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The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit

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Abstract Previous research has shown that a considerable number of primates can remember the location and fruiting state of individual trees in their home range. This enables them to relocate fruit or predict whether previously encountered fruit has ripened. Recent studies, however, suggest that the ability of primates to cognitively map fruit-bearing trees is limited. In this study, we investigated an alternative and arguably simpler, more efficient strategy, the use of synchrony, a botanical characteristic of a large number of fruit species. Synchronous fruiting would allow the prediction of the fruiting state of a large number of trees without having to first check the trees. We studied whether rainforest primates, grey-cheeked mangabeys in the Kibale National Park, Uganda, used synchrony in fruit emergence to find fruit. We analysed the movements of adult males towards *Uvariopsis congensis* food trees, a strongly synchronous fruiting species with different local patterns of synchrony. Monkeys approached within crown distance, entered and inspected significantly more *Uvariopsis* trees when the percentage of trees with ripe fruit was high compared to when it was low. Since the effect was also found for empty trees, the monkeys likely followed a synchrony-based inspection strategy. We found no indication that the monkeys generalised this strategy to all *Uvariopsis* trees within their home range. Instead, they attended to fruiting peaks in local areas within the home range and adjusted their inspective behaviour accordingly revealing that non-human primates use botanical knowledge in a flexible way.

Keywords Foraging cognition · Fruit finding strategies · Botanical knowledge · Seasonal food distribution · *Lophocebus albigena*

Introduction

Compared to other groups of mammals, non-human primates possess relatively large brains (Jerison 1973; Harvey and Krebs 1990). Neural tissue is metabolically expensive to maintain and needs a continuous supply of energy. Perhaps, more so than other groups of animals, non-human primates are forced to ensure a reliable and steady intake of high-energy nutrition throughout the year (Armstrong 1983; Aiello and Wheeler 1995). This may be particularly challenging in rainforests where numerous species, including many primates, compete for the same food resources (Houle et al. 2006) and where only a very small fraction of trees offer significant sources of food at any given time (Waser 1974; Milton 1981; Chapman et al. 1999).

The periodic cycle of many tropical rainforest plants (phenology) is relatively well described, which makes it possible to estimate the cognitive challenge faced by frugivorous primates, such as the grey-cheeked mangabeys

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(*Lophocebus albigena johnstonii*); the focus of this study. In Kibale National Park, Uganda, mangabeys consume fruit from more than 65 woody plant species (of about 260 species in total; Waser 1977; Barrett 1995; Olupot 1998; Struhsaker 1997). Taking into account tree density measures of the different species, the monkeys' home range is likely to contain about 125,000 trees, of which about 100,000 could contain fruit (Janmaat et al. 2009; Chapman et al. 1997). However, the probability that an individual will find ripe fruit in any of these trees at any given time varies from about 1 out of 10 to as low as 1 out of 1,000 trees (Chapman et al. 2004; Janmaat 2006). This suggests that random approach is an extremely inefficient and a potentially lethal strategy for non-human primates.

Rainforest tree species range from nearly continuous fruiting (asynchronous species) to temporally segregated fruiting peaks, where individual trees produce fruits simultaneously with other members of the species (synchronous species) (Hladik 1975; Milton 1980, 1981; van Schaik et al. 1993; Chapman et al. 1999, 2004). In Kibale National Park, the timing of peak fruiting of some species varies between years (Chapman et al. 1999, 2004). One of the most predictable species is *Uvariopsis congensis*, where 60% of trees fruit between June and July in most years. However, in one exceptional year, 50% of trees produced fruits in December and once the entire surveyed population failed to produce fruits for 4 years in a row (Chapman et al. 2004). For fruit eaters, such irregular patterns exclude localisation strategies that are based on monitoring photoperiod or successions of fruiting seasons, strategies that are feasible for temperate zones (e.g. raspberries, *Rubus idaeus*, traditionally fruit in July, followed by blackberries, *Rubus fruticosus* in August; Lamey and Grey-Wilson 1989). In addition to temporal variability, trees of most primate fruit species have a low density and tend to be widely dispersed (Milton 1977, 1981; Chapman et al. 1999; Vooren 1999), which increases the challenge of finding fruit even more.

Various authors have argued that rainforest primates possess sophisticated spatio-temporal abilities, which allow them to remember fruiting states and to predict fruit emergence and ripening rates of individual trees (Milton 1981, 1988; Potts 2004). Two recent studies have added relevant empirical evidence to this idea. First, the ranging behaviour of two species of mangabeys (sooty mangabeys, *Cercocebus atys atys*, and grey-cheeked mangabeys) suggested that these monkeys relied on memory of previous feeding experiences in a particular tree, to predict the current fruit availability of that same tree (Janmaat et al. 2006a). Second, grey-cheeked mangabeys of Kibale National Park were found to be capable of taking past weather conditions into account when searching for fig trees, whose fruits' ripening rates are dependent on solar radiation. The monkeys were more likely to revisit a tree with fruit following several days of warm and sunny weather compared to a cooler and cloudier period. These effects were only found for trees that had carried fruit at the previous visit, but not for trees that had carried none (Janmaat et al. 2006b). Similar studies demonstrating sophisticated spatio-temporal memory in non-human primates have been reviewed by Garber and Boinski (2000), Janson and Byrne (2007) and Zuberbühler and Janmaat 2010.

Other research emphasises the ways in which primates may be cognitively limited in mapping fruit-bearing trees and planning revisits. Noser and Byrne (2010), for instance, concluded that the cognitive maps of savannah-living baboons (*Papio ursinus*) either contained information on relatively few trees or of only a single route along which several trees were situated, leading to very limited planning abilities. A related study concluded that baboons did not have the ability to compute Euclidian relationships between locations (Noser and Byrne 2007a). Chimpanzees (*Pan troglodytes verus*) appear to remember a large number of trees of rare fruit species, but interestingly, there is no evidence that they rely on memory when foraging for high-density species (Normand et al. 2009). Chimpanzees also appear to be limited in their ability to remember distances between fruit-bearing trees in the periphery of their territory, presumably because these are lesser-known areas (Normand and Boesch (2009).

Such failures are not difficult to explain. The timing and occurrence of fruit emergence in individual fruit trees can be highly variable between years (Struhsaker 1997; Chapman et al. 1999; Janmaat et al. 2009) and fruiting periods of individual trees may be simply too short to enable primates to have a continuously up to date record on which trees carry fruit and which do not. It is very likely, therefore, that non-human primates, including chimpanzees, do not maintain a complete representation of the fruiting state of all relevant feeding trees. We thus propose an alternative, perhaps cognitively less challenging, strategy to predict the location of fruit, attending to synchrony patterns in fruiting behaviour.

Forest primates could make use of synchrony in fruit emergence to anticipate the current fruiting state of a large number of trees within one species. For example, after discovering a tree with fruit, primates could switch to an 'inspect-all' strategy and start visiting all other trees of the same species in their home range. Whether forest primates possess the ability to make use of synchrony cues and whether they can discriminate between synchronous and asynchronous species is currently unknown.

Menzel (1991), working with Japanese macaques (*Macaca fuscata),* was the first to suggest the presence of a *synchrony-based inspection strategy*. In his study, if the macaques were artificially provisioned with fruits of *Akebia trifoliate* vines, prior to their fruiting season, individuals were more likely to inspect other *Akebia trifoliate* vines than if they were provided with other food items. Intriguingly, the monkeys manipulated both *Akebia trifoliata* and *Akebia quinata* vines, although the fruits and leaves of this vine species taste and look 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, related or other simultaneous fruiting vine species.

The current study

Compared to the temperate zones of the Japanese woodlands studied by Menzel (1991), heights of fruiting peaks are much less predictable in tropical rainforests. Within a species, levels of synchrony vary in time and space and the discovery of fruits in one tree does not automatically predict the presence of fruit in other conspecific trees (Milton 1981; Chapman et al. 1999, 2004). For example, in May 1996, 60% of the *U. congensis* population in Kanyawara carried fruit, while none did at three other research sites that were all within 12 km distance (Chapman et al. 2004).

To investigate whether, despite this drawback, rainforest primates use a synchrony-based inspection strategy similar to Japanese macaques, we conducted a study with the frugivorous grey-cheeked mangabeys of Kibale National Park, Uganda—to our knowledge, the first study to investigate the use of synchrony in rainforest primates. The majority of the grey-cheeked mangabeys' diet in the Kibale National Park consists of fruit (59% of foraging time; Olupot 1998). A majority of these fruit species emerge synchronously (64%; Chapman et al. 1999). First, we investigated whether grey-cheeked mangabeys used a synchrony-based inspection strategy, as described by Menzel (1997). Our null hypothesis was that the monkeys inspected trees by random approach. We monitored the movement of the monkeys towards trees of a highly synchronously fruiting tree species (*Uvariopsis congensis*) in two different time periods—in and out of fruiting season. We expected that the monkeys inspected more trees during, than out of fruiting season (as assessed by the overall percentage of trees that carried ripe fruit). In addition, we expected the monkeys to inspect more trees when the percentage of fruit-bearing trees that they encounter per day increased. Second, we investigated whether grey-cheeked mangabeys generalised the synchrony-based inspection strategy to all trees of the same species within its fruiting season or whether they took local differences in synchrony levels into account during their search for fruit. We thus monitored the movement of the monkeys towards *U. congensis* trees in two different areas within their home range. We expected that the monkeys inspected more *U. congensis* trees in areas where a higher percentage of trees carried ripe fruit compared to areas with lower percentages, in the same time period. Lastly, we discuss the cognitive prerequisites for a synchrony-based strategy and assessed the monkeys' capacity to differentiate *U. congensis* trees from those of *Teclea nobilis,* a food tree species that has a highly similar visual appearance.

Methods

Study design

Within our study, we first assessed the synchrony levels of *U. congensis* trees during our observation periods. Secondly, we investigated the mangabeys' motivation to feed on fruits of *U. congensis*. Thirdly, we tested whether the mangabeys inspected more *U. congensis* trees in time periods when, or areas where, synchrony levels were high compared to low. For this, we compared inspection rates in and out of fruiting season. Within the fruiting season, we compared inspection rates between two different adjacent ranging areas that were expected to have different levels synchrony. We tested, in addition, whether inspection rate of *U. congensis* trees (full and empty) correlated with the percentage of *U. congensis* trees that the monkeys fed in per distance travelling per day. Lastly, we tested whether the mangabeys also inspected more trees of *T. nobilis* when the percentage of ripe fruit-bearing *U. congensis* trees was high compared to low.

Study animals and study site

Our study animals were members of a group of arboreal mangabeys in the Kanyawara study area in a lightly logged moist evergreen forest patch of Kibale National Park in Uganda (0°34′N, 30°21′W) (Struhsaker 1997; Chapman et al. 1997). At the beginning of the study, the group consisted of 20–27 independently moving individuals. During the study, the group split into subgroups I and II, consisting of 10 and 12 independently moving individuals, respectively. All individuals were well habituated to observers, allowing observations at a distance of 2 m. The group and subgroups covered a total area of 623 ha (Janmaat 2006). Nine days after the start of our study, the group started to forage in a new area in which it had not been observed for 6 years (17th September 2009; Janmaat et al. 2009). After the split, subgroup II remained in this newly explored area (range II). Subgroup I returned to the group's old area (range I). Data were collected on fruit localisation behaviour of individual adult males. We chose to work

Table 1 Number of 300–400 m trajectories used for analyses, total days, distance and duration of observation

	Individuals:	Bg	Ma	Sp	Me	Lb	Em	Ha	Pl	Mg	# Days	Distance (m)	Duration (min)
Period I (8 Sep 03–29 Nov 03)	Before split (23 Apr 04)	12	12	6	7	5	12	9			35	19,487	7,571
Period II (4 May 04–26 June 04)	Subgroup I	9				4			7	8	37	18,327	9,469
	Subgroup II		9	10	7	4							

Lb shifted from subgroup II to I halfway through the observation period. Em and Ha left the group after period I and were replaced by Pl and Sp in period II

with adult males because they are more independent in their foraging decisions than other group members (Waser and Floody 1974) and because they could be recognised individually most easily. Before the group split, we conducted observations on seven males. After the split, we followed three males in subgroup 1 and three males in subgroup II and one male who switched between subgroups (Table 1).

Target fruit species

To increase our chances of finding evidence for the use of a synchrony-based inspection strategy, we monitored the mangabeys' behaviour towards trees of a species that was likely to have high levels of synchrony during its fruiting season. We selected *Uvariopsis congensis* Robyns and Ghesq. (Family *Annonaceae*) that had shown a high temporal clustering in fruiting periods within the past 12 years (variance to mean ratio of 1.27; Sokal and Rohlf 1981; Chapman et al. 1999). Therefore, a high percentage of its trees were expected to carry fruit at the same time. *U. congensis* is a small under-story species with an average diameter at breast height (DBH) of 15.7 cm and a high density (of trees >10 cm DBH; 60.4 tree/ha; Chapman et al. 1999; Chapman unpublished data) and, according to the Morisita index (Poole 1974), a clumped (patchy) distribution (Barrett 1995). An individual *U. congensis* tree was said to belong to a patch if it was within a distance of two times the average crown diameter (8.0 m) of another *U. congensis* tree. Patch size was calculated by measuring the straight-line distance between the two outer trees in North–South and East–West direction. Patches have an average diameter of 111.9 m ± SE 35.7 m (NS) and 92.2 m ± SE 31.4 m (EW). *U. congensis* trees are ranked low on the mangabeys' preference list [19th, 16th and 42nd based on the percentage of time that mangabeys were feeding on any item from each tree species (20, 20 and 48 species, respectively)]. The rank numbers are calculated by Barrett (1995) and Janmaat based on feeding data collected from (1) the study group from November 2003 until July 2005 (R. L. Chancellor unpublished data), (2) a group ranging in the same ranging area as the study group from March 1972 until April 1973 (Waser 1977) and (3) a group that ranged in primary forest 12 km from the study area from August 1975 until May 1977 (Wallis 1979). Preference ranks were estimated using Ivlev's electivity indices that incorporate percentages of feeding time and relative tree density (Krebs 1989; Barrett 1995). Mangabeys feed on fruits, but not on leaves or flowers of *U. congensis* (Waser 1977; Barrett 1995; Olupot 1998).

Study period

In our first period of data collection, we followed our focal males between 8 September 2003 and 29 November 2003 for 37 observation days (Table 1). Period II started after the group split, when we followed males in subgroup I and II, between 4 May 2004 and 26 June 2004 on alternating days for 19 and 18 observation days, respectively. The start of the observation periods was based on 12 years of data from phenology transects that monitored the fruiting state of all primate fruit trees monthly. At the start of the first observation period, no *U. congensis* fruits were available. With the beginning of the second one, ripe *U. congensis* fruit started to emerge.

Measuring inspections in natural conditions

Without provisioning experiments that can be conducted in periods in which all fruit trees are empty, we had to rely on observations of the monkeys' reaction to finding fruit during the naturally occurring fruiting season. In natural conditions, approaches to *U. congensis* trees could be explained by monkeys having spotted ripe fruit, rather than attempts to inspect trees for the presence of ripe fruit, as observed in the Japanese macaques. To identify approaches that were likely to represent inspection, we therefore focussed on the approaches to empty trees. We have no doubt that in some instances the monkeys were able to spot fruits from considerable distances. However, visual detection of fruit was limited by dense vegetation in the understory of *U. congensis* trees (Struhsaker 1997). Moreover, *U. congensis* trees often carry fruit inside the dense tree crown that are difficult to spot from the outside. We therefore expected that the monkeys would need to approach and enter the trees to correctly assess their fruiting state and that as a consequence they would make ‘mistakes’ by entering empty trees. Hence, we studied the monkeys’ inspective behaviour by measuring the number of empty trees that were entered in and out of the season. During the fruiting season, we studied the monkeys’ inspective behaviour by measuring the number of trees that were *presumably* entered (i.e. the number of empty crowns that overlapped with a male’s travel route), as this allowed us to make a comparison with a control route (see description below). The trees whose crown overlapped with the male’s route were assumed close enough to have allowed the monkey to inspect their fruiting state.

Sampling methods

Male trajectories

To calculate our first measure of inspection, we recorded the number of empty trees that were entered by the male mangabeys along parts of their daily travel routes—a trajectory of between 300 and 400 m. This distance was assumed to be long enough to contain a sufficient number of *U. congensis* to test our predictions (pilot study April–July 2003). We stopped following the male when calculations of the sum of our step lengths showed that we had followed him for a distance of 300 m or more. Since these calculations were not feasible at all times during the follow, the length of the trajectories was variable, but always remained between 300 and 400 m. Along this male trajectory, we recorded the activity of the focal male for every minute that he was visible (one-zero sampling; Martin and Bateson 2007). For each minute, we recorded the distance travelled per minute (in steps), the number and species identity of food trees entered (including trees of *Teclea nobilis* Delile (Family of *Rutaceae*) and all other known food species) and whether the male was feeding inside a tree or not. If the focal animal was feeding, we specified whether this was on fruits or on other food items within the tree (e.g. young leaves). Data collection started by locating and identifying one of the focal individuals. Each focal male was followed for one trajectory of 300–400 m before the next available focal animal was chosen. If a focal male was lost, or could not be found within 1 h, the next male in the order was followed. If the observer managed to relocate a previously lost male later in the day, he was followed again until the trajectory of 300–400 m was completed. Deliberate search for particular males (e.g. according to a preset list) was not practical under field conditions, since males often lingered at the periphery or outside the group and locating them was extremely time consuming and often impossible to do within a day.

Control trajectories

The day after each focal follow, we created a control trajectory that was likely to be in the same *U. congensis* patch for each male trajectory, 15 m from and parallel to the male’s trajectory (Fig. 1). This was done for three different purposes. First, we created a control trajectory to verify the predicted high level of synchrony of *U. congensis,* within our observation period, in the focal animal’s daily ranging area. Synchrony levels were quantified as the percentage of trees that produced fruit simultaneously within a fruiting period along these control trajectories. Second, we created the control trajectory to make an estimate of the male’s motivation to find *U. congensis* fruit. It enabled us to assess whether the males had approached more fruit-bearing *U. congensis* trees than was expected by walking another route of similar length through the same forest area. The male’s trajectory was marked with visible markers (60 cm long traffic safety tape) about every 5 m, which allowed the observers to determine the location of the control trajectory the following day.

We placed the control trajectory within 15 m parallel to the male’s route because it was likely to be located in the same patch of *U. congensis* trees—a tree species that is, as discussed above, known to have a spatially clumped distribution and has an average patch size of about 100 m. By comparing the differences in density between a male’s chosen trajectory and an *adjacent* control trajectory (that was likely to be in the same patch), we accounted for the patchy distribution of this tree species and thus provided a better indication of the degree with which the male was

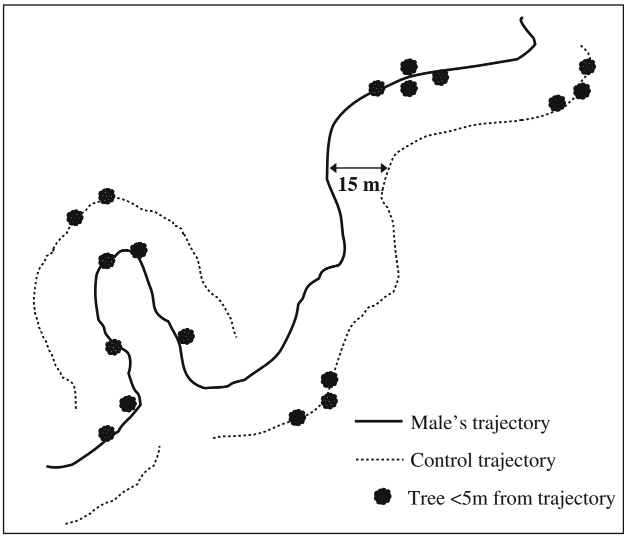

Fig. 1 Measuring approach behaviour. The schematic diagram illustrates part of a mangabey male’s trajectory and the control trajectory. We measured the number of tree trunks of *U. congensis* and the fruiting state of the trees within 5 m of each trajectory

actively approaching fruit in patches where it was available. To assess synchrony along a control trajectory, the observers mapped each *U. congensis* tree, with a trunk within 5 m from the control trajectory, and determined its fruiting state the day after each focal follow. We opted for a 5 m distance since our assistants were already trained in tree determination within this distance (botanical transects at Kibale have a standard width of 10 m; Chapman et al. 1997, 1999). To estimate each tree's fruiting state, the observers checked the crown for fruit from each wind direction using 25 × 10 Leica Trinovid binoculars. To assess the male's motivation, the observers, thereafter, also walked the male's trajectory of the previous day to collect the same measurements. Walking a parallel control trajectory was more time efficient than the alternative option of walking a set out 'randomly' placed trajectory within the presumed patch boundaries by the use of GPS and enabled us to finish both trajectories within the same day, which minimised influences of fruit consumption by other frugivores within our measuring period.

Relative localisation efficiency

Creating a control trajectory also enabled us to calculate a second measure of inspection that allows us to investigate the effect of local differences in synchrony levels on the monkeys' inspective behaviour during the fruiting season. For this, we calculated the relative localisation efficiency (RLE), as follows:

$$\mathrm{RLE} = \frac{(\#U.\,congensis\ \text{trees whose crown overlapped with the male's trajectory})}{(\#U.\,congensis\ \text{trees whose crown overlapped with the control trajectory} + 1)}.$$

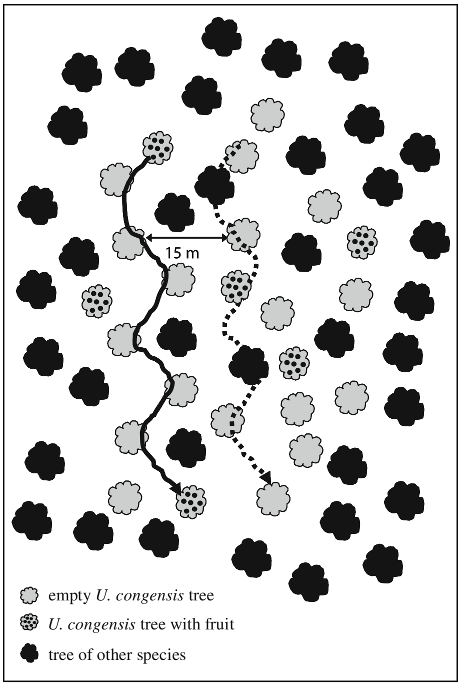

Fig. 2 Calculating relative localisation efficiency (RLE). The *schematic diagram* provides a visual example of how RLE was calculated for empty trees. The *grey coloured* trees represent a patch of *U. congensis* trees within a forest. In this example, six tree crowns of empty trees overlap with the male's trajectory (*full line*) and four overlap with the control trajectory (*dotted line*). This results in a RLE of 1.2 for empty trees

This measure allowed us to control for the use and entry of empty trees as travel substrate, when the monkeys moved from one fruit-bearing *U. congensis* tree to another within a patch (Fig. 2). In the above equation, we calculated the number of trees per 100 m travelling as the male and control trajectory were not always of equal length. We calculated separate RLE values for trees that carried ripe fruit and for empty trees. We added the value of 1 to the denominator to enable the use of a larger number of control trajectories (some did not contain ripe fruits). However, we only analysed trajectories in areas that contained *U. congensis*, i.e., in which at least one tree was observed either on the male's trajectory or in the control trajectory.

Measurements of motivation and inspection

In summary, our measure of motivation was the number of fruit-bearing *U. congensis* trees within 5 m of the male's trajectory compared to the number of fruit-bearing trees within 5 m of the control trajectory. Our first measure of inspection was the number of empty *U. congensis* trees entered per 100 m travelling in versus out of season. The second measure of inspection, used to compare behaviour between different areas, was the RLE of empty trees.

Observer reliability

Data were collected simultaneously by two teams of observers. Each consisted of one researcher (K. Janmaat, R. Meijer) and one local field assistant (J. Rusoke, P. Irumba, respectively). The researcher recorded the data dictated by the local assistant, who kept a constant eye on the focal male. To minimise observer bias effects, both male and control trajectories were always walked by the same team of observers. In addition, the two teams alternated after a similar number of days (5 days) keeping the number of days that each team recorded in each observation period or ranging area equal. Tree identification was done by the field assistants who had four and 9 years of experience. Inter-observer tests between the two field assistants were conducted on two 200 × 10 m transects, walked at the beginning of each observation period. Results revealed a percentage of agreement of 81–83% in determining the fruiting state and a reliability of 93–96% in estimating density of *U. congensis* and *T. nobilis* (index of concordance, Martin and Bateson 2007). We also conducted two intra-observer tests for each assistant, by walking two similar 200 m transects in opposite directions. This revealed a percentage of agreement of 83–85% for determination of fruiting state and 85–87% for estimating the density of *U. congensis* and *T. nobilis*. The researchers' step lengths were repeatedly calibrated over a stretch of 500 m within the forest habitat with varying elevation levels.

Statistical procedures

Since our variables were not normally distributed (also after transformations), we relied on non-parametric Wilcoxon signed rank tests, Mann–Whitney *U* tests and Spearman correlation analyses (Siegel 1956) using SPSS and *R* (Spearman exact test (1,000 permutations) written by Roger Mundry). All tests were two-tailed unless indicated differently. In each case, we assessed evidence about specific hypotheses and hence we do not adjust critical alpha levels using procedures such as Bonferroni correction factors (Perneger 1998). Most of the males were members of the same group; however, we assumed that the data collected on the foraging behaviour of the individual males were independent. This was justified because our study group rarely travelled as a cohesive unit; the average group spread was 98.0 m. (Janmaat and Chancellor 2010). Furthermore, adult males ranged relatively independently from other group members and were regularly found at the periphery of the group or even away from the group (Waser and Floody 1974; Waser 1985; Olupot and Waser 2001; Janmaat and Chancellor 2010). The trajectories for each male were separated by at least 1 day. Since the group travelled fairly large distances each day ($X \pm SD =$ 1,120 m ± 394 m; maximum 2,501 m; Waser 1974, 1975; Janmaat and Chancellor 2010) and mangabeys rarely back-tracked (Waser 1974; Barrett 1995), we assumed that each 300–400 m trajectory could be treated as an independent sample.

Results

Are mangabeys interested in *U. congensis* fruit?

Uvariopsis congensis rank low on the preference list of fruits consumed by the mangabeys, and it is possible that the monkeys bypass *U. congensis* fruit when more preferred fruit is available. In a first analysis, we therefore determined whether their route indicated whether the monkeys were interested enough in fruiting *U. congensis* to actively approach those that they had spotted on route (as opposed to randomly encountering them as part of their daily ranging). For this analyses [in the second observation period (i.e. in season)], we simply compared the density of *U. congensis* trees (*N* trees per 100 m) with ripe fruit along the focal male's trajectory with the density of trees with ripe fruit along its control trajectory. We did the same for trees that contained either ripe or unripe fruit. For the analyses, we calculated the number of trees per 100 m travelling in each trajectory. For each male, we calculated an average value by pooling all samples. These comparisons showed that the male trajectories had significantly higher densities of *U. congensis* trees with ripe fruit or both ripe and unripe fruit than their paired control trajectory (ripe fruits only: $T^+ = 28$, $N = 7$, $P = 0.016$; ripe or unripe fruit: $T^+ = 27$, $N = 7$, $P = 0.031$; Wilcoxon signed rank exact (WSR); $N =$ number of males; Fig. 3). These results suggest that the monkeys were changing their route to actively approaching fruit of *U. congensis* in season and were interested in feeding on it.

We found no indication that the monkeys showed more interest in feeding on *U. congensis* fruit during particular

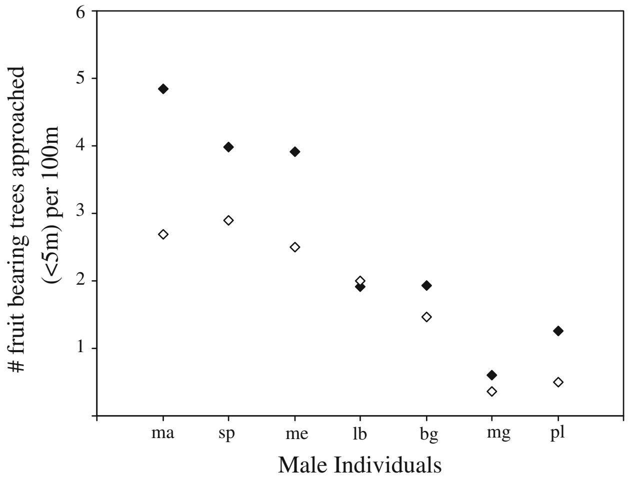

Fig. 3 Estimates of fruit approach behaviour in male individuals. Densities of *U. congensis* trees that carried ripe or unripe *U. congensis* fruit within 5 m of the male's trajectory (*closed circles*) compared to the densities within 5 m of the paired control trajectory (*open circles*)

times of the day, as no significant difference was found between the number of *U. congensis* trees fed in per 100 m, in the morning compared to the afternoon, in season ($U = 333.5$, $N_{\mathrm{morning}} = 35$, $N_{\mathrm{afternoon}} = 22$, $P = 0.41$, $N =$ number of male trajectories).

Synchrony levels of *U. congensis* in time and space

Synchrony levels of ripe and unripe fruits of *U. congensis* trees were higher in the second observation period (the predicted fruiting season) than in the first (Fig. 4). Within period II (in season), we found that the percentage of ripe fruit-bearing trees within 5 m of the control trajectory decreased in time, though not significantly, suggesting that the degree of synchrony remained fairly stable or declined marginally throughout the season (54 days; $N = 46$ $r_{\mathrm{s}} = -0.261$, $P = 0.067$, $N =$ number of control trajectories). This precluded measuring the monkeys' reaction to changes in synchrony levels within the fruiting season, but still allowed us to compare their behaviour in and out of season.

Due to a group split after the first observation period, we were able to measure differences in synchrony levels of ripe *U. congensis* fruit in two distinct ranging areas. During this period, a significant difference was found between the percentages of *U. congensis* trees with ripe fruit in subgroup I's and subgroup II's range (mean: 13.0 vs. 34.0, median: 7.0 vs. 41.0; $U = 177.0$, $P = 0.008$, $N_{\mathrm{period\ I}} = 24$, $N_{\mathrm{period\ II}} = 26$; $N =$ number of control trajectories). Calculations were based on control trajectories with at least five *U. congensis* trees within 5 m. Having confirmed that the monkeys were interested in feeding on *U. congensis* fruit and that there were differences in synchrony levels of this fruit in time and space we continued to investigate the monkeys' reaction to these differences.

Does a high synchrony level trigger inspection?

To investigate whether the synchrony level of ripe fruits influenced the males' inspection behaviour, we first compared the males' rates of entering trees of *U. congensis* in and out of season where synchrony levels were high versus almost zero, respectively (Fig. 4). Males entered significantly more *U. congensis* trees (with or without fruit) in season than out of season [$U = 28.0$, $N_{\mathrm{period\ II}} = 7$, $N_{\mathrm{period\ I}} = 7$, $P < 0.001$, $N =$ number of males (one-tailed)].

To test whether the monkeys indeed entered *U. congensis* trees with the purpose of inspecting, as opposed to getting fruit already spotted, we conducted a similar analysis for empty trees only (our first measure of inspective behaviour) and found that males also entered significantly more empty *U. congensis* trees in season than out of season [$U = 5.0$, $N_{\mathrm{period\ II}} = 7$, $N_{\mathrm{period\ I}} = 7$, $P = 0.005$ (one-tailed)]. In addition, the number of empty *U. congensis* trees entered was positively correlated with the percentage of *U. congensis* trees with fruit that were entered and fed on ($r_{\mathrm{s}} = 0.80$, $N = 14$, $P = 0.001$, $r^2 = 0.64$). These results suggest that the monkeys entered and presumably inspected more trees in season when the percentage of *U. congensis* trees that carry fruit was high and in times when the percentage of entered trees that the monkeys fed in was high.

Effects of spatial differences in synchrony levels on inspective behaviour

To investigate whether the monkeys inspected trees as a function of the spatial differences in synchrony levels, we compared the monkeys' relative localisation efficiency (RLE) for the ranging area of subgroup I and II (range I and II). The RLEs of trees with ripe *U. congensis* fruit was significantly higher in range II, where the synchrony level of ripe fruits was higher compared to range I [$U = 176.0$, $P < 0.001$, $N_{\mathrm{range\ II}} = 29$, $N_{\mathrm{range\ I}} = 28$, mean: 1.16 vs. 0.35, median: 1.20 vs. 0.00; $N =$ number of RLEs (one-tailed)]. Crucially, the males also (presumably) entered relatively more empty *U. congensis* trees in range II than I, as judged by their relative localisation efficiency of empty

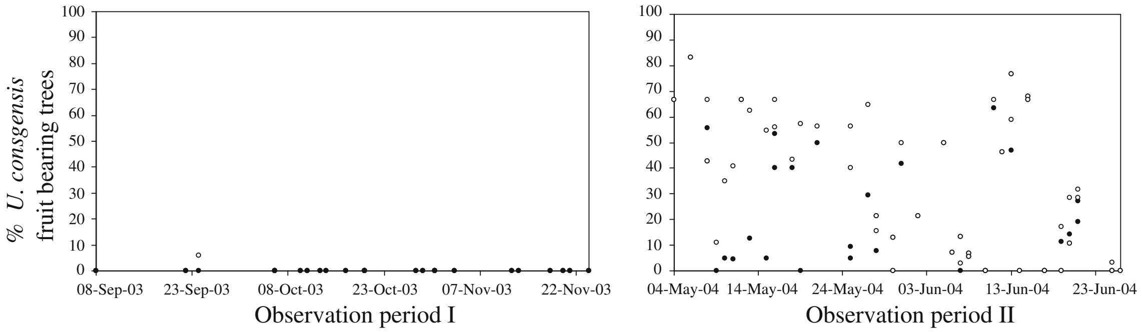

Fig. 4 Temporal distribution of synchronous fruit. Percentages of trees *U. congensis* that carried ripe (*closed circles*) and unripe (*open circles*) fruit within 5 m of the control trajectories plotted per observation day, within each observation period. Included were trajectories with at least five *U. congensis* trees

U. congensis trees, our second measure of inspective behaviour [$U = 271.0$, $P = 0.016$, $N_{\mathrm{range\ II}} = 29$, $N_{\mathrm{range\ I}} = 28$, mean: 1.00 vs. 0.67, median: 0.87 vs. 0.54 (one-tailed)]. There was no indication that the observed difference was due to differences in tree density, as the total number of *U. congensis* trees in the control trajectories did not differ significantly between both areas ($U = 312$, $P = 0.14$, $N_{\mathrm{range\ II}} = 29$, $N_{\mathrm{range\ I}} = 28$, median: 7.21 vs. 4.69, N = number of control trajectories). Neither could the results be explained by differences in the males' overall activity levels in both areas, assessed by the per cent time males spent feeding on fruit (of 28 species) nor the total number of fruit trees entered per trajectory between the two areas (per cent time: $U = 364$, $P = 0.51$, $N_{\mathrm{range\ II}} = 29$, $N_{\mathrm{range\ I}} = 28$, median: 1.32 vs. 0.93; number of trees entered: $U = 364$, $P = 0.38$, $N_{\mathrm{range\ II}} = 29$, $N_{\mathrm{range\ I}} = 28$, median: 7.95 vs. 7.36, respectively). Hence, males more actively approached and presumably inspected *U. congensis* trees in the area with a high level of synchrony than in the area with a low level, within the same time period.

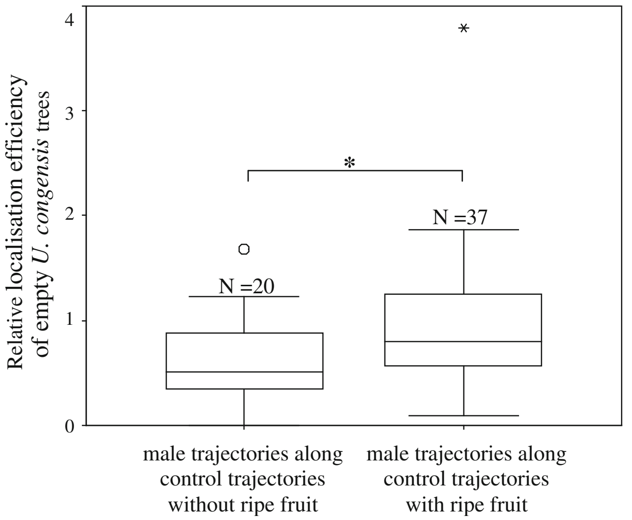

Fig. 5 Inspection of empty *U. congensis* trees in areas with and without ripe fruits. The *bars* represent the relative localisation efficiency of empty *U. congensis* trees of seven mangabey males, while the *top* and *bottom* of the *boxes* represent the 75 and 25 percentiles. The highest and lowest whiskers represent the highest and smallest values, which are not outliers. The *asterisks* represent an extreme value

To further control for effects of differences in overall fruit or tree availability between the two ranging areas, we conducted additional analyses. We pooled observations from both ranges and split the data in male trajectories from areas *with ripe fruit*, i.e., male trajectories with accompanying control trajectories, where the controls contained at least 5 trees each of which at least 1 bore ripe fruit, and male trajectories from areas *without ripe fruit*, i.e., male trajectories with accompanying control trajectories, where the controls contained at least five trees of which none bore ripe fruit. We found that, in season, the males' relative localisation efficiency of trees with ripe *U. congensis* fruit was significantly higher when the control trajectories contained ripe fruits than when they did not [pooled: $U = 112.0$, $P < 0.001$, $N_{\mathrm{ripe\ fruit}} = 37$, $N_{\mathrm{no\ ripe\ fruit}} = 20$, median: 0.94 vs. 0, N = number of RLEs (one-tailed)]. When we compared the average RLEs of individual males for which we had trajectory data in both areas, RLEs were also higher ($T^{+} = 21$, $P = 0.016$, $N = 6$, $\mathrm{median}_{\mathrm{ripe\ fruit}} = 0.91$, $\mathrm{median}_{\mathrm{no\ ripe\ fruit}} = 0.26$, N = number of males (one-tailed); number of male trajectories per individual: Male Ma: 8, Male Bl: 10, Male Lb: 7, Male Mg: 8, Male Pl:7 and Male Sp: 10). Crucially, the RLE of empty *U. congensis* trees was also higher when control trajectories contained ripe fruits than when they did not (pooled: $U = 238.0$, $P = 0.014$, $N_{\mathrm{no\ ripe\ fruit}} = 20$, $N_{\mathrm{ripe\ fruit}} = 37$, median: 0.80 vs. 0.51 (one-tailed); Fig. 5). When we compared the average RLEs of individual males for which we had trajectory data in both areas, RLEs of empty trees were significantly higher when control trajectories contained ripe fruit than when they did not [$T^{+} = 19$, $P = 0.046$, $N = 6$ $\mathrm{median}_{\mathrm{ripe\ fruit}} = 0.89$, $\mathrm{median}_{\mathrm{no\ ripe\ fruit}} = 0.55$ (one-tailed)]. This suggests that the males more actively approached and presumably inspected *U. congensis* trees in areas with ripe fruits than in areas without ripe fruits within the same time period.

Mangabeys' capacity to distinguish tree species with similar visual appearances

If mangabeys are indeed actively inspecting empty *U. congensis* trees, it implies that they use a memory of either the location of *U. congensis* trees or the visual or olfactory characteristics of the *U. congensis* tree irrespective of the presence of fruit. In other words, they either inspected the same tree individuals in which they fed previously or trees with the same species' distinguishing characteristics of trees they fed in earlier in time. The latter is not a trivial task, as fruitless trees from different species can appear very similar, at least to human observers. For example, inexperienced field assistants often identify trees of *Teclea nobilis* as *U. congensis* trees. Neither of the tree species produces obvious visual or olfactory cues, and human observers can only distinguish trees of both species by carefully comparing the leaf configuration or peeling the bark from the stem (Janmaat 2006; Zuberbühler and Janmaat 2010). We investigated if mangabeys could discriminate between the empty trees of these two species. If mangabeys could not discriminate between the two species, we would expect the number of *T. nobilis* trees entered to increase during the *U. congensis* fruiting season, in parallel with the increase in numbers of *U. congensis* entered. Since both species have a patchy occurrence, we only included trajectories in which the male trajectory contained at least one *T. nobilis* and one *U. congensis* tree within 5 m. We found that males did not enter more empty *T. nobilis* trees (N trees per 100 m) in the *U. congensis* season than out of season (pooled: $U = 53.0$, $N_{\text{period I}} = 13$, $N_{\text{period II}} = 9$, $P = 0.744$; $N =$ number of male trajectories). Furthermore, we found no relationship between number of empty *T. nobilis* trees entered (N trees per 100 m) and percentage of ripe fruit-bearing *U. congensis* trees within 5 m of the male's trajectory (pooled: $r_s = -0.218$, $P = 0.34$, $N = 21$). The results suggest that the males did not confuse two food species with a highly similar visual appearance.

Discussion

To our knowledge, this is the first study to investigate whether rainforest primates use synchrony in fruit emergence to locate fruit and to evaluate their flexibility in their use of botanical characteristics. We examined whether differences in synchrony levels in time and space affected the rate with which monkeys' inspected *U. congensis* trees. To make sure that the monkeys did not bypass fruit of *U. congensis* because of its low ranking on their preference list and the potential availability of more preferred food items, we first assessed the monkeys' interest in finding the fruit. We found that, in season, the monkeys approached more fruit-bearing trees compared to human observers walking a parallel control route, suggesting that the monkeys adjusted their travel path to find *U. congensis* fruit and thus were interested in finding this fruit.

Second, we found that as predicted from 12 years of phenology data, the percentage of ripe fruit-bearing trees (i.e. the synchrony level) was higher in observation period II (the predicted season) than in period I. In addition, we found clear local differences in the synchrony levels of ripe fruit-bearing *U. congensis* trees between two ranging areas within the season.

These observations allowed us to investigate the monkeys' reaction to different levels of fruiting synchrony. We found that the monkeys entered significantly more *U. congensis* trees in season than out of season. Crucially, this was also true for empty trees. Moreover, the number of empty *U. congensis* trees entered was positively related to the percentage of entered trees that they fed in and thus carried edible fruit. These results suggest that the percentage of ripe fruit-bearing trees observed in control trajectories and the percentage encountered by the monkeys both influenced the number of empty trees that they entered and presumably inspected.

Fourth, to investigate whether the monkeys took spatial differences in the synchrony levels into account, we investigated their *relative localisation efficiency* in different areas within the fruiting season. Using this measure, we found that males approached and presumably entered relatively more fruit-bearing trees per distance travelled (relative to the control trajectory) in areas with a high compared to areas with low percentages of fruit-bearing trees. Crucially, this was also true for approaches to empty *U. congensis* trees, suggesting that the inspection activity was influenced by the percentage of fruit-bearing trees encountered within an area. These results could not be explained by differences in activity levels (potentially caused by a higher overall fruit availability in range II) as we found no significant difference between the percentages of time that males spent feeding on fruit and the number of fruit trees they entered in both areas. The lack of significance is unlikely to be due to a small sample size as our other tests that assess the monkeys' activities, based on exactly the same number of trajectories, did reveal significant differences. To further control for differences in the overall food availability in both ranging areas, we conducted an additional analysis where we pooled the data from both areas. We found that the monkeys approached and presumably entered a relatively higher number of empty *U. congensis* trees per distance travelling, as judged by their relative localisation efficiency, if the control trajectory contained ripe fruits than if not.

Uvariopsis congensis trees are spatially clumped (Barrett 1995; KRL Janmaat unpublished data). Thus, differences in entering rates of empty *U. congensis* tree between fruit 'rich' and 'poor' areas could have been a simple by-product of the monkeys' increased foraging on ripe fruits inside a *U. congensis* tree patch. This could have resulted in an increased need to enter suitable substrates (e.g. empty *U. congensis* trees) to cross from one ripe fruit-bearing tree to another. If this was true, we should have found a similar amount of empty trees within the control trajectories located 15 m from the male's own trajectory, which was likely located within the same patch of *U. congensis* trees. However, the monkeys trajectory overlapped with relatively more empty tree crowns in 'fruit rich' than 'fruit poor' areas than the control trajectory. For this reason, we concluded that the monkeys did not just approach and presumably enter more empty trees in the 'fruit rich' area because they were using them as suitable travel substrate, but they were more actively inspecting empty trees of *U. congensis* for fruit in the 'fruit rich' area.

These results suggest that inspection activity is flexible and that rainforest monkeys do not inspect trees of a synchronous species after the encounter of any number of fruit of that same species, as was proposed for monkeys in more temperate zones (Menzel 1997). The monkeys presumably inspected more trees in periods and areas with a higher percentage of ripe fruit-bearing trees—a higher synchrony level. We found no indication that their inspective behaviour was affected by a generally higher density of *U. congensis* trees in the fruit rich areas, as no significant difference between tree densities was found. However, our sample size was small and effects of tree densities and synchrony levels were not always easy to separate. The effect of overall fruit availability should therefore be considered in future studies where primates feed on other fruit species.

Visually guided approach or active search?

We hypothesised that the activation of the observed inspective behaviour could be triggered by two forms of information processing. First, the monkeys were simply triggered to inspect trees that were of the same species in which they recently fed on fruit and that they happened to spot *en route*. Second, the encounter with ripe fruit triggered an anticipation of fruit finding expressed in active search. At a proximate level, it is possible that monkeys developed a 'search image', originally proposed by Tinbergen (1960), to explain predation events in which predators fed relatively more on certain prey species than was predicted from their density. In a similar way as predators change their 'search image' from prey A to B when prey B becomes more abundant, the monkeys may change their 'search image' for fruit when the percentage of fruit-bearing trees of species fruit B becomes higher than that of species A. The number of search images (food species) may, however, be considerably higher in the mangabeys than in other 'predators'. Within this study, mangabeys were observed to feed on 28 different food species, yet not all feeding events may have been a result of active search. Alternatively, the search could have relied on a spatial memory of tree patch locations that helped the monkeys travel towards areas with large numbers of *U. congensis* trees. Anecdotal observations on two gorilla species (*Gorilla gorilla beringei* and *Gorilla gorilla graueri*), making detours outside their normal ranging area to inspect bamboo groves at the beginning of the season, suggest the use of such a strategy (Byrne 1995). Even though the results of our study do not allow us to distinguish between these different forms of information processing, a combination of the use of fruiting synchrony, search images and spatial memory of tree patch locations is likely to result in highly efficient fruit finding, a topic for future study.

Categorising a tree species

If the monkeys were actively inspecting empty trees, how did they manage to recognise trees of the highly synchronous species? This question becomes especially interesting if we consider the fact that the 'fruit rich' area was an area of which the males had no or very limited knowledge about the location of individual *U. congensis* trees. During 6 years of observation, it was only 8 months before the start of the *U. congensis* fruiting season that the study group was first observed to enter the area (Janmaat et al. 2009, Janmaat and Chancellor 2010). Even if some of the males had been in the new area before on solitary foraging trips or before natal or secondary dispersal, it seems unlikely that the monkeys were able to visit and remember the location of all the trees visited in this study. The finding that the monkeys were actively inspecting empty trees of *U. congensis,* therefore, strongly suggests that they can identify the species of a tree without the presence of fruit by using some kind of representation or memory of visual features of the tree itself. The determination of a tree species is not a trivial task, as a *U. congensis* does not have a specific smell and visually resembles other sympatric species, such as *T. nobilis,* to a high degree (Janmaat 2006; Zuberbühler and Janmaat 2010). We found no indications that the mangabeys confused both types of empty trees (unlike human observers), suggesting that they were able to discriminate between tree species using very detailed characteristics of their food trees. Each *U. congensis* tree has a different visual appearance, due to the different micro-climatic and competitive conditions of the forest (Oldeman 1990; De Reffye et al. 1995). Hence, it is likely that the mangabeys based their decision whether or not to approach a particular tree on a categorisation that consists of detailed species-specific characteristics, such as leaf configuration or tree architecture. Similar categorisations were suggested to be used by pigeons (*Columba livia*) (trees; Herrnstein and Loveland 1964; Herrnstein et al. 1976; oak leaves; Cerella 1979). An ability of the monkeys to discriminate between two extremely similar food trees may imply that they categorise the trees by the use of a category boundary instead of mere stimulus generalisation—another topic for future study.

The adaptive value of a flexible synchrony-based inspection strategy

Within this study, we focussed on one fruit species only and we do not know how widely the strategy is used for other species. The finding that rainforest primates generally forage on a relatively small number of species per time period (Janson et al. 1986; Poulsen et al. 2001; Eckhardt and Zuberbühler 2004) is, however, consistent with a more general use of a synchrony-based inspection strategy.

Many Kibale fruit species for which long-term phenology records are available (12 years) have shown synchrony levels similar to those found for *U. congensis* in the fruit rich area (41%; Chapman et al. 2004), suggesting that the strategy could be used for a large number of fruit species. The strategy is furthermore not restricted to fruits with particular high preference scores, since *U. congensis* is not a preferred food for mangabeys.

As discussed, synchrony levels of tropical rainforest fruits can vary immensely between years. For example, the Kanyawara population of one of the mangabey fruit species *Strombosia scheffleri* was found fruiting only 4 times within 12 years and reached overall percentages of 3, 7, 11 and 55% of trees that carried ripe fruit, respectively (Chapman et al. 2004). As shown in our study, synchrony is also known to vary within species between locations (Chapman et al. 1999; Chapman et al. 2004). In addition, even when fruiting patterns appear highly synchronous, not all fruits within a species are qualitatively equal. Nutritional values of particular fruit species can vary substantially between different periods of the year and again between different locations within the forest (Chapman et al. 2003; Worman and Chapman 2005). For example, the lipid content of what appeared to a human observer to be ripe *Celtis durandii* varied from 0.03 to 30.8% over 6 months, with more fruit being eaten by the mangabeys when it contained more lipids (Worman and Chapman 2005). In some cases, the variation in fruit quality among sites can be greater than the differences among species (Chapman et al. 2003). Furthermore, fruiting seasons do not start abruptly; not all trees within a synchronous species carry ripe fruit from 1 day to the other. In addition, as fruits ripen, levels of edible fruit may stay low due to intense foraging activity. Observations of *D. abyssinica* indicate that the percentage of trees that carry ripe fruits can stay low for a considerable amount of time (79 days) despite the fact that a large number of trees carried unripe fruit throughout this period (Janmaat 2006). Considering the degree of unpredictability of fruit availability, it is essential that the monkeys can react to fruiting synchrony in a flexible way. A *flexible* inspection mechanism activated by high levels of synchrony would enable the monkey to deal with spatial and temporal fluctuations in quantity and quality by allowing them to adjust their travel accordingly. Such a strategy is therefore likely to be adaptive and viable alternative or additional strategy to the use of episodic-like memory and anticipation of fruit emergence in individual trees.

We do not deny that primates can find fruit by the use of a detailed cognitive map and that perhaps they even use these maps to plan foraging routes (Janmaat et al. 2006b, Valero and Byrne 2007; Cunningham and Janson 2007; Noser and Byrne 2007b; Normand et al. 2009). In fact, we know that mangabeys use spatial memory to relocate preferred fruit trees (Janmaat et al. 2006a). We also suspect that a cognitive ability to predict the ripening and emergence of fruit in individual trees of asynchronous high quality fall back fruits, such as figs, could have been a highly advantageous trait in periods of food scarcity. Yet, long-term data on tree phenology show us that the majority of African rainforest fruit emerges synchronously and can, in our opinion, more easily be found by the use of a flexible synchrony-based inspection strategy. Considering this botanical knowledge—the product of decades of research—we therefore encourage other cognitive scientists to consider this flexible, but fairly 'simple', fruit finding strategy as an alternative mean to find fruit in everyday foraging by primates.

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