individuals modelled, the behavioural complexity of individuals and the number of Monte Carlo simulations required. If movements can be affected by both memory and interactions among individuals, many replications of interacting groups will be needed to gain insight into the long-term expectation of space use. Overall, even modest increases in behavioural complexity in memory-driven models may lead to substantial increases in computational demands. Nevertheless, such approaches allow for the investigation of individual variation in exploratory behaviour that may be essential to understanding the role of memory in movement. Careful consideration of the appropriate parallel computing architecture and programming strategy will facilitate exploration of complex movement models involving memory (Tang & Wang 2009).

In a similar vein, mathematical analysis of partial differential equation models arising from random walks may provide a useful path forward. Such models can yield steady-state solutions equivalent to a home range or territory (Moorcroft & Lewis 2006), but they would be new to the memory-movement problem. One of the major challenges associated with this approach is that complex behaviours (such as discrete or continuous behavioural states, hierarchical perception and context-dependent resource selection) are difficult to capture in mathematical form. Further, these behaviours may not yield steady-state solutions – especially in the face of temporally and spatially dynamic resources. However, the nonlocal nature of this class of models should prove fertile ground for applied mathematicians. Going forward, key opportunities for analyses include development of relatively simple models that provide robust predictions of short-term space use, and models that examine how short-term expectations shift through time. Understanding the mechanistic links between fine-scale movement models and broad-scale shifts in short-term expectations will be a major goal of this approach, increasing opportunities for modellers to move forward when connecting to biological systems.

Models of movement that can accommodate interactions among moving individuals, such as interference and information-sharing, are challenging but essential for making the transition from individual-level issues to questions at the population- or species-levels. Overall, memory-based models incorporating interactions among individuals (whether intra- or interspecific) seem especially difficult but of potentially great value, particularly as a means of exploring the tension between individual and collective learning. Few models have actually explored the effects of memory in this context, but some conceptual frameworks exist (e.g. Sueur *et al.* 2011). An interesting opportunity would be to pivot from existing mathematical models that can accommodate fixed perceptual ranges (such as partial integrodifferential equations) to models where the perceptual range and structure is flexible and can be modified to reflect the benefits (or disadvantages) of collective learning. Game-theoretic approaches, in which the relative fitness of different strategies could be examined, should be especially beneficial here. Such approaches could build on ideas in Noonburg *et al.* (2007), which raised the game-theoretic question of how an animal might choose a movement behaviour so as to maximise its fitness when there are other players with similar goals. Biologging technologies can inform these models, and there are now transmitting/receiving 'business card' tags, which can identify when and where particular tagged animals associate with each other (e.g. Holland *et al.* 2009).

Connecting models with animal movement data is a particular challenge because the memory process itself is hidden. As with many complex models, maximization of multi-dimensional likelihood surfaces in memory-based movement models will be difficult, with the possibility of local peaks or ridges dominating the process. Recently, the method of data cloning (Lele *et al.* 2007) has been developed to aid model fitting, and this approach makes it possible to maximise complex likelihoods using a modified Monte Carlo Markov Chain. Approximate Bayesian computation (Csilléry *et al.* 2010) is another computationally intensive emerging area that seems promising for parameterising memory-based movement models with intractable likelihoods. With this technique, a metric describing an animal movement pattern is defined, and parameters are modified until the metric most closely represents the corresponding measure as calculated directly from movement data. As we collect more data at finer detail, we expect models to evolve from simple caricatures to more realistic and complex depictions of spatial memory and animal movement.

Functional navigation and mathematical representation of spatial memory

In computational modelling of memory-based movement, substantial progress towards a more robust representation of animals' functional navigation systems may be possible by borrowing approaches from computational cartography (Slocum *et al.* 2009). For example, memory-based movement models could employ a multi-'layer' approach, with each layer associated with a particular goal such as food acquisition, mate finding or territory defence. Coupled with a hierarchical decision-making system, such a layered approach to modelling would require the animal to first decide which goal it wanted to pursue, and then retrieve the appropriate layer. This modelling approach would greatly facilitate exploration of how moving animals prioritise the integration of information from different sources and at different spatiotemporal resolutions based on reliability and relevance. For example, desert ants in the genus *Cataglyphis* employ several navigation mechanisms to return to their nest and they are able to shift between these mechanisms based on available sensory information (Bühlmann *et al.* 2011). The biological process of memory decay (Fig. 2) could also be represented mathematically within this layered framework. For example, time-dependent changes in the intensity and precision of spatial memories could be included in mechanistic movement models through their influences on, respectively, the strength and directionality of movement vectors.

CONCLUSION

Although behavioural ecology, cognitive science, animal tracking and computational and statistical ecology are all well-established fields, movement ecology, at the confluence of these fields, is still in its infancy. We have outlined new synergies arising among these fields in studies of how memory influences animal movement. At this interdisciplinary intersection, theoretical behavioural ecology provides conceptual frameworks for exploring the interplay between movement behaviour and memory. Cognitive science yields neurological and behavioural details that lend realism to this theoretical framework. Advanced animal tracking technologies are providing large amounts of detailed data with which this theoretical framework can be confronted. Computational and statistical ecology are developing the tools necessary for sensible and robust confrontation. At this emerging research interface, as in many others, meaningful progress requires in-depth interdisciplinary efforts. We hope that this article will inspire such efforts to move the field forward into new directions.

ACKNOWLEDGEMENTS

We thank Banff International Research Station (BIRS) for hosting a Focused Research Group on Memory and Animal Movement in the fall of 2012. With animal tracks right outside our windows, BIRS was the inspiring environment where the review paper was conceived and started. Editorial assistance by Caroline Wick, Silvia Alvarez and Francisca Lorenzen was essential to manuscript development. We acknowledge the following grants for supporting this research: NSF Advances in Bioinformatics award 1062411 to TM and WFF, NSF Mathematical Biology award 1225917 to WFF, a Canada Research Chair, a Killam Research Fellowship and NSERC Discovery and Accelerator grants to MAL, Alberta Innovates Technology Futures graduate scholarship and the Killam trust scholarship to MAM, an NSERC Vanier CGS to TA, an NSERC Banting postdoctoral fellowship to GAB, NSF Integrative Organismal Systems award 0918268 to LL, an iCORE Graduate Recruitment Scholarship in Information and Communications Technology to UES, and funding from the Robert Bosch Foundation to TM.

AUTHOR CONTRIBUTIONS

William F. Fagan and Mark A. Lewis designed and organised the review, secured funding, and led writing of the manuscript. Marie Auger-Méthé, Tal Avgar, Simon Benhamou, Greg Breed, Lara LaDage, Ulrike E. Schlägel, Wen-wu Tang, Yannis P. Papastamatiou and James Forester contributed to the review and helped write the manuscript.

REFERENCES

Alonso-Alvarez, C. & Velando, A. (2012). Benefits and costs of parental care. In: *Evolution of Parental Care*. (eds Royle, N.J., Smitseth, P.T. & Kölliker, M.). Oxford University Press, Oxford, UK, pp. 40–61.

Anderson, J.R. (2000). *Learning and Memory: An Integrated Approach*, 2nd edn.. John Wiley, New York.

Asensio, N., Brockelman, W.Y., Malaivijitnond, S. & Reichard, U.H. (2011). Gibbon travel paths are goal oriented. *Anim. Cogn.*, 14(3), 395–405.

Avgar, T., Deardon, R. & Fryxell, J.M. (2013a). An empirically parameterized individual based model of animal movement, perception, and memory. *Ecol. Model.*, 251, 158–172.

Avgar, T., Mosser, A., Brown, G.S. & Fryxell, J.M. (2013b). Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *J. Anim. Ecol.*, 82(1), 96–106.

Aznar-Casanova, J.A., Matsushima, E.H., Pérez-Zapata, L., Ribeiro-Filh, N.P. & Da Silva, J. (2008). Interaction between egocentric and exocentric frames of reference as assessed by perceptual constancy parameters. *Cogn. Stud.*, 15, 1–16.

Baddeley, A.D. (2004). The psychology of memory. In: *The Essential Handbook of Memory Disorders for Clinicians* (eds Baddeley, A.D., Kopelman, M.D. & Wilson, B.A.). J. Wiley, New York, pp. 1–12.

Bar-David, S., Bar-David, I., Cross, P.C., Ryan, S.J., Knechtel, C.U. & Getz, W. (2009). Methods for assessing movement path recursion with application to African buffalo in South Africa. *Ecology*, 90(9), 2467–2479.

Barraquand, F. & Benhamou, S. (2008). Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. *Ecology*, 89, 3336–3348.

Benhamou, S. (1994). Spatial memory and searching efficiency. *Anim. Behav.*, 17, 1423–1433.

Benhamou, S. (1997). On systems of reference involved in spatial memory. *Behav. Proc.*, 40, 149–163.

Benhamou, S. (2006). Detecting an orientation component in animal paths when the preferred direction is individual-dependent. *Ecology*, 87, 518–528.

Benhamou, S. (2010). Orientation and navigation. In *Encyclopedia of Behavioral Neurosciences*, Vol. 2. (eds Koob, G.F., LeMoal, M., Thomson, R.F.). Academic Press, Oxford, UK, pp. 497–503.

Benhamou, S. & Riotte-Lambert, L. (2012). Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecol. Model.*, 227, 112–116.

Berger-Tal, O. & Avgar, T. (2012). The glass is half-full: overestimating the quality of a novel environment is advantageous. *PLoS ONE*, 7, 1–9.

Bestley, S., Jonsen, I.D., Hindell, M.A., Guinet, C. & Charrassin, J.B. (2013). Integrative modelling of animal movement: incorporating *in situ* habitat and behavioral information for a migratory marine predator. *Proc. Biol. Sci.*, 280(1750), DOI: 10.1098/rspb.2012.2262

Bingman, V.P. & Cheng, K. (2005). Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethol. Ecol. Evol.*, 17, 295–318.

Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008). Are there general mechanisms of animal home range behavior? A review and prospects for future research. *Ecol. Lett.*, 11, 637–650.

Bouton, M.E. (1993). Context, time, and memory retrieval in the interference paradigms of Pavlovian learning. *Psychol. Bull.*, 114(1), 80–98.

Boyer, D. & Walsh, P.D. (2010). Modelling the mobility of living organisms in heterogeneous landscapes: does memory improve foraging success?. *Philos. Trans. A Math. Phys. Eng. Sci.*, 368(1933), 5645–5659.

Brooks, C.J. & Harris, S. (2008). Directed movement and orientation across a large natural landscape by zebras, *Equus burchelli antiquorum*. *Anim. Behav.*, 76, 277–285.

Bühlmann, C., Cheng, K. & Wehner, R. (2011). Vector-based and landmark-guided navigation in desert ants inhabiting landmark-free and landmark-rich environments. *J. Exp. Biol.*, 214(17), 2845–2853.

Burns, J.G., Foucaud, J. & Mery, F. (2011). Costs of memory: lessons from 'mini' brains. *Proc. Biol. Sci.*, 278(1707), 923–929.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.*, 9(2), 129–136.

Clark, S.E. & Gronlund, S.D. (1996). Global matching models of recognition memory: how the models match the data. *Psychon. Bull. Rev.*, 3, 37–60.

Clayton, N.S. & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, 395, 272–274.

Collins, S.L., Bettencourt, L.M.A., Hagberg, A., Brown, R.F., Moore, D.I., Bonito, G. *et al.* (2006). New opportunities in ecological sensing using wireless sensor networks. *Front. Ecol. Environ.*, 4(8), 402–407.

Craik, F.I.M. & Lockhart, R.S. (1972). Levels of processing: a framework for memory research. *J. Verbal. Learning Verbal Behav.*, 11, 671–684.

Csilléry, K., Blum, M.G.B., Gaggiotti, O.E. & François, O. (2010). Approximate Bayesian computation (ABC) in practice. *Trends Ecol. Evol.*, 25(7), 410–418.

Dalziel, B.D., Morales, J.M. & Fryxell, J.M. (2008). Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. *Am. Nat.*, 172(2), 248–258.

Day, J.J. & Sweatt, J.D. (2010). DNA methylation and memory formation. *Nat. Neurosci.*, 13(11), 1319–1323.

Dukas, R. (1999). Costs of memory: ideas and predictions. *J. Theor. Biol.*, 197(1), 41–50.

Dukas, R. (2009). Learning mechanisms, ecology, and evolution. In *Cognitive Ecology II (7–26).* (eds Dukas, R., Ratcliffe, J.M.). University of Chicago Press, ???????.

Dukas, R. & Lange, A. (2009). Bayesian approximations and extensions: optimal decisions for small brains and possibly big ones too. *J. Theor. Biol.*, 259(3), 503–516.

Farnsworth, K.D. & Beecham, J.A. (1999). How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. *Am. Nat.*, 153(5), 509–526.

Fortin, D., Beyer, H., Boyce, M. & Smith, D. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86(5), 1320–1330.

Fronhofer, E.A., Pasurka, H., Poitrineau, K., Mitesser, O. & Poethke, H.J. (2011). Risk sensitivity revisited: from individuals to populations. *Anim. Behav.*, 82, 875–883.

Fronhofer, E.A., Hovestadt, T. & Poethke, H.J. (2013) From random walks to informed movement. *Oikos*, 122, 857–866.

Fryxell, J.M., Hazell, M., Börger, L., Dalziel, B.D., Haydon, D.T., Morales, J.M. *et al.* (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc. Natl. Acad. Sci. USA*, 105, 19114–19119.

Gautestad, A.O., Loe, L.E. & Mysterud, A. (2013). Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer *Cervus elaphus* movements with simulation models. *J. Anim. Ecol.*, 82, 572–586.

Girard, C., Benhamou, S. & Dagorn, L. (2004). FAD: Fish aggregating device or fish attracting device? A new analysis of yellowfin tuna movements around floating objects. *Anim. Behav.*, 67, 319–326.

Gleiss, A.C., Wilson, R.P. & Shepard, E.L.C. (2011). Making overall body dynamic acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.*, 2, 23–33.

Golledge, R.G. (1998). *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes.* Johns Hopkins University Press, Baltimore, MD.

Gould, K.L., Kelly, D.M. & Kamil, A.C. (2010). What scatter-hoarding animals have taught us about small-scale navigation. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 365(1542), 901–914.

Haas, C. (1998). Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk*, 115, 929–936.

Hagstrom, J.T. (2013). Atmospheric propagation modeling indicates homing pigeons use loft-specific infrasonic map cues. *J. Exp. Biol.*, 216, 687–699.

Hazen, E., Maxwell, S., Bailey, H., Bograd, S., Hamann, M., Gaspar, P. *et al.* (2012). Ontogeny in marine tagging and tracking science: technologies and data gaps. *Mar. Ecol. Prog. Ser.*, 457, 221–240.

Hein, A.M. & McKinley, S.A. (2012). Sensing and decision-making in random search. *Proc. Natl. Acad. Sci. USA*, 109, 12070–12074.

Holland, K.N., Meyer, C.G. & Dagorn, L.C. (2009). Inter-animal telemetry: results from first deployment of acoustic 'business card' tags. *Endanger Species Res.*, 10, 287–293.

Janmaat, K.R.L., Byrne, R.W. & Zuberbuhler, K. (2006). Primates take weather into account when searching for fruits. *Curr. Biol.*, 16, 1232–1237.

Kitchin, R. & Blades, M. (2002). *The Cognition of Geographic Space.* I.B, Tauris, London, UK.

Klaassen, R.H.G., Nolet, B.A., van Gils, J.A. & Bauer, S. (2006). Optimal movement between patches under incomplete information about the spatial distribution of food items. *Theor. Popul. Biol.*, 70, 452–463.

Klatzky, R. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In *Spatial Cognition: An Interdisciplinary Approach to Representing and Processing Spatial Knowledge.* (eds Freksa, C., Habel, C.). Springer, Heidelberg, pp. 1–17.

Körding, K. (2007). Decision theory: what "should" the nervous system do? *Science*, 318(5850), 606–610.

Lele, S.R., Dennis, B. & Lutscher, F. (2007). Data cloning: easy maximum likelihood estimation for complex ecological models using Bayesian Markov Chain Monte Carlo methods. *Ecol. Lett.*, 10(7), 551–563.

Lesku, J.A., Roth, T.C., Amlaner, C.J. & Lima, S.L. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *Am. Nat.*, 168(4), 441–453.

Li, Z., Han, J., Ding, B. & Kays, R. (2012). Mining periodic behaviors of object movements for animal and biological sustainability studies. *Data Min. Knowl. Disc.*, 24(2), 355–386.

Lihoreau, M., Chittka, L., Raine, N.E. & Kudo, G. (2011). Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. *Funct. Ecol.*, 25, 1284–1292.

Lima, S.L., Rattenborg, N.C., Lesku, J.A. & Amlaner, C.J. (2005). Sleeping under the risk of predation. *Anim. Behav.*, 70(4), 723–736.

March, D., Palmer, M., Alós, J., Grau, A. & Cardona, F. (2010). Short-term residence, home range size and diel patterns of the painted comber *Serranus scriba* in a temperate marine reserve. *Mar. Ecol. Prog. Ser.*, 400, 194–206.

McClintock, B., King, R., Thomas, L., Matthiopoulos, J., McConnell, B. & Morales, J.M. (2012). A general discrete-time modeling framework for animal movement using multistate random walks. *Ecol. Monogr.*, 82, 335–349.

McNamara, J.M. & Houston, A.I. (1987). Memory and the efficient use of information. *J. Theor. Biol.*, 125(4), 385–395.

Milinski, M. (1994). Long-term memory for food patches and implications for ideal free distributions in sticklebacks. *Ecology*, 75, 1150–1156.

Moorcroft, P. & Lewis, M.A. (2006). *Mechanistic Home Range Analysis*. Princeton University Press, Princeton, N.J.. 208 pp.

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. & Fryxell, J.M. (2004). Extracting more from relocation data: building movement models as mixtures of random walks. *Ecology*, 85, 2436–2445.

Mueller, T. & Fagan, W.F. (2008). Search and navigation in dynamic environments - from individual behaviors to population distributions. *Oikos*, 117, 654–664.

Mueller, T., Fagan, W.F. & Grimm, V. (2011a). Integrating individual search and navigation behaviors in mechanistic movement models. *Theor. Ecol.*, 4, 341–355.

Mueller, T., Olson, K.A., Dressler, G., Leimgruber, P., Fuller, T.K., Nicolson, C. *et al.* (2011b). How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Glob. Ecol. Biogeogr.*, 20(5), 683–694.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. *et al.* (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA*, 105, 19052–19059.

Noonburg, E.G., Newman, L.A., Lewis, M.A., Crabtree, R. & Potapov, A. (2007). Sequential decision-making in a variable environment: Modeling elk movement in Yellowstone National Park as a dynamic game. *Theor. Popul. Biol.*, 71, 182–195.

Normand, E. & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *For. Ecol. Manage.*, 77, 1195–1201. doi:10.1016/j.anbehav.2009.01.025.

O'Keefe, J. & Nadel, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford University Press, Oxford, UK.

Osborne, J. & Clark, S. (2001). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.*, 36, 519–533.

Papastamatiou, Y.P., Cartamil, D.P., Lowe, C.G., Meyer, C.G., Wetherbee, B.M. & Holland, K.N. (2011). Scales of orientation, directed walks and movement path structure in sharks. *J. Anim. Ecol.*, 80, 864–874.

Papastamatiou, Y.P., Meyer, C.G., Carlvaho, F., Dale, J.J., Hutchinson, M. & Holland, K.N. (2013). Telemetry and random walk models reveal complex patterns of partial migration in a marine predator. *Ecology*. In Press.

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends Ecol. Evol.*, 23(2), 87–94.

Paul, C., Magda, G. & Abel, S. (2009). Spatial memory: theoretical basis and comparative review on experimental methods in rodents. *Behav. Brain Res.*, 203, 151–164.

Perez, S.M., Taylor, O.R. & Jander, R. (1997). A sun compass in monarch butterflies. *Nature*, 387, 29.

Reid, C.R., Latty, T., Dussutour, A. & Beekman, M. (2012). Slime mold uses an externalized spatial "memory" to navigate in complex environments. *Proc. Natl. Acad. Sci. USA*, 109, 17490–17494.

Riotte-Lambert, L., Benhamou, S. & Chamaillé-Jammes, S. (2013). Periodicity analysis of movement recursions. *J. Theor. Biol.*, 317, 238–243.

Rosenzweig, M.L. (1981). A theory of habitat selection. *Ecology*, 62(2), 327–335.

Roth, T.C., Rattenborg, N.C. & Pravosudov, V.V. (2010). The ecological relevance of sleep: the trade-off between sleep, memory and energy conservation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 365(1542), 945–959.

Schacter, D.L. (1992). Priming and multiple memory systems: perceptual mechanisms of implicit memory. *J. Cogn. Neurosci.*, 4(3), 244–256.

van Schaik, C.P. (2010) Social learning and culture in animals. In: *Animal Behavior: Evolution and Mechanisms* (Ed. Kappeler, P.M.). Springer, Heidelberg, pp. 623–653.

Sih, A. & Del Giudice, M. (2012). Linking behavioral syndromes and cognition: a behavioral ecology perspective. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 2762–2672.

Slocum, T.A., McMaster, R.B., Kessler, F.C. & Howard, H.H. (2009). *Thematic Cartography and Geovisualization*. Pearson Prentice Hall, Upper Saddle River, NJ.

Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature*, 437(7063), 1272–1278.

Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C. *et al.* (2011). Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos*, 120(11), 1608–1617.

Sutherland, G.D. & Gass, C.L. (1995). Learning and remembering of spatial patterns by hummingbirds. *Anim. Behav.*, 50, 1273–1286.

Tang, W. & Bennett, D. (2010). Agent-based modeling of animal movement: a review. *Geography Compass*, 4(7), 682–700.

Tang, W. & Wang, S. (2009). HPABM: a hierarchical parallel simulation framework for spatially-explicit agent-based models. *Transactions in GIS*, 13(3), 315–333.

Thinus Blanc, C. (1996). *Animal Spatial Cognition: Behavioral and Brain Approach*. World Scientific Publishing, Singapore.

Tulving, E. (2000). *Concepts of memory*. The Oxford handbook of memory. New York, Oxford, pp. 33–44.

Van Gils, J.A. (2010). State-dependent Bayesian foraging on spatially autocorrelated food distributions. *Oikos*, 119, 237–244.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S. & Gaillard, J.-M. (2009). Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, 118(5), 641–652.

Von Frisch, K. (1967). *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA.

Wehner, R., Michel, B. & Antonsen, P. (1996). Visual navigation in insects: Coupling of egocentric and geocentric information. *J. Exp. Biol.*, 199, 129–140.

Weimerskirch, H., Pinaud, D., Pawlowski, F. & Bost, C.A. (2007). Does prey capture induce area restricted searching? A fine-scale study using GPS in a marine predator, the wandering albatross. *Am. Nat.*, 170, 734–743.

Wolf, M., Frair, J., Merrill, E. & Turchin, P. (2009). The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti *Cervus elaphus*. *Ecography*, 32, 401–410.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Jean Clobert
Manuscript received 20 June 2013
Manuscript accepted 12 July 2013