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Report

Primates Take Weather into Account when Searching for Fruits

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Summary

Temperature and solar radiation are known to influence maturation of fruits and insect larvae inside them [1–8]. We investigated whether gray-cheeked mangabeys (*Lophocebus albigena johnstonii*) of Kibale Forest, Uganda, take these weather variables into account when searching for ripe figs or unripe figs containing insect larvae. We predicted that monkeys would be more likely to revisit a tree with fruit after several days of warm and sunny weather compared to a cooler and more cloudy period. We preselected 80 target fig trees and monitored whether they contained ripe, unripe, or no fruit. We followed one habituated monkey group from dawn to dusk for three continuous observation periods totalling 210 days. Whenever the group came within a 100 m circle of a previously visited target tree for a second time, we noted whether or not individuals proceeded to the trunk, i.e., whether they "revisited" or simply "bypassed" the tree. We found that average daily maximum temperature was significantly higher for days preceding revisits than bypasses. The probability of a revisit was additionally influenced by solar radiation experienced on the day of reapproach. These effects were found only for trees that carried fruit at the previous visit but not for trees that had carried none. We concluded that these nonhuman primates were capable of taking into account past weather conditions when searching for food. We discuss the implication of these findings for theories of primate cognitive evolution.

Results and Discussion

Weather variables, such as temperature and solar radiation, are known to influence the ripening rates and growth of fruit [1–6, 8]. Temperature can also affect the development of larvae that are extracted by primates from infested fruit [7, 9]. We investigated whether gray-cheeked mangabeys (*Lophocebus albigena johnstonii*) of Kibale National Park, Uganda, take temperature and solar radiation into account when searching for figs. We predicted that monkeys would be more likely to revisit trees in which they had previously found fruits after a period of sunny and warm days, compared to after a cooler period with overcast skies.

We studied the ranging pattern of an observer-habituated monkey group in relation to a large number of preselected *Ficus* trees (n = 80) throughout the group's home range. Data collection began as soon as the group entered a critical 100 m radius circle around a target tree and proceeded to the trunk. We then determined whether or not the tree carried fruit. As soon as the group reentered the same circle for a second time, usually a few days later, we noted whether or not individuals proceeded to the trunk, i.e., whether they "revisited" or simply "bypassed" the tree (Figure 1).

The purpose of this study was to investigate whether the likelihood of revisiting or bypassing a target tree was related to the weather conditions experienced during the period since the previous visit. We thus determined the average daily temperature (maximum and minimum) and solar radiation (% high-level radiation) for the time interval between each visit and successive revisit/bypass. We expected averages to be higher during periods prior to revisits than bypasses, but only for trees that carried fruit at the previous visit.

Revisiting Is Influenced by Weather

The average maximum daily temperature was significantly higher when the group revisited than when it bypassed a tree. This was true only for trees that carried fruit during the group's previous visit (with fruit: U = 5476.0, $n_{revisit} = 143$, $n_{bypass} = 91$, $p = 0.041$; without fruit: U = 2107.5, $n_r = 49$, $n_b = 92$, $p = 0.526$; Figure 2). Logistic regression analyses showed that the probability of revisiting a tree increased with increasing average maximum temperature for trees that carried fruit (chi-square = 3.938, p = 0.047, df = 1; $\beta = 0.121$, p = 0.050, df = 1; Figure 3). No significant relationships were found between the monkeys' foraging decisions and average daily minimum temperature measured at night (fruit: U = 5951.0, $n_r = 143$, $n_b = 91$, $p = 0.271$; no fruit: U = 2112.0, $n_r = 49$, $n_b = 92$, $p = 0.539$).

We also investigated whether the mangabeys returned earlier to a fruit-bearing target tree after warm periods compared to cooler ones. We found a negative relationship between the average maximum temperatures and the number of days between a current and previous visit (n = 74; $r_s = -0.260$, p = 0.025), but only for trees that had particularly high fruit cover of at least 25% during the previous visit. Trees with such large amounts of fruit were unlikely to be depleted at the day of reapproach. If all trees were included, the relationship was no longer significant ($r_s = -0.09$, p = 0.171, n = 231).

For the third data collection period (n = 100 days), we additionally measured solar radiation. This second weather variable also influenced the monkeys' revisiting behavior but effects were weaker. The average daily percentage of high-level radiation tended to be higher for revisits than for bypasses, but only for trees that carried fruit at the previous visit (fruit: U = 1735.5, $n_r = 93$, $n_b = 46$, p = 0.071; no fruit: U = 642.5, $n_r = 23$, $n_b = 57$, p = 0.890; Figure 4). Additional logistic regression analyses

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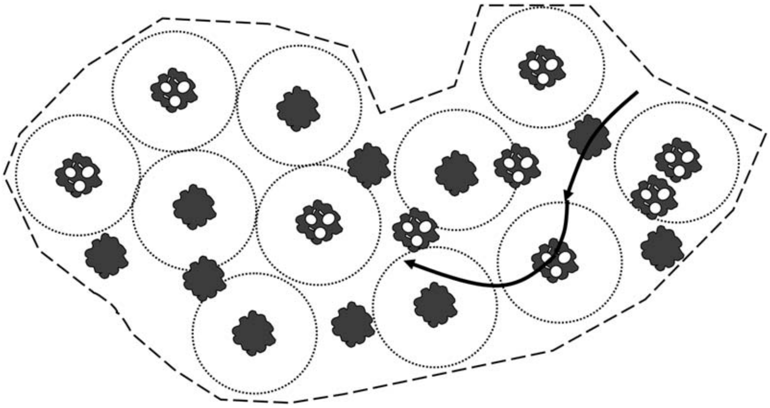

Figure 1. Measuring Revisiting Behavior

The diagram illustrates an example of part of the study group's daily route (arrows) among target trees, each surrounded by an imaginary 100 m radius circle (dotted line). Once the group entered the circle, one observer rushed to the tree to determine the fruiting state and whether the group came into sight and entered the tree. In this example, the group visited one tree with fruit and bypassed one without fruit.

did not reveal a significant relationship (chi-square = 0.28, p = 0.597, df = 1; p = 0.596, df = 1). There was no correlation between the length of the revisit interval and the average percentage of high-level radiation (all fruit-carrying trees: $r_s = -0.09$, p = 0.321, n = 133; trees with >25% fruit cover: $r_s = -0.223$, p = 0.136, n = 46).

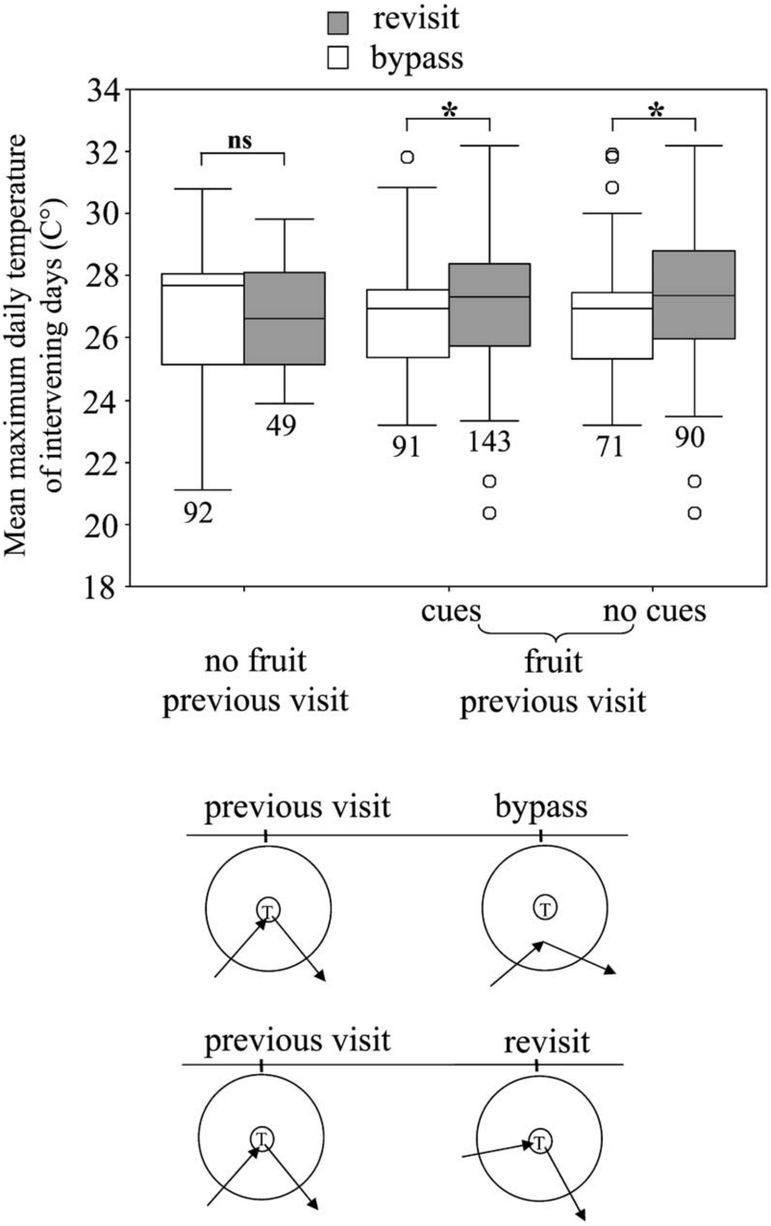

Figure 2. The Influence of Temperature on Revisiting Behavior

Average daily maximum temperature determined for the intervening period between the time the group entered the 100 m radius circle and the time the group last visited the same tree. Shaded boxes represent average temperature values for revisits; white boxes represent bypasses. Different clusters refer to trees that (1) did not carry fruit at the previous visit, (2) carried fruit at the previous visit, and (3) carried fruit at the previous visit but no longer offered any sensory cues. Bars represent the median values of the average temperatures; top and bottom of the boxes represent the 75 and 25 percentiles. Whiskers represent highest and lowest values; circles represent outliers.

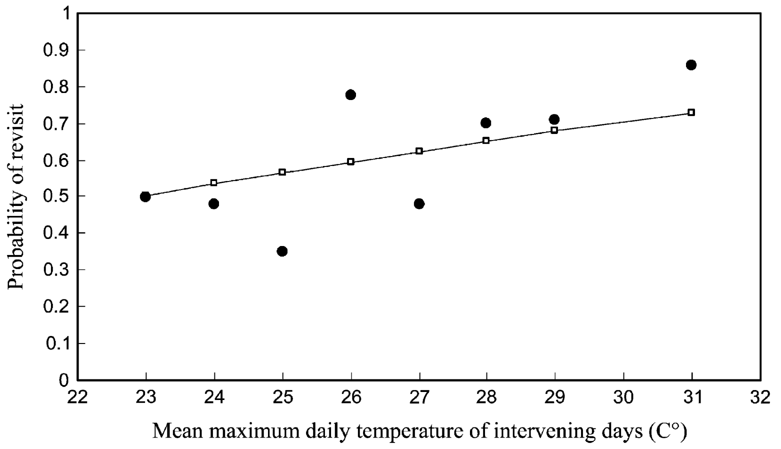

Figure 3. Probability of Revisit as a Function of the Mean Maximum Temperature of the Intervening Days between a Visit and a Reapproach

Average temperatures were calculated between the first visit and the subsequent reapproach. Temperature values were rounded to integers (e.g., 27° ranges from 26.5° to 27.4°). For each temperature interval, we calculated the observed revisiting probability (closed circles) as the proportion of times the monkeys entered the critical 100 m circle around a target fig tree and proceeded to the trunk ($n = 8–48$). Temperature intervals with less than four data points were considered unreliable and excluded from analysis. Predicted values (open squares) for the logistic regression were calculated as $Y = e^{\text{constant} + \beta^{*}X}/(1 + e^{\text{constant} + \beta^{*}X})$.

Is Revisiting Influenced by Sensory Cues?

An obvious alternative hypothesis suggests that the patterns described in Figures 2–4 are the result of monkeys' responding directly to the physical presence of ripe fruits while approaching a tree. For example, monkeys may be more likely to revisit a fruit-bearing tree after warm and sunny weather, simply because they are responding to visual or olfactory cues emitted by ripe fruits. To address this point, we repeated the same set of analyses for a subset of trees that carried fruit at the previous visit, but excluding all trees that carried ripe fruits at the current revisit or bypass. The majority of these trees carried unripe fruit, while some others were already depleted. This subset of trees was still valuable to the monkeys because unripe fruits were often infested by weevil larvae (69% of trees with unripe fruit visited). As the developmental state of the larvae cannot be assessed from the outside, monkeys have to inspect each fruit individually. Visual cues, in other words, do not offer reliable cues for foraging decisions with this subset of trees. Unripe fruit or the weevil larvae inside them did not emit any olfactory cues that could be detected from further than 20 cm, making it extremely unlikely that monkeys were able to use olfactory cues to take foraging decisions more than 100 m from a target tree.

For this subset of trees ($n = 31$), revisits were associated with higher average daily maximum temperature than bypasses ($U = 2502.5$, $n_r = 90$, $n_b = 71$, $p = 0.017$, Figure 2). Additional logistic regression analyses for trees of this subset showed that the probability of a revisit increased with increasing average maximum temperature (chi-square = 3.841, $p = 0.050$, df = 1; $\beta = 0.144$, $p = 0.054$, df = 1). A similar trend was found for the average percentage of high-level radiation ($n = 20$; $U = 871$, $n_r = 63$, $n_b = 36$, $p = 0.056$; Figure 4), although

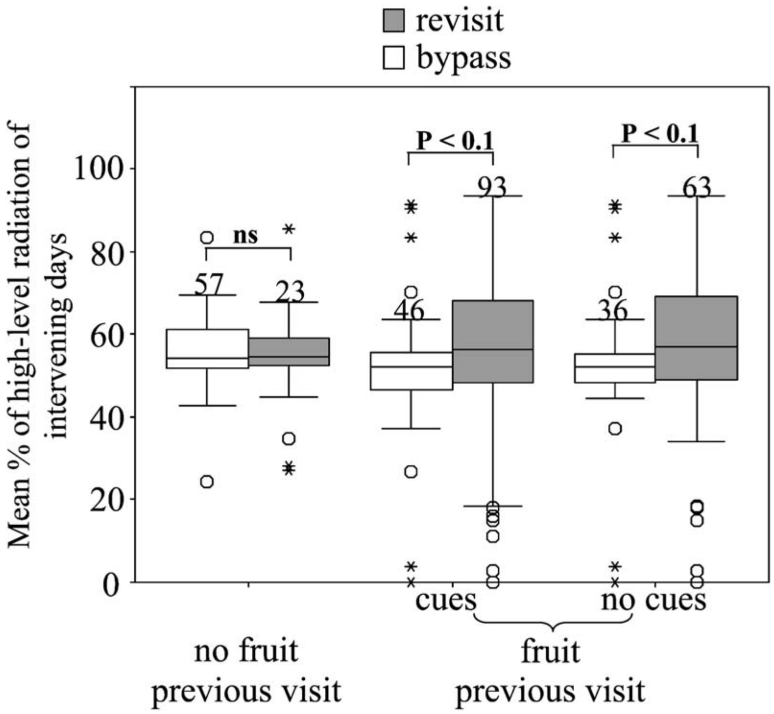

Figure 4. The Influence of Solar Radiation on Revisiting Behavior

Average percentage of high-level solar radiation determined for the intervening period between the time the group entered the 100 m radius circle and the time the group last visited the same tree. Shaded boxes represent average radiation values for revisits; white boxes represent values for bypasses. Each cluster refer to trees that (1) did not carry fruit at the previous visit, (2) carried fruit at the previous visit, and (3) carried fruit at the previous visit but no longer offered any sensory cues. Bars represent the median values of the average percentage of high-level solar radiation; top and bottom of the boxes represent the 75 and 25 percentiles. Whiskers represent highest and lowest values; circles and stars represent outliers and extreme values.

logistic regression analyses did not reveal a significant effect (chi-square = 1.283, $p = 0.257$, df = 1; $p = 0.261$, df = 1).

Is Revisiting Influenced by Weather Conditions on Particular Days?

Weather Conditions during First Visit

It could be the case that the monkeys returned earlier to a particular tree if the weather conditions were favorable during the day of the initial first visit. For example, finding fruit during hot and sunny days may establish special memories in the monkeys compared to when finding fruits during cooler, cloudy days. According to this hypothesis, monkeys may simply remember particular days of first visiting a tree, rather than integrating temperature over several days. However, we found that average daily maximum temperature measured at the first visit did not differ between subsequent revisits and bypasses ($U = 5723.0$, $n_b = 91$, $n_r = 143$, $p = 0.121$), and further logistic regression analyses did not indicate a significant effect of temperature either (chi-square = 1.946, $p = 0.164$, df = 1; $p = 0.163$, df = 1).

Weather Conditions during Reapproach

It may be the case that the monkeys' behavior was driven by the weather conditions of the day of reapproach, rather than the temperature integral of the previous time period. For example, if monkeys are more active on hot days, they will be more likely to come across trees with figs, regardless of weather conditions during the previous days. We found some support for this hypothesis because day journey length was significantly correlated with daily maximum temperature ($r_p = 0.247$, $n = 210$, $p = 0.001$). However, the general increase in activity during hot days did not explain the monkeys' visiting patterns of fig trees. Day journey lengths leading to revisits did not differ significantly from those leading to bypasses (all trees: $F_{1,\ 374} = 0.080$, $p = 0.252$; trees with fruit at previous visit only: $F_{1,\ 233} = 0.0$, $p = 0.233$).

To further investigate this hypothesis, we split the data and analyzed the monkeys' behavior on the day of reapproach and during all other days separately. We found no difference in the maximum daily temperature between revisits and bypasses on the day of reapproach ($U = 6001.0$, $p = 0.316$, $n_r = 143$, $n_b = 91$). Daily percentage of high-level radiation, however, tended to be higher on days of revisits than bypasses ($U = 1722.0$, $p = 0.062$, $n_r = 143$, $n_b = 91$). For all other days, the average maximum daily temperature was still significantly higher for revisits than bypasses ($U = 4876$, $n_r = 127$, $n_b = 91$, $p = 0.049$), but no effect was found for average radiation ($U = 1748.5$, $n_r = 81$, $n_b = 46$, $p = 0.566$).

We used multiple logistic regression analyses to investigate the effects of weather and activity on the monkeys' foraging behavior. These analyses showed that the probability of revisiting increased significantly with percentage of high-level radiation (hereafter RAD) on the days of revisit/bypass and with maximum temperature (hereafter Tmax; Table 1) of the interval prior to the day of revisit/bypass. Adding either RAD or Tmax to the respective univariate models (1 and 2; Table 1) increased the fit significantly (RAD: Δchi-square = 4.130, df = 1, $p = 0.042$; Tmax: Δchi-square = 6.527, df = 1, $p = 0.011$; Table 1; block entry method). Adding day journey length (hereafter DJL) to control for an increase in activity (see rationale above) did not lead to relevant effects (Δchi-square = 0.720, $p = 0.396$; Table 1). For trees that did not carry fruit during the previous visit, neither Tmax nor RAD was a significant predictor of revisiting probability (chi-square = 1.829, $p = 0.401$, df = 1; RAD: $p = 0.669$, df = 1, Tmax: $p = 0.229$, df = 1).

Table 1. The Relationship between the Probability of Revisiting and Weather Conditions

Model	Variable	Parameter Estimate (SE)	Probability	Total Model Chi-Square (df)
1	Constant	−0.337 (0.416)	—	
	RAD	1.660 (0.699)	0.017	5.883 (1)
2	Constant	−5.477 (3.303)	—	
	Tmax	0.217 (0.119)	0.068	3.486 (1)
3	Constant	−7.219 (3.530)	—	
	RAD	1.808 (0.727)	0.013	10.013 (2)
	Tmax	0.244 (0.124)	0.049	
4	Constant	−7.935 (3.659)	—	
	RAD	1.824 (0.731)	0.013	10.733 (3)
	Tmax	0.245 (0.125)	0.050	
	DJL	0.001 (0.001)	0.399	

Results of logistic regression analyses illustrate the probability of revisiting of trees that carried fruit at the previous visit. RAD represents the daily percentage of high-level radiation on the days of revisit/bypass; Tmax represents the average maximum temperature values measured between the previous visit and the day of revisit/bypass (excluding the day of revisit/bypass). DJL is the day journey length travelled by the monkeys on the days of revisit/bypass (in meters).

Weather Conditions between First Visit and Reapproach

Finally, perhaps mangabeys remembered particularly hot days in the time period between first visit and revisit/bypass, rather than integrating an averaged value of maximum temperature over several days. However, when considering the highest temperature value for each time period only, we failed to detect any differences between instances of revisits and bypasses ($U = 6162.5$, $n_r = 140$, $n_b = 91$, $p = 0.676$). The average maximum daily temperature for all days between the first visit and subsequent reapproach, but excluding these days, was higher prior to revisits than to bypasses for trees with fruit (trees with fruit at previous visit: $U = 2425.0$, $n_b = 73$, $n_r = 83$, $p = 0.032$; trees with fruit at previous visit, but no ripe fruit at current visit only: $U = 1141.0$, $n_b = 57$, $n_r = 57$, $p = 0.006$). Differences for average radiation between cases of revisit and bypass were not significant ($U = 881.0$, $n_b = 33$, $n_r = 56$, $p = 0.715$; $U = 525.0$, $n_b = 26$, $n_r = 41$, $p = 0.923$).

In sum, these additional analyses are consistent with the idea that the monkeys' foraging patterns could not be explained by events that took place on particular days, but that individuals integrated the weather conditions over larger periods of time.

Conclusions

The question of why primates, and especially humans, have more developed cognitive skills than other mammals has a long history in science. The most widely accepted notion has been that primates' superior cognitive abilities have evolved in the social realm. Many primate species live in complex societies and, the argument goes, this favored the evolution of especially developed social skills [10, 11]. Although there is much empirical evidence in favor of the social intelligence hypothesis, very little work has been conducted to address its alternative, the idea that primate cognition has evolved to deal with problems of an ecological nature, such as foraging for food.

With this research, we sought to address this anomalous gap. By following a group of wild monkeys from dawn to dusk in their natural habitat, we obtained an almost complete record of their foraging decisions in relation to their preferred food over three unusually long time periods. Our data showed that the monkeys were more likely to revisit trees after a period of warm and sunny days compared to cold and cloudy days, provided that they had found fruits during the previous visit. These findings are consistent with the idea that monkeys make foraging decisions based on episodic-like memories of whether or not a tree previously carried fruit, combined with a more generalized understanding of the relationship between temperature and solar radiation and the maturation rate of fruit and insect larvae. How exactly the monkeys managed to register the relatively subtle differences in average temperature values (Figure 2), however, remains elusive and a topic for further research.

The mangabeys' foraging behavior shows similarities with those of some birds, such as Brent geese (*Branta bernicla*), finches (*Fringillid sp.*), and scrub jays (*Aphelocoma coerulescens*) [12–15]. In these species, foraging decisions are influenced by the recovery rate of plants, the ripening rate of seeds, and the perishing rates of moth larvae and peanuts, respectively. Despite the similarities, our study is different in that we have shown that monkeys also take into account variation in weather conditions, rather than mere differences in elapsed time.

The fact that birds can demonstrate episodic-like memory when collecting cached food has led to a number of provocative theories concerning the evolution of cognitive abilities in nonhuman species [14, 15]. For noncaching species, such as nonhuman primates, a main selective benefit of episodic-like memories is to anticipate the emergence of new food sources, which is particularly relevant for fruit species that show no signs of synchronous ripening, such as figs [9, 16]. Kibale Forest has some of the highest primate densities ever recorded [17–19], and competition for food is consequently high [1, 20]. The ability to take weather-related ripening of fruits into account allows individuals to forage much more efficiently in order to thrive in an ecologically complex and highly competitive rainforest habitat [1, 17–19].

Experimental Procedures

Study Species

The group of gray-cheeked mangabeys was studied in the semi-logged moist evergreen forest of the Kibale National Park in Uganda (0°34′N, 30°21′W) [16, 21, 22]. The group consisted of 18–24 individuals that were well habituated to human observers. Figs (*Moraceae*) were among the most preferred foods of gray-cheeked mangabeys [16, 23–25]. We focused on the relatively common strangler fig *Ficus sansibarica* (density: 1.7 trees/ha [26]) that shows no synchrony in fruiting periods [9, 16]. Fruits can reach a diameter of 5.1 cm, with no obvious visual signs of ripeness, such as specific color or size. Chimpanzees and mangabeys assess edibility by squeezing individual fruits [9]. Unripe figs often contain weevil larvae, such as *Omophorus stomachosus* [23], which are extracted and eaten by the monkeys.

Data Collection

Prior to each observation period, we selected and labeled the maximum number of fruit-bearing fig trees within the 623 ha study area used by the group, such that individual trees were separated by at least 200 m (Figure 1). In regions without fruit-bearing trees, we identified fruitless trees by using the same distance criterion. In areas that did not contain any *F. sansibarica* trees, we included trees of other closely related fig species, for a total of 80 fig trees. The monkeys visited and reapproached only a subset of these, a total of 53 trees (22 with fruit, 18 without fruit, 13 changed fruiting state throughout the observation period). The majority of trees were of the species *F. sansibarica* (n = 42), the others were *F. exasperata* (n = 3), *F. sur forsk* (n = 3), *F. stipulifera* (n = 1), *F. natalensis* (n = 2), *F. mucuso* (n = 1), and *F. vallis-choudae* (n = 1). For the final study period (January to May 2004; n = 100 days), we also investigated whether average percentage of high-level solar radiation influenced revisiting behavior. Within this period, the group reapproached 14 trees with fruit, 9 trees without fruit, and 6 trees that changed fruiting state.

We followed the monkey group for three continuous periods of 50, 60, and 100 days between 24 March 2003 and 30 April 2004. Two observers followed each group from the first movement in the morning to final resting place at dusk. Whenever the group came within 100 meters of one of the target trees, the primary observer stayed with the group while the other observer rushed to the target tree to estimate (1) the quantity of fruits, (2) the ripeness state and presence of weevil larvae inside fallen fruits, (3) whether other frugivorous animals or group members were present, and (4) whether or not the monkeys entered the tree. To exclude the potential use of auditory cues to discover fruit availability, we analyzed approaches only where no other primate or any other frugivorous species, such as black-and-white casqued hornbills (*Bycanistes subcylindricus*), were present before the arrival of the study group. Adult males sometimes feed on their own away from the group. In a previous study, we have shown that the group was unlikely to be cued by the behavior of males [9].

The ranging of the group was determined by measuring its position every 10 min by means of a global positioning system (Garmin 12XL) and a trail system. Day journey lengths were calculated from hand-drawn daily maps [27]. Solar radiation was defined as the percentage of daily samples with high-level illumination (the upper threshold of a Gossen Lunasix 3 light meter when directed at the sun, 350,000 LUX). Samples were taken every 10 min between 07:30 and 17:30 hr. Temperature data were collected daily by the Kibale Fish and Monkey Project in the vicinity of the study area.

Statistical Analyses

The median interval until the group reapproached a target trees was 5.0 days. The number of daily revisits was randomly distributed in time (dispersion coefficient = 1.03 [26, 28]), suggesting that they were not restricted to particular periods of high fruit production. Whenever the group reapproached within 100 m of a target tree previously visited within the study period, we noted whether or not individuals proceeded to the trunk, i.e., whether they revisited or bypassed the tree. 95% of all repeated (<100 m) approaches to target trees were separated by at least one day, suggesting that they should be treated as independent events. In some rare cases, the group revisited a particular tree two or three times in the same day. We only included these revisits in our analyses if the group had moved out of the outer circle between successive revisits.

Since most of our variables were not normally distributed, we relied on nonparametric Mann Whitney U test and Spearman correlation analyses for the main bulk of our analyses. All tests were two tailed. In each case, we assessed evidence about specific hypotheses, and hence did not adjust critical α levels by Bonferroni procedures [29]. Whenever an effect was found to be statistically significant, we conducted a follow-up analysis by logistic regression analyses with SPSS 10.0, provided variables were statistically independent from each other [30]. The statistical significance of a variable in regression can be judged either by the probability level associated with its parameter or by the change in the overall goodness of fit of the model due to the addition of that variable. The latter procedure depends less on specific assumptions needed for parameter estimation and thus is preferred; we provide both the probability that a given variable's asymptotic parameter equals 0 (second p value), as well as the total model goodness of fit (first p value) (measured by the chi-square statistic against the null hypothesis of homogeneity).

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