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Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys

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We investigated the ranging behaviour of two groups of wild mangabey monkeys (sooty mangabeys, *Cercocebus atys atys*, and grey-cheeked mangabeys, *Lophocebus albigena johnstoni*) relative to a number of preselected target trees within their home range. We observed the groups' visiting patterns and speed when they approached within a critical distance of a target tree as a function of the tree's fruiting state. For both groups, the likelihood of coming into sight or actually entering these trees was significantly higher if fruit was available. Target trees with fruit were also approached significantly faster than were trees without fruits. These behavioural differences were unlikely to be the result of auditory, visual or olfactory cues available over long distances, suggesting that monkeys relied on spatial memory to relocate fruit trees and distinguish between trees that had and had not carried fruit in the immediate past. Results further indicated that the monkeys clearly distinguished between different types of fruit-bearing target trees. We suggest that the monkeys used memory of previous feeding experience to assess each tree's differences and were able to anticipate changes in fruit quality. We found no evidence that individuals belonging to a particular age or sex class led the group towards trees with fruit more often than did others.

Rainforest primates with a frugivorous diet are promising candidates for investigations of ecological intelligence. Tropical rainforests are characterized by a high diversity of tree species with low densities and species-specific fruiting patterns (e.g. Myers 1980; Chapman et al. 1999). Adding further complexity, individual trees tend to be widely dispersed throughout a group's home range and can fruit at different and irregular times throughout the year (e.g. Milton 1977, 1981; Chapman et al. 1999; Vooren 1999). At the same time, most primates operate under several constraints that lower foraging success: group living, large body size, high travel costs and specialized dietary requirements. One way of increasing foraging success in these circumstances is continuously to monitor and remember fruiting states of individual trees within the home range and to anticipate subsequent states (Milton 1981, 1988). It has been argued, therefore, that frugivorous rainforest primates have evolved a specialized cognitive apparatus that can trace changes in fruit availability in time and space (Milton 1981, 1988; Boinski & Garber 2000; Janson 2000). Although this hypothesis is plausible, little empirical work is available to support it.

Evidence for spatial memory mainly comes from experimental studies with captive animals (e.g. rats, *Rattus norvegica*: Tolman 1948; chimpanzees, *Pan troglodytes*: Menzel 1973; sticklebacks, *Gasterosteus aculeatus*: Girvan & Braithwaite 1998; nutcrackers, *Nucifraga columbiana*: Balda & Kamil 1998). Far less is known about how spatial memory is used in a natural habitat, that is, in evolutionarily relevant circumstances. For a number of animal species, limited evidence suggests that individuals have knowledge about the location of food sources in their natural habitat (e.g. sunbirds, *Nectarinia* spp.: Gill & Wolf 1977; nutcrackers: Van der Wall & Balda 1981; chimpanzees, *P. t. verus*: Boesch & Boesch 1984; hummingbirds, *Selasphorus rufus*: Armstrong et al. 1987; tamarins, *Saguinus* spp.: Garber 1989; macaques, *Macaca fuscata*: Menzel 1991). Possibly the best evidence for the use of a spatial memory in the wild comes from experimental field studies on digger wasps, *Ammophila campestris* (Tinbergen 1972), honeybees, *Apis mellifera* (Dyer 1996), and capuchin monkeys, *Cebus apella nigritus* (Janson 1998). For nonhuman primates, the use of spatial memory may be the dominant strategy used to relocate experimentally introduced food sources (Garber & Paciulli 1997; Janson & Di Bitetti

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1997; Bicca-Marques & Garber 2004). However, to our knowledge, there is still no good evidence that primates rely on spatial memory when searching for natural food sources in everyday foraging. In addition, little is known about what aspects of the natural food sources are remembered.

In the first part of this study, we investigated whether two species of rainforest primates, sooty mangabeys, *Cercocebus atys atys*, and grey-cheeked mangabeys, *Lophocebus albigena johnstoni*, possess a general knowledge of the location of food sources in their home range. We preselected a number of food trees and observed the mangabeys' ranging behaviour in relation to these target trees. We analysed the monkeys' visiting patterns and approach speed to these trees as a function of their current fruiting state. Speed is a good measure of individuals' expectations about the resources to be found (Sigg & Stolba 1981; Janson 1998; Pochron 2001).

Our null hypothesis was that monkeys used sensory cues to find natural food sources rather than relying on spatial memory. This hypothesis is plausible as well as parsimonious: indeed, it has been difficult to exclude the sensory cue hypothesis (e.g. Garber 1989). Visual cues are a particular problem: fruit trees often emerge from the rainforest canopy and become visible over considerable distances, even from the ground. Humans can easily spot fruit in an emergent tree from a distance of 150 m if the view is unobstructed, suggesting that other primates have comparable abilities (Golla et al. 2004; K.R.L. Janmaat, unpublished data). To minimize the value of sensory cues, we selected tree species that did not offer obvious visual or olfactory signals that might have allowed the monkeys to detect fruiting state over long distances. We investigated whether auditory cues were available using post hoc analyses.

METHODS

Study Species

The sooty mangabey group was studied in primary lowland rainforest of the Taï National Park in Ivory Coast (5°52′N, 7°20′W; $N = 5–7$ fully grown males, 35 fully grown females and 53–54 not fully grown yet independently travelling individuals; F. Range, unpublished data). Sooty mangabeys forage in a largely terrestrial way (McGraw 1996). The grey-cheeked mangabeys were studied in semilogged moist evergreen forest of the Kibale National Park, Uganda (0°34′N, 30°21′W; see Waser & Floody 1974, Chapman et al. 1997 for descriptions of the study area). The group consisted of 4–10 fully grown males, seven fully grown females and 9–10 not fully grown individuals. Grey-cheeked mangabeys are considered arboreal (Waser 1974); however, our study group regularly foraged on the ground (Janmaat 2006). Both groups were well habituated to human observers on foot, allowing observation as close as 2 m.

For sooty mangabeys, we investigated ranging behaviour in relation to *Anthonota fragans* trees (Ceasalpiniaceae), which accounted for 25.8% of the study group's diet when fruiting (Bergmüller 1998). *Anthonota* fruit consists of 6–12-cm-long capsules, with no smell that can be detected by humans beyond 20 cm. Sooty mangabeys eat the seeds inside the capsules at every stage of ripeness. In the peak of the fruiting season, the mangabeys in our study visited up to 20 trees per day (K.R.L. Janmaat, unpublished data). The fruit was eaten by these monkeys even long after it had fallen to the ground but the fruit appeared to be ignored by other frugivorous species, possibly because it contains bitter chemicals (Voorhoeve 1965; Bergmüller 1998). Fallen *Anthonota* fruits have a brown, velvety skin and are hard to spot in the leafy ground substrate, making them ideal for exploring the use of spatial memory.

For grey-cheeked mangabeys, we focused on the strangler fig, *Ficus sansibarica* (Moraceae), a highly preferred food of grey-cheeked mangabeys (Waser 1974, 1977; Barrett 1995; Olupot 1999). The ripe fruit ranged in diameter from 1.4 to 5.1 cm. Individuals mainly ate ripe fruit but sometimes also the seeds of unripe fruit (K.R.L. Janmaat, unpublished data). Individual trees show marked differences in the amount of fruit produced during different fruiting periods, suggesting little relation between the size of a tree and its crop (Chapman et al. 1992). The fruit shows no obvious visual signs of ripeness, such as colour or size. Chimpanzees assess edibility by entering trees and squeezing individual fruits (N.J. Dominy, P.W. Lucas, R.W. Wrangham & L. Ramsden, unpublished data). Unripe figs are also attractive to the mangabeys because they often contain weevil larvae, such as *Omophorus stomachosus* (Waser 1977). These unripe fruits produce no smell that humans can detect from further than 20 cm. Mangabeys identify infested fruits by turning them, presumably to check for the distinctive small black spots made by the weevils. *Ficus sansibarica* trees tend to produce fruit in an asynchronous manner (Waser 1975), so we were able to test for the mangabeys' ability to distinguish two types of trees without fruit, those that had recently been depleted and those that had not yet grown fruit, as well as to collect data throughout the year. In sum, the strangler fig was an ideal choice because of its complex fruiting pattern and because long-range visual cues (the size of the tree and the characteristics of its crop) were unlikely to allow monkeys to make judgements about the suitability of the tree as a food source.

Data Collection

Target trees

Both mangabey groups had a large home range (sooty mangabeys: 700–800 ha over ca. 32 months Bergmüller 1998; Förderer 2001; F. Range, unpublished data; grey-cheeked mangabeys: 300–600 ha over ca. 38 months: Olupot 1999; G. Arlet, unpublished data; Janmaat 2006), which enabled us to investigate the groups' behaviour towards a relatively large number of target trees. Before each observation period, we located trees of the chosen tree species and then selected and labelled a number of them that had fruit. These trees were selected so that a maximum number of trees could fit in the study area, under the condition that