



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.

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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 norvegicus*: 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 nigrurus* (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 pre-selected 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 (Ceasalpinia-ceae), 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

individual trees were separated by at least 300 m (*A. fragrans*) or 200 m (*F. sansibarica*). We chose a smaller critical distance for *F. sansibarica* because the mean \pm SD group spread of grey-cheeked mangabeys (57.0 ± 31.2 m; Olupot et al. 1997) was smaller than that of the sooty mangabeys (102 ± 52 m; K.R.L. Janmaat, unpublished data). In regions without fruiting exemplars of the target species, we identified trees without fruit using the same distance criteria. This resulted in a roughly equal number of target trees with and without fruit. In Tai forest, we selected 33 *A. fragrans* trees, 16 of which carried fruit at the beginning of the study (natural tree density 0.5 trees/ha; Bergmüller 1998). In Kibale forest, we selected 56 *F. sansibarica* trees, 27 of which carried fruit at the beginning of the study period (natural tree density 1.7 trees/ha; Chapman et al. 1999).

For each tree, we measured the diameter at breast height (DBH) and that of the crown by averaging the north–south and east–west projections on the ground. We only included trees with DBH and crown diameters greater than the smallest tree ever observed with fruit during the study period. For *F. sansibarica*, we analysed data only of target trees that had been observed to bear fruit before, during or after the observation period. We also excluded target trees that appeared to have other food items inside, such as fruit from host trees or lianas. Some areas of the group's home range did not contain *F. sansibarica* trees, so we also collected data on two closely related fig species, *F. exasperata* ($N = 6$) and *F. natalensis* ($N = 6$). From the data collected on these trees, we only analysed observations of fruit-handling behaviour.

Foraging behaviour

We followed each monkey group for several continuous periods of several months between 31 January 2002 and 30 April 2004. The sooty mangabey group was followed during two continuous periods of 30 days each. The grey-cheeked mangabey group was followed during three continuous periods of 50, 60 and 100 days. Two observers followed each group from the first movement in the morning to the final resting place at dusk. Whenever a group entered a specified critical radius surrounding one of the target trees (sooty mangabeys: 150 m; grey-cheeked mangabeys: 100 m; Fig. 1), the primary observer stayed with the individual closest to the tree to measure approach speed, while the other observer rushed to the target tree to estimate the quantity of fruits and whether other frugivorous animals or group members were present. To keep each other informed about the position of the tree in relation to the moving group, the two observers communicated via calling, producing click sounds or using a walkie-talkie. Fruit quantity was scored (1–4) according to the percentage of branches containing fruit: 0 (no fruit), 1 (1–25%), 2 (26–50%), 3 (51–75%) and 4 (76–100%). Additional notes were made on the presence of young fruit buds in *F. sansibarica*. The observer at the tree then measured (1) the time that the first individual came into sight and its age–sex class, (2) the time that the first individual entered the tree (for both species) or walked underneath it (for sooty mangabeys) and its

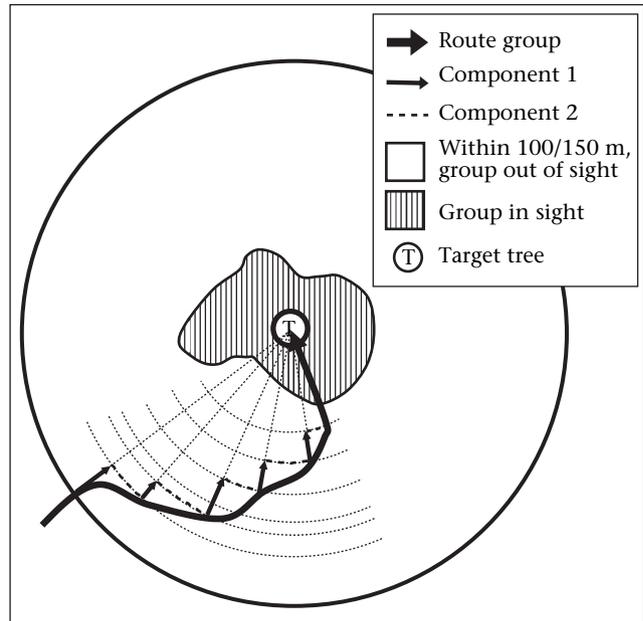


Figure 1. Illustration of the method used to measure speed towards a target tree. The observer followed the group while staying within 5 m of the individual closest to the target tree. Following took place in two components of direction, either along component 1 (small arrow), directed towards the tree trunk, or component 2 (thick dotted line), directed along the imaginary circle around the tree trunk. Speed was determined by counting steps/min in the direction of the tree (component 1). The primary observer was updated on the direction of the tree trunk by calling or clicking by the secondary observer, who waited under the tree trunk. The outer circle had a radius of either 100 m (grey-cheeked mangabeys) or 150 m (sooty mangabeys). Hatching shows the area in which the group came in sight of the observer waiting under the tree.

age–sex class, (3) the number of individuals that entered and left the tree (for both species) or the area underneath it (for sooty mangabeys) and (4) whether individuals ate the fruit.

At the same time, the primary observer measured the speed at which the group moved towards the tree (in steps/min; the observer's step lengths were calibrated over a stretch of 500 m within the forest habitat with varying elevation levels; Fig. 1). Speed refers to the component of movement towards the tree only (see Fig. 1 legend). Data on speed were analysed post hoc over different stretches, according to the tree species. For both tree species, we began to measure speed from about 150–50 m from the trunk, depending on how quickly the observer was able to reach the front of the group. We stopped before visual access to assessment cues might have been available. *Anthonota fragrans* fruit was eaten in any ripening state, so the monkeys could assess a tree's suitability from the moment that it came into their sight. Therefore, we stopped measuring speed 5 m before the tree became visible to the primary observer. For *F. sansibarica* we are confident that the mangabeys could not visually assess the edibility of the fruit from outside the tree (see above), so we analysed speeds measured up until the first individual began to climb the trunk. To exclude the potential use of auditory cues to fruit availability, we only analysed

approaches where no other group member or frugivorous species, such as black-and-white casqued hornbills, *Bycanistes subcylindricus*, were present before the arrival of the study group.

Once the group had entered a target tree, the primary observer recorded the total number of fruits eaten or rejected (by touch of hand or nose) by the first mangabey observed in the tree. The same observer also recorded whenever the individual changed its location on fruit-bearing branches. When the view was obstructed, observation switched to the next individual that came into sight until 10 min of data were collected. We determined whether the individuals ate ripe fruits, weevil larvae or seeds of unripe fruits, using direct observations and by inspecting dropped fruit. As soon as the first monkey moved out of sight, the primary observer continued to follow the group. As soon as all individuals had left the tree, and the main part of the group had left the predefined outer circle (Fig. 1), the secondary observer returned to the group or moved directly to another target tree.

The 10-min focal data were collected by two observers who were both experienced in the use of focal animal sampling (Altmann 1974). Interobserver tests were not conducted, because few places allowed two independent observers a similar view of a monkey high up in a fig tree, but we analysed an equal number of 10-min observations per fig species for each observer.

Assessing tree quality

Ideally, the quality of a tree is defined by the number of edible fruits. However, the edibility of *F. sansibarica* fruits cannot be determined by visual cues. Furthermore, the density and developmental state of weevil larvae and fruit are likely to vary within the crown (Houle 2004), making assessments of tree quality by sampling fruits impractical. Hence, we instead defined tree quality (Q) as the cumulative number of monkeys inside the tree/min, provided that at least one individual was feeding on figs (see also White & Wrangham 1988 and Garber 1989; Chapman et al. 1992 showed a similar behavioural variable to be correlated to the visual estimation of fruit quantity for species with large fruit). Q values varied between visits, as did the fruit quantity class. These data were collected by different observers (in Tai: $N = 2$; in Kibale: $N = 5$). Interobserver reliability was strongly correlated for simultaneously collected data on both variables (Spearman rank correlation: Q values: $0.758 < r_s < 0.964$, $P < 0.001$; fruit quantity: $0.830 < r_s < 0.928$, $P < 0.001$).

Statistical Analyses

Ninety-three per cent of all repeated approaches to trees were separated by at least 1 day, suggesting that repeated approaches should be treated as independent events. In rare cases, the group approached a particular tree two or three times in the same day. We included these visits in our analyses only if the group had moved out of the outer circle between successive visits (Fig. 1). Most data were analysed with nonparametric Spearman correlation analyses and chi-square tests, which are sensitive to proportions

and frequencies (Sokal & Rohlf 1995). Data on speed and number of fruits eaten or rejected were transformed into normal distributions using a log and square-root function, allowing us to use independent-sample *t* tests and Pearson correlation analyses. All tests were two tailed. In each case we assessed evidence about specific hypotheses, so we did not adjust significance criteria with the Bonferroni method (Perneger 1998).

RESULTS

Can Mangabeys Distinguish Fruiting States?

Sooty mangabeys

During the two observation periods, the group came within the critical distance of 150 m of, respectively, 11 and nine *A. fragans* trees with fruit and 14 and 14 trees without fruit ($N = 184$ approaches). The two observation periods were pooled for analysis.

We found a significant association between the frequencies with which the group, once they approached within 150 m, continued into sight of a target tree and the probability of this tree carrying fruit (chi-square test: $\chi_1^2 = 6.26$, $P < 0.05$, Phi = 0.184, $P < 0.05$). The same was true for the frequencies with which the group proceeded underneath or entered the tree ($\chi_1^2 = 20.6$, $P < 0.001$, Phi = 0.333, $P < 0.001$). The proportion of times that the group came into sight or went under or in the tree was higher for target trees with than without fruit (Fig. 2). The group also approached target trees with fruit significantly faster than they did trees without fruit ($N_{\text{trees with}} = 8$, $N_{\text{trees without}} = 12$; independent samples *t* test: $t_{14.54} = -3.500$, $P < 0.01$; Fig. 3).

Grey-cheeked mangabeys

During the three observation periods, the group came within a critical distance of 100 m of, respectively, 11, 20 and 28 *F. sansibarica* trees with fruit and 20, 24 and 31 target trees without fruit ($N = 577$ approaches). Data from the three observation periods were pooled for analysis.

We found a significant association between the frequency with which the group, once within 100 m, continued into sight of a target tree and the probability of this tree having fruit (chi-square test: $\chi_1^2 = 42.11$, $P < 0.001$, Phi = 0.270, $P < 0.001$). We found the same significant association for the frequencies with which the group proceeded and climbed the tree once they had come within sight of it ($\chi_1^2 = 71.10$, $P < 0.001$, Phi = 0.351, $P < 0.001$). The proportion of times that the group came within sight of or entered the tree was higher for target trees with than without fruit (Fig. 2). The group also approached target trees with fruit significantly faster than they did trees without fruit ($N_{\text{trees with}} = 34$, $N_{\text{trees without}} = 27$; independent samples *t* test: $t_{93.63} = -3.052$, $P < 0.01$; Fig. 3).

Do Mangabeys Rely on Visual Cues or Memory?

The findings presented so far indicate that both groups distinguished between trees that did and did not carry

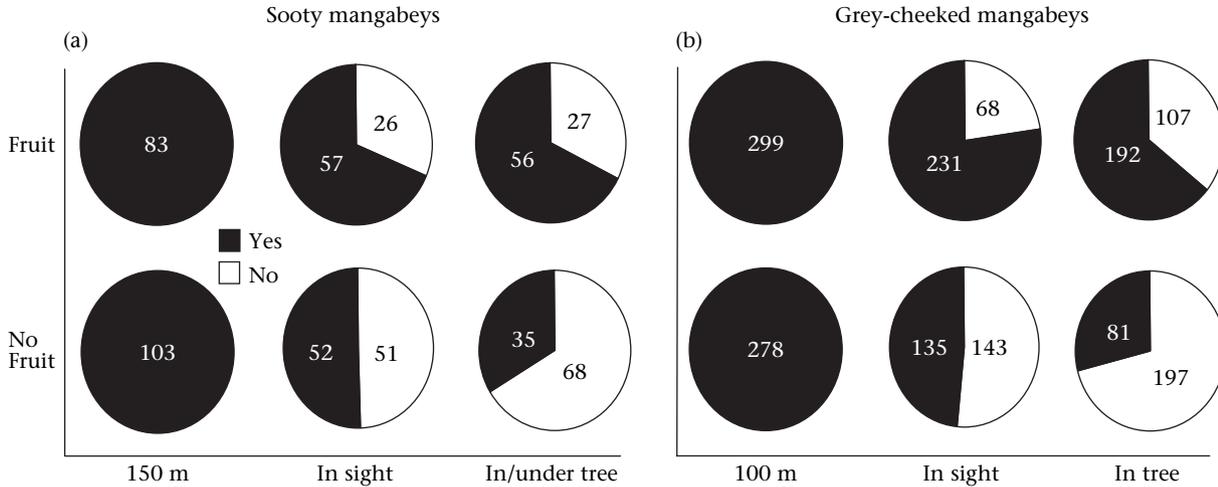


Figure 2. Ranging behaviour of (a) sooty mangabeys towards target trees of *Anthonota fragans* and (b) grey-cheeked mangabeys towards target trees of *Ficus sansibarica* with and without fruits. Circles represent the proportion of time that the group 1) approached the trees within (a) 150 m or (b) 100 m, 2) was visually detected from under the tree (a, b) and 3) entered (a, b) or passed under the crown of the tree (b). Numerals in white: number of occurrences; numerals in black: number of occurrences in which the group approached the tree but did not come in sight of, enter or pass under its crown.

fruit. To assess whether this could result from mangabeys' use of visual cues, we conducted the following analyses.

Visiting pattern of trees with empty crown

Sooty mangabeys. During the observation periods, 12 *A. fragans* trees had empty crowns (no fruit or flowers) but much fruit was still available on the ground; thus, no visual cues were available from a distance. We used this subset of target trees conducting the same series of analyses, to investigate whether the visiting pattern shown above resulted from distant inspection. We found a significant association between the frequencies with which the group, once they approached within 150 m, continued into sight of a target tree and the probability of this target tree having fallen fruit (chi-square test: $\chi^2_1 = 10.87$,

$P < 0.001$, $\Phi = 0.295$, $P < 0.01$). We found the same significant association for the frequencies with which the group proceeded underneath or entered the tree ($\chi^2_1 = 10.87$, $P < 0.001$, $\Phi = 0.295$, $P < 0.01$). The proportion of times that the group came into sight or went into or under the tree was higher for target trees with fruit on the ground than for trees without fruit (came into sight or entered, respectively: $N_{\text{trees with}} = 4, 9$, $N_{\text{trees without}} = 14, 14$; Fig. 4). These results do not differ from those for all *Anthonota* trees, suggesting that distant inspection did not influence the monkeys' behaviour.

Grey-cheeked mangabeys. Unlike *Anthonota* fruit, *Ficus* fruit is consumed only when it is on the tree. Fruit hanging in a tree is much easier to spot than is fruit on the ground, especially by the more arboreal grey-cheeked

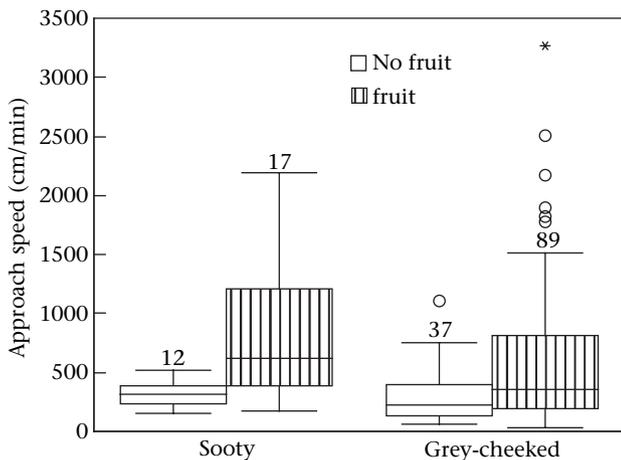


Figure 3. Speed of approach to trees with and without fruit. Bars: median speeds; top and bottom of boxes: 75 and 25 percentiles, respectively; Whiskers: highest and lowest values that are not outliers; circles outliers; asterisks: extreme values. Numbers above box plots: sample sizes.

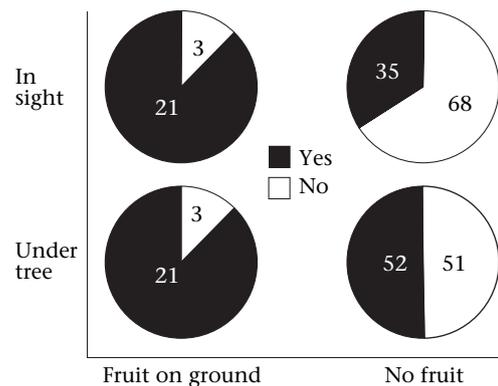


Figure 4. Ranging behaviour of sooty mangabeys towards target trees with fruit on the ground and trees without fruit. Each circle represents the proportion of times that the group came in sight of or entered the area under the target trees once they had approached within 150 m. Numerals in white: number of times that individuals came in sight of or entered the area under it. Numerals in black: number of times that these individuals did not.

mangabeys. To investigate whether the grey-cheeked mangabeys relied on distant visual cues to distinguish between potential food trees, we analysed their behaviour towards target trees that carried no fruit. We compared the monkeys' behaviour towards two types of trees that were alike in not carrying fruit or fruit buds, but different because of their potential to grow new fruit; i.e. we compared depleted trees and trees that had not had fruit within the observation period. We predicted that mangabeys would regularly check empty trees that had no fruit yet, but would avoid empty trees depleted during the observation period.

We found a significant negative association between the frequencies with which the group, once they approached within 100 m, continued to approach within sight of a tree and the probability of this tree being depleted (chi-square test: $\chi_1^2 = 4.20$, $P < 0.05$, $\Phi = 0.120$, $P = 0.040$). We found the same association for the frequencies with which the group entered both tree types ($\chi_1^2 = 5.22$, $P < 0.05$, $\Phi = 0.135$, $P = 0.022$). The proportion of times that the group came into sight or proceeded to enter the tree was lower for the depleted target trees ($N = 25$) than for the trees that did not have fruit within the observation period ($N = 50$; Fig. 5). We also found that the interval differed between the times at which the group came into sight of both tree types and the times at which they reapproached into sight after leaving the critical radius (Mann–Whitney U test: $U = 501$, $N_1 = 33$, $N_2 = 45$, $P < 0.05$). The reapproach interval was longer for depleted target trees ($N = 15$) than for the trees that had not yet had fruit within the observation period ($N = 18$). The crowns of both tree types were empty, so the monkeys could not have relied on visual, olfactory or auditory cues to assess their difference.

Edibility judgements of figs

To investigate whether grey-cheeked mangabeys relied on visual or olfactory cues when approaching target trees with fruit, we also observed their fruit-handling behaviour inside target trees of three fig species. In two species, *F. exasperata* (Fe) and *F. natalensis* (Fn), the figs undergo obvious colour changes during ripening and in the third,

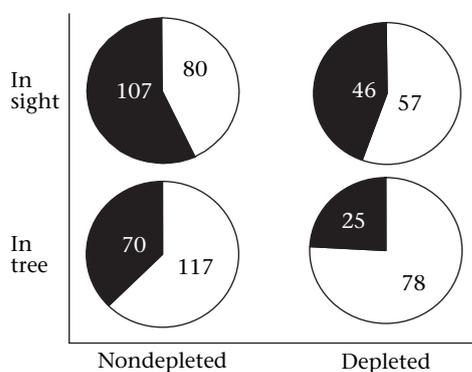


Figure 5. Ranging behaviour of grey-cheeked mangabeys towards depleted and nondepleted trees. Numerals in white: number of times that individuals entered trees of each type; Numerals in black: number of times that they did not.

F. sansibarica, colour change is unrelated to ripening state (Sumner & Mollon 2000; Dominy & Lucas 2004; N.J. Dominy, R.W. Lucas, R.W. Wrangham & L. Romsden, unpublished data).

In line with these differences, fruit of *F. sansibarica* was regularly touched by hand or nose without being eaten or picked from the tree. In contrast, fruit of *F. natalensis* and *F. exasperata* were hardly ever rejected by touch. For the three species, touching of fruit was significantly related to species (chi-square test: $\chi_1^2 = 721.68$, $P < 0.001$, $F_n: N = 6$, $F_e: N = 6$, $F_s: N = 15$; Fig. 6).

For *F. sansibarica*, the number of fruits rejected by touch and those eaten was significantly related (Pearson correlation: $r_{30} = 0.664$, $P < 0.001$, log-transformed), suggesting that monkeys had to rely on tactile information to judge edibility of individual fruits, but visual information was potentially available for the other two fig species. A similar relation was found for *F. sansibarica* trees with only unripe fruits that were attractive because of the chance of finding weevil larvae and edible seeds ($r_{21} = 0.569$, $P < 0.01$, square-root transformed). Infested fruits can be recognized by small black spots, so these results further suggest that the mangabeys required close-range visual inspection to assess the possibility of finding edible weevil larvae inside fruits.

Can mangabeys remember previous feeding experiences?

Over one-third of the *F. sansibarica* trees that carried fruit were not entered (Fig. 2). This result suggests that not all trees that carry fruits were valued similarly. To investigate whether mangabeys remembered differences in quality of trees encountered in the past, we conducted additional analyses.

We first examined the groups' revisiting behaviour towards *F. sansibarica* trees with fruits. We compared the

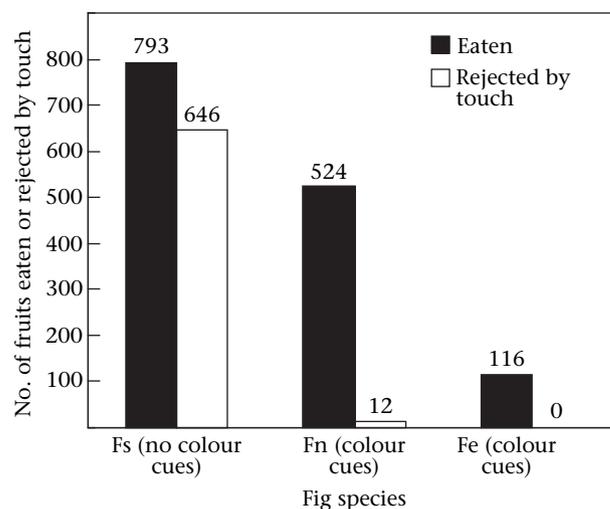


Figure 6. The number of fruits that were touched and rejected within the first 10 observable minutes after the group entered *Ficus sansibarica* (Fs), *F. natalensis* (Fn) and *F. exasperata* (Fe) trees in relation to the number of fruits that were eaten. Numbers above bars show sample sizes.

quality values of current visits with the previous ones and found several patterns. First, previous quality values of target trees that were re-entered were significantly different to those not re-entered (Mann–Whitney U test: $U = 4496$, $N_1 = 89$, $N_2 = 142$, $P < 0.001$, $N_{\text{trees}} = 32$; Fig. 7), suggesting that previous experience with a particular tree guided the monkeys' foraging behaviour. The same was true for target trees that carried unripe fruit at the current visit (which were attractive because of the chance of finding weevil larvae or seeds), demonstrating that olfactory cues could not have influenced the monkeys' behaviour ($U = 1841$, $N_1 = 83$, $N_2 = 56$, $P < 0.05$, $N_{\text{trees}} = 27$).

However, the quality values at previous and current visits were significantly related (Pearson correlation: $r_{32} = 0.433$, $P < 0.01$; log transformed), so we used the speed data to determine the origin of this effect, i.e. whether the monkeys relied on either a 'frozen memory' of the previous quality or a knowledge of the current quality while approaching a target tree.

We analysed data for trees with unripe fruit (no odour cues) only. Approach speed (S , log transformed) was significantly positively related to quality of the previous visit (Q_p ; Pearson correlation: $r_{41} = 0.302$, $P < 0.05$, $N_{\text{trees}} = 17$). If current quality (Q_c) was kept constant (using partial-rank correlation), then approach speed and previous quality were no longer significantly related (partial-rank correlation coefficient: $r = 0.063$, $N = 34$, $P = 0.715$). However, if previous quality was kept constant, approach speed remained significantly related to current quality ($r = 0.520$, $N = 34$, $P < 0.01$). These results suggest that the monkeys' behaviour was caused by knowledge of the current quality state of each target tree. To investigate whether this knowledge was assessed

via detection of visual cues emitted by the fruit-bearing trees, or whether it was computed from the monkeys' ability to combine knowledge of the past fruiting state with that on changes in larvae development or fruit depletion, we conducted the following analyses.

Approach speed was not correlated with the estimated quantity of unripe fruit in target trees (Spearman rank correlation: $r_s = 0.168$, $N = 80$, $P = 0.137$, $N_{\text{trees}} = 23$), nor was it correlated with the DBH or crown diameter of the target trees with unripe fruit (DBH: $r_s = 0.163$, $N = 80$, $P = 0.642$; crown diameter $r_s = -0.057$, $N = 80$, $P = 0.731$, $N_{\text{trees}} = 23$), suggesting that the monkeys did not rely on long-distance visual cues, such as the number of fruits or the size of a target tree.

Approach speed was unlikely to be related to differences in hunger level. The monkeys did not approach trees with fruit faster in the morning (0700–1000 hours) than during the rest of the day (Mann–Whitney U test: $U = 847.0$, $N_1 = 28$, $N_2 = 74$, $P = 0.156$, $N_{\text{trees}} = 32$). Instead, speed was positively related to the average quality values of the target trees (Pearson correlation: $r_{21} = 0.513$, $P = 0.012$), suggesting that approach speed was related to the characteristics of the target trees.

Who Knows Best?

To investigate whether group members differ in their ability to distinguish between trees with and without fruit, we recorded, when possible, the sex and age class of the first individual that arrived within sight and went under or in the target trees. We analysed the results for three age–sex classes: fully grown males, fully grown females and not fully grown but independent travelling individuals.

In sooty mangabeys, fully grown males arrived into sight first and in or under the tree most often (respectively, 67% and 48%). However, there was no relation between the frequencies with which individuals of each age–sex class, once they approached within 150 m arrived into sight and in or under the target tree, and the probability of the target tree carrying fruit (chi-square test, arrived into sight: $\chi^2_2 = 0.137$, $N = 79$, $P = 0.755$, under or in trees: $\chi^2_2 = 0.122$, $N = 69$, $P = 0.804$).

In grey-cheeked mangabeys, fully grown males arrived first into sight and went into the tree most often (53% and 57%). There was again no relation between the frequencies with which individuals of each age–sex class arrived into sight or in the target tree and the probability of the target tree carrying fruit (chi-square test, arrived into sight: $\chi^2_2 = 3.801$, $P = 0.149$, $N = 257$, under or in trees: $\chi^2_2 = 0.764$, $P = 0.682$, $N = 200$).

These results suggest that, within both groups, neither fully grown males and females nor fully grown individuals and those that had not yet reached adult size differed in their ability to distinguish between trees with and without fruits.

DISCUSSION

Both sooty and grey-cheeked mangabeys appear to have knowledge about the fruiting state of various trees within

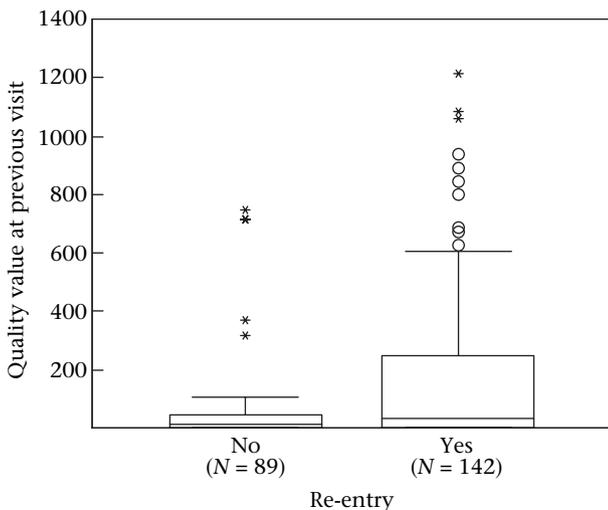


Figure 7. Revisiting pattern, by grey-cheeked mangabeys, of *Ficus sansibarica* trees with fruit with different past quality values (where quality is the cumulative number of monkeys in the tree/min). Right box: past quality values of trees that had been re-entered the next time that the group came within 100 m; left box: past quality values of trees that had not. Bars: median past quality value; top and bottom of the boxes: 75 and 25 percentiles, respectively; whiskers: highest and lowest values that are not outliers; circles and asterisks: outliers and extreme values, respectively.

their home range. Once the monkeys were within a critical distance from a target tree, beyond the average visual range in the forests, they were more likely to visit and approached faster if the tree carried fruit, suggesting that they assessed fruit availability without the use of visual cues. However, groups often came into clear sight of target trees without fruit but then did not enter them (Fig. 2), indicating that the monkeys were able to spot the presence or absence of fruits from greater distances (e.g. emergent trees, local clearings). To address this possibility, we carried out further analyses that showed that foraging patterns in these monkeys could not have been guided by visual assessment alone.

First, sooty mangabeys distinguished between two types of *Anthonota* trees with empty crowns, those with fruit scattered on the ground and those with no fruit. It is improbable that the monkeys were able to discriminate the brown, inconspicuous fruits among the leafy substrate of the forest floor from a distance further than the point at which the monkeys were visible to a human observer under the tree. Nevertheless, target trees with fallen fruit were associated with relatively more visits and approaches to within sight. The assumption that the monkeys could not have seen the fruit is supported by comparative studies indicating that visual acuity thresholds are lower for human than for nonhuman primates, which have typically smaller eyes and hence smaller retinal image size (e.g. Cavonius & Robbins 1973; Merigan & Katz 1990; Golla et al. 2004). We excluded all cases in which other mangabeys, the only species that has been observed to eat *Anthonota* fruits (Bergmüller 1998), were present in or under the tree before the arrival of the group, so it is also unlikely that the group relied on auditory cues to make the distinction between the two tree types. We cannot exclude the possibility that auditory cues were heard from other mangabey groups before the moment that the group came within 150 m of the target tree. It seems unlikely, however, that the group would be able to locate the target tree among the approximately 502 other trees with a DBH of greater than 30 cm within the 150-m circle (Vooren 1999), just by remembering the direction of an intermittent auditory cue that was heard from a distance of more than 150 m. Furthermore, in only 3% of the cases were other mangabeys present under or in the tree when the group had entered the 150-m circle (these approaches were not analysed), strongly suggesting that the use of auditory cues cannot explain the observed behaviour either. We also cannot exclude the possibility that the group used the clicking and calling sounds made by the observers to locate the tree. However, this communication was done at both tree types, so it does not explain why the group went more often to target trees with fallen fruits than towards those without. Nonhuman and human primates fall within the same range of olfactory performance with regard to sensitivity to isoamyl acetate, the major component in a large variety of fruit odours (Laska & Freyer 1997; Laska et al. 1999, 2000, 2003), so we also consider it unlikely that the mangabeys were able to smell the fruit. Humans could not detect the fruit's odour from further than 20 cm, so mangabeys were unlikely to have done so from further than the point at which the first individual

came into sight of the tree. We conclude that the most likely explanation of the observed behaviour is that the sooty mangabeys remembered the fruiting state of the target trees and used this memory to relocate them.

Second, grey-cheeked mangabeys behaved differently towards trees that had been depleted recently than to trees that had lacked fruit for longer periods and thus had more potential to carry new fruit. When grey-cheeked mangabeys came within 100 m of a tree without fruit, the proportion of times that they approached into sight and entered a tree was lower for recently depleted target trees than for trees that had not produced fruits within the study period. In addition, the interval between the times that the group came into sight and re-entered into sight was longer for the depleted target trees. Both tree types had an empty crown that showed no obvious differences in appearance. The depleted trees did not contain obvious signs of a fruiting history, such as hanging branches (fruit grows only on the trunk and heavy branches), nor did the trees show early signs of fruiting, such as fruit buds. Therefore, this pattern is best explained by the hypothesis that memories of previous visits guided the monkeys' visiting patterns.

Grey-cheeked mangabeys do use visual cues to assess edibility of fruits if these cues are available. With the two fig species (*F. exasperata* and *F. natalensis*) that show an obvious colour change during ripening, mangabeys seldom touched and discarded fruits. *Ficus sansibarica*, on the other hand, offers no colour cues for edibility, and monkeys determined the edibility using tactile cues.

One unexpected finding was that mangabeys did not enter about one-third of fruit-bearing target trees. To investigate whether grey-cheeked mangabeys chose not to enter a particular tree because they remembered its low value from a previous visit, we first analysed the monkeys' revisiting behaviour. Revisited target trees had been valued higher at the previous visit than trees that were avoided. This was also true for target trees with unripe fruits that were attractive because of the weevil larvae or edible seeds. We also found that the speed with which the group approached target trees with unripe fruits was significantly correlated with the quality values measured at the previous visit. These results initially suggested that the monkeys were able to remember differences in the quality experienced at previous visits. However, subsequent partial-correlation analyses showed that past and current quality values were related, and that the above relation may have been an effect of only current quality values. No difference was found between the speed of approach measured early in the morning and later in the day, suggesting that the relation between speed and current quality value was not a function of differences in hunger. The relation between average quality values and average speed of approach also indicates that speed was related to the value of individual trees and not simply to the level of hunger. The finding that the grey-cheeked mangabeys approached faster towards high-valued *F. sansibarica* trees is best explained by the hypothesis that individuals did not rely on a 'frozen memory' of the past fruiting state, but instead that they were able to assess knowledge of the current fruiting state and could anticipate what they were going to find inside the tree.

Although sensory cues are likely to be important in the mangabeys' foraging behaviour, it is unlikely that the mangabeys used sensory cues to anticipate the quality of the target trees with unripe fruits; to do so, they would have needed to detect the content of the fruits (hatched larvae or edible seeds) from before the point that the group entered the tree. Even if the characteristics of the black spots could reveal the developmental state of the weevils inside, observations of fruit handling indicated that close-range inspection would be necessary. Furthermore, we found no correlation between the speed with which the group approached a tree and either the number of fruits in a tree or its size. Finally, it is unlikely that the monkeys could use olfactory cues to detect edible unripe fruits, because the unripe fruits produce almost no smell detectable to humans. We are confident that no obvious sensory cues were available, so we suggest that the monkeys anticipated the quality of a target tree by using their memory of the latest fruiting state in combination with knowledge of the rate of larvae development and/or fruit depletion Janmaat et al. 2006.

Even though we followed the groups continuously for long periods, the mangabeys might have used knowledge from visits that were undetected by the observers. In both mangabey species, males sometimes leave the group temporarily (Waser & Floody 1974; Olupot 1999; Range 2005) and solitary males have been observed to feed in fig trees up to 500 m from their group (K.R.L. Janmaat, unpublished data). The finding that fully grown males were often the first to arrive near or at target trees suggests that they might lead the group towards good-quality trees. However, male early arrival was not significantly related to the fruiting state of the tree, suggesting that arrival time was a by-product of males' peripheral foraging behaviour. We found no evidence that the males had foreknowledge about the state or value of target trees from their solitary exploration trips.

Taken together, these results indicate that both species of mangabeys have a sophisticated spatial memory of fruit availability, providing the monkeys with information on the present and previous fruiting state and possibly its present quality. This memory seems to contain information not only about the condition of trees with fruit but also about differences between different types of empty trees. The results also suggest that the mangabeys used their memory in combination with available visual cues.

One particular anecdote further supports the hypothesis that mangabeys use memory to find fruit. After one of the best-quality target trees had been depleted, we were surprised to observe that the sooty mangabeys nevertheless approached the tree at high speed. However, the monkeys approached not the tree itself but a small pool of water next to it, which formed part of a small river. As the dry season progressed, the water level in the river continued to drop and fruit that had fallen into the pool gradually became accessible to the mangabeys. After arriving at the site, the monkeys immediately began to reach into the pool and retrieve the sunken fruit, suggesting they had remembered the site for a significant interval; this behaviour would be comparable to the ability of food-caching birds to remember specific locations over

long intervals (e.g. Balda et al. 1987; Clayton & Dickinson 1998).

Primates will travel to more distant resources if the quality of the distant source is sufficiently high (Boesch & Boesch 1984; Garber 1989; Janson 2000; Cunningham 2003). Our findings raise the possibility that mangabeys may make finer categorizations of fruit trees on the basis of their future potential. First, grey-cheeked mangabeys seem to be able to anticipate the quality value of a target tree without the use of obvious sensory cues. They also seem to be able to anticipate differences in fruiting potential. That grey-cheeked mangabeys visited depleted target trees less often than nondepleted ones might simply reflect avoidance of depleted trees. The results, however, are also consistent with the possibility that nondepleted trees were avoided less often because the mangabeys knew that these trees were more likely to grow new fruit than were the recently depleted ones. Approach speed may serve as a valuable variable to assess such forms of prospective behaviour. Each study group travelled significantly faster towards target trees with fruit than towards those without; they also travelled faster towards trees of higher overall quality. These results suggest that the monkeys approached faster if they expected to find food, and that approach speed was related to the quality of food that they expected to encounter. It will be of interest to examine further the approach speeds of successive visits, ideally between the first and second times that the group eats in a particular fruiting tree or when the quality values have changed substantially. Such studies may identify whether monkeys understand the concepts of depletion, renewal and emergence rates of new fruits. Investigations on the existence of such abilities and their distribution among frugivorous species should improve understanding of relevant selection pressures favouring intelligent behaviour.

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