

# What wild primates know about resources: opening up the black box

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**Abstract** We present the theoretical and practical difficulties of inferring the cognitive processes involved in spatial movement decisions of primates and other animals based on studies of their foraging behavior in the wild. Because the possible cognitive processes involved in foraging are not known a priori for a given species, some observed spatial movements could be consistent with a large number of processes ranging from simple undirected search processes to strategic goal-oriented travel. Two basic approaches can help to reveal the cognitive processes: (1) experiments designed to test specific mechanisms; (2) comparison of observed movements with predicted ones based on models of hypothesized foraging modes (ideally, quantitative ones). We describe how these two approaches have been applied to evidence for spatial knowledge of resources in primates, and for various hypothesized goals of spatial decisions in primates, reviewing what is now established. We conclude with a synthesis emphasizing what kinds of spatial movement data on unmanipulated primate populations in the wild are most useful in deciphering goal-oriented processes from random processes. Basic to all of

these is an estimate of the animal's ability to detect resources during search. Given knowledge of the animal's detection ability, there are several observable patterns of resource use incompatible with a pure search process. These patterns include increasing movement speed when approaching versus leaving a resource, increasingly directed movement toward more valuable resources, and directed travel to distant resources from many starting locations. Thus, it should be possible to assess and compare spatial cognition across a variety of primate species and thus trace its ecological and evolutionary correlates.

**Keywords** Cognitive map · Primate · Foraging · Ecology · Psychology

## Introduction

Although there is abundant evidence that wild animals navigate adaptively through familiar spaces (e.g., Gallistel 1990; Shettleworth 1998), there is still much to learn about how spatial relationships are encoded (e.g., landmark-based vs. geometric cognitive maps: Byrne 2000; Vlasak 2006), how well animals learn renewal rates of resources (Schwagmeyer 1995), to what extent they can associate distinct renewal rates with different resources, and how they use that information to make decisions (for instance, do they plan optimal travel routes or just move to nearby resources: Cramer and Gallistel 1997). In most cases, answers to these questions for wild animals depend on inferring process from patterns of movements between unmanipulated resources. Even in the case of experiments in the field or captivity, to infer what navigational processes an animal is using, it is often necessary to guess what cues it perceives. Thus, we are faced with the proverbial “black box” problem,

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in which an engineer has to figure out the circuit within a sealed box by introducing different inputs and observing the outputs. In theory such inference can work, if the set of possible processes is limited and well known. Unfortunately we generally do not know the complete list of possible processes for most animals' minds. The remaining article will focus on this problem primarily from the point of view of the study of primates, as the cognitive maps of primates may be more complex than those of most other animals (Shettleworth 1998) and at the same time, it is often difficult to do experiments on primates in the wild because they range large distances, are diet generalists, and live at low population densities compared to many smaller animals.

Because of these limitations, we discuss in detail the kinds of descriptive data that may reveal some aspects of what primates know about their resources when experiments cannot be done, and what kinds of data or processes can only be measured by experiments. For either descriptive or experimental data, we emphasize the need to compare observed movements with specific quantitative models of 'random' movement behavior that incorporate an understanding of how animals detect new resources. Although models of 'random' movement can often mimic some aspects of spatial movement patterns of primates, detailed analyses of spatial foraging behavior and resource choices reveal preferences that are difficult to interpret unless the monkeys know about the state of ripeness and productivity of the resources they visit.

### **How can we expect to learn what animals know and how they use that knowledge?**

When we study wild animals, it is tempting to infer cognition in our study subjects by using our intuition about the possible goals that may be important to our study on animals. Thus, it is common for students of primate behavior to claim that straight-line travel is 'goal-oriented' because such travel frequently ends in a food resource, water hole, or sleep site. When the travel behavior of the primates is very repeatable, or the number of possible goals few, such an inference is likely to be correct. However, when Noser and Byrne (2007) used the 'natural experiments' of intergroup encounters to examine these assumptions, they concluded that baboons lacked the ability to compute Euclidian relations among out-of-sight locations. For most fruit-eating primates in rainforests, the researcher's problem is greater: because the number of possible fruiting trees in a home range is large, straight-line travel in almost any random direction would eventually lead to a food source (see Janson 1998). Similarly, if one assumes that minimizing distance traveled to food sources is an overall goal of primate foraging strategy, then the observation that they usu-

ally move to the closest available resource is consistent with the notion that they know where alternative resources are and choose the closest (Garber 1989). However, to be certain that a given resource is the closest available is difficult, because it requires the observer to define what is available for the animals. In some cases, such as escape burrows for meerkats, the availability of resources is relatively easy to determine, and the presumption that the animal would prefer to find the nearest one in an emergency is reasonable (Manser and Bell 2004). For fruit or leaf resources, defining availability is tricky and usually requires a complete list of potential foods, phytochemical analyses, how the forager ranks those food items by preference, and detailed phenology of each food type. Because of the enormity of the work involved, researchers have often used the primates' feeding behavior to tell them what counts as an available resource, a procedure which risks logical circularity. The purpose of this article is to state clearly what types of information can be used to support different kinds of spatial knowledge in wild animals using either pure observations or field experiments.

### **Inferring process from outcomes: two approaches**

There are two broad classes of methods that allow more confident inferences about the mental processes and purposes underlying animal movements. The first of these is to perform experiments. These can be done in captivity or the wild. The advantage of captive experiments is the much tighter control over extraneous variables, but a serious drawback is both the lack of natural context (e.g., a lack of predation risk or competing groups) and the small spaces within which captive experiments are typically performed. For instance, Cramer and Gallistel (1997) found that macaques in an outdoor enclosure of 0.01 ha seemed to be able to solve the 'traveling salesman problem', choosing the shortest route over a set of four food locations. Yet, similar experiments designed to test the same rule in wild capuchin monkeys over a period of 10 years in a home range of more than 150 ha failed to find evidence of complex travel decisions. Instead the results suggested that the monkeys mostly just visited the nearest food source (C.H. Janson, unpublished data). The difference between results could be due to several factors: (1) the species may differ intrinsically in cognitive use of spatial knowledge, (2) the wild monkeys have to deal with much larger spaces across which they cannot see their foraging goals and thus cannot precisely estimate the distances to each goal, let alone the distances between them, (3) the wild monkeys are hungrier and discount more distant resources so heavily that they do not include them in their decisions, (4) the wild monkeys may benefit from foraging in nearby areas they already know to be free from competitors—and the list could go on.

Although both results are intriguing, the captive result may tell us little about how a cognitive potential is used in the wild.

Conversely, experiments on captive animals may underestimate the abilities of their wild relatives to navigate landscapes. For instance, work on captive capuchin monkeys suggests that they learn only simple associations between a goal and a local landmark, not among two or more goals and a landmark (Poti 2000). This result would appear to preclude any use of ‘traveling salesman’-type foraging routes as postulated by Cramer and Gallistel (1997), which requires planning ahead and a precise knowledge of the full set of distances among all potential goals. Nevertheless, wild capuchin groups appear to use information about the location of at least two resources relative to each other to decide on a foraging route (Janson 2007). Thus, their apparent limitations in captive tests either do not apply to the wild or they use some other mechanism to circumvent this cognitive limitation. This caution applies particularly in the case of captive-reared primates, which may not have had the experience to develop or practice navigation abilities in large-scale space (Menzel and Beck 2000).

Compared to studies in captivity, field experiments have the contrasting characteristics of reduced control over the design variables, but potentially greater relevance to understanding the selection pressures that have contributed to the animal’s current capacities and decisions. Ideally a combination of both approaches would be used for each species, but field experiments are difficult in many cases, and many species do not thrive in captivity. The extensive work on bird foraging decisions in captivity and the wild (reviewed in Shettleworth 1998) is an excellent example of this approach, but one that has not yet been implemented for primates, despite a wealth of studies on cognition in this group.

The second major method of strengthening an inference about mental processes and goals is to compare observational data to predictions from explicit quantitative models based on each process or foraging goal (in some cases, even qualitative models can give clear results, e.g., Janmaat et al. 2006; Noser and Byrne 2007). Statistical analyses, although apparently assumption-free concerning mental processes, in fact are consistent with only limited kinds of external constraints. For instance, testing to see if primates preferentially visit closer resources rather than more distant ones is not itself informative about spatial knowledge, as the conventional null hypothesis (a slope or parameter of zero for the effect of distance on probability that a resource is visited) *cannot* be true under any reasonable model of two-dimensional spatial search. Simply put, it is always more probable that animals will encounter by chance closer resources before they find more distant ones. Thus, a statistical null hypothesis is that the probability of visiting a

given resource should decline with distance. The question of exactly how much decline is expected depends on assumptions about how the animal moves and detects resources (e.g., Janson 1998). More realistic null models incorporate more detail: the distribution of distances moved, the distribution of angles turned between movement ‘segments’, and possibly the dependence between the distance moved and angle turned (e.g., Ramos-Fernandez et al. 2004; see also Valero and Byrne 2007). Once such a model is constructed and parameterized correctly, it can be run repeatedly to test how often *non*-goal-oriented travel will result in encounters with desirable goals as a function of time or distance (e.g., Janson 1998); these modeled rates of encounter can then be compared statistically to observed rates. Even when the details of the movement process are not known, comparisons of travel paths produced by various orienting cues (vision, smell, memory) can be enlightening when compared to real travel paths (e.g., Garber and Hannon 1993; Boyer et al. 2004). If observed movements are found to be inconsistent with null models of random search, data can be compared to additional models that suppose that the forager knows the spatial location of resources, but not of other characteristics (quantity of food, temporal pattern of availability, variance in reward, predation risk, etc.).

One shortcut to using such models is to focus analysis on particular resources that a priori produce qualitative null expectations. For instance, Janmaat et al. (2006) documented the approach behavior of groups of mangabeys toward pre-selected distant (out of sight) trees of a single species that did or did not have ripe fruit. The qualitative prediction was that the groups should navigate more directly toward distant trees with fruit than without fruit. Significant differences in the approach behavior of the groups were found, suggesting that they knew of the tree’s fruiting state before being able to see it.

## Review of evidence about what primates know about resources

What choices do primates make when moving among resources? The most common pattern reported is that groups move to the nearest available resource (e.g., Menzel 1973; Garber 1988; Janson 1998). In these studies, potentially available resources were determined either by the experimenter (Menzel 1973; Janson 1998), or by virtue of the fact that the primate population had a very simple diet at the time of year studied (Garber 1988). Although such ‘nearest-neighbor’ movement is a commonly cited ‘rule’, the actual proportion of such ‘nearest-neighbor’ moves in these studies is 44–85%, meaning that a substantial minority or even a majority of moves is not to the closest

resource; it is difficult to decide if this fraction is different than expected from random search without building explicit models with known or measurable parameters (e.g., Janson 1998).

When the next site visited is not the closest to the previous one, the resources visited are usually much more productive than those passed by (e.g., Garber 1989; Janson 1998; Cunningham and Janson 2007a) or essential and irreplaceable (e.g., water holes: Sigg and Stolba 1981; Noser and Byrne 2007). Although such seemingly strategic foraging decisions are consistent with spatial memory of resources, there are other reasons that more productive resources may be visited more often and following longer travel segments than less productive resources. For example, more productive resources may be larger, and larger targets are visible from longer distances than smaller ones (Janson and Di Bitetti 1997; Noser and Byrne 2006, 2007).

The paths used by primates when foraging among spatially fixed resources often appear to be goal-oriented. In nearly all cases, routes taken between known resources are either approximate straight lines (e.g., Janson 1998; Pochron 2001; Cunningham and Janson 2007a; Valero and Byrne 2007) or sequences of a few straight-line segments (Di Fiore and Suarez 2007; Noser and Byrne 2006, 2007). However, animals may have reasons to travel in (nearly) straight lines even if they do not know the locations of discrete resources. First, many primates are territorial or monitor their home range on a regular basis; monitoring boundaries or traversing the diameter of their home range periodically may require relatively long and rapid travel that is best accomplished in straight lines (e.g., Terborgh and Stern 1987). Second, some primates rely on topographic or boundary features of their environment to orient or travel (Menzel 1997; Di Fiore and Suarez 2007; Noser and Byrne 2007); many of these features are linear over long distances. Third, traveling in a straight line may be a simple heuristic to avoid backtracking and thus revisiting recently used resources (Pyke 1978). Finally, nearly straight-line travel may simply be the result of averaging the tendencies of many independent travel decisions among social animals that wish to stay together; thus, species like gnus and bison that forage on vast expanses of renewing grass often move in straight lines even when they may not have to do so to reach good foraging areas (although in these cases, a few knowledgeable individuals could guide a large group to resources: Couzin et al. 2005).

One way to counter such arguments is to show that the degree of directedness toward a goal depends on the reward. Foods with large, predictable rewards should be worth traveling to directly (without detouring to other possible resources), whereas small or unpredictable rewards should not be (Janson and Di Bitetti 1997). Exactly such patterns have been found in baboons (Pochron 2001) and

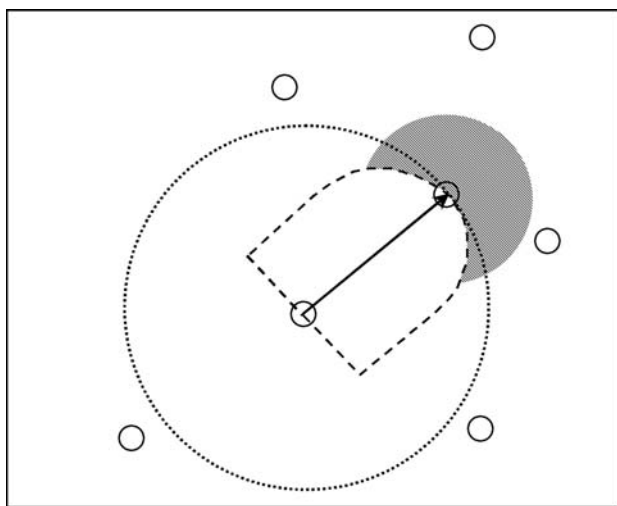
saki monkeys (Cunningham and Janson 2007a), and an analogous result was found for meerkats in locating escape burrows (Manser and Bell 2004). It is important for field researchers to record any usable resources that the forager passes by without stopping, because an apparent bias toward remembering the locations of more valuable resources could arise from a simple foraging strategy that does not require spatial memory. Suppose animals generally move in a relatively straight line until they stop to feed at a resource. If they follow optimal patch-foraging rules (Stephens and Krebs 1987), they will tend to skip over the less valuable resources they encounter and stop mostly at more valuable sites. Thus, the length of a movement towards a valuable goal will be the sum of the distances between all less-valuable resources encountered and skipped over since the last-visited resource. In contrast, a movement preceding a visit to a less valuable resource will usually include fewer previous skipped resources and thus will be shorter. In this case, there would emerge a correlation between movement segment length and resource value even though the forager does not know where resources are located. However, if the observer records resources that are skipped, and the animal's search is not guided by spatial memory, then the segment lengths should not correlate with the size of resource encountered (including those skipped over).

Changes of movement speed could be used to infer goal-directed travel and hence presumptive knowledge of the location of the goal. A common pattern of movements of capuchin monkeys is that groups move relatively slowly away from food patches and begin to speed up as they approach the next resource (Janson and Di Bitetti 1997). This could be interpreted as the outcome of scramble competition, as individuals approaching a known goal race each other to be the first to arrive to harvest it. However, the goal could be 'known' because the animals just perceived it, rather than its location remembered from previous experience. Therefore, independent evidence is needed to show that the change in movement speed started at distances well in excess of the distance at which resource perception occurs (Pochron 2001; Janmaat et al. 2006). If animals are found to travel more quickly toward more valuable resources (Janmaat et al. 2006), it is important to have independent assessments of resource value, not based on the animal's own behavior. Lacking such independent evidence, it is not easy to rule out the possibility that both the speed of approach and the apparent value of the resource depend on other, unmeasured behavioral variables (e.g., hunger).

After animals leave a resource, they may change direction relative to previous travel, yet maintain a consistent direction over most of the distance to the succeeding resource (e.g., Valero and Byrne 2007). This pattern is consistent with

spatial memory if animals both know where the next few closest resources are and preferentially travel to the nearest one, which is quite likely to lie anywhere within about  $100^\circ$  of the direction of previous travel (Fig. 1; see also Boyer et al. 2004). However, models of spatially naive foragers often use the turning angle as a parameter, and angles with modal values far from  $0^\circ$  can be adaptive if resources are clumped spatially (e.g., Pyke 1978). Thus, sharp turning angles following a stop at a resource could arise from patterns of foraging that do not incorporate knowledge of individual resource location. However, in this case, the sharp turning angle would not be clearly directed toward a preferred next goal—one that is closer or more productive than other resources. Thus, if sharp turning angles after a visit to a resource are used only when a group travels to preferred (closer or more productive) goals, this would be stronger evidence of goal directed movement, assuming the resource is not within sensory detection range. Although not a direct application of this criterion, more circuitous routes have been found in baboons and spider monkeys in wet periods when resources are abundant and no resource is especially valuable (Pochron 2005; Valero and Byrne 2007).

Some studies compare the observed values of specific or composite aspects of animal movement to those expected



**Fig. 1** When a forager searches from a resource (small circle at base of arrow), it traces out a path of searched area (inside of dashed oblong outline). When it leaves a resource, such as at the arrow tip, it searches for the next resource. If it uses its senses to inspect a fixed search field, as shown here in the shaded area, it will not find food in the direction it just came from, because any food located there would already have been detected and should have been consumed. If the forager uses a cognitive map to find the closest available resource, then the area inspected in this case is inside the large dashed circle, because by definition no other resource could be closer to the base of the arrow than the one chosen. The next resource to be used cannot lie within this area already inspected. Thus, in either case, the forager will usually end up moving in a direction within about  $90\text{--}100^\circ$  of the previous direction of movement—the shaded area not within previously searched areas

of random movement models (Garber and Hannon 1993; Janson 1998). The study of Garber and Hannon (1993) compared the general patterns of movement expected of animals searching for food using different sensory modalities—vision, memory, olfaction. They concluded that olfactory search modes were quite inconsistent with the long, straight movement segments observed in most primate studies. Janson (1998) assumed a more explicitly visual random search model, but with a variety of possible parameters for the length of movement segments, turning angles after each segment, and search field widths. He modeled three observable parameters of primate movements: (1) distance to the next used resource, (2) the angular deviation between the direction initially chosen after leaving a resource and the exact direction from the previous resource to the next used one, and (3) the probability of choosing each of the alternative resources starting from each given resource, based on either a geometrical model or computer simulations. Critical to comparing the field data to the model was knowing the search field width, which was possible in a rigorous way only because the study was experimental and used artificial feeding sites (platforms). For these sites, the process of detection of novel (newly-placed) feeding sites could be monitored and the mean detection field measured (Janson and Di Bitetti 1997). The results of this experimental system showed that the movements of the monkey group were indeed too straight and too directed to be consistent with any reasonable search process, given the known search field width. However, if the search field width was free to vary, a random-search model could match any one of the observable parameters, although not all the field parameters combined could be matched with a single set of assumed model values in Janson's (1998) simulations. Manser and Bell (2004) used a similar addition of experimental resources in their study on spatial knowledge of escape burrows by meerkats. Accurate spatial knowledge of burrow location, at least on a local scale, was supported by the fact that the meerkats located previously used burrows far more rapidly than new experimentally provided burrows, whether the latter provided only visual, only olfactory, or both visual and olfactory cues.

An ingenious alternative to testing observed movement patterns against hypothetical random models is to compare the movement behavior of a forager or group when they are displaced from a goal. This is the classic experimental method used to test for the existence of geometric versus landmark-based cognitive maps in honeybees (e.g., Gould 1986; Dyer 1991). Using 'natural experiments' caused by encounters between groups of baboons provides a similar sudden displacement that may reveal the cues used to navigate between major resources (Noser and Byrne 2007). Such situations reveal that both honeybees and wild baboons appear to use landmark-based cognitive maps in

most cases, apparently lacking the ability to plan novel routes on the basis of geometric knowledge.

An approach similar to the previous one is to compare the movements of a forager when its state of knowledge about resources is experimentally changed by the researcher. In an experiment on wild Japanese macaques by Menzel (1991), commercial ripe persimmons were placed out in the home range of a group when the wild trees still had only unripe fruit. The macaques, which had not been visiting persimmon trees before the experiment, shifted suddenly to focused travel among wild persimmon trees after the experiment, suggesting that they both knew where the fruit trees were and that they usually ripened close to the same time of the year.

Although most studies on spatial foraging focus on spatial parameters of the foraging animals, repeated use of a finite set of resources will lead to temporal patterns of visit intervals to each resource. These patterns can be compared to various statistical null models (Janson 1996; Thomson et al. 1997) or explicit models of random movements. In general, random models will show a decided bias toward short return intervals, with the mode close to zero, whereas observed distributions often have a more ‘normal’ shape with few very short intervals (e.g., Kamil 1978). However, if a forager or a group shows a strong ‘inertial’ bias toward forward movement (leaving a resource in the same general direction as the forager arrived), the resulting pattern of return intervals may be unimodal with a mode far from zero (C.H. Janson, unpublished results). In this case, explicit modeling of the forager’s movement patterns is needed to distinguish return intervals resulting from inertial local movements versus from global systematic foraging choices.

### Review of the goals of spatial foraging in primates

We next review the spatial organization of primate foraging to address the question “How do animals use resource knowledge to increase their fitness?” This question is relevant because the ultimate (fitness-enhancing) purpose of a foraging strategy is often assumed by researchers when they interpret observed patterns of primate foraging behavior as being consistent or inconsistent with resource knowledge (e.g., Menzel 1973; Garber 1989; Pochron 2001).

#### Immediate distance minimization

The notion that animals make decisions that minimize the delay to the next resource is a common idea in experimental psychology (Fantino and Abarca 1985; Tobin et al. 1996) and is often implicit in observational tests of primate foraging decisions. Observed movements usually are to the closest available resources (e.g., Garber 1989; Janson 1998). How-

ever, this is not always the case; primates can sometimes or even routinely bypass close resources to visit more distant but more productive ones (Garber 1989; Janson 1998; Cunningham and Janson 2007a; Noser and Byrne 2006; Valero and Byrne 2007), suggesting that they may maximize yield, rather than merely minimize travel. In either case, it is difficult to know if the observed pattern is different from that expected of random foraging unless it is tested against explicit simulated models of random movements (e.g., Janson 1998).

#### Long-term distance minimization

Altmann (1974) was among the first to suggest explicitly that primates might minimize the total distance traveled to acquire a given set of resources, although the idea was implicit in Menzel (1973). This problem is not solved by simply moving from each resource to its nearest neighbor, although that simple rule is usually not more than 20% longer than the shortest possible overall path (Anderson 1983). There is currently no evidence that primates can find the shortest overall path among a set of out-of-sight resources in the wild, although they may be able to do so within a small arena in captivity (Gallistel and Cramer 1996; Cramer and Gallistel 1997).

#### Minimizing travel effort

Although primates are often said to minimize foraging ‘effort’, this is usually equated with distance. However, when the terrain in a home range is very broken or hilly, distance and effort can become uncoupled (Milton 2000). Suarez (2003) used GIS and detailed topographic maps to show that spider monkeys may minimize elevation change along their travel routes even if that requires longer total distances to move from one resource to the next. The set of effort-minimizing routes in a mountainous landscape may be very limited, leading to the establishment of habitual or traditional routes (Di Fiore and Suarez 2007).

#### Reduced memory load

Di Fiore and Suarez (2007) suggest that the use of habitual travel routes may simplify the problem of remembering where resources are by arraying the resources along a small number of well-known routes. If this is the case, then one should expect to find frequent habitual travel routes used by primates even when they are not constrained by difficult terrain to follow a small set of energy-efficient paths. Although repetitive use of foraging pathways has been described for several primate species (e.g., Sigg and Stolba 1981; Terborgh 1983; Noser and Byrne 2006, 2007), such highly predictable pathways have not been reported for most species with well-documented daily movements.

### Return to resource when fully recovered

Nearly all studies of primate movements remark that primate groups rarely retrace their immediate pathways. Such a pattern could be due to pervasive scramble competition (van Schaik et al. 1983). When a cohesive group forages, it leaves a depleted swath behind it, so that individuals seeking unforaged areas or unused resources will generally move to the front of the group (see Janson 1990); repetition of this behavior leads to a forward movement bias. Such a forward movement bias does not require any explicit knowledge of resource location, but will also occur if a forager using a cognitive map moves from one known resource to the nearest available unused one (Fig. 1). No matter what the cause, a forward bias can lead to long and consistent delays in returning to a given resource even if the forager has no sense of time or resource renewal (Anderson 1983; C.H. Janson, unpublished data). A simple, albeit incomplete, way to visualize this is to imagine a toy boat with an electric motor in a bath tub—if the boat only moves forward, it will eventually hit the wall of the bath tub and start to circle the tub. An alternative adaptive model, suggested by researchers of species that ‘trapline’ renewing resources, is that animals regulate their return intervals to a resource so that the resource is recovered (or nearly so) by the time it is visited again, hence producing a deliberate cycle of re-visits. In support of this assumption, experiments with traplining hummingbirds by Gill (1988) showed that they returned more quickly when feeding stations renewed faster. Williams and Thomson (1998) tested for predictability in bumblebee foraging, and found that individual bees had significantly regular arrival and departure schedules, but that they did not return to the target plant when resources were more available. Janson (1996) tested whether capuchin monkeys appeared to understand the regularity of renewal of food on experimental platforms. The groups rarely revisited a site in less than 24 h (the shortest interval at which they would again receive food at that site), but the renewal interval was not varied, so it was unclear if the monkeys were responding to the renewal interval of the platforms or simply had foraging routes that usually kept them away from a site for more than a day.

### Reduce daily overlap in foraging areas

If primates use up the resources in the areas that they forage, they may need to avoid using the same areas or food sources for several hours to days. In this case, one should find a tendency for groups to avoid revisiting areas that were used recently. DiBitetti (2001) tested for and found such a pattern by wild capuchin monkeys in Argentina. This pattern implies at least that the animals remember areas in their home range, if not specific resources.

### Monitoring food resources

Although primate ecologists suggest that their study species monitor the ripening state of fruit trees (e.g., Terborgh 1983), obtaining direct evidence of such monitoring is difficult as it is usually performed while the monkeys are moving between other known food sources, or when they are foraging for invertebrates. Thus, most tests of this idea have been indirect. For instance, Di Fiore (2003) showed that foraging effort by woolly monkeys did not correlate well with ripe fruit abundance, even though this was the majority of the diet. Instead, their foraging effort was better predicted by the availability of unripe fruit, and he suggests that woolly monkey foraging routes might be dictated more by the need to monitor the state of unripe fruit trees than by the availability of ripe fruit. A subtler test of monitoring would be to analyze if the monkeys are more likely to return to a tree with fruit that was almost ripe when last visited than to one with less-ripe fruit. A conceptually similar study by Schwagmeyer (1995) found that male ground squirrels visited many females during the mating season, but they were more likely to return to a female’s territory when the female was in peak estrus (even if the female had been experimentally removed). Olupot et al. (1998) tested the monitoring hypothesis for a mangabey group by comparing their visitation rate to non-fruiting individuals of preferred versus non-preferred food trees, but found no difference and concluded that mangabeys do not monitor their food trees. However, Janmaat et al. (2006) compared the approach behavior of mangabeys toward pre-selected focal trees of one species, which did not have any fruit on them, but differed in whether they had recently finished fruiting (and thus were unlikely to produce new crops soon) or had not yet produced fruit during the study (increasing the chance that they would produce fruit in the future). Because both sets of trees lacked fruit, they should not have differed in any sensory cues for the mangabeys. Janmaat et al. (2006) found that the mangabeys were more likely to approach and inspect the trees that had not yet fruited, suggesting that the monkeys keep track of information on a particular tree’s fruiting history and monitor trees that are more likely to produce fruit in the future.

### Minimizing competition

Based on the fact that saki monkeys routinely skip over small trees with ripe fruit to visit more productive trees, Cunningham and Janson (2007a) suggested that saki monkeys attempt to reduce within-group feeding competition in tree crowns. The alternative hypothesis, that they are simply maximizing foraging gain rates by the selective use of more productive trees, could be tested by comparing the use of trees by groups of different sizes. Smaller groups

should show much greater use of small-crowned trees if food competition is the main cause of skipping small trees (Janson 1988). Instead, if small trees are passed by because they are less productive and so provide lower feeding rates than do larger trees for groups of all sizes, then there should be little effect of group size on the tendency to skip trees.

#### Other criteria

Many other possible goals of spatial foraging decisions can be imagined but are not tested at all. These include: minimizing or balancing variance in food intake rate; balancing fruit versus other diet components (Hladik 1977); minimizing intake of toxic leaves (Glander 1978), etc.

### Discussion

What do primates know about their food sources?

Laboratory and field experiments provide strong evidence that several species of primates remember the locations of some of their food sources (Menzel 1973; Janson 1998). This conclusion is further supported and enriched by descriptive analyses of spatial movements in the wild. The latter studies show that primate groups move preferentially, more directly, and faster toward more productive resources of a given type (e.g., Janson 1998; Pochron 2001; Janmaat et al. 2006; Cunningham and Janson 2007a; Noser and Byrne 2006, 2007), especially when the latter are scarce (Pochron 2005; Valero and Byrne 2007). This common observation suggests that primates anticipate the quantity of resource to be obtained at a particular location. Although return intervals to a food source may be consistent with anticipation of renewed food rewards (Janson 1996), direct tests for monitoring behavior have been indirect and weak. Nonetheless, Japanese macaques do appear to understand that fruits ripen relatively synchronously and will search preferentially for fruit trees of a given species once exposed experimentally to ripe fruit of that species (Menzel 1991). Mangabeys may distinguish between individual trees that are unlikely to produce fruit from those more likely to produce fruit, even in the same species (Janmaat et al. 2006).

There is less evidence and less consensus about how spatial and other information about resources is organized in primate memory. Some lab studies suggest that some primates have only egocentric views of space (Poti 2000), and this is consistent with evidence that they navigate through their home range by using local landmarks (Noser and Byrne 2007) or topographic features (Di Fiore and Suarez 2007). An egocentric view of space could also explain the frequent observation that primate groups typically move from one resource to the nearest available resource (e.g.,

Menzel 1973; Garber 1988; Janson 1998) or sometimes directly to the most productive of a set of nearby resources (Garber 1988; Janson 1998). However, it is not consistent with the observation that some primates appear to be able to plan routes that minimize distance across a set of resources (Cramer and Gallistel 1997) or will visit a small resource en route to a more productive one only if the detour required to reach the small resource is short (Janson 2007).

#### Observational support for resource cognition in wild animals

The preceding observations of primate spatial foraging provide evidence that there are many ways to show that foraging decisions are *consistent* with models of spatial foraging that assume knowledge of spatial location. However, except when detailed data are available on the possible detection methods and capacities of primates for particular foods, these observational data are usually also consistent with one or more null models of random movement that do not assume knowledge of spatial location (e.g., Janson 1998). Although field experiments can often resolve whether the movements are consistent with plausible models of movement that assume no spatial knowledge, such experiments are not always feasible. The point is not that primates or other animals are likely to lack spatial knowledge, but rather that it is difficult to demonstrate such knowledge when plausible models of random movement can reproduce the gross movement behavior of primate groups rather well. Is it then impossible to provide strong inferential support for spatial knowledge of food resources by primates (or other animals) using only field observations?

There is hope. The detection ability of an animal for its resources is a vital parameter needed to model the foraging process, but it can be estimated experimentally (Janson and Di Bitetti 1997) or by using human senses as a plausible substitute for animal ones (Janmaat et al. 2006; Noser and Byrne 2007). The latter strategy is likely to work best for animals that are relatively closely related to humans, such as primates, or for species that use senses similar to ours (dominated by vision, such as diurnal birds). It is important to keep in mind that detection distance will vary between resource types (Noser and Byrne 2007) and between different sizes of resources of a single kind (Janson and Di Bitetti 1997). Even if the detection distance cannot be estimated precisely, random models may converge on observed behavior only for values of detection distances so extreme as to be implausible (Janson 1998; Valero and Byrne 2007). In addition, the particular values of detection distances needed to make the random models fit observed behaviors change depending on the kind of behavior being examined (Janson 1998). For instance, in Janson's analysis, a random



search process could match the distribution of distances moved between goals if one assumed that the monkeys could detect food sources 250 m away, but this search field in the random model did not reproduce the observed sequence of movements among goals or the directness of travel among goals. To match the observed sequence of movements, the random search process required assuming a search field of 310 m and to match the directness of travel required a search field of 350 m. Thus, a random foraging model using one particular detection distance may fit one observed behavior but leave others unexplained. If no random model (assuming only one detection distance) is consistent with all the observed behaviors, which are instead overall consistent with an assumption of spatial knowledge, the latter receives more support.

If the detection ability of the animals for the resource is at least approximately known, many patterns that can be observed in wild animals may become difficult to explain as part of a foraging strategy that does not use knowledge of the spatial location of resources. For instance, if a foraging group shows increased movement speed as it approaches a food source that is not within detection range, this change would imply foreknowledge of the resource and thus the involvement of spatial memory (Pochron 2001). If the forager shows more directed travel toward more productive or scarce resources than to unproductive or easily replaced ones, the forager may be using knowledge of resource value (Janmaat et al. 2006). The ability of a forager to move toward a resource out of detection range in reasonably straight or efficient paths from many starting places (including natural or experimental displacements) argues for the use of at least a fine-grained landmark map if not a true geometric map (Garber 1988; Cunningham and Janson 2007a).

#### Future challenges

Integration of captive and field studies on the same species could help to clarify cognitive constraints on foraging in the wild and the adaptive value of particular cognitive capacities known from captivity. What can captive studies contribute to the interpretation of wild primate spatial foraging? There are many manipulations of the forager's world that are not feasible in the wild. For example, tests of long-term memory ideally require that the environment remain unchanged between trials separated by long intervals (e.g., Cunningham 2003). Similarly, for group-living primates, tests of foraging cognition necessarily take place in a social context, so it is not clear whether the behaviors observed are limited by or adjusted specifically to group foraging. Isolating an individual from a group allows the researcher to address what an individual knows or values when only its own foraging success is at stake.

Likewise exposure of one foraging individual in controlled social contexts can reveal what aspects, if any, it is noticing in the foraging behavior of others (e.g., Whiten et al. 1996; Hare et al. 2000; Hare et al. 2003; Bugnyar and Heinrich 2005; Bonnie and de Waal 2007). Adroit use of experimental manipulations in captive animals can reveal what sensory and cognitive processes they have been selected to possess in the wild (e.g., see Timberlake 2002 for examples with rodents). For instance, capuchin monkeys were shown to use tools in captivity for a long time before this ability was found to have any survival value in the wild (reviewed in Fragaszy et al. 2004). Similarly, the demonstration by Tobin et al. (1996) that primates can delay gratification (accept a large future reward instead of a small immediate reward) much better than rats or pigeons suggests that the food resources of primates are comparatively clumped and stable over time, as indeed fruit trees are.

Another challenge is to integrate the results of experimental studies, whether in the wild or in the captivity, to predict the movements of animals on unmanipulated resources in the wild. Ideally, one ought to be able to predict with high accuracy the movements of an individual or a group, if one possessed the same information that they do about food source location, the costs of potential travel paths, resource value and preference, the foraging strategies of other group members, non-foraging costs (such as predation risk) across the landscape, and the history of use of the resources and their recovery from such use. This predictive exercise would require a vast quantity of knowledge of the animal's perception of their resource characteristics, but it may be possible to obtain such data for animals foraging in simple habitats or in lean seasons when few species of foods are available.

Finally, an area of foraging cognition about which we have no more than small hints for any species is temporal knowledge or understanding. Do monkeys or other animals really understand the 'ripening' process in fruiting or flowering trees? Do they estimate the present value of resources depending on how long ago they were last visited, the size of the resource, and the probability that a competitor used the resource in the meantime? Or do they use some very simple rule of thumb, such as "stay away for a day, then expect the same amount of food we ate the last time"? Does an individual adjust its judgment of resource value depending on how many other animals were feeding in the resource and when during the feeding bout it was able to feed? Answers to these questions are vital if we are to understand the foraging behavior of animals using renewing resources, but will require focused experiments both in captivity, to assess the potential to learn temporal patterns, and in the wild, to see if this potential is used in practice when faced with resources of many different sizes, renewal

rates, and values, along with possible competition from a few to many dozens of species of competitors.

## References

- Altmann SA (1974) Baboons, space, time, and energy. *Am Zool* 14:221–248
- Anderson JD (1983) Optimal foraging and the traveling salesman. *Theor Popul Biol* 24:145–159
- Bonnie KE, de Waal FBM (2007) Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Anim Cogn*. doi:10.1007/s10071-006-0069-9
- Boyer D, Miramontes O, Ramos-Fernandez G, Mateos JL, Cocho G (2004) Modeling the searching behavior of social monkeys. *Physica A Stat Mech Appl* 342:329–335
- Bugnyar T, Heinrich B (2005) Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proc R Soc B Biol Sci* 272:1641–1646
- Byrne RW (2000) How monkeys find their way. Leadership, coordination, and cognitive maps of African baboons. In: Boinski S, Garber P (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 491–518
- Couzin ID, Krause J, Franks NR, Levin SA (2005) Effective leadership and decision making in animal groups on the move. *Nature* 433:513–516
- Cramer AE, Gallistel CR (1997) Vervet monkeys as travelling salesmen. *Nature* 387:464
- Cunningham EP (2003) The use of memory in *Pithecia pithecia's* foraging strategy. PhD dissertation, Anthropology, City University of New York. Available from: University Microfilms, Ann Arbor 64-03: 973
- Cunningham EP, Janson CH (2007a) Integrating information about location and value of resources by white faced-saki monkeys (*Pithecia pithecia*). *Anim Cogn*. doi:10.1007/s10071-007-0077-4
- Cunningham EP, Janson CH (2007b) A socioecological perspective on primate cognition, past and present. *Anim Cogn*. doi:10.1007/s10071-007-0078-3
- Di Fiore AD (2003) Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuni National Park, Ecuador. *Am J Primatol* 59:47–66
- Di Fiore A, Suarez SA (2007) Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Anim Cogn*. doi:10.1007/s10071-006-0067-y
- DiBitetti MS (2001) Home-range use by the tufted capuchin monkey (*Cebus apella nigrinus*) in a subtropical rainforest of Argentina. *J Zool* 253:33–45
- Dyer FC (1991) Bees acquire route-based memories but not cognitive maps in a familiar landscape. *Anim Behav* 41:239–246
- Fantino E, Abarca N (1985) Choice, optimal foraging, and delay-reduction hypothesis. *Behav Brain Sci* 8:315–330
- Fragaszy DM, Visalberghi E, Fedigan LM (2004) *The complete Capuchin: the biology of the genus Cebus*. Cambridge University Press, Cambridge
- Gallistel CR (1990) *The organization of learning*. Bradford Books/MIT Press, Cambridge
- Gallistel CR, Cramer AE (1996) Computations on metric maps in mammals: getting oriented and choosing a multi-destination route. *J Exp Biol* 199:211–217
- Garber PA (1988) Foraging decisions during nectar-feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*). *Biotropica* 20:100–106
- Garber PA (1989) Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *Am J Primatol* 19:203–216
- Garber PA, Hannon B (1993) Modeling monkeys: a comparison of computer-generated and naturally occurring foraging patterns in two species of neotropical primates. *Int J Primatol* 14:827–852
- Gill FB (1988) Trapline foraging in hermit hummingbirds: competition for an undefended renewing resource. *Ecology* 69:1933–1942
- Glander KE (1978) Howling monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery GG (ed) *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C. pp 561–574
- Gould JL (1986) The locale map of honey bees: do insects have cognitive maps? *Science* 232:861–863
- Hare B, Addessi E, Call J, Tomasello M, Visalberghi E (2003) Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? *Anim Behav* 65:131–142
- Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. *Anim Behav* 59:771–785
- Hladik CM (1977) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In: Clutton-Brock TH (ed) *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. Academic, London, pp 481–501
- Janmaat KRL, Byrne RW, Zuberbühler K (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Anim Behav* 72:797–807
- Janson CH (1988) Intra-specific food competition and primate social structure: a synthesis. *Behaviour* 105:1–17
- Janson CH (1990) Social correlates of individual spatial choice in foraging brown capuchin monkeys (*Cebus apella*). *Anim Behav* 38:910–921
- Janson CH (1996) Toward an experimental socioecology of primates: examples from Argentine brown capuchin monkeys (*Cebus apella nigrinus*). In: Norconk MA, Rosenberger AL, Garber PA (eds) *Adaptive radiations of neotropical primates*. Plenum, New York, pp 309–325
- Janson CH (1998) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Anim Behav* 55:1229–1243
- Janson CH (2007) Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Anim Cogn*. doi:10.1007/s10071-007-0079-2
- Janson CH, Di Bitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behav Ecol Sociobiol* 41:17–24. doi:10.1007/s002650050359
- Kamil AC (1978) Systematic foraging by a nectar-feeding bird, the Amakihi (*Loxops virens*). *J Comp Physiol Psychol* 92:388–396
- Manser MB, Bell MB (2004) Spatial representation of shelter locations in meerkats, *Suricata suricatta*. *Anim Behav* 68:151–157
- Menzel CR (1991) Cognitive aspects of foraging in Japanese monkeys. *Anim Behav* 41:397–402
- Menzel CR (1997) Primates' knowledge of their natural habitats: as indicated in foraging. In: Whiten A, Byrne RW (eds) *Machiavellian Intelligence II: extensions and evaluations*. Cambridge University Press, Cambridge, pp 207–239
- Menzel CR, Beck BB (2000) Homing and detour behavior in golden lion tamarin social groups. In: Boinski S, Garber PA (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 299–326
- Menzel EW Jr (1973) Chimpanzee spatial memory organization. *Science* 182:943–945
- Milton K (2000) Quo vadis? Tactics of food search and group movement in primates and other animals. In: Boinski S, Garber PA (eds) *On the move: how and why animals travel in groups*. University of Chicago Press, Chicago, pp 375–417
- Noser R, Byrne RW (2006) Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. *Anim Behav*. doi:10.1016/j.anbehav.2006.04.012

- Noser R, Byrne R (2007) Mental maps in chacma baboons (*Papio ursinus*): using intergroup encounters as a natural experiment. Anim Cogn. [10.1007/s10071-006-0068-x](https://doi.org/10.1007/s10071-006-0068-x)
- Olupot W, Waser PM, Chapman CA (1998) Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? Inter J Primatol 19:339–353
- Pochron ST (2001) Can concurrent speed and directness of travel indicate locational knowledge in free-ranging yellow baboons (*Papio h. cynocephalus*) of Ruaha National Park, Tanzania? Inter J Primatol 22:773–785
- Pochron ST (2005) Does relative economic value of food elicit purposeful encounter in the yellow baboons (*Papio hamadryas cynocephalus*) of Ruaha National Park, Tanzania? Primates 46:71–74
- Poti P (2000) Aspects of spatial cognition in capuchins (*Cebus apella*): frames of reference and scale of space. Anim Cogn 3:69–77
- Pyke GH (1978) Optimal foraging: movement patterns of bumblebees between inflorescences. Theor Popul Biol 13:72–97
- Ramos-Fernandez G, Mateos JL, Miramontes O, Cocho G, Larralde H, Ayalda-Orozco B (2004) Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). Behav Ecol Sociobiol 55:223–230. [10.1007/s00265-003-0700-6](https://doi.org/10.1007/s00265-003-0700-6)
- Schwagmeyer PL (1995) Searching today for tomorrow's mates. Anim Behav 50:759–767
- Shettleworth SJ (1998) Cognition, evolution, and behavior. Oxford University Press, New York
- Sigg H, Stolba A (1981) Home range and daily march in a Hamadryas baboon troop. Folia Primatol 36:40–75
- Stephens DW, Krebs JR (1987) Foraging theory. Princeton University Press, Princeton
- Suarez SA (2003) Spatio-temporal foraging skills of white-bellied spider monkeys (*Ateles belzebuth belzebuth*) in the Yasuni National Park, Ecuador. PhD Thesis, Dept of Ecology and Evolution, Stony Brook University, Stony Brook, 336 p
- Terborgh JW (1983) Five new world primates. Princeton University Press, Princeton
- Terborgh JW, Stern M (1987) The surreptitious life of the saddle-backed tamarin. Am Sci 75:260–269
- Thomson JD, Slatkin M, Thomson B (1997) Trapline foraging in bumble bees: II. Definition and detection from sequence data. Behav Ecol 8:199–210
- Timberlake W (2002) Niche-related learning in laboratory paradigms: the case of maze behavior in Norway rats. Behav Brain Res 134:355–374
- Tobin H, Logue AW, Chelonis JJ, Ackerman KT (1996) Self-control in the monkey *Macaca fascicularis*. Anim Learn Behav 24:168–174
- Valero A, Byrne RW (2007) Spider monkey ranging patterns in Mexican subtropical forest: Do travel routes reflect planning? Anim Cogn. [10.1007/s10071-006-0066-z](https://doi.org/10.1007/s10071-006-0066-z)
- van Schaik CP, van Noordwijk MA, de Boer RJ, den Tonkelaar I (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). Behav Ecol Sociobiol 13:173–181
- Vlasak AN (2006) Global and local spatial landmarks: their role during foraging by Columbian ground squirrels (*Spermophilus columbianus*). Anim Cogn 9:71–80
- Whiten A, Custance DM, Gomez J-C, Teixidor P, Bard KA (1996) Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). J Comp Psychol 110:3–14
- Williams NM, Thomson JD (1998) Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. Behav Ecol 9:612–621