

REVIEW

Spatial mapping memory: methods used to determine the existence and type of cognitive maps in arboreal mammals

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ABSTRACT

1. Researchers have used multiple methods to understand spatial mapping memory used by arboreal mammals for orientation: the change-point test, measures of path tortuosity, field experiments with feeding platforms, nearest-neighbour feeding tree methods, complex calculations of travel route parameters, and theoretical models.
2. This literature review provides details of all of these methods, highlights previous results from spatial mapping memory studies, and discusses perspectives for future studies.
3. Previous studies have shown that various arboreal mammals, mostly in the order Primates, can memorise spatial environments using a cognitive map. Two types of maps are characterised: the topological map, based on landmarks and reused routes, and the Euclidean map, including the ability to create shortcuts by measuring distances and distinguishing between directions. Most of the studies showed that mammals do not travel randomly but, due to the difficulty of determining which spatial map is used, the use of cognitive maps remains hypothetical.
4. When studying spatial mapping memory, data collection and analysis should account for the species' characteristics, such as the home-range size, food preferences, and types of movements. The role of sensory cues (visual, auditory, olfactory) is crucial to understanding spatial orientation. The most relevant way to determine how arboreal mammals orientate themselves in space is by using a mix of methods: random theoretical models, collecting data in a controlled environment, measuring different parameters of travel patterns, and considering the use of sensory cues and environmental factors of the study sites.
5. Research pertaining to spatial mapping memory in arboreal mammals and forest-dwelling mammals is important for understanding cognitive abilities in mammal species, and more studies are needed in mammals of various orders.

Mots clés

carte cognitive, écologie du mouvement, mammifères arboricoles, mémoire spatiale, navigation dans l'espace, orientation, Primates

RÉSUMÉ EN FRANÇAIS

1. La communauté scientifique s'est servie de multiples méthodes afin de comprendre la mémoire spatiale utilisée dans l'orientation des mammifères arboricoles: le «change-point test», des mesures de linéarité de trajets pris par les individus étudiés, des expériences sur le terrain utilisant des plateformes approvisionnées en nourriture, la mesure des arbres les plus proches autour

- du site de nourriture, des calculs complexes sur les paramètres des trajets, et des modèles théoriques.
2. Cette revue présente toutes ces méthodes, expose les résultats des études précédentes sur la mémoire spatiale et propose des pistes de recherche pour les études futures.
 3. Les études précédentes ont montré que les mammifères arboricoles, en particulier chez les Primates, peuvent mémoriser leur environnement en utilisant une carte cognitive. Deux types de cartes ont été caractérisés : la carte topologique, basée sur des points de repères et sur la réutilisation de certaines routes, et la carte Euclidienne, permettant la création de raccourcis et la mesure de distances ainsi que la distinction de directions. La plupart des études ont montré que les mammifères ne s'orientent pas de façon aléatoire, mais due à la difficulté à déterminer le type de carte cognitive utilisée, l'utilisation de celles-ci ne reste encore qu'une hypothèse.
 4. L'étude de la mémoire spatiale doit prendre en compte dans la collecte et dans l'analyse de données les caractéristiques des espèces étudiées comme la taille du territoire, le type de nourriture consommée et le type de locomotion utilisé par l'espèce. Le rôle des indices sensoriels (visuel, auditif et olfactif) est crucial pour comprendre l'orientation spatiale. La façon la plus appropriée pour déterminer comment les mammifères arboricoles s'orientent dans l'espace est d'utiliser plusieurs méthodes pour une même étude : des modèles théoriques aléatoires, collecter des données dans un environnement contrôlé, mesurer différents paramètres de trajets et considérer l'utilisation d'indices sensoriels ainsi que les facteurs environnementaux du site d'étude.
 5. La recherche se focalisant sur la mémoire spatiale chez les mammifères arboricoles et les mammifères vivant en forêt tropicale est importante pour comprendre les capacités cognitives des différentes espèces de mammifères, plus d'études sont nécessaires chez les mammifères incluant différents ordres.

INTRODUCTION

Animal movements are involved in important needs such as food acquisition, travel to sleeping and reproduction sites, and escape from predators. Consequently, many animal species demonstrate capacities to move efficiently in their environment and save time and energy. Several approaches using mathematical models have been developed to study animal movements (Gurarie et al. 2009, 2016). These methods allow researchers to describe movements, by identification and quantification of the structure of the movement path (a.k.a exploratory analysis; Gurarie et al. 2016), but it remains difficult to identify the behavioural mechanisms and cognitive processes that underlie observed movement patterns.

To travel among different feeding, sleeping, or important sites, animals can use sensory cues such as odours or sight (Nevo & Heymann 2015). However, using only sensory cues for orientation and navigation appears challenging, especially in environments with dense vegetation. For

example, canopy density in tropical forests reduces visibility for diurnal arboreal apes foraging on fruits (visibility estimated at only 21 m; Joly & Zimmermann 2011). The ability to remember important locations and efficient paths is advantageous in environments where sensory cues cannot be used exclusively. Therefore, memory is one of many cognitive and information-use processes involved in movement, orientation, and navigation.

It is suggested that some species living in a complex environment create a cognitive map that allows them to orientate themselves within a certain space (Poucet 1993). The existing literature describes the concept of a cognitive map with different definitions, sometimes contradictory or imprecise (Bennett 1996, Trapanese et al. 2018). A cognitive map has been defined as “an internal representation (or image) of an external environmental feature or landmark” (Tolman 1948), as “the representation of a group of places, some related to others by means of a set of rules of spatial transformation” (O'Keefe & Nadel 1978), but also as “a representation of (at least some) geometric relationships

among a home site, terrain surrounding the home site, goals to be visited and the terrain surrounding those goals – a representation used for navigation” (Gallistel & Cramer 1996). In this review, the term cognitive map refers to a mental representation of the physical environment allowing the acquisition, storage, and decoding of spatial, temporal, and ecological information.

Two types of cognitive maps have been proposed that explain the possible spatial strategies used by non-human primates for moving between distant sites: the topological map (a.k.a. network map, route-based mental map; Byrne 2000, Di Fiore & Suarez 2007) and the Euclidean map (a.k.a. mental map, vector map, coordinate-based mental map; Poucet 1993, Normand & Boesch 2009). The topological map is a representation of a space based on key locations and using familiar landmarks and travel routes. Novel travel paths can be generated, but they will always be close to landmarks and familiar routes (Dolins & Mitchell 2010). Alternatively, a Euclidean map includes an internal representation, allowing the use of direct routes and novel paths. The Euclidean map allows individuals to compute distances and directions from any location and to create shortcuts (O’Keefe & Nadel 1978). As a Euclidean map is more flexible than the topological map, an animal using a Euclidean map rarely uses the same travel paths and does not abide by a specific set of landmarks (Normand & Boesch 2009). However, the use of repeated routes is not necessarily evidence that an animal lacks a Euclidean map and navigates only by using a topological map (Presotto & Izar 2010).

Spatial mapping memory refers to the memory responsible for the recording of information about one’s environment and spatial orientation using cognitive maps. Understanding cognition-based movements in relation to dynamic environments and resources, and the role of memory in animal movement, will provide a deeper understanding of animal space-use patterns and their responses to environmental change (Fagan et al. 2013, Schlägel et al. 2017).

Tropical forests are complex environments with an unpredictable distribution of resources and exceptional biodiversity of plant and animal species. Terrestrial species have a larger choice of paths that can be used to travel from one spot to another than arboreal species, which are constrained by the availability and resistance of branches and trees; this is even more true for species with restricted movement abilities such as moving by hanging (e.g. sloths, Folivora). Arboreal foraging proves to be difficult, as food spots are distributed within large areas (relative to the species’ body size), sometimes over hundreds of hectares (Di Fiore & Suarez 2007, Suarez et al. 2014).

Numerous studies have been focused on how arboreal mammals, mostly primates, orientate themselves within space, but a limited number of investigations have been conducted

on the type of cognitive map used by specific species (Table 1). In this literature review, we present and discuss the different spatial mapping memory methods utilised by researchers to understand and define the types of cognitive maps used by various arboreal mammal species.

METHODS

A detailed search of publications relating to spatial mapping memory in arboreal mammals was undertaken using the website Google Scholar. Data search was conducted using the keyword combinations of “spatial mapping,” “spatial mapping memory,” “spatial navigation,” “Euclidean map,” “route-based mental map” OR “topological map” AND “arboreal mammals,” “arboreal species” OR “Primates.” After a first overview of the knowledge about spatial mapping in arboreal mammals, more specific combinations were used: “Change Point Test method,” “Circuitry Index” OR “Nearest-Neighbour method” (referring to the methods used by researchers and described in this review) AND “spatial mapping,” “spatial mapping memory” OR “spatial navigation” AND “arboreal mammals,” “arboreal species” OR “Primates.” Afterwards, more articles were selected by reviewing author bibliographies and reference lists of the articles of interest.

One main limitation of the data search was the taxonomy of the study species. The studies we found on spatial mapping memory in arboreal species were focused on the order Primates, though many other arboreal mammal species may use spatial mapping memory. Studies on spatial mapping memory in arboreal mammals are focused on primates, because they are known to have highly developed cognitive abilities. Additionally, they usually occupy large home ranges and travel long distances every day to reach goals such as food and sleeping sites, which make them ideal subjects for investigating spatial cognition (Byrne 2000, Janson & Byrne 2007).

RESULTS: METHODS USED TO STUDY SPATIAL MAPPING MEMORY IN ARBOREAL MAMMALS

Twenty-six studies were analysed, dating from 1989 to 2019 and including information from 18 species of arboreal mammals, all in the order Primates. Table 1 details the species and the six different methods used to study spatial mapping memory in these arboreal mammals: 1) the change-point test; 2) the measure of path tortuosity (Circuitry Index, CI); 3) field experiments with feeding platforms; 4) the nearest-neighbour feeding tree method; 5) route analysis; and 6) theoretical models. The results of these studies and the type of mapping identified in them are also described.

Table 1. Studies on spatial orientation and navigation conducted in 18 species of arboreal mammals, all primates, the type of cognitive mapping identified, and methods used to study spatial mapping memory

Species	Methods used to study spatial mapping memory	Type of mapping	Exclusion of sensory cues?	Number of individuals tested	Home-range size	References
Grey mouse lemur <i>Microcebus murinus</i>	Circuitry Index + field experiment with feeding platforms + Theoretical model (random walk model)	Topological map	Olfactory: change of baiting patterns	8 individuals: 2 females and 6 males	1–2 ha (Garbutt 2007)	Lührs et al. (2009)
Red-fronted lemur <i>Eulemur rufus</i>	Change-point test + Theoretical model (heuristic random travel model)	Undetermined	Visual: assumption of visibility range	7 individuals (only females)	1–2 ha (Garbutt 2007)	Joly and Zimmermann (2011)
	Measure of path tortuosity + nearest-neighbour feeding tree method	Topological map suggested	Visual: assumption of visibility range	2 groups: group 1: 6 individuals (1 male, 3 females, 2 juveniles) and group 2: 4 individuals (3 males and 1 female)	<100 ha	Erhart and Overdorff (2008)
Silvery woolly monkey <i>Lagothrix poeppigii</i>	Route analysis (representation of daily path in Arcview and calculations)	Topological map	No	18–25 individuals	110–1000 ha	Di Fiore and Suarez (2007)
Mantled howler <i>Alouatta palliata</i>	Behavioural data + Circuitry Index	Topological map	No, but possibility of visual cues suggested	26–29 individuals including 10 adult females and 12 adult males	3.9 ha	Garber and Jelinek (2005)
	Direct observations + theoretical models	Use of spatial memory	Visual: assumption of visibility range	18 individuals	44 ha	Hopkins (2015)
Guatemalan black howler <i>Alouatta pigra</i>	Map of travel paths + theoretical models (linear mixed models)	Topological map	Visual: creation of buffers every 5 m from the centre of each quadrat of the travel routes up to 35 m (assumed visibility range)	5 groups varying from 3–4 to 7–9 individuals per group	7.1–15.3 ha	Guinea et al. (2019)
Milne-Edwards's sifaka <i>Propithecus edwardsi</i>	Measure of path tortuosity + nearest-neighbour feeding tree method	Topological map suggested	Visual: assumption of visibility range	7 individuals: 4 males, 2 females, 1 juvenile	56 ha	Erhart and Overdorff (2008)
White-faced saki <i>Pithecia pithecia</i>	Direct observations + theoretical models (step model and geometric model)	Use of spatial memory, Euclidean map suggested	Visual: assumption of visibility range. Olfactory: fruits not smelly. Auditory: assumption that the presence of other individuals is not involved in orientation	6 individuals: 2 adult males, 2 adult females, 1 subadult female and 1 juvenile male	12.8 ha	Cunningham and Janson (2007)

(Continues)

Table 1. (Continued)

Species	Methods used to study spatial mapping memory	Type of mapping	Exclusion of sensory cues?	Number of individuals tested	Home-range size	References
Red-backed bearded saki <i>Chiropotes chiropotes</i>	Route analysis (representation of travel paths and calculations) + Theoretical model (random walk model)	Goal-directed travel with distance-minimising movements between high-quality food patches	No	38 ± 15 individuals	Not specified	Shaffer (2013)
White-headed capuchin <i>Cebus capucinus</i>	Field experiment with feeding platforms	Topological map	Visual: platform baiting with plastic bananas Olfactory: platform baiting with banana skins	10–12 individuals	20 ha	Garber and Paciulli (1997)
Brown capuchin <i>Cebus apella</i>	Circuitry Index + field experiment with feeding platforms + Theoretical models (step model and geometric model)	Straight-line movement and a preference for closer feeding sites, use of spatial memory suggested	Visual: implementation of a new feeding platform to determine visual detection field (41 m). Olfactory: method of providing fruits reduced possible long-distance cues of fresh fruit odours	15 individuals: 3 adult males, 5 adult females, 5 juveniles, and 2 infants	Not specified	Janson (1998)
	Field experiment with feeding platforms	Undetermined	No	2–3 adult males, 1–2 subadult males, 6–14 adult females, and 15–22 juveniles and infants	Not specified	Janson (2007)
Black capuchin <i>Cebus nigrinus</i>	Route analysis (representation of daily path and calculations) + Theoretical model (three-dimensional model)	Use of both topological and Euclidean map suggested	Visual: line-of-sight analysis	14 individuals: 2 adult males, 3 females, 3 infants, and 6 juveniles	400 ha (2006–2008)	Presotto and Izar (2010)
Black-striped capuchin <i>Cebus libidinosus</i>	Change-point test + Theoretical model (resistance model)	Undetermined. Travel in zones with low landscape resistance	Auditory: call-back technique	8 individuals	Not specified (approximation using the figures: 12–56 ha)	Howard et al. (2015)
	Change-point test	Topological map	Visual: line-of-sight analysis	17 individuals: 2 adult males, 2 subadult males, 3 adult females, 1 subadult female, 4 juveniles, 5 infants	354 ha	Presotto et al. (2018)
Lar gibbon <i>Hylobates lar</i>	Change-point test + theoretical model (heuristic random travel model)	Undetermined, Euclidean and topological maps suggested	Visual: assumption of visibility range	11 groups from 3 to 6 individuals each	13–27 ha	Asensio et al. (2011)

(Continues)

Table 1. (Continued)

Species	Methods used to study spatial mapping memory	Type of mapping	Exclusion of sensory cues?	Number of individuals tested	Home-range size	References
Moustached tamarin <i>Saguinus mystax</i>	Nearest-neighbour feeding tree method	Undetermined, goal-oriented foraging and ability to compare distances and directions	Olfactory: examining the patterned use of specific pathways and new routes taken to important feeding sites	13 individuals: 7 adults, 2 subadults, 2 juveniles, and 2 infants	40 ha	Garber (1989)
	Circuitry Index + theoretical models	Undetermined, use of spatial map and olfactory cues suggested	Olfactory: creation of a model	Unknown	40 ha	Garber and Hannon (1993)
Brown-mantled tamarin <i>Saguinus fuscicollis</i>	Nearest-neighbour feeding tree method	Undetermined, goal-oriented foraging and ability to compare distances and directions	Olfactory: examining the patterned use of specific pathways and new routes taken to important feeding sites	9 individuals: 6 adults, 1 juvenile, and 2 infants	40 ha	Garber (1989)
	Circuitry Index + theoretical models	Undetermined, use of spatial map and olfactory cues suggested	Olfactory: creation of a model	Unknown	40 ha	Garber and Hannon (1993)
	Circuitry Index + field experiments with feeding platforms	Topological map	Visual: assumption of visibility in a straight line	4–5 individuals	35.5 ha (in 2009) and 28.8 ha (in 2011)	Garber and Porter (2013)
Weddell's brown-mantled tamarin <i>Saguinus fuscicollis weddelli</i>	Circuitry Index	Topological map	No	5 individuals: 1 adult female, 3 adult males and 1 juvenile	25.5–35.5 ha	Porter and Garber (2012)
White-fronted spider monkey <i>Ateles belzebuth</i>	Route analysis (representation of daily path in Arcview and calculations)	Topological map	No	Group 1: 3 females/ Group 2: 23 individuals	100–400 ha (300 ha and 266 ha in that study)	Di Fiore and Suarez (2007)
	Circuitry Index + theoretical models (comparison of two variations of computer simulated null models with observed foraging behaviour)	Undetermined, goal-oriented foraging	No	3 individuals (females) from a community of 16 individuals	300 ha	Suarez et al. (2014)
Geoffroy's spider monkey <i>Ateles geoffroyi yucatanensis</i>	Direct observations + Circuitry Index + route analysis (GPS mapping and calculations of diverse characteristics of the travel paths)	Use of spatial memory and straight-line travel, change of direction	Visual: visibility not possible because resource far away	11 individuals (+9 babies or juveniles)	155 ha	Valero and Byrne (2007)

The change-point test

The change-point test (CPT) is a mathematical equation created by Byrne et al. (2009) and used to identify changes of direction independently of the possible reasons for the changes. This method requires an accurate travel path of the animal to be known and represented by using a series of waypoints. The CPT is applied to daily travel paths by calculating travel segments starting from the last resource (i.e. food source, duet site, resting site or intergroup encounter site) until a change point is discovered. These short linear segments are considered as vectors (Byrne et al. 2009). Then, the CPT is applied with this new location (the change point) as a starting point until the next change point is determined and so on, until no further change points are detected for a daily path.

Figure 1 explains how change points are detected using the CPT. By using vector collinearity, the CPT determines the occurrence of significant changes of direction of q vectors (change points). Although this method allows the detection of change points, genuine change points can be missed, especially for small values of k . In addition, the number q of vectors impacts the test's sensitivity: for a small value of q , a change point is almost undetectable, but running the test with a high value of q (a large set of vectors) can also cause a decrease in detection of change points because the corresponding segments are likely to include more and conflicting directional changes, resulting in a decrease of the test's sensitivity. Therefore, an intermediate q seems to be most suitable to keep a balance

between sensitivity and precision (Byrne et al. 2009). Additionally, the choice of the most adapted significance level α implies a trade-off between statistical robustness of the results and the number of locations identified as change points (Byrne et al. 2009). Thus, the choice of q and α is crucial for the interpretation of the results and should be considered carefully according to what the researchers want to investigate, and the scale and pattern of travel of the particular species under study (Byrne et al. 2009).

Byrne et al. (2009) studied changes of direction in synthetic data and data from two terrestrial mammals, chacma baboons *Papio ursinus* and common chimpanzees *Pan troglodytes*. Their analysis demonstrated that the CPT successfully detected change points and allowed interpretations of the results about travel patterns in these two species. By choosing species whose ranging varies in several ways, due to travel constraints about sleeping sites, spatial distribution, habitat, and foraging configurations, Byrne et al. (2009) created an approach to study route patterns that can be applied to a wide range of species. Consequently, the CPT method has been applied to the study of spatial orientation in arboreal mammals (Asensio et al. 2011, Joly & Zimmermann 2011, Howard et al. 2015, Presotto et al. 2018).

Asensio et al. (2011) showed that lar gibbons *Hylobates lar* travel in a goal-oriented manner (compared with a heuristic travel model based on straight travel paths in random directions), and change direction primarily at preferred fruit sources. Joly and Zimmermann (2011) showed that grey mouse lemurs *Microcebus murinus* do not forage

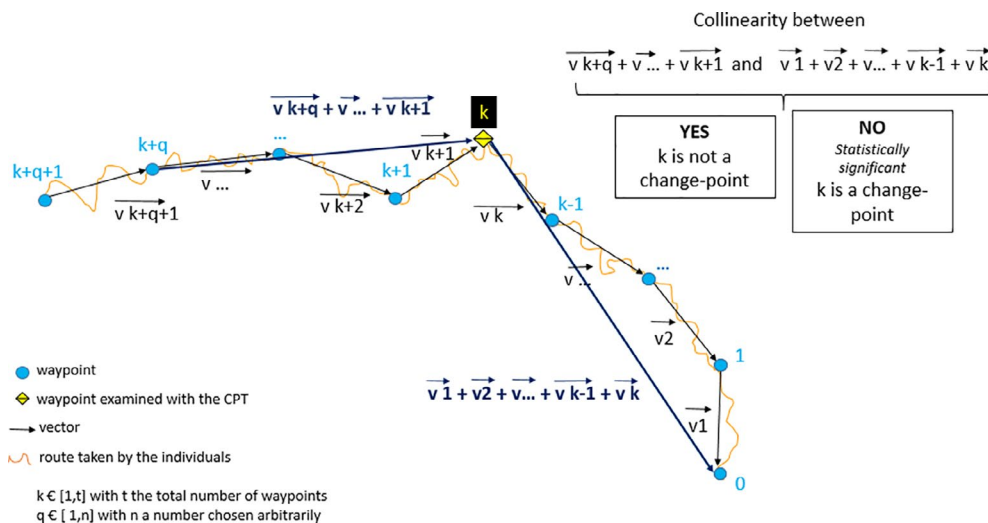


Fig. 1. Schema of the method used to detect a change point with the change-point test (CPT). Each time it is applied, the CPT compares a set of vectors on one side of a possible change point k with a set of vectors on the other. The vector v_1 leads to the potential goal location, v_2 leads to v_1 , and so on. Similarly, the q vectors describe travel before the potential change point and are labelled v_{k+1}, \dots, v_{k+q} , with v_{k+1} leading to the putative change point, v_{k+2} leading to v_{k+1} , and so on. If the two resulting vectors $v_k + \dots + v_1$ and $v_{k+q} + \dots + v_{k+1}$ are found to be significantly collinear, a change point is identified and the test is applied again at the next point, working backwards along the travel path (Byrne et al. 2009).

in random directions, since the individuals are more efficient at detecting resources than expected from a heuristic random travel model. Results negated the hypothesis that lar gibbons and grey mouse lemurs use exclusively visual cues to orientate themselves and forage (Asensio et al. 2011, Joly & Zimmermann 2011). Howard et al. (2015) and Presotto et al. (2018) used the CPT to evaluate travel paths in black-striped capuchins *Cebus libidinosus*. Howard et al. (2015) considered landscape features by combining the landscape of the monkeys' home range from satellite imagery with point data on the monkeys' patterns of movement. The results showed that the natural monkey's empirical travel path was the most similar to the straight-line path model in its landscape resistance (the inverse of habitat suitability), but not in its geometry.

All four studies identified change points as key locations in spatial orientation by their study species, and the results from the CPT coincided with the conclusions of Byrne et al. (2009) about the test (Table 2).

The preliminary results of Byrne et al. (2009) about the choice of q coincide with the results of the other studies: the optimal q is an intermediate value among the variants of the test. All studies found a trade-off between the robustness of the test and the number of change points by taking a level of significance between 0.01 and 0.05 (Table 2). As suggested by Byrne et al. (2009), the CPT can be applied to species of mammals with different ecological characteristics.

The CPT is a useful tool to determine locations where the studied animals reorient themselves. However, this method does not identify the cause of the route deviation. There may be numerous reasons for a change of direction that are not goal-oriented, such as social factors (e.g. presence of a predator, competitors) or ecological factors (e.g. physical barrier). Considering this, the results obtained by the CPT should not be interpreted independently, but should be combined with behavioural observations and ecological data.

Another method has been used by researchers to detect change points in animal movements. Gurarie et al. (2009) created a robust and efficient method allowing the

identification and characterisation of significant behavioural shifts based on movement data, named behavioural change-point analysis. The method consists of the transformation of step lengths and turning angles into orthogonal persistence and turning components of velocity, and then, these parameters are characterised as continuous autocorrelated time series described by a mean, a variance, and a continuous autocorrelation. Moments where the parameters' values change significantly can be identified and correspond to a change of behaviour. This method allows the identification of change points in movement data with temporal gaps and heterogeneous behaviours, and without any prior assumptions (Gurarie et al. 2009, 2016). However, to our knowledge, this method has not been used yet to study movements in arboreal mammals.

Measure of path tortuosity

The degree of path tortuosity estimates the efficiency of an animal to reach a spot of interest (e.g. a feeding spot), whether or not the animal travels towards a known goal (Beisner & Isbell 2009). Different metrics can be measured to characterise the tortuosity of an animal's path: a straightness index (a.k.a. linearity ratio, used by Valero & Byrne 2007) corresponding to the ratio of the straight-line distance to the distance of the studied trajectory and used when the animal performs an oriented movement; a sinuosity index (introduced by Bovet & Benhamou 1988) used for random search movements and combining the mean cosine of changes of direction with the mean step length of a trajectory; and fractal dimensions (Benhamou 2004, Seidel et al. 2018).

Studies focusing on movement ecology in arboreal mammals used the Circuitry Index (CI) which corresponds to one divided by the straightness index. To be coherent with the described studies, we use the term Circuitry Index in this review. The CI is the path length of an individual divided by the straight-line distance of the path. It was first used by Garber and Hannon (1993) to study foraging patterns in moustached tamarins *Saguinus mystax* and brown-mantled tamarins *Saguinus fuscicollis*. Multiple

Table 2. Change-point tests: choices of the level of significance (α), the number of variants of the test (q), and the optimal value of q in studies of spatial orientation in arboreal mammals using the change-point test

Species	Level of significance α	Number of variants of the test q	Optimal value of q	References
Chacma baboon <i>Papio ursinus</i>	0.01	1–10	6	Byrne et al. (2009)
Common chimpanzee <i>Pan troglodytes</i>	0.05	1–6	4	Byrne et al. (2009)
Lar gibbon <i>Hylobates lar</i>	0.01	1–8	6	Asensio et al. (2011)
Grey mouse lemur <i>Microcebus murinus</i>	0.05	1–6	5	Joly and Zimmermann (2011)
Black-striped capuchin <i>Cebus libidinosus</i>	0.01	1–10	5	Howard et al. (2015)
Black-striped capuchin <i>Cebus libidinosus</i>	0.05	4–8	4	Presotto et al. (2018)

studies on spatial mapping memory in arboreal mammals included CI calculations in their analysis (Table 3).

Porter and Garber (2012) formulated three hypotheses about spatial orientation, as summarised in Fig. 2. In their study, CI values did not get lower over time when the monkeys were frequently visiting the same sites, and the individuals did not take novel shortcuts to reach feeding sites. According to the hypotheses formulated previously, the brown-mantled tamarins did not use a Euclidean map but a topological map to navigate in the forest.

While the studies of Porter and Garber (2012) and Garber and Porter (2013) suggest that brown-mantled tamarins do not travel in straight lines between feeding sites (CI between 1.25 and 1.47), Garber and Hannon (1993) suggested that moustached tamarins and brown-mantled tamarins travelled in relatively straight lines (CI = 1.19). These contradictory results question the ability of tamarins to travel directly to their goals and the interpretation of the CI. None of the studies states a threshold value for CI, below which travel is considered to be direct (straight line). Also, straight-line travel might be used in specific conditions, in terms of landscape features for example, but evidence of non-direct travel does not exclude

the ability to use straight-line travel in any given species. More comparative studies should be conducted to investigate this last point.

Field experiments with feeding platforms

Numerous researchers implemented feeding platforms in the home ranges of their study animals, to investigate spatial mapping memory in arboreal mammals (Garber & Paciulli 1997, Janson 1998, Lührs et al. 2009, Garber & Porter 2013). They used direct modification of feeding sites by installing feeding platforms and by controlling the food available on these platforms. Garber and Paciulli (1997) and Lührs et al. (2009) tested the ability of white-headed capuchins *Cebus capucinus* and grey mouse lemurs *Microcebus murinus*, respectively, to use visual and olfactory cues, spatial information, and their ability to have expectations about the amount of food at a given feeding site. The experiments conducted by Garber and Paciulli (1997) are summarised in Appendix S1. Both studies (Garber & Paciulli 1997, Lührs et al. 2009) revealed that the movements of white-headed capuchins and grey mouse lemurs were not random but goal-directed and flexible.

Table 3. Results of Circuitry Index (CI) calculations to measure path tortuosity in studies on spatial mapping memory in arboreal mammals. SD, standard deviation

Species	CI values	Conclusions of the authors	References
Moustached tamarin <i>Saguinus mystax</i>	Subject's travel route: CI = 1.19 Two-step olfactory navigation model CI = 2.25	Possible use of olfactory cues, but foraging patterns are better explained by the use of a spatial map	Garber and Hannon (1993)
Brown-mantled tamarin <i>Saguinus fuscicollis</i>	Three-step olfactory navigation model CI = 1.75 Steepest ascent model: CI = 1.10 and with degree adjustment CI = 1.16 Spatial mapping model: CI = 1.28 for trees visited for the first time and CI = 1.12 for previously visited trees		
Weddell's brown-mantled tamarin <i>Saguinus fuscicollis weddelli</i>	Subject's travel route: CI = 1.47 ± 0.66	No straight-line travel	Porter and Garber (2012)
	Subject's travel route: CI = 1.37 for data collected in 2009 and CI = 1.25 for 2011	No straight-line travel	Garber and Porter (2013)
White-fronted spider monkey <i>Ateles belzebuth</i>	78% of route segments with linearity ratios above 0.8, and the remaining 22%, above 0.6, which correspond respectively to CIs of 1.25 and 1.67 Subject's travel route: CI = 1.4 ± SD 0.7 Random foraging model: CI = 4.8 ± SD 7.7 Route model: CI = 3.6 ± SD 5.1 Scrambled route model: CI = 3.3 ± SD 5.0	Relative straight-line travel Goal-directed travel	Valero and Byrne (2007) Suarez et al. (2014)
Grey mouse lemur <i>Microcebus murinus</i>	Subject's travel route: CI between 1.03 and 1.30	Values not reflecting the actual routes due to the restricted observation protocol and the results of a test of turning angles showing that the lemurs did not consistently move directly forward	Lührs et al. (2009)
Mantled howler <i>Alouatta palliata</i>	Subject's travel route: CI between 1.00 and 1.35	Reuse of the same travel paths with direct or relatively straight-line routes	Garber and Jelinek (2005)

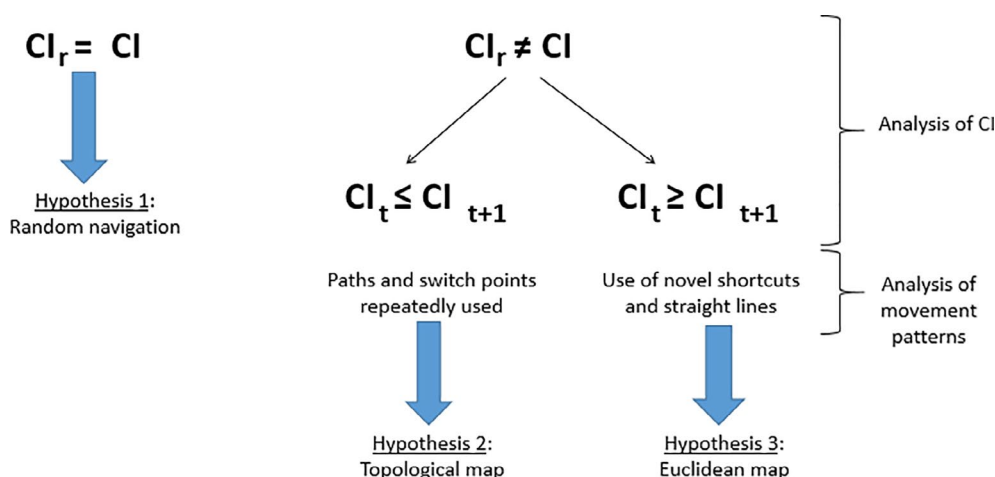


Fig. 2. Schema of hypotheses about the use of cognitive maps based on Circuitry Indices (CIs). CI_r represents the Circuitry Index of a random travel path. CI represents the Circuitry Index of the travel path of the study animal. CI_t represents the Circuitry Index of the study animal at the time t . CI_{t+1} represents the Circuitry Index of the study animal at the time $t + 1$, when the individual revisits a feeding or resting spot. Hypothesis 1: The study animals travel randomly and do not use a cognitive map to orientate themselves in their environment. Hypothesis 2: The study animals use a topological map to orient themselves in their home range. Hypothesis 3: The study animals use a Euclidean map to orient themselves in their home range.

Garber and Porter (2013) examined the paths taken by Weddell's brown-mantled tamarins *Saguinus fuscicollis weddelli* when they incorporated new feeding sites into their daily foraging itinerary. To understand how goal-directed travel is impacted by landscape variables, Howard et al. (2015) conducted experiments in which they manipulated the travel goals of black-striped capuchins *Cebus libidinosus* by training them to respond to an auditory cue signifying the presence of a high-value provisioned food item. They showed that the monkeys used more linear routes irrespective of the resistance of the landscape to reach the feeding platforms. Janson (1998) investigated spatial memory in wild brown capuchins *Cebus apella* by implementing feeding platforms by comparing empirical data with a step model and a geometric model. The study demonstrated that the capuchins travelled more often to the closer platforms and in straighter lines than predicted by the random search models using their observed detection field of 82 m. Given the results, Janson (1998) suggested that capuchins used spatial memory to move between feeding sites, but he considered that straight-line movements and a preference for closer feeding sites are convincing evidence for spatial memory only if the detection field of the forager for the resources is known.

Using field experiments to study spatial orientation in arboreal mammals appears to be an efficient method to collect relevant data and to control some aspects of location, quantity and cues given by food items. When a study does not include feeding platforms but is only based on field observations, it is difficult to draw conclusions about the travelling patterns. However, the reasons study subjects decide to orientate their foraging travel to one direction can be directly explained by the presence of

a feeding platform. The expectation of having food in a specific spot means that the subjects tend to travel in a straight line towards it.

The nearest-neighbour feeding tree method

In the nearest-neighbour feeding tree (NNFT) method, researchers identify the potential feeding tree (defined by food abundance or preferred species) that is nearest to the tree where the subject is currently feeding, and examine whether or not the subject will transfer to that nearest tree.

Garber (1989) used the NNFT method to determine how frequently the nearest tree of a given species was selected by brown-mantled tamarins *Saguinus fuscicollis* and moustached tamarins *Saguinus mystax* as their next feeding spot, and Erhart and Overdorff (2008) applied the NNFT method to food patches for red-fronted lemurs *Eulemur rufus* and Milne-Edwards Sifakas *Propithecus edwardsi*, where a patch is defined by a single tree or liana. To determine whether the feeding sites were encountered by chance or whether the travel pathways were goal-oriented, calculations of the probability that any tree encountered by the tamarin groups would be the NNFT of that species were made (Garber 1989). An index of turning was calculated by Garber (1989) and Erhart and Overdorff (2008) to differentiate straight-line travel from recrossing or backtracking displacements.

These studies suggest that moustached and brown-mantled tamarins, red-fronted lemurs and Milne-Edwards Sifakas travel using a goal-oriented approach. All studied species

selected the closest feeding spots more than half of the time (moustached tamarins: 70%, brown-mantled tamarins: 71%, red-fronted lemurs: 79%, and the two groups of Milne-Edwards Sifakas: 57% and 82%). Additionally, moustached and brown-mantled tamarins and Milne-Edwards Sifakas travelled in relatively straight lines. The results show that tamarins are able to compare distances and directions between their position and the positions of several potential feeding trees. Erhart and Overdorff (2008) suggested that red-fronted lemurs and Milne-Edwards Sifakas use a topological map to orientate themselves in space, because individuals use well-known travel routes. However, if no shortcuts are used by the study subjects, as in the study of Erhart and Overdorff (2008), it appears difficult to determine whether the individuals used a Euclidean map with the NNFT method. Nevertheless, this method provides information about decision-making in animal foraging and, combined with route analyses, allows us to make suggestions about the use of a cognitive map.

Route analyses

In route analyses, different calculations based on field observations of daily travel paths can be made for route segments such as travelled and direct distances, feeding time at the stop site or food identity (Di Fiore & Suarez 2007, Valero & Byrne 2007, Presotto & Izar 2010, Shaffer 2013).

These calculations, combined with other methods or in isolation, can lead to conclusions about the type of spatial map used. For example, Di Fiore and Suarez (2007) showed that silvery woolly monkeys *Lagothrix poeppigii* used a topological map to orientate themselves within a space, and Presotto and Izar (2010) found that black capuchins *Cebus nigrinus* used both a topological and a Euclidean map to navigate, depending on the quality and distribution of the food resources they encountered. By analysing different features of travel paths, it is possible to investigate changes of direction, straight-line travel, and minimisation of distance travelled to specific feeding sites by the study animals (Valero & Byrne 2007, Shaffer 2013).

Theoretical models

Random-walk models are extremely useful to determine whether a travel path is goal-oriented or not. A random-walk model is a travel simulation based on the observed characteristics of a mammal's travel path obtained from field observations. Several researchers have run such models and compared them with the actual travel path of the study animals (Garber & Hannon 1993, Garbutt 2007, Asensio et al. 2011, Shaffer 2013, Suarez et al. 2014). Theoretical models offer the possibility to investigate the choice of the most productive foraging sites, the nearest

foraging site, and the use of different paths to reach the same site (Cunningham & Janson 2007).

Step models generate a dataset containing different steps, using the distance travelled between each global positioning system data point and the turning angles from one point to the next. The models randomly select steps from that dataset and generate the path of a given target distance (e.g. 100, 105, 110 m, etc.). Cunningham and Janson (2007) used two models (a step model and a geometric model, both adaptations of models created by Janson 1998 and Janson & Di Bitetti 1997) to demonstrate that white-faced sakis *Pithecia pithecia* directed their travel to the most productive foraging sites, not the nearest foraging site, and used different paths to reach the same site, indicating the use of a Euclidean map. Garber and Hannon (1993) included olfactory cues in their analysis by using a 'two- and three-step olfactory navigation model', which hypothesises that the direction of each foraging step is based on the ability to detect, remember, and compare odour concentrations. Additionally, Garber and Hannon (1993) ran a 'steepest ascent model' gathering a set of memory and olfactory cues that achieved a level of foraging performance comparable to that of wild monkeys, and a 'spatial mapping model' assuming that individuals foraged by using a mental map, which implies that they can remember locations of previous feeding spots and efficient travel routes to forage. This model is based on determining the most efficient travel route (in terms of minimising distance) between several distributed feeding sites, also known as the 'travelling salesperson problem'.

Other models have been run to study spatial mapping memory in arboreal mammals, such as models of decision-making (movement to core home-range areas instead of individual trees, travel along a sensory gradient, movement along with arboreal pathway networks without a predetermined destination, straight-line travel in a randomly chosen direction, and random walks; Hopkins 2015), or linear mixed models allowing researchers to determine the influence of food resource distribution and landscape attributes, such as slope, elevation, and presence of canopy gaps, on the location of routes within a route network (Guinea et al. 2019).

DISCUSSION

Comments on the methods

The CPT provides information about travel paths by identifying a series of places at which travel direction changed towards locations, and determines whether the travel path of an individual is random or goal-directed. Additionally, the CPT can be considered as a useful tool to interpret decision-making in animals under natural conditions. According to Byrne et al. (2009), change points often

correspond to the outcomes of decision-making processes. For example, points where changes of direction occur could be reflections of immediate responses to the detection of other individuals. King and Sueur (2011) also support the use of the CPT to assess decision-making, by suggesting that, over a long time, researchers could use the CPT to detect when and where change points occur; using targeted observations at these locations, they would be able to study how and why the decisions were made. However, this method does not allow researchers to draw conclusions about the type of cognitive map used by the subjects. To investigate spatial orientation and the role of cognitive maps in detail, the CPT should be used alongside other methods. Additionally, other methods investigating changes in movement patterns, such as behavioural change-point analysis, could be applied to movements of arboreal mammals. Behavioural change-point analysis has the advantage that it can be used to study movement data with temporal gaps and heterogeneity in behaviour, and without any prior assumptions.

Path tortuosity can be studied to determine whether a travel path is random or goal-oriented, and the type of cognitive map. However, straight-line movements alone should not be treated as proof of goal-oriented travel, because an individual foraging in a straight line will ultimately find a food spot (Janson 1998). Nevertheless, there should be a measurable difference between a goal-oriented straight line and a random straight line in terms of the degree of directness related to the spot characteristics (Janson & Byrne 2007). When using CI values, it appears important first to state the value from which the path is considered as direct. Additionally, a lack of proof of straight-line travel does not signify a lack of spatial map, as the forest features need to be considered as well in the analysis. Many factors may explain why an individual is not taking the most direct path to its goal, such as broken branches, the presence of predators or competitors. Thus, the results of CI calculations must be combined with other data (behavioural and landscape features) to make correct interpretations about the use of cognitive maps by the study subjects. Finally, different names are attributed to the same metrics measuring the straightness of a path, which leads to confusion when comparing studies. Future researchers should be sure to use the correct mathematical appellations when calculating metrics related to path tortuosity.

Field experiments with feeding platforms can be used to determine the type of cognitive map used and are extremely practical for testing the role of sensory cues in spatial orientation because they allow researchers to control food availability on the feeding platforms and regulate information available to the study subjects. A study based on field experiments including different baiting parameters such as quantity, olfactory, visual and auditory cues, change

of locations, and determining changes of direction and straightness of travel patterns would be thorough, and could provide valuable information regarding spatial mapping memory. Field experiments and observations provide valuable data but have limitations. It is not always possible to replicate experiments or observations under controlled conditions, as ecological conditions can be unstable, in terms of climate or tree productivity for example (Petrovskii & Petrovskaya 2012).

The NNFT method allows researchers to determine whether a travel path is goal-oriented and to make suggestions about the type of cognitive map (Garber 1989, Erhart & Overdorff 2008). The examination of NNFTs in a travel path can provide information about decision-making. As additional analysis to the CPT method, the NNFT analysis could be conducted on every change point to determine whether the change was made in the direction of the NNFT or not. However, although Joly and Zimmermann (2011) and Asensio et al. (2011) included data on preferred feeding spots in the CPT method, they did not consider the NNFT in their analysis. Porter and Garber (2012) used the NNFT analysis to determine the distribution (clustered, random, or dispersed) of sites in the tamarins' home range according to their productivity. However, they did not collect information on the location or productivity of potential feeding trees that were not visited by the tamarins; thus, they were not able to determine whether the monkeys chose the most productive or the nearest feeding sites among all that were available. Additionally, evidence of straight-line travel and selection of NNFTs by using the measure of path tortuosity and the NNFT method indicates an ability to compare the distance and the direction between sites in a habitat (Garber 1989). Finally, the NNFT method, completed with productivity data, provides information about the trade-off between distance and productivity that animals have to make (Cunningham & Janson 2007). However, the NNFT method requires an extensive amount of work, as the entire studied area has to be mapped with all the potential feeding trees.

In route analysis, field observations and location records allow the creation of daily travel paths and the identification of feeding spots. Based on these data, measures of route concordance across time can be calculated, and by superimposing the daily paths connecting these locations, sets of repeatedly used routes and intersections among these routes can be identified (Di Fiore & Suarez 2007). To study spatial mapping memory in arboreal mammals, this first step is necessary and extremely useful to determine the implication of a topological map in arboreal foraging. By dividing travel routes into route segments and analysing the linearity of each segment and the collinearity between segments, it is possible to draw conclusions about the straightness of travel between feeding sites and about the direction of the general travel route (Valero & Byrne 2007).

The use of theoretical models compensates for the limitations of field studies by creating a convenient 'virtual environment' and provides a valuable supplement to ecological studies (Petrovskii & Petrovskaya 2012). Modelling can be used to assess the efficiency of foraging strategies based on species' characteristics and previous travel patterns, and to determine which strategy is the most likely to be used by the species (Garber & Hannon 1993). It also allows comparison between actual travel paths and theoretical paths, including assumptions about straightness, resource detection field, or direction of departure (Cunningham & Janson 2007, Suarez et al. 2014).

All in all, the most relevant way to investigate spatial orientation in arboreal primates may involve using a mix of methods: random theoretical models, collecting data in a controlled environment (e.g. using field experiments with feeding platforms), measuring different parameters of travel patterns (e.g. path tortuosity, change points, route analysis), and considering the use of sensory cues and environmental factors of the study sites (e.g. nearest-neighbour feeding tree method).

Use of random models

Random models can be a powerful tool to examine whether a travel path of an individual is randomly directed or goal-oriented. Due to the limited paths that an arboreal species can take, the ideal random model should only consider travel segments used at least once by the study animals, to avoid the generation of random paths that are impossible for the animals to use. Travelled distances and the home range of the study animals are parameters that must be considered for the use of random models as well.

Random models have been used extensively in movement ecology (Thurjell et al. 2014, Gurarie et al. 2016, Bailey et al. 2018). For instance, the step-selection function is a powerful technique using random models to identify the habitats that animals choose to travel through, which could be used to understand animal decision-making better and at finer spatial and temporal scales (Thurjell et al. 2014). Even though complex and efficient methods involving path selection models have been developed to study movement ecology, these techniques are not used to investigate spatial mapping memory in arboreal mammals; therefore, future studies should integrate into their analysis more recent techniques used in the broad field of movement ecology.

A controlled environment

Field experiments allow observations of animals in their natural environment while controlling variables of interest

such as food quantity, and visual and olfactory cues (Garber 2000). For example, studies not using field experiments assume or suggest that animals do not, or do not only, rely on olfactory cues for foraging (Garber 1989, Garber & Hannon 1993), whereas studies including field experiments can assess the importance of olfactory cues on foraging decisions, using evidence (Garber & Paciulli 1997, Lührs et al. 2009). The regulation of food availability and information available to the study subjects allows a better understanding of the relationship between stimuli and behavioural responses, and more direct testing of hypotheses about, for example, the influence of visual or olfactory cues (Zuberbühler & Wittig 2011). Observations without field experiments can lead to the same results, but usually require more observation efforts (Zuberbühler & Wittig 2011). However, there are advantages and drawbacks. Field experiments allow researchers to determine travel goals of the study subjects, such as food spots or specific locations, but large-scale studies encounter practical difficulties, such as the risk of the non-detection of a feeding platform by the study animals (Byrne et al. 2009). Additionally, feeding platforms attract different animals, and researchers need to keep in mind that the study animals will not necessarily arrive first at the platforms. On the other hand, collecting data in strictly natural conditions can provide a lot of relevant data for the study of spatial orientation, but their interpretation can be difficult, specifically in relation to the reason an individual directs its travel to a particular location (Byrne et al. 2009). Controlled environments provide a strong tool to study the use of spatial information and to test the implications of using sensory cues in foraging. They also deliver information on spatial and temporal learning. For instance, putting different amounts of food on the platforms gives the opportunity to test the memory of the study animals about the best food spots and the representation of quantity. However, this method may not always be possible or ethical. Altering the feeding patterns of wild animals can potentially make them dependent on a non-reliable food source provided by humans while also teaching them that humans may give them food (Fedigan 2010).

Use of olfactory, visual, and auditory cues

Some, but not all, of the studies in this review investigated the potential role of sensory cues in spatial orientation. And yet, sensory cues might play an important role in spatial orientation, especially for species with well-developed organs for transmission and reception of sensory signals. Different species can detect resources according to their visibility range or from particular food resource odours (Dominy et al. 2001, Garber & Jelinek 2005, Siemers et al. 2007). Additionally, some species may follow a known path if they marked it

previously using scent glands or by using auditory cues such as the call of a conspecific or a sound emitted by the prey (Dominy et al. 2001, Siemers et al. 2007). Thus, to investigate the role played by sensory cues, different parameters can be determined such as the visibility range, the presence and use of scent glands, and the efficiency of the auditory and olfactory organs (Garber 1989, Garber & Hannon 1993, Garber & Paciulli 1997, Dominy et al. 2001, Cunningham & Janson 2007, Valero & Byrne 2007, Erhart & Overdorff 2008, Asensio et al. 2011, Joly & Zimmermann 2011). Ecological aspects may affect the visibility range of animals, including landscape features and characteristics (forest density, fragmentation, darkness, and uniformity), as well as the way they travel in terms of height in the forest (travelling in the canopy, along ridges or low within the forest; Garber & Jelinek 2005, Di Fiore & Suarez 2007).

Implementing feeding platforms and modifying the baited resources in terms of vision, odour, and sound appear to be a reliable method to assess the implications of sensory cues in spatial orientation (Garber & Paciulli 1997, Lührs et al. 2009). Using sensory cues does not exclude the use of a cognitive map, but if there is no evidence that the individuals rely on any sensory cue, then the use of a cognitive map can be assumed (Garber & Hannon 1993, Garber & Jelinek 2005, Cunningham & Janson 2007).

Considerations during analysis

Species-specific differences in locomotor abilities should be considered in the analysis of data on spatial orientation. Based on morphological differences, some species have more possible ways to travel from one spot to another (e.g. jumping, swinging). Some travel routes are avoided by certain individuals because of gaps in the forest cover, such as rivers, roads, or damaged trees. The presence of predators or conspecifics can also affect preferred pathways. The nearest-neighbour rule, while logical because it reduces energy spent during foraging, is not always accurate because of variables such as tree productivity, nutritional quality, and access to other resources (e.g. water holes; Janson & Byrne 2007).

Spatial representation

Studies on spatial mapping memory show that it is possible to prove that foraging in arboreal mammals is not random but goal-oriented by using various methods (Garber 1989, Suarez et al. 2014). It is possible to validate the existence of a cognitive map with multiple methods based on spatial data of travel paths (Di Fiore & Suarez 2007, Porter & Garber 2012). The analysis of daily travel paths of study subjects allows us to make solid conclusions about the use of key locations, landmarks, and familiar routes, implicating the existence of a mental representation of the physical

environment. However, it is extremely difficult to draw firm conclusions about what kind of spatial representation is utilised. Indeed, topological maps may include many landmarks and travel routes, making them even harder to differentiate from Euclidean maps. Moreover, researchers found it was difficult to demonstrate the use of a Euclidean map for animals in their natural environment because it is difficult to prove the use of novel shortcuts: there is a possibility that a novel shortcut is not truly novel or that familiar landmarks are being recognised from a new angle (Bennett 1996).

Using one type of map is not exclusive. A small number of studies suggest that some species orient themselves in a given space by using a combination of topological and Euclidean maps (black capuchin *Cebus nigritus*: Presotto & Izar 2010, white-headed capuchin *Cebus capucinus*: Urbani 2009, and Geoffroy's spider monkey *Ateles geoffroyi yucatanensis*: Valero & Byrne 2007).

Challenges and prospective studies

One of the main challenges for future studies on spatial mapping memory in arboreal mammals will be to find the appropriate method to distinguish between topological and Euclidean maps. The ability to use novel shortcuts could be a promising aspect of animal orientation, as it is one of the features of the use of Euclidean maps, which is not present in the use of topological maps. Taking novel shortcuts is not common in arboreal species, and it might take time to observe such behaviour; thus, field experiments could be extremely useful for investigating this ability, as they allow experimenters to control and modify features of the environment (e.g. food availability and location). Additionally, investigating differences in movement patterns between the peripheral and central areas of individuals' home ranges could be another promising technique to differentiate the use of topological maps and Euclidean maps. For example, Normand and Boesch (2009) studied these differences to prove that common chimpanzees *Pan troglodytes verus* use a Euclidean map.

The current literature provides an overview of spatial mapping memory in arboreal mammals, but multiple aspects of spatial orientation warrant further exploration. Some suggestions for future investigations are as follows: mechanisms of information exchange between conspecifics, the effects of feeding choices earlier in the day on feeding choices later in the day, and differences in foraging between group-living and solitary individuals.

The studies in this review show that order Primates species from distinct suborders and families use different spatial mapping representations. Lührs et al. (2009) demonstrated that a small-brained solitary mammal, the grey mouse lemur *Microcebus murinus*, has spatial cognitive abilities that are similar to those of large-brained and highly

social mammals such as monkeys and apes. These findings question the relation between cognitive abilities, brain size, and sociality. Spatial mapping memory has mostly been studied in primates, but what about the other arboreal mammals? More investigations should be conducted on other arboreal orders such as Diprotodontia (e.g. koalas, possums, tree kangaroos) and Pilosa (e.g. sloths, anteaters), and even more widely in mammals in general. Indeed, comparing spatial mapping memory between arboreal and terrestrial mammals would bring new perspectives to mammal cognition. Several questions related to the advantages of an arboreal lifestyle for foraging and the proneness to develop spatial maps compared with a terrestrial lifestyle remain underinvestigated. These studies could aid in understanding the effects of morphology and locomotory abilities on cognitive mapping types, as well as help us to investigate the evolution of spatial mapping memory through time, and would provide more knowledge about the cognition of mammals.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Summary of field experiments by Garber and Paciulli (1997).