CHAPTER 4

Foraging Cognition in Nonhuman Primates

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FORESTS AS PRIMATE HABITATS: COEVOLUTION OF PRIMATES AND FRUIT

In terms of total biomass, primates are very successful vertebrates in most undisturbed tropical forests (Chapman et al., 1999a; Fleagle & Reed, 1996). Many primate species are forest dwellers, and the forest habitat is likely to have had a major impact on primate evolution. This is especially true for the great apes, whose changes in diversity have followed climate-related retractions and expansions of wooded habitats since the late Miocene (Potts, 2004). Most primates, including typical leaf-eaters, consume considerable amounts of fruits as part of their daily diets (e.g., Korstjens, 2001). Fleshy fruits and the arthropods that associate with them are highly nutritious, which provide arboreal animals, such as primates, birds, and bats, with a stationary and relatively reliable source of energy (Janmaat et al., 2006a). Primates and fruiting trees have shared a long evolutionary history, and the arrival of angiosperm fruits and flowers may have been of particular importance in primate evolution (Soligo & Martin, 2006; Sussman, 1991, 2004). About 85 million years ago, a trend toward increased fruit size can be found (Eriksson et al., 2000), roughly coinciding with the radiation of early ancestors of today's primates, about 82 million years ago (Tavaré et al., 2002).

Compared to other groups of animals, primates possess a number of adaptations that make them particularly suited for arboreal foraging on fruit. Many primate species have opposable thumbs and toes, allowing them to grasp and reach fruit at the terminal tree branches, which are inaccessible to many other animals. Hindlimb dominance and grasping ability enable many primates to leap between trees in an energetically efficient way, in contrast other arboreal mammals such as most tree squirrels (Gebo, 2004; Sussman, 1991; Taylor et al., 1972). Other adaptations concern forward-facing eyes and stereotypic vision, which facilitates hand–eye coordination and foraging at high speed (Cartmill, 1972; Gebo, 2004). Similarly, diurnal activity, high visual acuity, and color vision enable spotting of fruit and their nutritional value from large distances (Barton, 2000; Polyak, 1957; Riba-Hernández et al., 2005; Sumner & Mollon, 2000). Diurnal foraging is also beneficial because ripening rates of fruits tend to be highest in the early afternoon following high midday incident radiation and ambient temperature (Diaz-Perez et al., 2002; Graham et al., 2003; Houle, 2004; Spayd et al., 2002).

EVOLUTIONARY THEORIES OF PRIMATE COGNITION

Primates, and especially humans, have relatively larger brains than other groups of mammals (Harvey & Krebs, 1990; Jerison, 1973). It has also been noted that a variety of brain size variables in primates correlate positively with measures of social complexity, such as group size, deceptive behaviour, or strength of social bonds (Barton, 1996, 1999; Byrne & Corp, 2004;

Dunbar, 1998; Dunbar & Shultz, 2007). This has been taken to suggest that large groups, and social complexity that emerges from them, have acted as a primary selection force favouring the evolution of increased brain size. This is because high social intelligence is likely to provide individuals with a competitive and reproductive advantage over their less socially skilled conspecifics.

As appealing as it is, the social intelligence hypothesis has a number of problems. Large promiscuous multimale/multifemale groups, the presumed breeding grounds for high social intelligence, are the exception in primate societies (Smuts et al., 1986) and it is often not specified how group size relates to social complexity. Moreover, although food competition is likely to increase with group size, larger groups also benefit from increased search swath and accumulated knowledge of individuals to locate food sources, avoid predators, and deal with neighboring groups (Garber & Boinski, 2000; Janson & Di Bitetti, 1997). Individuals are especially likely to benefit from older and more knowledgeable group members during periods of food scarcity when long-term experience is more crucial (Byrne, 1995; Chauvin & Thierry, 2005; van Roosmalen, 1988). The social intelligence hypothesis also struggles to explain how exactly primates were able to grow expensive large brains in the first place. Why did primates benefit more than other social animals from increased encephalization? The relationship between neocortex and group size is certainly real, but the causal arrow could also point the other way: Primates have evolved large brains for nonsocial reasons, which enables them to live in larger groups, form more complex social systems, and maintain more complex social relations than other smaller-brained species (Müller & Soligo, 2005).

A main contender of social intelligence is the "ecological intelligence" hypothesis developed by Milton (1981). Large brains, according to this idea, are the evolutionary products of extensive mental mapping requirements faced by frugivorous species, a hypothesis that emerged from empirical work comparing highly encephalized and frugivorous spider monkeys (*Ateles geoffroyi*) with less encephalized folivorous howler monkeys (*Alouatta palliata*). It is interesting that in diurnal frugivorous primates, relative brain enlargements are primarily found within the visual system, while in nocturnal species enlargements are in the olfactory structures (Barton et al., 1995), suggesting that the brain has directly responded to the demands of foraging. In addition, increases in the degree of orbital convergence (associated with stereotypic vision) correlate with expansion of visual brain structures and, as a consequence, with overall size of the brain (Barton, 2004).

Compared to other body tissues, brains are metabolically expensive organs, requiring a continuous and reliable flow of nutrients (Armstrong, 1983; Mink et al., 1981). According to recent analyses, relative brain size is positively correlated with basal metabolic rate, indicating that larger brains may be a reflection of being able to sustain higher basal energy costs (Isler & van Schaik, 2006a). Any increase in relative brain size, therefore, may only be possible in populations that have managed to either improve their access to nutrition or decrease other existing energy demands. Energy can be saved, for example, by reducing an organism's locomotor costs (Isler & van Schaik, 2006b) or reducing the metabolic requirements of other expensive tissues, such as the digestive system (Aiello & Wheeler, 1995). Higher-quality foods, such as fruit and animal matter, are easier to digest than other material, allowing the organism to reduce the size of its digestive tract. This hypothesis is supported by the findings that frugivorous primates usually have relatively larger brains and smaller digestive systems than folivorous primates (Barton, 2000; Clutton-Brock & Harvey, 1980; Hladik, 1967).

The various special adaptations for harvesting the fruits discussed in the previous section enabled primates to monopolize one of the most nutritious food sources in these forests. This may have allowed primates, especially haplorhines (see Chapter 1) that live in areas with relatively high fruit production, to afford larger brains than other groups of animals (Cunningham & Janson, 2007; Fish & Lockwood, 2003). What benefits they gain

from this relatively costly trait and what selection pressures have favored its evolution is subject of an ongoing debate.

In sum, a more complete understanding for why primates have relatively bigger brains than other groups of animals requires evidence at the ultimate and proximate level (Tinbergen, 1963). The current literature favors social explanations, mainly because of what is available in terms of empirical studies, but we have outlined a number of reasons for caution. By contrast, we discuss recent empirical progress on understanding the impact of foraging problems on cognition. The studies we review all have been conducted with the intent to investigate the cognitive capacities employed by nonhuman primates in relation to finding food in their natural habitats, and we contend that some of these findings are of direct relevance to the ecological intelligence hypothesis.

HOW DO FOREST PRIMATES KNOW WHERE TO FIND FRUIT?

A large-bodied monkey group's home range can contain as many as 100,000 trees (e.g., *Lophocebus albigena johnstonii*; Waser, 1974), yet only a small fraction of these trees will carry ripe fruit at any given time. Estimates for some forests vary anywhere from 50 to 4,000 trees per average home range (Janmaat et al., submitted). Are primates able to find these trees, and how efficient are they at doing so? A number of studies found that wild primates were more efficient in finding food than predicted by random search models, suggesting that individuals use some mental heuristics to locate food (e.g., Cunningham, 2003; Garber & Hannon, 1993; Janson, 2000; Milton, 2000; Valero & Byrne, 2007). In our own studies on gray-cheeked and sooty mangabeys (*Lophocebus albigena johnstonii*; *Cercocebus atys atys*), we found that monkeys were more likely to approach and search for fruit under or in trees that had produced fruits than empty trees of the same species (Janmaat et al., 2006b; Figs. 4.1 and 4.2).

We also found that target trees with fruit were approached significantly faster and with sharper angles than trees without fruit (Janmaat, 2006;

Figure 4.1   A gray-cheeked mangabey (*Lophocebus albigena johnstonii*) feeding on purple flowers of *Milettia dura*. Picture by Rebecca Chancellor.

Janmaat et al., 2006b; Figs. 4.3 and 4.4). When we measured the number of trees that were encountered while following individual monkeys, we found that they encountered or approached significantly more fruit-bearing trees than during control transects (i.e., when the observer walked a path parallel to the monkey's own route) (Janmaat, 2006; Janmaat et al., submitted).

It has been argued that the most efficient way to optimize foraging success is to mentally represent the location of all fruit trees in a home range as well as their fruiting state and overall temporal patterning, that is, to maintain a cognitive map (Milton, 1981, 2000). According to most definitions, cognitive maps are mental representations of the real world, as if viewed from above, a Euclidian representation of landmarks with vector distance and angular relationships between them (O'Keefe & Nadel, 1978; Tolman, 1948).

Figure 4.2 Terrestrial sooty mangabeys (*Cercocebus atys atys*) foraging for insects in dead wood. Picture by Karline Janmaat.

However, current evidence suggests that it is not very likely that nonhuman primates, or even humans, represent their home ranges in such a way (Byrne, 1979; Janson & Byrne, 2007). One crucial empirical test for the cognitive map hypothesis concerns the responses of individuals to obstacles on a foraging route (Bennett, 1996), that is, whether they are capable of finding an efficient detour. So far, wild primates have failed this test. In one study, the behavior of wild Chacma baboons (*Papio ursinus*) was studied when encountering neighboring groups on their habitual foraging routes. Individuals did not take detours around such groups to get to their foraging goal, but either waited for them to pass by or simply abandoned their goal completely (Noser & Byrne, 2007a). Some support for

something like a cognitive map comes from a captive study with a young bonobo (*Pan paniscus*) that was tested with an artificial lexigram system, but it is unclear to what degree primates use this capacity in the wild (Menzel et al., 2002).

SPATIO-TEMPORAL MENTAL REPRESENTATIONS IN THE NATURAL HABITAT

Apart from the general difficulties of providing empirical evidence for a cognitive map, no one seriously doubts that primates are able to mentally represent space in some way, although in many cases it is not clear what exactly these representations consist of, especially in the
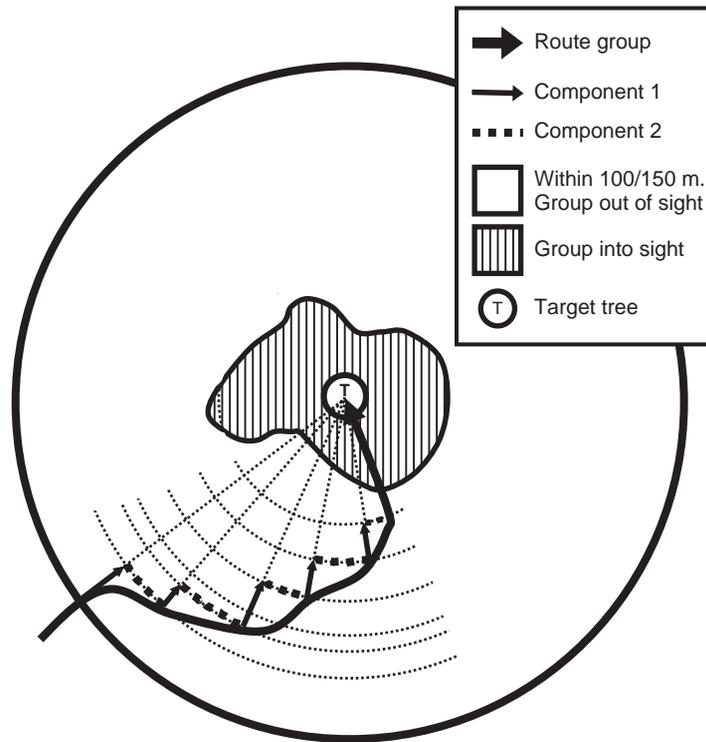
Figure 4.3 Illustration of the method used to measure speed toward a target tree. The observer follows the group while staying within a 5-m distance of the individual that is closest to the target tree. Following took place in two components of direction, either along (a) component 1 (arrow) that is directed toward the tree trunk or (b) component 2 (thick dotted line), which is directed along the imaginary circle around the tree trunk. Speed was determined by counting steps per minute when walking in the direction of the tree (component 1) only. The observer was updated on the direction of the tree trunk by the calling or clicking sounds produced by a second observer, who was waiting under the tree trunk. The outer circle has a radius of 100 or 150 meters dependent on the species. The shaded area represents the area in which the group comes into sight of the second observer waiting under the tree.

natural habitat. A major challenge in field studies is to determine if primates reach a resource by goal-directed travel, an indicator of mental representations of space, or by chance. It is important to consider that the shortest route is not always the most efficient one, and that animals could combine different goals in one single route, and that they could monitor food without exploiting it (Sigg & Stolba, 1981). Some researchers have generated geometric or step models combined with sophisticated statistics to determine the likelihood of whether spatial representations are involved in travel decisions (Bates, 2005; Cunningham & Janson, 2007; Garber &

Hannon, 1993; Janson, 1998; Milton, 2000; Noser & Byrne, 2007a; Valero & Byrne, 2007).

In one experiment with Argentinean capuchin monkeys (*Cebus apella nigritus*), three feeding sites were arranged in a triangle and provisioned once per day. Once a monkey group had chosen a site, its next choice was between the two remaining sites, a close one with less food and a far away one with more food. The surprising finding was that capuchins generally chose the closer feeding site, even when the more distant site offered up to 12 times as much food (Janson, 2007). Should we conclude that the monkeys did not possess a mental
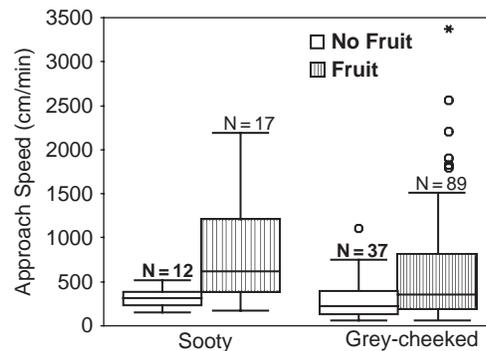
Figure 4.4 Speed of approach to trees with and without fruits. For both mangabey groups, bars represent the median speeds, while the top and bottom of the boxes represent the percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. Circles and stars represent outliers and extreme values.

representation of the locations and value of the provided food? Alternatively, did they simply weigh up travel distance and likelihood of arriving at the food in time in the highly competitive situation of a rainforest? Further experiments will be required to determine what exactly influenced the monkeys' foraging decisions.

Similarly, a recent study on Chacma baboons (*Papio ursinus*) showed that the sleeping cliff, a presumably important goal, was not always approached fast and in a straight line, because the group was regularly foraging for seeds close to the sleeping site (Noser & Byrne, 2007b). Spider and woolly monkeys (*Ateles belzebuth*; *Lagothrix poeppigii*) travel through their home ranges along repeatedly used paths, which has been taken as evidence that spatial mental representations are in the form of route-based or network maps (De Fiore & Suarez, 2007). Nonrandom foraging patterns have also been reported from tamarins (*Saguinus mystax, S. fuscicollis*) in the Amazon of northeastern Peru (Garber, 1989). For great apes, the empirical evidence for spatial cognition is surprisingly weak. One study on tool-transporting behavior in wild chimpanzees (*Pan troglodytis*) concluded that subjects remembered distances between different nut-cracking sites and different stone hammers, as if using Euclidian space, but this interpretation is controversial (Boesch & Boesch, 1984).

The Role of Secondary Cues

One problem with field studies is that it is often difficult to make reliable assumptions about how far an individual can detect, using both visual and olfactory sensory information, a target resource. Moreover, travel decisions may be influenced by other secondary cues, such as food calls of other species. The availability of visual cues is particularly difficult to assess in a rainforest where fruit trees are sometimes visible over considerable distances, even from the ground. Humans are capable of spotting fruits in emergent trees from a distance of 150 m if the view is unobstructed, suggesting that other primates may possess comparable abilities (Golla et al., 2004; Janmaat, unpublished data).

Only a small number of field studies have been able to convincingly reject the use of such sensory cues to find resources (Garber & Paciulli, 1997; Janson, 1998; Janson & Di Bitetti, 1997; Sigg & Stolba, 1981). For example, departure latency in Chacma baboons was significantly shorter before traveling to scarce mountain figs compared with traveling to other more abundant fruit sources. Because the fig trees were approximately 700 m from the sleeping site, visible to human observers only from short distances, it was unlikely that the monkeys were guided by any secondary cues (Noser & Byrne, 2007b). In another study, the

ranging behavior of sooty mangabeys was studied in relation to Anthonota trees with empty crowns (Janmaat et al., 2006a; Fig. 4.5). Monkeys approaching within 150 m of empty trees were more likely to approach if the tree was surrounded by fruits that had fallen to the forest floor than if the tree had not produced any fruit. The authors were able to rule out the possibility that the monkeys had seen any of the inconspicuous fallen fruits in the leafy substrate, indicating that the monkeys used spatial knowledge acquired during previous feeding experiences to relocate trees with fruit (Janmaat et al., 2006b).

In a similar way, gray-cheeked mangabeys that came within 100 m of an empty *Ficus sansibarica* tree were less likely to enter if the tree had recently been depleted than if the tree had not produced any fruits so far (Fig. 4.6). Since both tree types had empty crowns, with no differences in overall appearance, the visiting pattern was best explained by memories of previous visits (Janmaat et al., 2006b).

In sum, it seems safe to assume that navigation of primates in their natural habitats involves some kind of mental representations of space, but it is often unclear how enduring and rich these memories really are. Memories of spatial locations could be relatively short lived (a few days), and there is no good evidence for a geometric representation of space (Byrne, 2000; Janson, 2000).

## EVIDENCE FOR FRUIT LOCALIZATION STRATEGIES

Another characteristic of forest fruits concerns their ephemeral nature. Temporal patterns of emergence can be complex, and fruits are often present for short periods only (Chapman et al., 1999b; 2004; Janmaat et al., submitted; Milton, 1981, 1988). Many fruit tree species rely on animals for seed dispersal and have evolved features that make their fruits appeal to a large number of species, leading to high levels of inter- and intraspecies competition (e.g., Hauser & Wrangham, 1990; Houle et al., 2006; McGraw & Zuberbühler, 2007; Sterck, 1995). Early arrival is therefore advantageous, and natural selection is likely to favor any cognitive strategy that makes this behavior possible. In the following final section, we discuss a number of behavioral strategies, and their potential underlying cognitive processes, that enable free-ranging primates to deal with these temporal constraints.

Monitoring Individual Trees

Gray-cheeked mangabeys have been observed to bypass about a third of all available fruit-bearing fig species (Janmaat et al., 2006b). The monkeys were more likely to revisit trees in which they had good feeding experiences before, compared to trees in which they were less successful. Similar

Figure 4.5 A sooty mangabey eating *Anthonota fragans* fruit (left). Picture by Karline Janmaat. Ripe *Anthonota fragans* fruits are harvested by the monkeys after they have fallen into the leaf litter underneath the tree (right). Picture by Ralph Bergmüller. Used with permission.
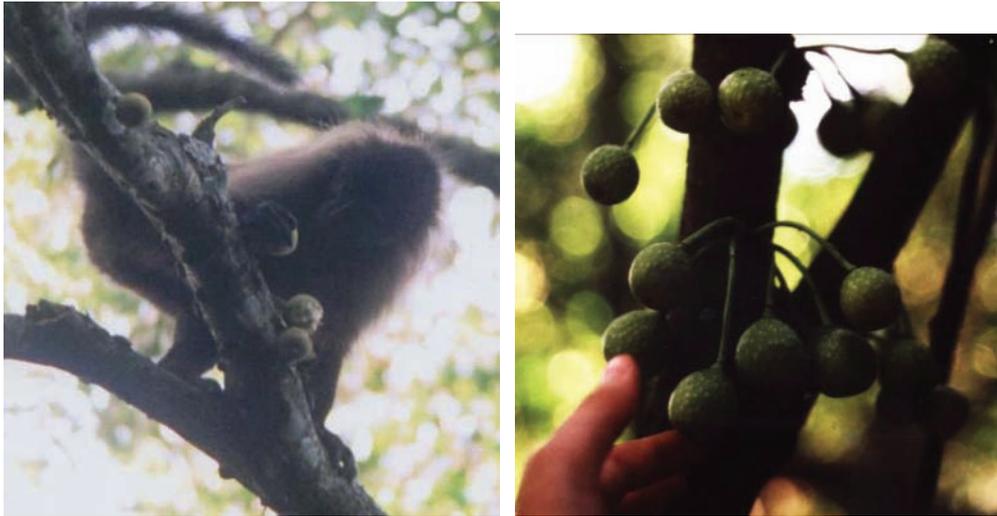
Figure 4.6 A gray-cheeked mangabey inspecting the ripening state of *Ficus sansibarica* fruit (left), *F. sansibarica* fruit (right). Pictures by Karline Janmaat. Used with permission.

patterns have been reported from a study on wild tamarins (Garber, 1989). For the mangabeys, intriguingly, this was also the case for fig trees with unripe fruits. Unripe figs are attractive to these monkeys because some of them contain weevil larvae or edible seeds. Monkeys have to inspect each fig individually, an interesting fact for the purpose of cognitive studies, because it effectively rules out the possibility that the monkeys responded to long-distance visual or olfactory cues (Janmaat et al., 2006a). In addition, the authors also found that the average speed with which the group approached such trees was significantly correlated with their average prior feeding experience in that tree (Fig. 4.7). Similar results have been reported from free-ranging sakis (*Pithecia pithecia*) in Venezuela. These primates bypassed a majority of fruit-bearing trees without feeding because they preferentially revisited specific trees, which they already knew as highly productive from prior visits (Cunningham & Janson, 2007).

In sum, there is good evidence that primates are able to distinguish between individual trees, which they assess in terms of quality, and that they use such memories in their daily foraging decisions.

Monitoring Meteorological Cues

Work on captive primates has shown that they can readily learn to anticipate delayed food rewards (Dufour et al., 2007; Ramseyer et al., 2005) and that they can trade off reward
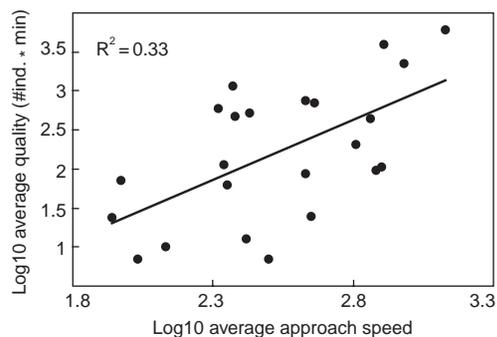
Figure 4.7 Approach speed to trees of different quality. The sum of quality values per tree is plotted in relation to the average of the total speeds with which the gray-cheeked group traveled toward that tree. Each dot represents the values of a target tree that carried unripe fruits. Values are based on an average number of three visits ($N_{min} = 1$, $N_{max} = 11$).

amount versus time delay (Stevens et al., 2005). Similar suggestions for a rudimentary ability to anticipate future events have also been made for wild primates, but only a few good empirical studies are available (Janmaat et al., 2006a; Janson, 2007; Noser & Byrne, 2007b; Sigg & Stolba, 1981; Wrangham, 1977).

Temperature and solar radiation influence ripening rates of fruits as well as the maturation of insect larvae inside them (e.g., Adams et al., 2001; Diaz-Pérez et al., 2002; Houle, 2004; Mazzei et al., 1999; Morrison & Noble, 1990), making the emergence of edible fruits somewhat predictable. A recent study on free-ranging mangabeys investigated whether these primates were able to take previous weather conditions into account when deciding to revisit particular fruit trees (Janmaat et al., 2006b). For this purpose, a study group was followed from dawn to dusk for three continuous long observation periods totalling 210 days, yielding an almost complete record of all revisit decisions toward 80 preselected fruit trees (Fig. 4.8).

The results were consistent with the idea that these monkeys made foraging decisions based on episodic-like memories of whether or not a tree previously carried fruit, combined with a more generalized understanding of the relationship

between temperature and solar radiation and the maturation rate of fruit and insect larvae (Fig. 4.9). How exactly the monkeys managed to register the relatively subtle differences in average temperature values was not addressed, a topic for further research.

Monitoring Competitor Behavior

The presence of other fruit-eating individuals may also serve as a reliable indicator of the presence of edible fruits, especially for tree species that do not have predictable patterns of fruit emergence and that do not offer conspicuous secondary cues of edibility. In free-ranging tamarins (*Saguinus imperator* and *S. fuscicollis*), high-ranking individuals tended to monitor the activities of other group members, rather than to initiate their own food searches, providing evidence that these primates were able to associate social cues with the presence of foods (Bicca-Marques & Garber, 2005). Similarly, Tonkean macaques, *Macaca tonkeana*, kept in a large outdoor enclosure used food odor cues, acquired by smelling the mouths of other group members, to guide their own search for food (Chauvin & Thierry, 2005).

Primates also use auditory cues, such as feeding calls of group members, to find fruit
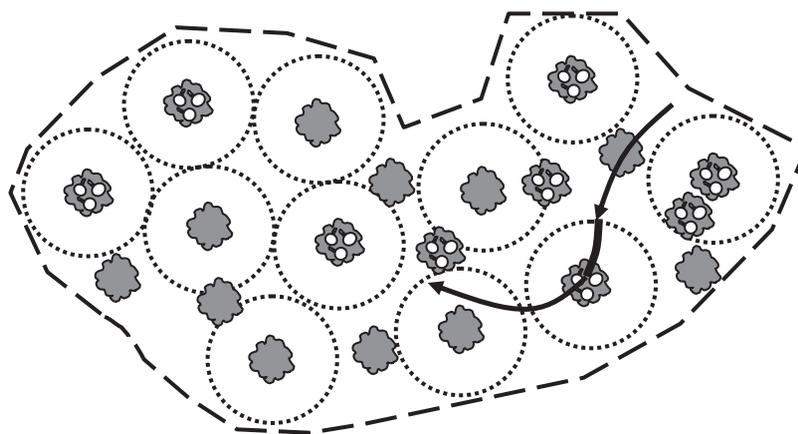
Figure 4.8 Measuring revisiting Behavior. The diagram illustrates an example of part of the study group's daily route (arrows) among target trees, each surrounded by an imaginary 100-m radius circle (dotted line). Once the group entered the circle, one observer rushed to the tree to determine the fruiting state and whether the group came into sight and entered the tree. In this example, the group visited one tree with fruit and bypassed one without fruit.
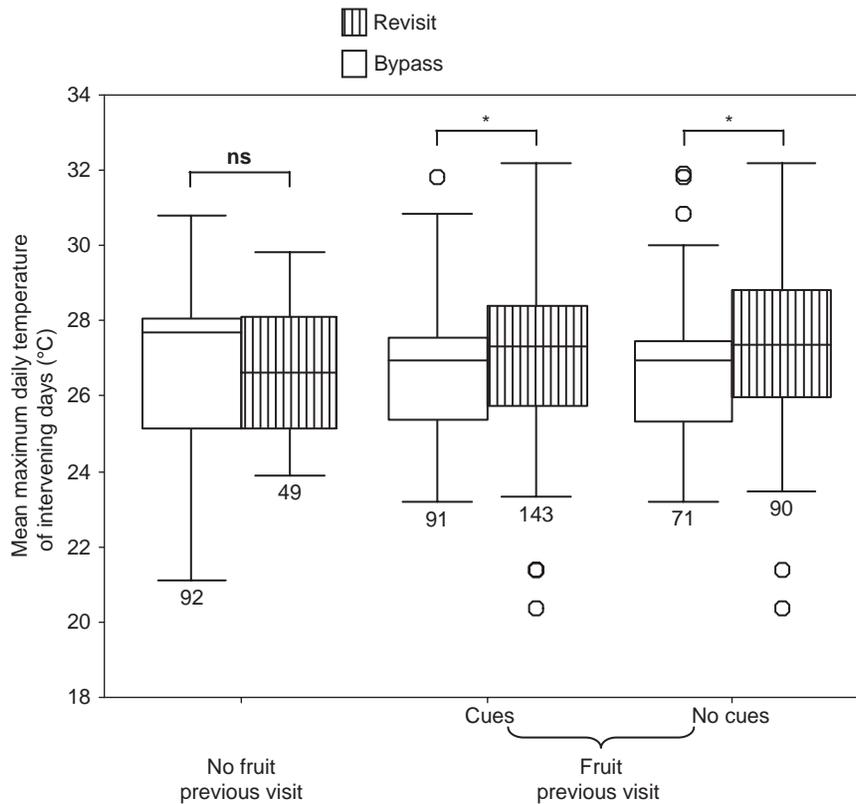
Figure 4.9 The influence of temperature on revisiting behavior. Average daily maximum temperature determined for the intervening period between the time the group entered the 100-m-radius circle and the time the group last visited the same tree. Shaded boxes represent average temperature values for revisits; white boxes represent bypasses. Different clusters refer to trees that (1) did not carry fruit at the previous visit, (2) carried fruit at the previous visit, and (3) carried fruit at the previous visit but no longer offered any sensory cues. Bars represent the median values of the average temperatures; top and bottom of the boxes represent the 75 and 25 percentiles. Whiskers represent highest and lowest values; circles represent outliers. Results showed that average daily maximum temperature was significantly higher for days preceding revisits than bypasses. These effects were found only for trees that carried fruit at the previous visit but not for trees that had carried none, providing empirical evidence that these primates were capable of taking into account past weather conditions when searching for food.

(e.g., tamarins, *Saguinus labiatus*: Caine et al., 1995; macaques, *Macaca sinica*: Dittus, 1984). Red-tailed monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), and gray-cheeked mangabeys have been suggested to recognize the food-arrival calls of sympatric frugivores (Hauser & Wrangham, 1990).

In Kibale National Park, Uganda, fig trees that carried fruit contained a significantly larger number of noisy frugivorous animals, such as chimpanzees or hornbills, than fig trees that carried none, suggesting that primates could use the sound of sympatric foragers as an indicator for fruit availability (Janmaat, 2006). We thus analyzed the behavior of our mangabey study group on 10 different occasions when they discovered newly emerged or newly ripened fruits (Janmaat, 2006). In 2 out of 10 encounters, the tree was already occupied by a chimpanzee or hornbills feeding inside the tree, and interestingly in these cases the speed of approach was much higher than in the other eight cases (Fig. 4.10).
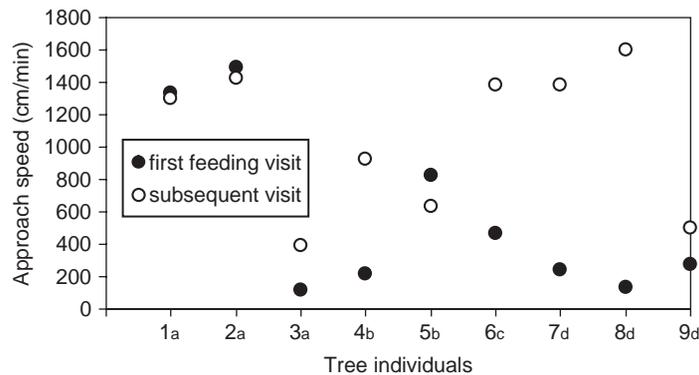
Figure 4.10   Speed of approach at discoveries of new edible figs. Closed circles represent the speed with which a mangabey group approached a fig tree in which the group was thought to discover newly emerged edible fruits. Open circles represent the speed with which the group approached the same tree at the subsequent visit. Trees 1 and 2 were occupied by other frugivores before the group's arrival. a, b, c, and d represent the type of discovery visit: type (a) a feeding visit that succeeds a visit in which the group entered but did not eat; (b) a feeding visit in which the tree had grown new fruits during the observation period (50, 60, or 100 days); (c) a feeding visit in which the tree had grown new fruits during the observation period and that succeeds a visit in which the group entered but did not eat; and (d) the first time that feeding was observed in a tree after a period of at least 40 days in which the group did not come within 100 m of the same tree.

Olupot and colleagues (1998) found that mangabeys were more likely to travel in the direction of areas from which hornbills (*Bycanistes subcylindricus*) were calling earlier in the day compared to other areas. Of course, it is possible that the monkeys already knew that the targeted area contained fruit from previous visits, regardless of the hornbills' behavior. Apart from these and other anecdotes (e.g., Kinnaird & O'Brien, 2000), little systematic experimental research on the use of auditory cues in fruit finding has been conducted.

To address the issue, we conducted a series of playback experiments in which we played different animals' sounds from fig trees that either carried no fruit or only unripe, inedible fruits. We used calls produced by hornbills or chimpanzees, which were recorded while individuals were feeding inside fig trees (Fig. 4.11). As a control, we used the territorial calls of a local bird species, the yellow-rumped tinkerbird (*Pogoniulus bilineatus*). KJ carried out all experiments with the help of field assistants. For each trial the speaker was positioned at an elevation of at least 12 m within a fig tree.

Our observations suggested that the presence of chimpanzees did not stop the mangabeys from approaching fruit trees, despite the fact that chimpanzees are notorious monkey predators. During continuous observation periods totaling 210 days, we observed seven times that the study group was feeding in a fig tree when chimpanzees arrived. Three times the mangabeys left the tree after being chased by male chimpanzees, which were in groups of more than four. Four out of seven times, however, the monkeys continued feeding together with the chimpanzees, but these were usually single individuals or small groups. Twice, one of the mangabey males even chased a female chimpanzee out of the tree. On a further six occasions, the mangabeys encountered chimpanzees that were already feeding inside a fig tree. In all cases, the study group eventually entered the tree, five times within 100 minutes after waiting at the same spot, and one time only after 6 hours, after some additional traveling.

To investigate systematically whether these monkeys took the presence of other frugivorous species into account when trying to locate food

Figure 4.11   Chimpanzees often produce pant-hoot and rough grunts before feeding on *Ficus capensis* fruits. Picture by Karline Janmaat. Used with permission.

trees, we conducted two playback experiments. The first consisted of a small number of calls (hornbill and chimpanzee), played from inside fig trees, with variable fruiting states, at a distance of 50 m to 200 m from five different mangabey groups. The second type consisted of a large number of hornbill or tinkerbird calls, played from inside fig trees, regardless of whether we knew of the presence of any monkeys nearby.

After playing back hornbill vocalizations, the experimental tree was reliably approached by other hornbills, suggesting that the playback stimuli were effective. However, we never managed to attract any mangabeys in response to playback of chimpanyee or hornbill calls compared to tinkerbird control calls. When comparing latency and duration of looking towards the speaker, we did not find any differences between the hornbill calls and tinkerbird control calls. We also failed to detect any differences in these measures when comparing playbacks of

chimpanzee feeding grunts, played from within a fig tree, with chimpanzee pant hoot vocalizations, played from the forest floor. Finally, the monkeys did not respond differently to chimpanzee feeding grunts played from empty trees or trees with potentially ripe fruits (Janmaat 2006). An alternative explanation is that the mangabeys had previously visited the experimental trees and already knew that the tree did not carry any edible fruits.

Monitoring Synchronicity

Most rainforest trees produce fruits synchronously with fruit production peaking some time of the year (Chapman et al., 1999b; van Schaik et al., 1993). In these species, finding fruit in one tree can be a reliable indicator for the presence of fruit in other trees of the same species, potentially allowing primates to make predictions about where to find fruit without having to remember the fruiting states of individual trees. Japanese macaques (*Macaca*

fuscata), artificially provisioned with fruits of the *Akebia trifoliate* vines prior to fruiting season, were more likely to inspect other *Akebia trifoliate* vines than if they were provided with other food items (Menzel, 1991). Intriguingly, the monkeys manipulated both *Akebia trifoliata* and *Akebia quinata* vines, although the leaves and fruits of this vine species look very different. Both *Akebia* species fruit simultaneously, suggesting that the monkeys were not simply searching for the original source of the presented fruit, but used the discovery of a fruit as an indicator for the presence of fruit in vines of the same or other simultaneous fruiting vine species.

Compared to temperate zones of the Japanese woodlands, seasonality is much less pronounced in African rainforests (Walter, 1984; Worman & Chapman, 2005). In Kibale forest, Uganda, a majority of tree species fruit synchronously (64%), but the percentage of trees that carry fruit during fruiting peaks differs substantially between species, and within species between years and areas (Chapman et al., 1999b; Janmaat et al., submitted). For example, *Strombosia scheffleri* produced fruits only four times within 12 years (Chapman et al., 2004), with variable peaks from 5% to 50%. In May 1996, 60% of the *Uvariopsis congensis* population at the Kanyawara research site carried fruit, while none did at three other research sites, all within a 12-km distance (Chapman et al., 2004).

In a recent study, Janmaat and colleagues (submitted) investigated the foraging behavior of gray-cheeked mangabeys in relation to different levels of synchronicity in rainforest fruit species. Results showed that active searching was only triggered if the monkeys encountered high frequencies of trees with ripe fruits in the same area. Thresholds for switching to an "inspect-all" strategy appear to vary between different tree species, perhaps influenced by the nutrition value and productivity of the trees. Such a strategy is likely to be adaptive for the monkeys, because it allows them to flexibly respond to frequent and irregular fluctuations in fruit production and differences in nutritional value between species (Chapman et al., 1999b, 2003, 2004; Janson et al., 1986; Worman & Chapman, 2005). The results were also consistent with the findings that primates generally forage on a relatively small number of commonly distributed species per time period (Eckardt & Zuberbühler, 2004; Janson et al., 1986) and "trap-line" trees of species that have a high density and high fruit production (Janson et al., 1986; Milton, 2000; Terborgh & Stern, 1987). At a proximate level, it is possible that monkeys develop a "search image," originally proposed to explain the behavior of predators (Tinbergen, 1960). Identifying trees by their visual features is not a trivial task, as trees of different fruit species can resemble each other to a high degree (Janmaat, 2006; Fig. 4.12). During the entire study period the mangabeys fed on 28 different fruit tree species, suggesting that the monkeys must be able to retain a long-term memory of the specific visual characteristics of a large number of fruit tree species, which could require substantial processing power (Barton, 2000; Fagot & Cook, 2006).

CONCLUSIONS

Several decades ago, Eisenberg (1973) and Napier (1970) described what sets primate societies apart from those of other long-lived animals. The suggestion was that primates were equipped with brains able to store and retrieve a great deal of independently acquired information about the environment and able to apply considerable degrees of behavioral plasticity in responding to specific situations. In searching for food, primates could be more skilled than other groups of animals in their abilities to combine and integrate different types of information. For example, in order to use synchronicity in fruit emergence, monkeys need to keep track of the local density of several fruit species, recognize the visual characteristics of fruits and trees that show local abundance, and/or remember the location of the trees or patches of trees that have started fruiting (Janmaat et al., submitted). There is currently no strong evidence that primates use olfactory cues or the sounds made by other animal species to locate fruit trees, but it is likely that such cues are integrated with spatial knowledge of likely food sources (Janmaat, 2006). Before revisiting particular trees, primates appear to combine weather conditions with
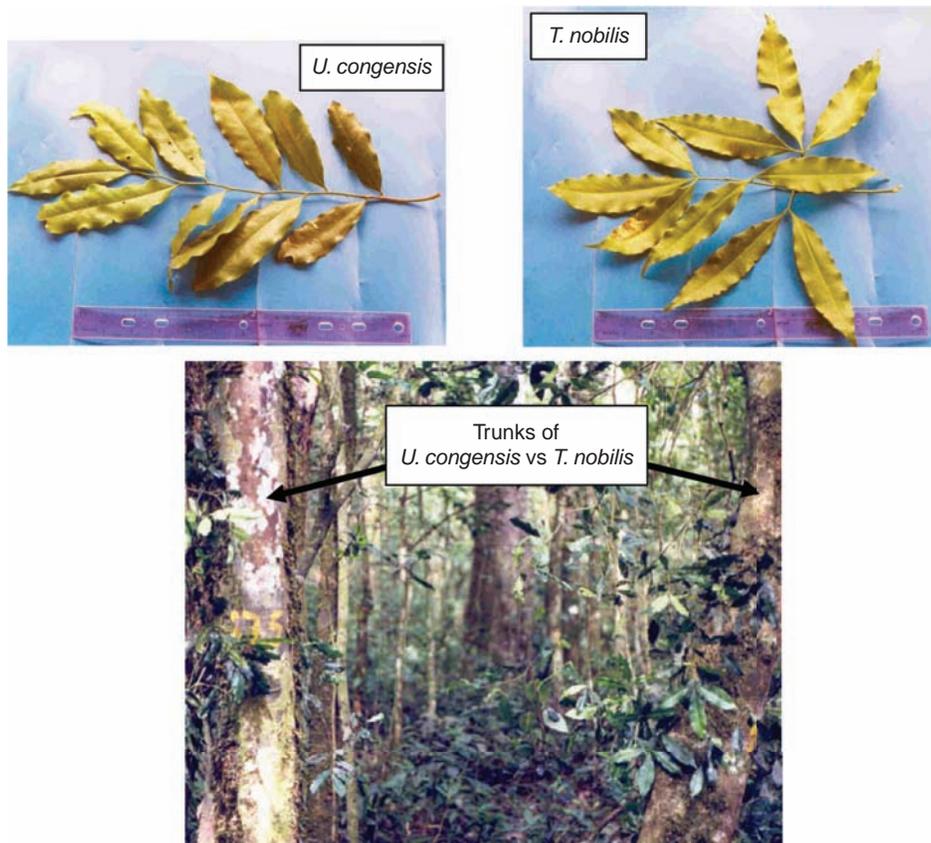
Figure 4.12 Illustration of the similarity in appearance of *U. congensis* and *T. nobilis* trees. Leaf shape, color, and configuration of *U. congensis* (top left) and *T. nobilis* (top right) and a close-up of the (yellow marked) trunks of both tree species (bottom). Despite the similarity, mangabeys did not enter more *T. nobilis* trees in *U. congensis* season than out of season, or in areas with higher ripe *U. congensis* fruit densities, suggesting that the monkeys use a memory of the visual characteristics of the trees or the locations of the tree patches of each species when searching for fruit (Janmaat 2006). Used with permission.

memories of previous fruiting states of trees, and they may even have some rudimentary understanding that high temperature and radiation accelerates fruit ripening (Janmaat et al., 2006b). One emerging point from the studies reviewed is that successful foraging depends on various cognitive skills, much beyond simply remembering the spatial location of a number of food trees throughout a home range. The degree to which nonprimate species possess comparable abilities is an important question, but unfortunately the answer is largely unknown.

How are these foraging abilities relevant to the more general question of why primates have relatively larger brains than other animals? Fieldwork in different parts of the world has shown that primates have been exceptionally successfully in monopolizing the arboreal space of most tropical forests, much more so than other groups of animals. Moreover, primates possess a number of morphological adaptations that make them especially well suited for arboreal foraging. The brain is an expensive organ, and primates' reliable access to the highest-quality nutrition available

in this habitat may have enabled them to afford unusually large brains.

Fruit-eating bats and birds also feed on arboreal fruit, but these competitors are perhaps more constrained by their specialized locomotor apparatus, which also prevents them from manipulating and harvesting difficult-to-open fruits (Isler & van Schaik 2007b; Ross, 1996). Parrots, often noted for their exceptional cognitive abilities, are somewhat of an exception as their tongue, feet, and toes are highly mobile, allowing them to manipulate and discard lower-quality portions of food items (Milton 2001). Isler and van Schaik (2007b) report a negative relationship between brain size and the relative mass of pectoral muscle in birds, which are crucial for taking in air. It is interesting that some forest birds appear to minimize these costs by climbing up trees with their hooked claws (Hoatzin bird; *Opisthocomus hoazin*). Primates are less constrained in these ways, which may have allowed them to evolve larger bodies and brains while accessing the most nutritious foods, including young leaves, fleshy fruits, and the arthropods associated with them (Kay, 1984; Martin, 1990). As a result, primates have been able to evolve more complex behavioral strategies and mental capacities when dealing with both environmental and social problems. Various studies reviewed in this chapter indicate that primates engage in a number of complex cognitive foraging strategies, which gives them an advantage in competing over food with other species, reinforcing their chosen strategy to invest in brain size. Although not very popular at the moment, the ecological intelligence hypothesis appears to be more parsimonious than its rivals in the evolutionary scenario it presupposes: Overall, primates have been more successful in exploiting sustained high-quality nutrition from their habitats compared to their competitors, which has allowed them to evolve an unusually large brain. The sophistication seen in primates' social behavior as well as other aspects of their cognitive sophistication may be a by-product of their highly encephalized neural system, afforded by their special adaptations to the ecological conditions of the forest habitat.

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