

## RESEARCH ARTICLE

### Primate Spatial Strategies and Cognition: Introduction to this Special Issue

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Wild primates face significant challenges associated with locating resources that involve learning through exploration, encoding, and recalling travel routes, orienting to single landmarks or landmark arrays, monitoring food availability, and applying spatial strategies that reduce effort and increase efficiency. These foraging decisions are likely to involve tradeoffs between traveling to nearby or distant feeding sites based on expectations of resource productivity, predation risk, the availability of other nearby feeding sites, and individual requirements associated with nutrient balancing. Socioecological factors that affect primate foraging decisions include feeding competition, intergroup encounters, mate defense, and opportunities for food sharing. The nine research papers in this Special Issue, “Primate Spatial Strategies and Cognition,” address a series of related questions examining how monkeys, apes, and humans encode, internally represent, and integrate spatial, temporal, and quantity information in efficiently locating and relocating productive feeding sites in both small-scale and large-scale space. The authors use a range of methods and approaches to study wild and captive primates, including computer and mathematical modeling, virtual reality, and detailed examinations of animal movement using GPS and GIS analyses to better understand primate cognitive ecology and species differences in decision-making. We conclude this Introduction by identifying a series of critical questions for future research designed to document species-specific differences in primate spatial cognition. *Am. J. Primatol.* 76:393–398, 2014. © 2014 Wiley Periodicals, Inc.

**Key words:** spatial memory; foraging; problem-solving; navigation; decision-making

#### INTRODUCTION

This Special Issue of the *American Journal of Primatology* is dedicated to the memory, intellectual contributions, and scholarly creativity of Dr. Emil W. Menzel, Jr, a pioneering figure in the study of primate spatial memory. Emil Menzel passed away on April 7, 2012. The goal of this special issue is to present and explore new theoretical perspectives and empirical data to better understand primate spatial memory, cognition, and decision-making, building on the intellectual foundation that Dr. Menzel established.

Compared to many other mammals, primates are characterized by relatively large brain size, particularly in the area of the prefrontal association cortex, and by functional changes in neural architecture and neural integration [Park & Friston, 2013; Rapoport, 1999] resulting in enhanced problem-solving skills and socio-cognitive complexity [Barrett et al., 2003; Barton, 2006; Goldman-Rakic, 2010; Rilling, 2006; Tomasello & Call, 1997]. A critical question in primate evolution is how do prosimians, monkeys, apes, and humans encode, internally represent, and integrate spatial, temporal and quantity information

in efficiently locating and relocating productive feeding sites [Garber et al., 2009; Janmaat et al., 2006, 2013]? Moreover, given differences in diet, home range size, group size, group cohesion, predation risk, and daily ranging patterns, it is likely that different primate species encounter foraging challenges that require alternative cognitive solutions and problem-solving skills [Barrett et al., 2003]. For example, a group of six pygmy marmosets (*Cebuella pygmaea*) that exploits a home range of less than 1 ha and concentrates its feeding efforts on a small number of exudate-producing trees is likely to face very different social and ecological challenges in locating and monitoring resources than a multilevel

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society of 100–200 golden snub-nosed monkeys (*Rhinopithecus roxellana*) that exploits tens of food patches in a single day and utilizes a home range of 2,000 ha [Qi et al., 2009].

Recent neurobiological studies indicate the existence of specialized cells in the primate hippocampus (border, head-direction, and place cells) and entorhinal cortex (EC) (grid cells) that encode spatial information with respect to an animal's movement, present location, and the direction of its or another animal's gaze [Arajo et al., 2001; Killian et al., 2012; Solstad et al., 2008; Whitlock et al., 2008]. The sequence, pattern, and intensity with which these cells fire enable primates to form a highly complex and detailed representation of their environment by identifying salient objects, locations, or environmental features as landmarks or spatial anchors whose positions are fixed relative to one another [Killian et al., 2012]. Grid cells, for example, are thought to create or overlay a regular metric framework upon a spatial representation and thereby enable a forager to update its location relative to other points encoded in a mental map [Fyhn et al., 2007; Killian et al., 2012; Solstad et al., 2008]. Moreover, given evidence that grid cells are stimulated even when monkeys view visual images on a screen, it appears that "spatial representation in primates can arise during visual exploration at a distance, without requiring an actual visit to that place" [Killian et al., 2012, p 763]. These data suggest that several brain regions (posterior parietal cortex, EC, and hippocampus) interact dynamically to enable an individual to locate, alter, and update its position, and chart a trajectory of travel relative to other encoded points within its environment [Whitlock et al., 2008]. In addition, new technologies such as the use of virtual reality and MRI [De Lillo et al., this issue; Dolins et al., this issue; Phillips & Thompson, 2013] offer opportunities to investigate these phenomena in multiple modalities through behavioral, cognitive, and neural correlates.

Our current understanding of primate spatial memory principally comes from studies of wild primates navigating in large-scale space or captive studies that examine cognitive capacities in small-scale space. Few studies have examined decision-making and foraging in the same species across both spatial scales [but see Garber & Porter, this issue; Schreier & Grove, this issue]. The degree to which primates use different spatial representations and landmark cues when navigating or orienting between large- and small-spatial scales remains unclear. In an effort to bridge this gap, this special issue aims to examine the ability of monkeys, apes, and humans to internally represent spatial information across a range of spatial scales and to compare species differences and flexibility in the types of information used and integrated in forming internal spatial representations across a range of foraging and social

challenges. Data presented focus on a diverse set of primate taxa and include research conducted in both wild and experimental settings.

We begin by offering a working definition of small-scale and large-scale space. Small-scale space and large-scale space are not defined by distance. Small-scale space is defined as the area in which a forager can obtain multiple views of the same set of salient points or places in their environment such as landmarks, topological features, and feeding sites from different directions and perspectives. For primates exploiting open terrestrial habitats, small-scale space could represent an area of over a 1 km<sup>2</sup>. For arboreal primates inhabiting dense evergreen forest, small-scale space could represent the area contained in a circle with a radius of only 10–30 m, with the canopy acting as a filter limiting the use of more distant visual cues. In the absence of this spatial information, the forager may not be able to compute a straight-line route of travel between out-of-view feeding sites. However, within both large- and small-scale space, primates are likely to maintain flexible spatial strategies that allow them to represent "place" in several ways. These may include a combination of ego-centric (relationship of self to object) and allocentric (relationship of object to object) spatial coding systems (frame of reference) [Dolins & Mitchell, 2010] including path integration, gauge distance by effort, and the ability to mentally rotate landmark arrays [Barton, 2006; Byrne, 2000; Dolins, 2009; Dolins & Mitchell, 2010; Garber & Brown, 2006; Garber & Porter, this issue].

In addition, it has been argued that several primate species encode spatial information in a topological or route-based mental map, which is associated with the ability of a forager to use and reuse a series of familiar travel routes (networks) and landmarks as orientation or switch points in order to navigate to and relocate feeding and resting sites. As suggested by Dolins & Mitchell [2010], within a route-based spatial framework foragers can generate novel routes of travel. These routes, however, are constrained by their proximity to familiar landmarks (switch points or nodes) and pre-established intersecting travel routes. Alternatively, animals may represent spatial information in the form of a coordinate-based mental map (a Euclidian map or a "view from above") in which the precise locations of salient features of the environment are encoded and recalled as *x* and *y* coordinates. Using such a system, animals are expected to compute relatively accurate distances and directions from their current location to their goal and travel using direct routes and novel short-cuts, even to goals that lie far outside their field of view. Evidence supporting a coordinate-based spatial representation in large-scale space has been reported for chimpanzees [Normand & Boesch, 2009] and humans [Spiers, 2012; but see Foo et al., 2005 for an alternative explanation]. It has been argued that

even if other primate species possess the cognitive abilities to compute coordinate-based spatial relationships in small-scale space, in the absence of obtaining the appropriate “views” needed to assign  $x$  and  $y$  coordinates to a given point, these same individuals are likely to form a route-based spatial representation in large scale space [Garber & Porter, this issue; Poucet, 1993]. Thus, primates may use multiple spatial strategies interchangeably and show considerable flexibility in associating spatial information with other forms of sensory input and cognitive search strategies.

In this Special Issue we feature articles that focus on several themes related to furthering our understanding of primate navigation and movement within small- and large-scale space and the types of representations primates generate in response to spatial scale and landmark arrays. Two key questions addressed are: (1) what topographical information present in the environment (e.g., landmarks or natural features) may trigger decisions associated with changes of travel direction within a local area and/or travel to a distant location, and (2) do primates employ different spatial strategies when navigating in small and large scale space? Specifically, a number of authors within this issue apply and test models of random movement and optimal search to examine primate travel and decision-making strategies. The comparisons of wild primate species’ movement patterns to models integrating spatial scale, local environmental features, and landmarks, with analyses of travel paths used during repeated visits to the same feeding site and to first-time feeding sites offer critical insight into how spatial and temporal information are internally represented and integrated during decision-making.

Noser & Byrne [this issue] examine the distribution of change points in the travel patterns of wild baboons (*Papio ursinus*) inhabiting a dry woodland savannah. Applying the Change Point Test [Byrne et al., 2009] to analyze movement patterns, the authors determined that a significant clustering of directional changes occurs at “nodes” associated with productive fruiting areas [also see Garber & Dolins, 2010; Garber & Porter, this issue]. One-third of the change-points were not associated with any discernible resources, however. In these cases, change-points were associated with prominent landmarks. The authors conclude that there is little evidence to support the contention that baboons use a Euclidean frame of reference in either small- or large-scale space. Instead, the data support the use of a route-based (network) map in which travel is re-oriented in relation to known landmarks and commonly used routes.

Janson’s paper [this issue] applies the Traveling Salesman Problem (TSP) to determine the degree to which wild primates plan a daily travel route. The TSP model assumes three processes, that subjects

have distinct memories for multiple food/goal locations, that they employ efficient paths between these locations (minimize distance and effort), and that they plan a multistep or daily travel itinerary in large-scale space.

Realistic limitations that affect the efficacy of the TSP model include tradeoffs between resource distribution and patch productivity, competition from neighboring troops or other species for valued resources, predation risk, and age, sex, or individual differences in nutritional requirements. In his paper, Janson used previously published data sets from multiple primate species in order to test the TSP model. He concludes that primates generally traveled to nearby areas that contained multiple high reward feeding sites using a two-step additive-gravity rule (although in some cases there was support for a three-step look-ahead rule) rather than planning a daily travel route that minimizes total distance traveled as suggested by the Traveling Salesmen model.

Garber & Porter’s paper [this issue] examined the foraging and spatial strategies of wild saddleback tamarins (*Saguinus fuscicollis weddelli*) in Bolivia. They present data on daily travel routes, direction of travel, circuitry index (CI: distance actually traveled/straight-line distance), and identification of switch-points (also referred to as “change-points” and “nodes” by other authors, this issue) to revisit feeding sites and experimental feeding platforms. They found that in both large- and small-scale space, saddleback tamarin foraging behavior was most consistent with route-based travel and attention to local landmarks. These authors also provide evidence that by not traveling in a straight-line to revisit nearby feeding sites, the tamarins were able to update ecological information on resource availability and distribution. Thus the costs of not taking the most efficient path appear to be offset by the benefits of using multiple spatial strategies and travel patterns to more effectively locate and monitor new feeding sites.

Schreier & Grove [this issue] focus on differences in spatial strategies used by hamadryas baboons (*Papio hamadryas*) when navigating in small- and large-scale space. These authors hypothesize that resource density and distribution affect primate foraging behavior and that when traveling between distant feeding sites a random search strategy is considerably less efficient than when searching for food items within a food patch that has a more uniform distribution of food. The authors applied a partial sum method and distribution-fitting analyses to identify patterns of area-restricted search from patterns of more variable movement. Using this approach there was evidence that the hamadryas baboons reused a set of travel routes to reach important feeding areas (large-scale space) and then altered their movement patterns at so-called “tipping points” or areas of their home range (small-scale space) characterized by high-density food

patches. These data are consistent with other articles in this volume indicating that primates employ multiple spatial strategies in locating feeding sites.

Articles by Shaffer [this issue] and Suarez et al. [this issue] share a related approach by comparing mathematical and computer-generated models of movement to actual observations of monkeys' travel patterns. Shaffer compares the movement patterns of wild bearded sakis (*Chiropotes sagulatus*) to that of Brownian random walks (measured in "step lengths" that reflect an exponential probability distribution) and Lévy walk patterns (also a random walk analysis, measured in "step lengths" and "waiting times," and alternates between intensive (small step) and extensive search modes (large step)). In examining patch use and patch quality, distance traveled between patches, step-lengths, waiting times, turning angles, and instances of straight-line travel between feeding patches compared to alternative routes algorithmically generated, Shaffer found that bearded sakis used relatively straight-line travel paths when moving between distant feeding sites. The analysis of step lengths fit a Brownian walk pattern, while waiting times were better suited to a Levy walk pattern. Shaffer concludes that bearded sakis encoded spatial and ecological information regarding the location and availability of high quality food patches to navigate between patchily distributed feeding sites. The sakis traveled directly to targeted areas of high quality food, minimizing distance, while opportunistically feeding from lower quality food patches encountered on route.

Suarez et al. [this issue] compared the travel patterns of wild spider monkeys (*Ateles belzebuth*) with a modified random-walk model (which alternates 100-m steps with turn angles) and a route-based model of navigation using a computer-simulated data set. The goal of this research was to test the hypothesis that in large-scale space, a route-based navigation strategy would be more efficient than a random-walk strategy. Their results indicated that the travel patterns of wild spider monkeys were more efficient than either a random-walk or a route-based simulation model, with the simulated route-based monkeys outperforming the random-walk modeled monkeys. Overall, the authors found that wild spider monkeys encoded and integrated ecological information on patch size and patch quality with the spatial locations of familiar travel routes to encounter feeding sites.

De Lillo et al. [this issue] and Dolins et al. [this issue] both employed a novel methodology, virtual reality (VR), to investigate spatial patterns of movement within simulated environments containing landmarks and variable resource distributions. Using virtual reality allows for a controlled investigation of an individual's attention to specific landmarks, travel trajectories, and the distribution of food items to attain a specific goal. In three experiments,

De Lillo et al. compared adult humans' search organization within and between feeding sites to examine perceptual grouping processes (e.g., chunking) that underlie efficient foraging behavior and serial spatial recall. This is particularly interesting when subjects do not have an overview of a defined space but are limited to the structural spatial information at "eye-height" with minimal perceptual access to what lays beyond, except through navigation during exploration. In De Lillo et al.'s first experiment, participants explored an immersive search space (virtual foraging task) containing multiple locations based on two geometric arrangements that maintained a constant spatial relationship, either a cluster or a square matrix. The results showed that humans organized their exploratory trajectories in a way that reduced requirements for recall while maintaining efficiency of the foraging task. The second experiment made use of the Immediate Serial Spatial Recall (ISSR) task, which is a computerized version of the Corsi task. In this paradigm, identical icons are present, flashing in different colors to create patterns and identify locations. The participants are required to repeat the pattern from memory in a recall phase. The results indicate that providing a perceptual overview of the spatial configuration of the search space enhances the participants' ability to explore and recall that search space. In the third experiment, the size and distance between foraging sites (presenting both clustered and square matrix configurations) were made variable in order to test for recall of the order in which these sites had been explored. The results of this experiment indicated that participants' recall was better for structured space rather than unstructured space, regardless of path length.

Dolins et al. [this issue] compared adult chimpanzees' and humans' of four age groups (younger children (3–4 and 5–6 year olds), older children (11–12 year olds) and adults) efficiency of travel in increasingly complex virtual (VR) environments simulating small- and large-scale spatial challenges. The spatial task required participants to navigate using a joystick while attending to spatial information (landmarks, structure of the environment, orientation) required to localize the goal site. The VR environments increased in size and complexity from open space (small-scale) environments (1-barrier and 2-barrier) where participants could obtain a partial overview, to large-scale environments where participants' view was blocked by the structure of the environment. The results indicated that both species and all age groups displayed a clear ability to effectively discriminate between the positive ("proceed") and negative ("don't proceed") landmarks. The assessment of path efficiency revealed that both species and all age groups used relatively efficient, distance reducing paths in both small- and large-scale environments. Comparing performance across

all participant groups, the chimpanzees' performance was similar to that of the younger children (both 3–4 and 5–6 year olds). There were differences, however, between the chimpanzees and humans, and between the age groups of humans tested. Compared to the chimpanzees and adult humans, the younger children's (3–4 and 5–6 year olds) performance decreased as maze complexity and environment size increased. Young children, compared to the adult chimpanzees, adult humans, and the older children (11–12 year olds), showed greater deviation from optimal routes when navigating in more complex mazes (e.g., 2T- and 3T-mazes and 2-barrier environment compared to the 1T-maze and 1-barrier environment).

Mendes & Call [Mendes and Call, 2013] this issue] experimentally examined short-term and long-term memory in captive chimpanzees to determine their capacity and accuracy in retaining spatial and temporal information needed to relocate feeding sites. In this study, the chimpanzees, after minimal exposure to being fed at four specific locations, were tested in pairs on their ability to recall these food locations after 24 hours, after 4 days, and after a period of three months. The chimpanzees displayed accurate recall for the locations in which they previously found food during each of these distinct time intervals. This study adds to the growing body of literature on nonhuman primate spatial and temporal short- and long-term memory [e.g., Clayton et al., 2003; Dolins, 2009; Garber & Paciulli, 1997; Janmaat et al., 2006; Janson, 1998; Menzel, 2010] and provides significant insight into the cognitive capacity with which primates attend, encode and recall ecological information.

We end by presenting a series of research questions that are discussed in this special issue and are critical to the study of primate spatial cognition. These include:

1. Do primates represent spatial information differently in large- and small-scale space?
2. To what degree does the physical structure of the local environment, resource density, canopy openness, and forest phenology influence how an individual or species internally represents spatial information?
3. Do primates plan sequential or daily foraging routes in an attempt to maximize the efficiency of travel relative to their resource needs?
4. Is the ability of some primate species to solve the Traveling Salesperson Problem in captivity an artifact of small-scale space and experimental design?
5. Given that resources vary in quality, quantity, nutrient content, proximity, visibility, and ease of acquisition, do primates prioritize foods based on some measure of expected value, and visit feeding sites according to their rank in priority rather than based on the distance between feeding sites?
6. Do primates adjust their travel strategies and foraging routes in order to monitor and track fruit production in their home range, and to take advantage of individual tree species fruiting patterns to predict the availability of new feeding sites?
7. Do primates pay attention to the vocal signals or nearby presence of neighboring groups and does this affect the focal groups foraging decisions and ranging patterns?
8. Does virtual reality allow us to address difficult but ecologically valid questions that cannot be easily answered from studies of wild and captive populations of primates, such as comparing spatial strategies in small- and large-scale space, comparing net gains from selecting different paths to foraging sites that vary in productivity, and/or varying the number, type, and configuration of landmarks presented?
9. Should virtual environments presented to captive primates incorporate ecological variables that more closely simulate natural environments such as bird and other primate vocalizations, direction of the sun as it moves throughout the day, wind currents, and predator sightings?
10. How can we best use virtual reality and GPS/GIS technology and analyses to address new research questions regarding changes in foraging strategies and spatial cognition under different social and ecological constraints and information sets?

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