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Wild capuchin monkeys anticipate the amount of ripe fruit in natural trees

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Abstract Tropical forests have a high diversity of tree species which have very low densities and vary across time in their seasons of peak fruiting and maturation rates. As evidence of the ability of primates to track or anticipate changes in fruit production at individual trees, researchers have used the increased speed of primate groups toward more rewarding food patches. We analyzed the speed of approach to natural trees of wild capuchin monkeys under the effect of scramble competition, after excluding any plausible visual, olfactory and auditory cues. We conducted all-day group follows of three habituated capuchin groups at Iguazú National Park, Argentina, collecting data on ranging behavior and patterns of visits to fruit trees in relation with their location and fruit availability. Travel speed varied according to the expected reward at a feeding tree, increasing as rewards increased from low values, but decreasing again at very high values. Also, travel speed varied with time of day, decreasing from the time of first activity as the monkeys became less hungry, and increasing again toward late afternoon. Measures of unripe fruit cover

did not explain variation in travel speed at any distance from a focal tree. Our data imply that, after excluding sensory cues, capuchins appear to anticipate time-varying ripe fruit quantity of natural resources, suggesting that they use memory of tree location and anticipation of fruit maturation. We also confirm that speed is a good measure about expectations of resources, as has been shown in previous studies.

Keywords Spatial memory · Fruiting trees · Expectation · *Cebus* · *Sapajus nigritus*

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Introduction

Tropical forests have a high diversity of tree species, most of which have very low densities and vary across time in their seasons of peak fruiting and maturation rates (Milton 1981). Fruit-feeding animals with a complex and seasonally varying diet face the problem of visiting several resources in the course of each foraging trip (Noser and Byrne 2010). The ability to remember tree features and to travel efficiently among feeding patches would help them to minimize energy expenditure by reducing the time and energy spent searching for food items in a random pattern (Janson 1998; Milton 2000).

Speed can be a good measure of expectation about a resource to be found (Pochron 2001; Janson and Byrne 2007). In terms of behavioral changes, researchers have used the increased directedness or speed of primate groups toward more rewarding food patches as evidence of anticipation of both the resource's location and of its expected value (Sigg and Stolba 1981; Janson 1998; Janmaat et al. 2006; Noser and Byrne 2007; Janmaat et al. 2014).

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Higher travel speed is expected along trajectories toward known resources than toward unknown ones (Janson and Di Bitetti 1997; Janmaat et al. 2006; Noser and Byrne 2007). This higher speed could reflect a higher motivation to reach a valuable resource (similar to higher rates of activity approaching the time of the next reward in classical conditioning, Gallistel and Gibbon 2000), or a reduced trade-off between travel speed and searching ability when search is not needed (e.g., Gendron and Staddon 1983). However, the goal could be 'known' because the animals just perceived it, rather than remembering its location from previous experience (Janson and Byrne 2007). If travel speed reflects perception of goal value, we would expect travel speed to increase uniformly with resource productivity (Fig. 1a). Independent evidence is needed to show that the change in movement speed started at distances that exceed the range at which resources are typically perceived (Pochron 2001; Janmaat et al. 2006).

Changes in travel speed toward a known resource might also reflect individual strategies during spatial food competition. A common pattern of movements of capuchin monkeys is that groups move relatively slowly away from food patches and begin to speed up as they approach the next resource (Janson and Di Bitetti 1997). This could be interpreted as the outcome of scramble competition, as individuals approaching a known goal race each other to be the first to arrive to harvest it (Janson and Byrne 2007). A group's overall travel speed should increase as the number of individuals participating in the 'race' increases. The number of individuals that can benefit from early arrival at a food source increases initially with its productivity, but will eventually plateau or may even decline as food availability becomes large enough to allow all group members to feed well. In this case, we would expect a hump-shaped (concave-downward) relationship between travel speed and food availability of the targeted food patch (Fig. 1b).

Capuchins also showed high levels of contest competition (Janson 1985), and speed is expected to increase as the group approaches known resources because subordinates specifically can avoid aggressive competition within the resource by arriving there before the dominants (e.g., Di Bitetti and Janson 2001). If direct competition were the only factor favoring higher travel speeds, we would expect travel speed to be highest at small food sources (Janson 1985, 1996), where subordinates are most directly impacted by the presence of dominants, and should decline as resource size increases (Fig. 1c).

Many studies show that primates move toward food patches in a manner that is consistent with goal-directed behavior implying spatial knowledge about food location (Menzel 1973, 1991; Milton 1981; Garber 1989;

(a) Increased perceptual stimulus

(b) Scramble or indirect competition for food

(c) Contest or direct competition for food
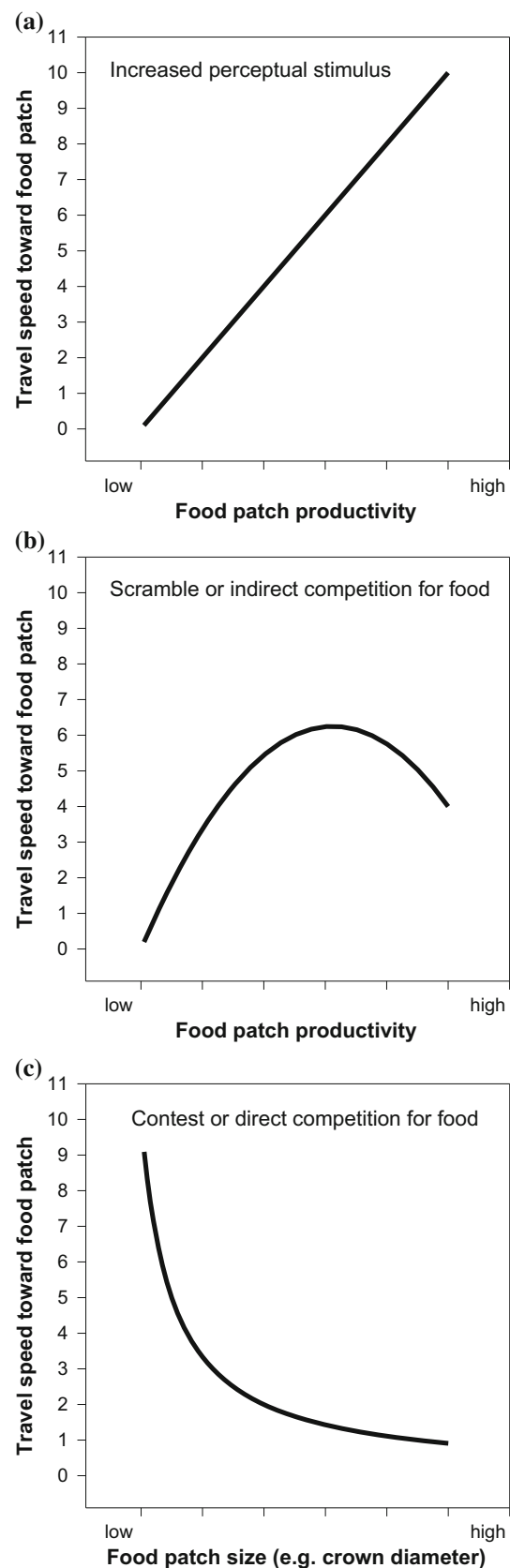
◀ **Fig. 1** Hypothesized relationships between group travel speed toward food patches and food patch productivity or size. **a** Sensory summation: speed toward a patch will increase in proportion with the amount of ripe fruit, which is the source of the sensory stimulus; **b** scramble or indirect competition: speed will increase from low to medium values of ripe fruit as more individuals race each other to reach the patch early, but will decline at the highest productivities where scramble competition is weak; **c** contest or direct competition: speed will decline from physically small to larger food patches, as subordinates incur smaller competitive costs in larger patches and have less incentive to arrive early

MacDonald and Wilkie 1990; Roberts et al. 1993, MacDonald 1994; MacDonald et al. 1994; Garber and Dolins 1996; Platt et al. 1996; Garber and Pacuilli 1997; Janson and Di Bitetti 1997; Janson 1998; MacDonald and Agnes 1999; Gibeault and MacDonald 2000; Pochron 2001; Scheumann and Call 2006; Cunningham and Janson 2007). Also, a few studies analyzed the quantity of reward to be obtained during movements to food patches (Garber and Pacuilli 1997, Janson 1998) and some kind of temporal knowledge about ripening states (Janmaat et al. 2006; Cunningham and Janson 2007; Anzelc 2009; Janmaat et al. 2012; Janson 2016).

There is limited evidence that primates are able to distinguish between fruiting states of trees of the same versus different species (Janmaat et al. 2006; Cunningham and Janson 2007, Janmaat et al. 2012; Ban et al. 2014; Suarez 2014; Tujague et al. 2016). Janmaat et al. (2006) studied spatial movements of two wild groups of *Cercocebus atys atys* and *Lophocebus albigena johnstoni* during daily visits to previously selected fruiting trees and concluded that monkeys used information about previous visits to anticipate state and quantity of fruit in future visits. In another study about daily movements of *Pithecia pithecia*, Cunningham and Janson (2007) found that monkeys used a combination of knowledge obtained through the repetitive use of their home range with information about location and condition of resources, taking more time to return to unripe fruiting trees. Janmaat and co-workers (2012) found that monkeys (*Lophocebus albigena johnstoni*) use synchronized fruiting patterns as an indicator of the presence of fruit on trees.

In more recent studies, Ban et al. (2014) found that chimpanzees (*Pan troglodytes verus*) travelled longer distances to trees at which they had previously made food grunts and had rejected fewer fruits, suggesting that individuals were able to anticipate the amount of fruit that they would find in the trees in future visits. Also, in his study about the ecological factors that predicted foraging decisions of wild spider monkeys (*Ateles belzebuth*), Suarez (2014) found that monkeys moved to nearby, large canopy trees, in which previous feeding success was high and which were visited after an interval of 3.5 days.

Finally, using Janmaat's observational method (2006), Tujague et al. (2016) recorded visits by known capuchin groups to pre-selected target trees at Iguazú National Park, Argentina, as a function of the tree's amount of fruit. Tujague and co-workers found that capuchin monkeys traveled faster to trees that carried fruit in comparison with empty ones, accelerating as they were getting closer to the target tree. Results showed that monkeys had a higher probability of visiting a tree when it had versus when it did not have fruit. To analyze whether groups increased their speed when traveling toward an out of sight tree, they compared speed before, after and at the critical visual detection radius. They found that speed increased significantly as the group approached the tree. These results suggest that once monkeys had entered a critical detection radius around the tree, they had an expectation of whether or not they would find fruit there. Preliminary analysis did not provide evidence that the monkeys responded to fruit availability by faster travel at the critical detection distance (Tujague et al. 2016).

The aim of this study is to expand the previous analysis (Tujague et al. 2016) by looking at changes in group travel speed for all distance categories as well as to examine the alternative hypothesis that the monkeys might increase travel speed when there is *less* ripe fruit available because of the greater importance of scramble competition when resource availability is low. We hypothesize that a monkey group will travel more quickly during approaches to some fruit trees according to fruit amount and quality. Capuchins might gain from faster travel because of the benefits for an individual to arrive earlier at a food source than other group members. This behavior is the embodiment of indirect or scramble competition (Janson and van Schaik 1988). Scramble competition is expected to be especially beneficial when the available resource is limited relative to the metabolic needs of the foragers. Because capuchin monkeys at Iguazu keep track of the location, size and fruiting status (fruiting vs. non-fruiting) of their food trees (Janson 1998, 2007; Tujague et al. 2016), they may be expected to modulate their approach speed in anticipation of the amount of reward available at the goal. However, we do not expect a simple response to reward amount. If the amount of food is very small, then the total reward is small even to the first forager arriving to the resource. A small benefit should not favor rapid travel in the face of its potentially large costs (see below). Conversely, when the total benefit is very large, little is gained by being the first to arrive as the most productive food trees often carry enough fruit to satiate all group members (e.g., Janson 1988). Therefore, we expect that travel speed would have a saturating or even possibly quadratic relationship with expected food amount. In the context of other studies on ecological cognition of capuchin monkeys, we were

especially interested in whether they behaved differently toward trees with different levels of fruit ripeness, although we included other metrics of total fruit crop size, both a priori (diameter at breast height, tree crown volume) and a posteriori measures (total group feeding minutes during a particular visit).

An assumption common to these arguments is that more rapid travel is costly. Energetic costs of animal travel are typically expressed as cost per unit distance (e.g., for capuchins, these are estimated at 123.9 kJ per km in travel costs, Janson 1988), but more rapid travel may have additional fitness costs for at least three reasons. First, faster travel limits opportunities to detect potential food sources or predators (e.g., Gendron and Staddon 1983; Janson and Di Bitetti 1997). Second, faster travel may increase the chance of monkeys falling from trees when they misjudge characteristics of their travel path (Janson, personal observation). Third, faster individuals end up at the front of a social group, where they may be more exposed to predation risk as they enter recently unexplored areas where a predator may be waiting—in rainforests; it is not uncommon to find major aerial predators waiting in the vicinity of fruit trees (van Schaik and van Noordwijk 1989). Thus, we expect that monkeys would travel more quickly only if there were greater benefits to be gained.

The benefits of accessing food depend not only on the amount and quality of food consumed, but on how hungry the animal is: The fitness value of food is higher when an animal is hungrier (e.g., Stephens and Krebs 1983; Janson and Vogel 2006). All else being equal, we expect that animals would compete more strongly soon after beginning activity in the morning, as they have just finished a 10–12-h fast. Indeed, fruit-feeding activity is highest in the morning, gradually decreasing toward midday, at which time the monkeys usually devote increasing time toward foraging for invertebrates or to resting (during the hottest periods of the year). Regardless of the intervening activity, there is usually a second minor peak of fruit-feeding in the late afternoon, which may denote increased hunger then as well. Thus, we expected that there might be both linear (decreasing with time of day) and quadratic (higher early and late) patterns of travel speed toward fruit trees. Finally, scramble competition should be more intense in larger groups (Janson and Goldsmith 1995), so we expect that group travel speed would be higher in larger groups, all else being equal.

Methods

Study site and subjects

The study was conducted in Iguazú National Park, a 60,000 ha preserve in northeastern Argentina (25°40′S,

54°30′W). The site is a semi-deciduous forest at the southern border of the Atlantic forest, characterized by a humid, subtropical climate (Brown and Zunino 1990). Fruit productivity is seasonal, with lowest production between June and August, and highest between October and November (Janson and Di Bitetti 1997). Most of the tree species have short fruiting periods (a month or less) with productivity of species varying from one month to the next (Placci et al. 1994). Because critical feeding sites are heterogeneously distributed (Di Bitetti 2001), remembering their location is important to improve foraging efficiency.

The tufted capuchin monkey (Cebus = Sapajus nigritus) is a small-bodied, diurnal primate and is the only primate species commonly found at Iguazú. At Iguazú, capuchins live in multi-male, multi-female groups with typically 7–45 independent individuals and predominantly male dispersal (Di Bitetti 1997, Janson et al. 2012). About 90% of their energy intake is from fruit, although 55% of their daily activity budget is spent foraging for dispersed arthropods and other food items (Janson 1990). Capuchins show high variability in space and time in allocation of feeding time, ranging from 81.2 to 53% of their feeding time spent on ripe fruit (Chapman and Fedigan 1990).

In the current study, data were collected for three habituated groups: Macuco (10–14 males, 17–18 females and a total of 27–32 individuals), Gundolf (7–9 adult males, 13–14 females and a total of 20–23 individuals) and Rita (5–12 males, 7 females and a total of 12–19 individuals), during September–December and March–April of 2008–2011. All group members were individually recognized by facial marks, color pattern and body size.

Data collection

We conducted all-day group follows collecting data on ranging behavior. Each group was followed for two continuous periods, according to fruiting seasons: Macuco—two periods of 27 and 40 days, respectively, during November to December 2008 and November to December 2009, Gundolf—two periods of 37 and 31 days, respectively, during September to October 2009 and November to December 2010, and Rita—two periods of 35 and 34 days, respectively, during March to April 2010 and March to April 2011. These long group follows were designed specifically to allow the authors to analyze travel behavior toward fruit patches that the monkeys had definitely visited previously and for which the monkeys might therefore have memories of the tree's size and ripening state (cf. Janmaat et al. 2006).

A modified form of the focal tree method (Janmaat et al. 2006) was used to assess the traits of focal trees that the groups visited; we also recorded traits of focal trees that were not visited, but they are not analyzed here (see

Tujague et al. 2016). Observers previously selected focal trees (FT) of 17 species without evident visual and olfactory fruit ripeness cues (Azota caballo: *Luehea divaricata;* Aguaí: *Chrysophyllum gonocarpum;* Burro Caá: *Casearia sylvestris;* Camboatá: *Matayba eleagnoides;* Cancharana: *Cabralea canjerana;* Carayá bola: *Guarea pohlii;* Guazatumba: *Casearia decandra;* Guabira: *Campomanesia xanthocarpa;* Higuerón: *Ficus* sp; Laurel: *Nectandra* sp./ *Ocotea* sp; Mboreví caá: *Coussarea contracta;* Mora amarilla: *Maclura tinctoria; Miconia* sp; Ñandipá: *Sorocea bonplandii;* Tala trepador: *Celtis iguanaeae;* Ubajai: *Eugenia piryformis* and Yvaporoití: *Plinia rivularis*—see Tujague et al. 2016 for a complete list of species consumed). Patches of two vine species were also included (*Trichostigma octandrum* and *Dicella nucífera*) since they were considered to function as fruiting trees. Although monkeys also approach other fruit trees, visits to these trees were excluded from the analysis because of their conspicuous fruit size (e.g., Araticú, *Rollinia* sp., or citrus species), coloration (e.g., Cocú, *Allophyllus edulis*, or citrus) and/or smell (e.g., *Hovenia dulcis*). Our selected studied trees were not notably odiferous, and human observers at the study site were not able to smell fruits from our focal trees until they are nearly under the tree. We also collected phenological data of each FT, as well as structural data: DBH = diameter at breast height and crown volume estimated from the formula of an ellipsoid (Janson 1988, see Table 1 for details). We did not collect either structural measure for individuals of the two vine species.

Two observers followed the group from the first movement in the morning to the final sleeping site at dusk collecting data of group's visits to FT. Ripe and unripe fruit quantity was scored 0–4 for each FT according to the percentage of branches containing fruit (Janmaat et al. 2006): 0 (no fruit), 1 (1–25%), 2 (26–50%), 3 (51–75%), 4 (76–100%). We visually divided the crop in four quadrants following the cardinal points and visually estimated the average percentage of branches containing fruit. A tree with category 4 had all the branches containing fruit. When a tree did not have branches in one of the quadrants, then that quadrant was assigned as category zero. Every time it was possible to distinguish between ripe and unripe fruit, we counted number of branches separately and we averaged the percentages across quadrants. Since trees could change fruiting states and quantities inside the same individual tree as a result of the influence of sun and temperature (Houle et al. 2007), this detailed methodology allowed some measurement of this variable. In the case of fruits that change color between ripe and unripe states, we use this feature to estimate ripe and unripe fruit quantities. In the case of *Maclura tinctoria* fruits, which remain green at maturity, we considered the fruit as ripe when it had lost trichomes and we started seeing the exterior creases

characteristic of that fruit when it increases in size (De Oliveira Oyama and De Souza 2011). With respect to *Ficus* sp., ripe fruit size differs between individual trees (Tujague, personal observation) so it was necessary to analyze each tree as a separate case. We observed and touched ripe fruits that had dropped to the ground and took these as a reference point to visually estimate ripe and unripe fruit on the tree. Monkeys have been seen to visually inspect and touch *Ficus* sp. fruits before eating them (Tujague, personal observation). We also excluded FT that appeared to carry another kind of food inside (lianas or host trees that also carried fruit). In order to exclude the potential use of auditory cues to infer fruit availability, we did not include in our analysis visits when any other frugivorous species was eating in the FT before the group arrived.

Average group spread was estimated from previous studies in this population that described a typical spread of 57×42 m for a group of 15 individuals (Janson and Di Bitetti 1997; Janson 1998). The average group spread of capuchin groups at Iguazú during this study varied according to group size and was observed to be similar to previously recorded estimates (Hirsch et al. 2013). To ensure that every visit to each FT was independent, we established a minimal distance between FT equal to twice the average group longitudinal spread during slow forage. These minimum distances varied from 100 m (Rita 2010) to 240 m (Macuco 2009; see Tujague et al. 2016 for details). We excluded from our sample any potential FT that was closer than the minimum distance (for each study group and sample year) from any FT already in the sample. To be sure that the tree was considered an important resource for the monkeys, we only considered visits to trees when at least one-third of the individuals of the capuchin group entered the tree to consume fruit.

At Iguazú, the expected minimal detection distance during slow forage (defined as the distance at which the focal animal, generally at the edge of the group, detects a resource while moving at 2 m/min) is 29.5 m (Janson and Di Bitetti 1997). We defined, for each group, a critical radius (CR) around each tree as half the minimal distance between FT described above (½ the minimal distance from the FT to the nearest other FT). We consider this distance to be a conservative estimate of the distance of visual detection since it was higher than 29.5 m in every case (Tujague et al. 2016). This distance of detection during slow forage was calculated experimentally by Janson and Di Bitetti (1997) using platforms provisioned with tangerines that are easier to detect because of their size and color than natural fruiting trees. Although fruiting trees are not the same as experimental platforms, our FT have an average height of 11.3 ± 3.6 meters SD, while the canopy at Iguazú reaches a height of about 25–30 m (Tujague, personal observation). Thus, we

Table 1 Variables and their descriptions

Variable	Description
Group identity	Identification of each studied group which varied in individual composition
Year	Study period for each studied group
Tree species	Tree categorization according to species selected for the study
Tree individual	Identification of each individual tree in relation with its location along the study area
After CR (speed before versus after CR)	Categorical variable which took values of 0 to denote speed before and 1 to denote speed after the critical radius.
Observation	Identification of each distinct approach to a focal tree. Treating the observation as a random effect helps to control for the correlation between speed before and after critical radius in each approach.
Group size	Number of individuals for each studied group
Time of day and time of day^2	Hour of the day at which the visit occurred. Both linear and quadratic (^2) terms
Ripe/unripe fruit cover and ripe/ unripe fruit cover^2	During data analysis, we converted fruit scores to % fruit cover by using the midpoint of the range of percentage of fruit cover corresponding to each score category: category 0 = 0%; category 1 = 12.5%; category 2 = 37.5%, category 3 = 62.5% and category 4 = 87.5%. Both linear and quadratic (^2) terms
Tree DBH	Diameter at breast height
Crown volume	Volume of the tree crown estimated from the formula of an ellipsoid: VOL = $R^2 D \pi 4/3$, where R is the crown radius and D is the crown depth, form lowest to highest fruit-bearing branch
PC1 and PC1^2	First principal component as a result of the principal component analysis of ln(DBH) and ln(CrownVolume) measures across the independent observations. Both linear and quadratic (^2) terms
Group-minutes and Group-minutes^2	Total duration from the start to the end of the visit, subtracted any periods when there where no monkeys in the patch, then multiplied the resulting time by the total number of individuals that visited the patch, and divided by the total group size. Both linear and quadratic (^2) terms

Random effects are underlined; fixed effects in bold

believe it was not easy for a monkey feeding at the top of the tree to see the next focal tree (considering that the minimum distance between FT was at least 5 times the experimentally derived visual detection distance). We used this CR to measure changes in speed of approach to FT before and after entering the CR.

To collect data on a group's visits to FT (Vogel and Janson 2007), one observer was always in the front of the group and went to the FT that monkeys were expected to visit sensu Janmaat et al. (2006). Before the group arrived, the observer collected data on the presence/absence of frugivores at the FT and scored the amount of ripe/unripe fruit according to the categories described above.

While following the group, we recorded the UTM coordinates for the spatial location of the group center (Janson 1990) using a handheld Garmin 60Cx GPS (≤10 m error) at 10-min intervals. When a GPS point could not be obtained directly from the center of the group, the coordinates of the group center were projected using the direction and distance from the observer. When the group approached the CR for a given focal tree, UTM coordinates were taken at least once prior to entering the CR, and once shortly after entering the CR, regardless of the time interval (Fig. 2). These data were used to estimate group speed during travel to FT (Noser and Byrne 2007) as follows:

Speed before critical radius (BCR): group speed (m/ min) before entering a critical radius, calculated as the distance in meters between the two UTM coordinates just before entering the CR (latest UTM coordinates position collected before approaching the CR) divided by the time elapsed between the two measures.

Speed after critical radius (ACR): group speed (m/ min) immediately after entering a critical radius calculated as the distance in meters between the last UTM coordinate position collected before approaching the CR and the first UTM coordinate position after entering the CR, divided by the time elapsed between the two measures.

We defined a visit as an entry to a FT and/or tree patch in which at least one-third of the group had eaten at least once at the site. It did not include visits of isolated individuals to isolated trees or patches. We defined a patch as a set of more than one tree of the same specie separated from the other by no more than 10 m, a distance chosen to make it possible to see the entire group at the same time; we considered a visit to a patch as a visit to one FT. For each visit, we defined a measure, Group-minutes, of time that the group invested in a food patch (see Table 1 for details
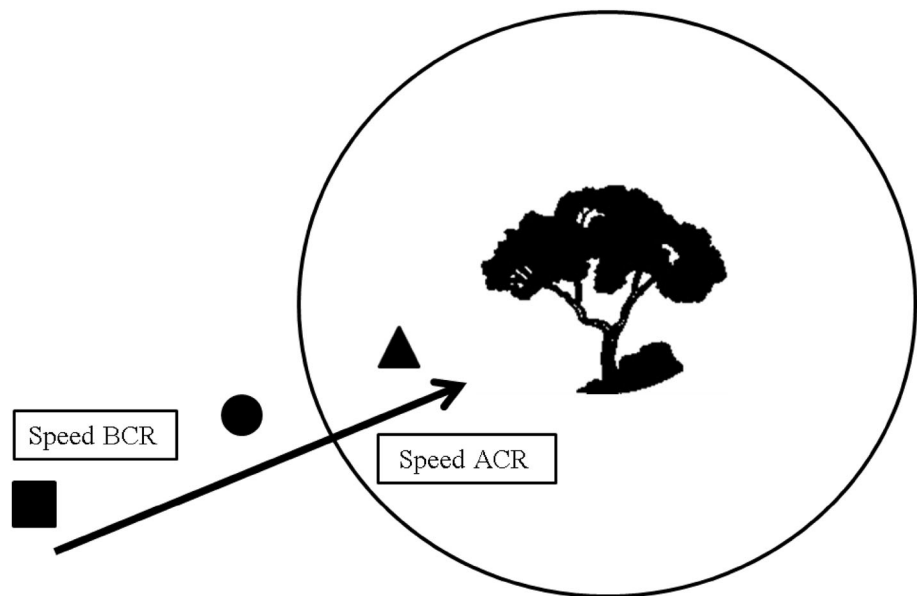
of the defined measure). We treated successive visits to a single FT as independent visits only if the monkeys left the FT and traveled a distance greater than the CR before returning.

Data analysis

An independent visit to a FT had a unique date and time of the visit, along with a known tree species and individual, and fruit cover values taken before the start of the visit. For each independent visit of a group to a FT, we treated the two estimates of travel speed (BCR and ACR) as distinct measures of travel speed, nested within a single 'observation,' which was treated as a random effect. The 'observation' random effect was nested within a second random effect, the year of the sample. We also included tree species as a random effect, because some species might be more highly preferred (and thus might encourage faster travel). Initially, we also included tree individual (nested within tree species) and group identity as random effects, but these consistently had zero or near-zero variance components in the model and thus were excluded from further analyses. As independent fixed effect variables, we used (1) a categorical variable for whether the speed was measured 'before' versus 'after' entering the CR, (2) group size, and (3) linear and quadratic terms for all the variables describing potential feeding benefits: ripe fruit cover, unripe fruit cover, group-minutes, DBH and crown volume (see Table 1 for details). To reduce notable skewness in measures of group size, group-minutes, DBH and crown volume, we took the natural logarithm of the raw measures; doing so reduced the effect on the analysis of large but rare values of these fixed effect variables.

To increase the robustness of the analysis, we took steps to reduce notably high pairwise correlations between the fixed effect variables. Because DBH and crown volume are both measures of tree size and were moderately highly correlated ($r = 0.53$), we carried out a principal component analysis of ln(DBH) and ln(CrownVolume) measures across the independent observations. As a final measure of FT size for a given observation, we used the observation's score on the first principal component. The first principal component (PC1) explained 77% of the combined variation in the original variables. In addition, to avoid strong correlations between the linear and quadratic terms for any fixed effect variable in the analysis, we centered each linear variable so that the mean of the variable was zero; the quadratic term was the square of the centered value of the linear variable. Before centering, the pairwise correlations between the linear and quadratic terms of fixed effect variables ranged from 0.77 for ln(group-minutes) to 0.99 for time of day; after centering, they ranged from -0.12 for ln(group-minutes) to 0.77 for ripe fruit cover. The complete model to analyze speed of approach (ESM1) had three random effects (tree species, year and observation nested within year) and 12 fixed effects (see Table 1 for details).

We analyzed the complete model as a generalized linear mixed model (GLMM) in R (R Development Core Team 2011) using the function lmer in lme4 package version 1.1-8 (Bates et al. 2015). For all inferential tests comparing any two models, we refitted the models using ML (maximum likelihood procedure) instead of REML (restricted maximum likelihood procedure). Of particular interest for this study was the effect of phenological measures of fruit availability—if the best statistical model included

phenological measures of fruit cover, such a result would be consistent with the possibility that the monkeys can anticipate the tree's phenological condition despite its variation across time. Because of strong directional expectations of the predicted trends for each variable, we used one-tailed probability values for all tests of fixed effect hypotheses.

Results

The total number of visits to selected trees varied between groups and years (Macuco: N 2008 = 52, N 2009 = 83; Gundolf: N 2009 = 48; N 2010 = 86; Rita: N 2010 = 59, N 2011 = 78). We excluded visits to trees that had other frugivores eating before monkeys arrived (birds and/or coatis), to avoid the possibility that the group was attracted by the sound of other animals feeding at the site (Macuco 2008 N = 2/2009 N = 6, Gundolf 2010 N = 2, Rita 2011 = 9).

There was considerable variation in fruit availability across time in individual tree crowns. For trees visited at least twice, the mean ripe fruit score was 1.312, while the within-tree SD was 0.593, yielding a coefficient of variation (CV) of 45.2%. The corresponding value for unripe fruit scores was 1.273 and 0.905, for a CV of 71.1%.

The GLMM model with all the fixed and random effects variables (Table 2) was significantly different from the model with only random effects (all main effects, Table 3). Travel speeds before and after passing the critical radius of a FT were significantly different, with ACR being on average 52% greater than BCR (speed after vs. before CR,

Table 3, Fig. 3). Travel speed increased significantly toward FT with greater ripe fruit cover, reaching peak speeds at intermediate cover values ($\sim$ 26–50%) and declining thereafter (ripe fruit cover and ripe fruit cover^2, Table 3, Fig. 4). The quadratic effect of ripe fruit cover on travel speed was significant (Table 3) in the expected negative direction based on theory and prior evidence from capuchin monkeys that scramble competition should be relaxed at high food availabilities (Janson 1988). Travel speeds were highest in the morning, declining significantly toward midday before increasing again toward evening (time of day and time of day^2 Table 3; Fig. 4). Travel speed did not appear to depend on any measure of unripe fruit cover, nor on measures of either tree size (score on PC1 and PC1^2) or actual feeding success (group-minutes and group-minutes^2; Tables 2, 3). The variances of the random effects tree species and year were generally small (absolute value and percentage of total variation: TreeSp = 0.01070, 2.52%; year = 0.04217, 9.93%). However, variation associated with observation (nested within year) was substantial (0.07515, = 17.7% of total variation), suggesting that variation in travel speeds among observations depended on unknown factors in addition to the tested variables. Finally, since speed BCR and ACR varied according to percentages of ripe and unripe fruit, and all the possible combinations of those categories in each tree, we refer to descriptive details of speed with mean and standard deviations to be found in Tujague (2013) and Tujague et al. (2016).

We accounted for possible temporal variation or clustering of travel speeds that did not depend on the variables described in our hypotheses. First, we treated the year of

Table 2 Results of the full GLMM analysis

Dependent variables	Parameter estimate	±SE	T
Intercept	1.249840	0.616784	2.026
After CR (speed after versus before CR)	0.459562	0.063126	7.280
Group size	0.010422	0.191508	0.054
Time of day	0.790644	0.269031	−2.939
Time of day^2	9.191018	1.974020	4.656
Ripe fruit cover	0.845644	0.406826	2.079
Ripe fruit cover^2	−2.023339	1.133070	−1.786
Unripe fruit cover	−0.081789	0.225148	−0.363
Unripe fruit cover^2	0.445422	0.669139	0.666
PC1	0.012523	0.045700	0.274
PCI^2	0.006681	0.015190	0.440
Group-minutes	0.031464	0.035948	0.875
Group-minutes^2	−0.008876	0.013058	−0.680

The values are the estimated parameter, standard error (±SE) and the *t*-values (T) of the variable in the complete model. ^2 = quadratic term of the variables. In bold are the fixed effects that were significant during the hypothesis tests. Random effects are included in the statistical model but not reported here, as the R program (lmer) does not report inferential statistical tests for random effects variables

Table 3 Summary of individual hypothesis test results

Fixed effects included	N	Change in −2*log-likelihood	df	Direction of effect	P(X df), one-tailed
All main effects	221	79.21	12	**NA**	**5.84E − 12**
After CR (speed after versus before CR)	221	41.545	1	**Positive**	**0.57E − 10**
Group size	221	0.03	1	Positive	0.431
Time of day	221	9.2036	1	**Negative**	**1.21E − 03**
Time of day^2	221	21.514	1	**Positive**	**1.75E − 06**
Ripe fruit cover	221	4.7718	1	**Positive**	**0.015**
Ripe fruit cover^2	221	3.5923	1	**Negative**	**0.029**
Unripe fruit cover	221	0.2314	1	Negative	0.185
Unripe fruit cover^2	221	0.5885	1	Positive	0.279
PC1	221	0.1494	1	Positive	0.35
PCI^2	221	0.2787	1	Positive	0.20
Group-minutes	221	0.8282	1	Positive	0.1814
Group-minutes^2	221	0.484	1	Negative	0.2433

The 'all main effects' test compares the complete model (Table 2) to the model with only random effects included. In each other case, we compared via ANOVA the complete model with all main effects to a reduced model that omits the fixed effect of interest. *N* number of observations, $-2*LL$ Chi-square values; *df* degrees of freedom; *P(X df)* probability values; ^2 quadratic term of the variables. In boldface are the effects that were statistically significant

the sample as a random effect, to account for possible large-scale temporal patterns (e.g., variation in climate or annual plant productivity) not captured by our hypotheses. Second, we tested for possible effects of sequential sampling on our results. We added the travel speed of the previous observation as a fixed effect variable to the complete model given in Table 2. The contribution of prior travel speed to the expanded model was small and not statistically significant ($t = 0.23$, $P = 0.82$), suggesting that each observation of travel speed to a FT was conditionally independent of previous observations.

We examined possible interactions between some of the variables, to test whether the analytic model we used was sufficient to describe the pattern of variation in speed of approach to a FT. First, it is possible that the effects of feeding benefit (fruit cover, tree or crop size) on travel speed would be more notable at large group sizes, in which scramble competition would be expected to be strongest. However, we found no significant interactions of group size with fruit patch variables either individually (ripe fruit cover: $t = -0.08$, $P = 0.94$; unripe fruit cover: $t = 0.09$, $P = 0.92$; tree size (PC1): $t = 1.04$, $P = 0.30$; log of group-minutes: $t = 0.24$; $P = 0.81$) or collectively (complete model vs. extended model including all interactions: Chi-square $= 1.37$, $df = 4$, $P = 0.85$). Third, we attempted to include all fixed effect by random effect interactions ('random slopes' model), according to the recommendations of Barr et al. (2013). Unfortunately, the full random slope models did not converge in lme4 even after 5,000,000 iterations. As recommended by Barr et al. (2013)

in cases of non-convergence of the full model, we tried a slightly simplified version of the random slopes model by disallowing a correlation between the intercept and slope. However, this model also failed to converge after 5,000,000 iterations in lme4. Thus, no random slopes model preferred by Barr et al. (2013) was feasible with our data set.

Discussion

Results from the present study provide evidence that wild capuchin monkeys changed their travel speed during approaches to trees with different rewards without any obvious perceptual knowledge of tree condition, given that all major sensory cues (visual, olfactory and auditory information) were controlled or minimized.

We predicted that travel speed would vary according to the expected reward at a given feeding tree in a nonlinear way, increasing as rewards increased from low values, but plateauing or even possibly decreasing again at very high values. We also expected that travel speed would vary with time of day, decreasing from the time of first activity as the monkeys became less hungry, and possibly increasing again toward late afternoon. Both patterns were confirmed in our analyses (Table 3; Fig. 4), but the effect of time of day was the strongest. The predicted hump-shaped relationship between travel speed and ripe fruit cover was statistically significant. The studied groups increased travel speed toward trees with more ripe fruit only up to a score
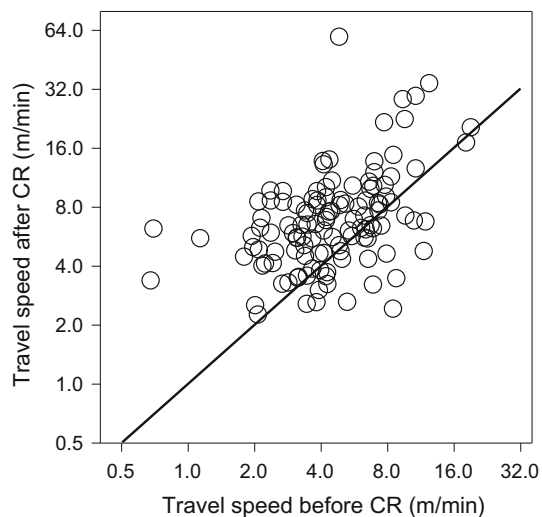
Fig. 3 Travel speed (meters per minute) before and after critical radius (CR) is positively related (orthogonal regression with equal variances for x- and y-axes, $r = 0.44$, $\ln(\text{ACR}) = 0.42 + 0.994 \cdot \ln(\text{BCR})$, $P < 0.0001$)

corresponding to 26–50% fruit cover, above which travel speed declined. At the highest fruit cover values, monkeys appear to have less urgency to be among the first to arrive at the food source. This is consistent with the idea that faster travel toward food patches is the result of scramble competition to reach the resource (Fig. 1b), rather than a simple response to greater food-related cues or larger potential rewards (Fig. 1a). Measures of unripe fruit cover did not explain variation in travel speed at any distance from a focal tree. The fact that travel speed increased notably at distances from a feeding tree that were at least 5 times the known detection distance of capuchin monkeys for experimentally provided food sources (Janson and Di Bitetti 1997) suggests strongly that they were responding to the memory of the resource characteristics from prior visits rather than to immediate food-related cues. Although the locations of UTM coordinates before and after entering the CR were highly variable, we, nonetheless, found a consistent pattern of speed related to ripe fruit cover, supporting the validity of our results. The detected changes in travel speed suggest that the monkeys used memory of fruit quantity and ripening state. In at least some cases, this memory was long term, lasting across several days since a prior visit to a given focal tree.

Our findings about speed in relation to time of the day support the results from Janson (2007) who found that capuchin groups moved faster when they were hungry or close to a goal, although his study was carried out using experimental platforms and during winter when resources are scarce and platforms were the only concentrated resource available. However, Janmaat and co-workers (2006) found that approach speed to trees by mangabeys
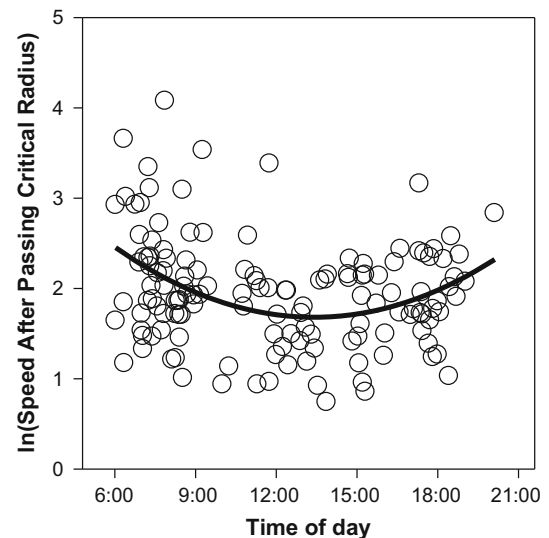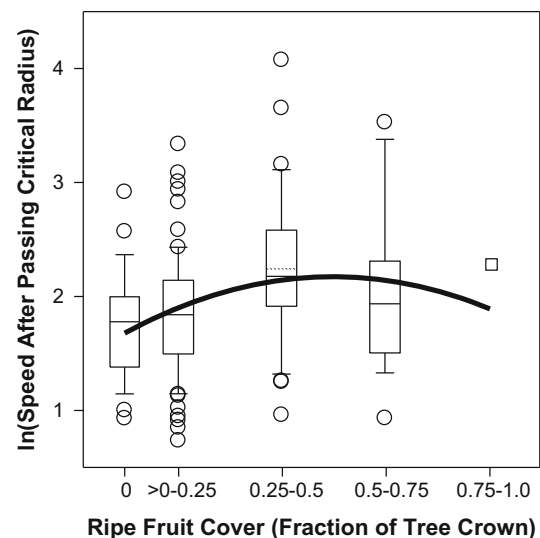

Fig. 4 Group movement speed (m/min) after passing the critical radius toward a focal tree, plotted as a function of ripe fruit cover and time. For ripe fruit cover, the travel data are shown for each value of phenological cover score as box plots (median *line*, upper and lower box bounds of 25 and 75% of the data, whiskers at 10 and 90% of the data, plus individual points for all data outside the 90% limits). Regression lines are based on bivariate results only, not on the complete model. Program used: R

did not change in relation to hunger levels (as assessed by time of day). Yet, they did not test for a curvilinear effect of time, but instead compared only morning (0700–1000 h) against the rest of the day. If we restrict our analysis of travel speeds in the same way as Janmaat et al. (2006), we also find no effect of time of day for BCR (*t* test, $P = 0.33$) but do find a significant difference for ACR (*t* test, $P < 0.005$). Thus, it is unclear whether the pattern we describe, in which travel speed increases when animals are likely to be hungry (Fig. 4),

is confined to this study site and species, or is more general.

Other metrics of tree size or fruit amount eaten (DBH and crown volume; total group feeding minutes) had no detectable effects on monkey's travel speed toward trees, after including phenological measures of ripe fruit availability and a random effect for tree species. Other studies found that measures of tree size did predict the selection of trees by spider monkeys (Suarez 2014) as well as by capuchins in the same population using experimental feeding sites (Janson 1998, 2007). Our present results suggest that monkeys pay more attention to anticipated ripe fruit cover than to whether a tree is large or small. However, all the focal trees in our analysis were ones at which at least one-third of the group members fed, thus biasing the sample toward more productive patches overall. Given other evidence from the same site that capuchins are able to track elapsed time since a prior visit to each of multiple feeding sites (Janson 2016), their ability to anticipate ripe fruit cover may depend on a similar cognitive capacity.

The increase in travel speed toward trees with higher ripe fruit cover (until it reaches the plateau) is consistent with the effect of indirect or scramble competition during the visits to fruiting trees (Fig. 1b). Although it is expected that scramble competition should be greater in larger groups (Janson and Goldsmith 1995), we did not find an effect of group size on the approach speed toward fruit trees. Perhaps variation in group size between studied groups was simply not large enough to be detected by the analysis. Finally, if increased direct competition over food were an additional factor favoring higher travel speeds, we would have expected to find that speeds were higher when tree size was smaller, all else being equal. However, the PC1 variable (which combines DBH and crown volume) had no significant effect on travel speed.

A cautionary note in interpreting our patterns is our inability to estimate the true value of feeding trees (Ban et al. 2014). Many fruit species in our study do not change color during maturation and thus require elasticity measurements to assess ripeness/sweetness (Janmaat et al. 2006); we were not able to take such measurements on actual fruits in our rainforest trees that were up to 40 m high and contained more than a thousand fruits. Nutritional value of fruits can vary tremendously within a tree but also between trees of the same species (Houle et al. 2007). In some cases, the variation in the nutritional values among tree sites can be greater than the differences among tree species (Chapman et al. 2003). Also, monkeys are able to regulate their nutritional state through selecting complementary combinations of foods to achieve a nutritionally balanced diet (Felton et al. 2009). Thus, fruit cover may not always be an accurate guide to the nutritional value of a fruit crop to its consumer. Incorporating measures that use

the animal's behavior to estimate the value of food such as fruit rejection ratios may prove beneficial for such studies (Ban et al. 2014).

Taking into account both quantity and fruiting state of resources allow researchers to analyze primate's spatiotemporal behavioral variation. How much they will eat on a given visit will depend on their own past behavior (Janson 2000). Tujague and Janson (in press) suggested that capuchins shortened their revisit intervals when a tree had more unripe fruit relative to mature fruit, even though the monkeys did not consume the unripe fruit: the time until the next revisit for a given tree decreased independently with increasing amounts of both ripe and unripe fruits in the crown at the end of the visit. The presence of only ripe fruit (with no unripe fruit) promoted shorter return intervals than for trees bearing only unripe fruit, regardless of fruit quantity (3.85 vs. 6.5 days, respectively). Revisit intervals to trees that had no fruit (empty trees, category 0) were the longest (11.8 days; Tujague and Janson, unpublished data). The higher travel speeds that Tujague and co-workers (2016) found when an entry to a critical radius ended in a visit to trees that carried fruit support these conclusions. Capuchins increase speed while they were closer to a focal tree, indicating that they had an expectation about what they were going to find (presumably based on their previous visit or visits). Monkeys accelerated progressively while the resource was out of sight to finally reach speeds close to their maximum velocity after entering the critical radius.

Non-human and human primates show a very similar pattern of discrimination in odor performance (Laska and Freyer 1997) and the same range of olfactory performance with regard to sensitivity to aliphatic esters related to the degree of ripeness of fruit (Maarse 1991). Also, it has been proved that functional olfactory genes or neuroanatomical olfactory features are poor indicators to predict olfactory performance since non-human primates species show different functional genes and neuroanatomical features but similar performances (Laska et al. 2004). Studies have concluded that olfactory cues are heavily used by nocturnal primates and visual cues are relied on by diurnal primates (Bicca-Marques and Garber, 2004), including capuchin monkeys (Bolen and Green 1997). Although we cannot exclude the possibility that the noses of capuchin monkeys might be more trained than those of humans or that odors can be transported over long distances by the wind, it seems unlikely that our studied groups relied on olfactory signals during approaches to trees. Given that the monkeys were very unlikely to see the trees at the critical distance (Janson and Di Bitetti 1997), we conclude that speed is a good measure about expectation of resources, as was shown in previous studies for the same specie (Janson and Di Bitetti, 1997; Janson 1998) and others (*Papio*

hamadryas: Sigg and Stolba 1981; *Papio hamadryas cynocephalus*: Pochron 2001; *Cercocebus atys atys* and *Lophocebus albigena johnstoni*: Janmaat et al. 2006; *Papio urcinus*: Noser and Byrne 2007).

Compliance with ethical standards

Conflict of interest The authors disclose no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All research reported in this manuscript adhered to the International Primatological Society and the American Society of Primatologists Principles for the Ethical treatment of Non-human Primates, and complied with the protocols approved by the Animal Care and Use Committee and the Argentine Research Council (CONICET). It also adhered to the legal requirements of Argentina.

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