Anim Cogn (2014) 17:1353–1364
DOI 10.1007/s10071-014-0771-y

ORIGINAL PAPER

Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances

Simone D. Ban · Christophe Boesch ·
Karline R. L. Janmaat

Received: 31 January 2014 / Revised: 29 May 2014 / Accepted: 3 June 2014 / Published online: 21 June 2014

Abstract The use of spatio-temporal memory has been argued to increase food-finding efficiency in rainforest primates. However, the exact content of this memory is poorly known to date. This study investigated what specific information from previous feeding visits chimpanzees (*Pan troglodytes verus*), in Taï National Park, Côte d'Ivoire, take into account when they revisit the same feeding trees. By following five adult females for many consecutive days, we tested from what distance the females directed their travels towards previously visited feeding trees and how previous feeding experiences and fruit tree properties influenced this distance. To exclude the influence of sensory cues, the females' approach distance was measured from their last significant change in travel direction until the moment they entered the tree's maximum detection field. We found that chimpanzees travelled longer distances to trees at which they had previously made food grunts and had rejected fewer fruits compared to other trees. In addition, the results suggest that the chimpanzees were able to anticipate the amount of fruit that they would find in the trees. Overall, our findings are consistent with the hypothesis that chimpanzees act upon a retrieved memory of their last feeding experiences long before they revisit feeding trees, which would indicate a daily use of long-term prospective memory. Further, the results are consistent with the possibility that positive emotional experiences help to trigger prospective memory retrieval in forest areas that are further away and have fewer cues associated with revisited feeding trees.

Keywords Prospective memory · Memory retrieval · Emotional salience · *Pan troglodytes* · Foraging cognition · Food value

Introduction

Food acquisition is one of the main daily activities performed by wild animals to ensure their survival and reproduction (Schoener 1971; Pyke et al. 1977). Efficient localization of food is expected to reduce direct and indirect competition (Cunningham and Janson 2007) and increase energy gain and fitness (Emlen 1966; Schoener 1971). In tropical forest habitat, fruit production is ephemeral and irregularly distributed (Milton 1981; Van Schaik et al. 1993; Janmaat et al. 2006). For instance, an individual tree can bear ripe fruits for an average of 0.8 months per year with individual fruits remaining edible for only three to six days (Milton 1981). This ephemeral nature of ripe fruit in combination with low visibility associated with dense rainforests (Janmaat et al. 2013a;

Electronic supplementary material The online version of this article (doi:10.1007/s10071-014-0771-y) contains supplementary material, which is available to authorized users.

S. D. Ban (✉) · C. Boesch · K. R. L. Janmaat
Max Planck Institute for Evolutionary Anthropology,
Deutscher Platz 6, 04103 Leipzig, Germany
e-mail: simone_ban@eva.mpg.de; bdagui@yahoo.fr

C. Boesch
e-mail: boesch@eva.mpg.de

K. R. L. Janmaat
e-mail: Karline_Janmaat@eva.mpg.de

S. D. Ban
Centre Suisse de Recherches Scientifiques, 01 BP 1303,
Abidjan 01, Côte d'Ivoire

S. D. Ban
UFR Biosciences, Université Félix Houphouët Boigny,
22 BP 1106, Abidjan 22, Côte d'Ivoire

Janson and DiBitetti 1997) complicates fruit-finding and places a premium on individuals that are able to use sophisticated spatial cognitive abilities to relocate fruit (Janson and Chapman 1999). The difficulties in finding ripe fruit may be especially relevant for chimpanzees who base their diet essentially on ripe fruits (Wrangham et al. 1998; in the Taï forest 85 % of feeding time; Goné Bi 2007) that can only be eaten for a limited period of time (Milton 1981) but provide high amounts of digestible energy (Carlson et al. 2013) needed to maintain a large brain (Zuberbühler and Janmaat 2010). Having accurate spatio-temporal knowledge on the location and value of ripe fruit-bearing trees and travel distances between these trees is expected to decrease searching time (Janmaat and Chancellor 2010), freeing up energy and time that can then be used to defend the territory or perform other social activities (Boesch and Boesch-Achermann 2000). Hence, it is not surprising that frugivorous rainforest primates were shown to remember fruiting states of food trees and to distinguish between sites that did and did not have fruit in the immediate past (e.g., Janson 1998; Janmaat et al. 2006). In addition, primates appear to remember the amount of fruit they fed on (e.g., Garber 1988; Noser and Byrne 2007; Normand et al. 2009; Cunningham and Janson 2007) and to avoid low-quality food sources (Glander 1978). These studies indicate that wild primates remember information about their food. However, little is known about the exact content of this memory and what attributes of the food are indeed remembered (Fagan et al. 2013). Most studies to date use a limited set or single measures to estimate the value of a food source to the forager (e.g., individual feeding duration, the number of minutes that all group members were feeding, food quantity or food type; Garber 1989; Janmaat et al. 2006; Noser and Byrne 2007; Martin-Ordas et al. 2010; Sayers and Menzel 2012; Porter and Garber 2013). Very few studies have measured the food source properties as well as the forager's feeding behaviour during feeding events and have investigated the importance of each in a comparative approach.

The aim of this study was to determine what information chimpanzees in the Taï National Park, Côte d'Ivoire, observe and store during feeding visits and how they integrate this information when they return to previous feeding trees, in addition to the location of those trees. By following five adult females for exceptionally long consecutive periods (maximum consecutive sequence of 44 days, total of 275 full days), we had the unique opportunity to know the exact feeding tree properties (e.g., crown size) as well as the chimpanzees' last feeding experiences (e.g., feeding duration) over continuous intervals of time. Estimating a feeding tree's value is notoriously difficult, as it requires a visually based estimation of the ripeness, taste and nutritional values of fruits that are being eaten (Chapman et al. 1992; Janmaat et al. 2006). To circumvent this problem, we also recorded feeding behaviours to help us estimate the tree's value, such as the ratio of fruit that was rejected by the chimpanzees (Janmaat et al. 2006; Hiramatsu et al. 2009) or the production of food calls, as this was proposed to indicate edible fruit quantity (Hauser and Wrangham 1987) and desirability (Goodall 1986). To gain insight in the nature of information that chimpanzees integrate when they return to feeding trees, we investigated their use of prospective memory—their ability to keep in mind a "to be performed task", i.e., the ongoing anticipation of approach and feeding at a tree that they had fed on earlier (Thorpe et al. 2004; Crystal 2013). We investigated what type of information would influence the distance at which females would start anticipating feeding at fruit trees by measuring at what distances they changed their travel direction towards these trees. We predicted that the chimpanzee females would target their travel towards trees from further distances when the trees had (1) larger crown sizes, (2) a larger proportion of their crown covered in fruit at the moment of the previous departure, and when the females had (3) fed longer, (4) rejected fewer fruits, (5) higher intake rates and (6) made food grunts compared to other revisited trees.

The last prediction was based on an additional expectation that emotions associated with prior feeding events would affect memory retrieval (Hamann et al. 1999; Kano et al. 2008). In fruit scarce periods, Taï chimpanzees feed on average in 7 trees each day (range 1–21; Janmaat et al. 2013b). This means that when revisit intervals were long (mean = 2.5, max = 26 days), a chimpanzee potentially experienced up to 182 different feeding contexts since its last visit to a target tree. As the amount of information as well as the daily amount of social information (Boesch and Boesch-Achermann 2000) keeps increasing, the likelihood that two sources of retained information will interact or confound also increases (known as retroactive and proactive interference; Kane and Engle 2000; Fagan et al. 2013). Foraging animals, therefore, are argued to profit from a mechanism that prioritizes information storage based on the importance of memory for food acquisition efficiency (Fagan et al. 2013). Hence, we investigated whether emotional salience that is known to affect reactivation or retrieval of the chimpanzees' memory could be such a mechanism. Pleasant or aversive events are known to modulate memory retrieval, and both humans and chimpanzees have been shown to have a more accurate and accessible memory of events that are associated with strong emotions as opposed to more neutral events (Hamann et al. 1999; Kano et al. 2008). Previous studies have investigated the role of emotional salience on memory tasks by combining feeding events with the presence or absence of a distressing "waa" call in chimpanzees (Rosati and Hare

2012). We chose a similar approach, yet instead of investigating the effect of a distressing call, we investigated the effect of calls proposed as being linked to positive emotion, namely the production of food grunts (Goodall 1986; Parr 2001). Food grunts are graded call types (also called rough grunts; Marler and Tenaza 1977) that are flexibly produced (Schel et al. 2013; Fedurek and Slocombe 2013) during feeding events. They are thought to indicate food quantity, food preference (Slocombe and Zuberbühler 2006) as well as positive emotional excitement about feeding (Goodall 1986; Hauser 2000; Parr 2001; Sayers and Menzel 2012). We expected that memories of feeding experiences that were associated with food grunts would be more salient and were therefore more likely to be reactivated outside the close surroundings of revisited trees, in forest areas that had fewer cues associated with the revisited trees, than memories of feeding experiences without food grunts. Hence, we predicted that chimpanzee females were especially more likely to target their travel towards trees from further distances when they had made food grunts at the previous visit compared to when they had not.

Methods

Study site and subjects

Data were collected from 16 April 2009 to 30 August 2011. We followed five adult habituated female chimpanzees for successive continuous periods ranging from 4 to 8 weeks totalling 275 full days. Their territory (south group; 26.5 km^2) was located in the Taï National Park (TNP), the largest remaining protected area of primary lowland rainforest in West Africa covering 5, 363 km^2, and located in southwest Côte d'Ivoire (Boesch and Boesch-Achermann 2000; Boesch et al. 2008; N'Goran et al. 2012). The TNP harbours an estimated amount of 1,300 tree species (Guillaumet 1967). During our data collection, each of females had infants ageing from 0 to 7 and their community consisted of an average of 28 individuals including an average of four adult males and six adult females.

Data collection

Behavioural data

We followed each of five focal females from the point of waking until construction of an evening sleeping nest and noted their activity, including all feeding activities, using continuous focal sampling (Martin and Bateson 2007). All plants on which the females fed on fruit were recorded with the GPS and were marked with brightly coloured spray paint. To estimate the focal animal's location at all times, we used the GPS's track log function (see Janmaat et al. (2013a) for accuracy measurements and data cleaning procedures). To decrease the chance of disease transmission from humans to chimpanzees, females were typically followed by one observer at a time and observers took care to remain at least 7 m away from the chimpanzees at all times (Boesch 2008). We used GPS (global positioning system; Garmin 60CsX) and a voice recorder to record the duration and location of each activity. Two observers (K.J. and S.B.) followed a given female on alternate days. Interobserver reliability tests for the scoring of feeding duration ($r_s = 0.93$, $N = 96$; see Janmaat et al. 2013a), rejection ratio ($r_s = 0.92$; $N = 25$) and food grunt presence (Kappa coefficient: $k = 0.73$; $N = 43$) revealed a good agreement between observers. To determine the females' feeding experience, we collected the following measures: Within the first 10 min after the focal female started feeding at a fruit tree, we recorded the rate with which she consumed fruits (*intake rate*) as well as a *rejection ratio*, which was equal to the number of fruits rejected divided by the total number that was picked (rejected or consumed; Janmaat et al. 2006; Hiramatsu et al. 2009). In addition, we recorded the duration for which the females foraged on the fruit for the entire feeding period (*feeding duration*). Lastly, we recorded whether a food grunt was emitted by the focal female during the feeding event (*food grunt* (*yes*/*no*); Goodall 1986; Slocombe and Zuberbühler 2006). To control for the potential use of auditory cues, we furthermore recorded whether other animals (squirrels, birds or primates) were in the tree at the moment of arrival (*other animals in tree* (*yes*/*no*)).

Tree property data

Chimpanzees fed on fruit in trees, strangler figs and lianas. For matters of simplicity, we refer to these fruit-bearing plants as *trees* in the remaining of the manuscript. To measure the tree properties that were expected to represent the tree's value, trained assistants relocated each marked tree the day after each focal observation. Information on each visited tree was collected by (1) identifying the tree species, (2) estimating the crown size and (3) measuring the fruit production class. The crown size was estimated by tape-measuring (1) the Diameter at Breast Height (DBH) for trees, (2) crown radius in all wind cardinal directions for figs and (3) the circumferences of the roots that reached the forest floor for lianas (Leighton and Leighton 1982; McFarland Symington 1988). See details on how crown size was estimated and turned into a *standardized crown size* and made comparable in the supplementary materials and also in Janmaat et al. (2013a). *Fruit production class* was estimated by checking the tree crown from all wind directions using binoculars and ranked with classes of 0, 1–25, 26–50, 51–75 and 76–100 % of the crown being covered in fruit (Peres 1991; Goné Bi 2007; Chapman et al. 1992). Kappa coefficients for agreement on tree species identity and fruit production class ranged between 1 and 0.99 ($N = 81$) and between 0.71 and 0.78 ($N = 112$), respectively; see Janmaat et al. (2013a) for further details. The visual and olfactory detection distance of the tree trunk and crown was estimated by tape-measuring the distance at which the trained assistants could last smell the fruit and see the trunk and crown when walking away from the tree trunk in the arrival direction of the chimpanzees (the track path of the chimpanzees was uploaded in the assistant's GPS the night before). Interpretation of these measurements was based on studies demonstrating that (1) visual acuity thresholds of humans are lower than non-human primates, meaning that humans can spot fruits from further distance since they typically possess larger eyes and hence larger retinal image size (Cavonius and Robbins 1973; Merigan and Katz 1990; Golla et al. 2004), and (2) non-human and human primates fall within the same range of olfactory performance with regard to sensitivity to isoamyl acetate, the major component in a large variety of fruit odours (Laska and Freyer 1997; Laska et al. 1999, 2000, 2003). As only 3 % of travel bouts occurred within trees (N travel bouts = 16,856), we measured detection distances only from ground level.

Data analyses

To gain insight into the content of the chimpanzees' memory of feeding events, we investigated from what distances the females directed their travels towards previous feeding trees to subsequently feed at them (a revisit; in sensu Normand et al. 2009). To minimize the possibility that sensory cues influenced their approach distance, we determined the distance from the last *decision point* to the moment the female entered the tree's *maximum detection distance* (in sensu Noser and Byrne 2007; Fig. 1) and defined this distance as the *out-of-sight approach distance.* We defined a *decision point* as being the last significant change in travel direction (*change point*) before the moment the female re-entered the tree's detection field (Fig. 1). To determine change points, we used the "change point test", a statistical method that objectively determines directional changes in animal travel routes (Byrne et al. 2009). We used a significance criterion of 0.05, step interval = 5 min and $q = 4$, which has been argued to be best for chimpanzees in rainforest habitat (Byrne et al. 2009). The *maximum detection distance* was equal to the maximum of the visual and olfactory detection distances measured by trained assistants the following day (see suppl. materials for details on estimation of the maximum detection distances). To determine the locations at which the female's travel route (using the cleaned GPS data) crossed the tree's maximum detection distance and to calculate the distance between the decision point and the entry in the detection field, we used a combination of programs written by R. Mundry in R and did a manual check of these programs in ArcGis 9.2. Crucially, for the analysis, we only considered revisits for which we followed the target female without interruption since the previous visit. In this way, we had accurate knowledge of the values of the tree properties and feeding experiences at the last visits of the same tree. To estimate the potential influence of female's energy balance on the approach distance, we calculated their *relative energy balance* at the respective decision points using the methods in N'Guessan et al. (2009); see supplementary materials for details on calculations of relative cumulative energy balance at the decision point.

Statistical analyses

Modelling the effect of tree characteristics and feeding experiences on out-of-sight approach distance

To investigate the combined effect of feeding experience variables and tree properties measured at a previous feeding visit on the out-of-sight approach distances preceding revisits, we designed two general linear mixed models (GLMM) (Baayen 2008) fitted with Gaussian error function and identity link. We included predictor variables representing (1) feeding experience: feeding duration, rejection ratio, presence or absence of feeding grunts, and (2) tree properties: standardized crown size and previous fruit production class. Since intake rate and rejection ratio were correlated ($r = 0.5$), we excluded intake rate from the model to avoid collinearity issues. To control for the possibility that the females travelled further simply because they were hungrier, we also included the estimated cumulative energy balance measured at the decision point. To control for the possibility that the females were guided by the sounds of other animals at the feeding trees, we included whether other animals were present in the tree at the moment of revisit as a control predictor. To consider the possibility that our estimation of the tree's detection distance was underestimating the chimpanzee's sensory abilities, we also included whether the fruit had an obvious smell (yes or no; see details in the supplementary materials Table S2). A fruit was defined to have an obvious smell (odiferous) if fruits could be detected from 10 cm away from the human nose (Janmaat et al. 2013a). We furthermore included the fruit production class at the moment of revisit (*current fruit production class*) to further control for visual and olfactory cues. Chimpanzees are known to use fruiting synchrony (Janmaat et al. 2013b) and exhibit

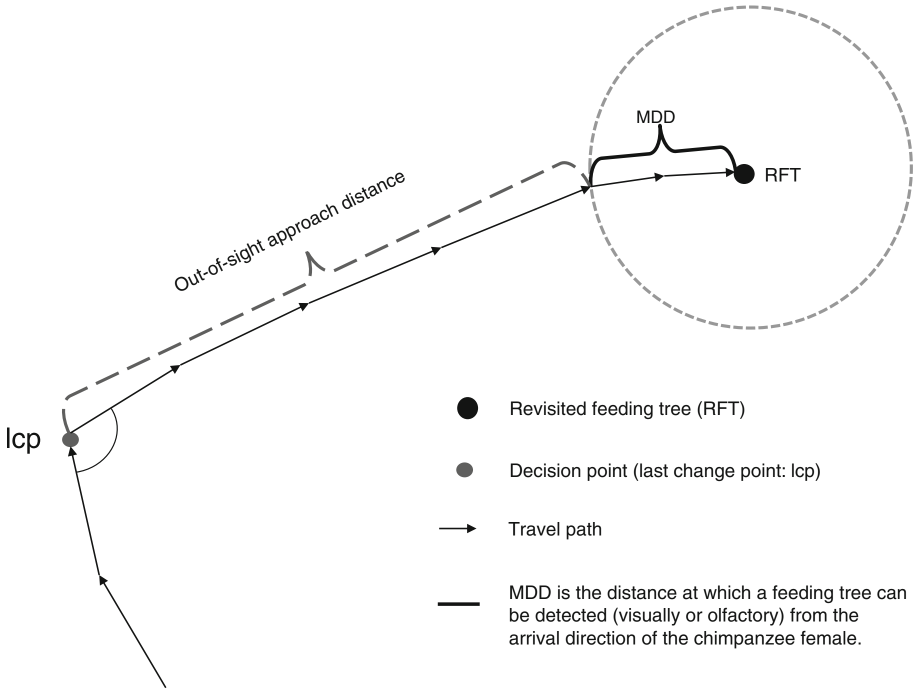

Fig. 1 Schematic of measurements of out-of-sight approach distance travelled by the chimpanzee between the last significant change point and entry in the maximum detection distance of the previously visited feeding tree

periods in which they feed on rare versus common or more spatially clustered fruit species. We therefore expected that approach distances would be somewhat clumped in time, with some time periods with on average larger approach distances compared to other periods with shorter approach distances. To control for this possibility, we included a *temporal autocorrelation term* in the model. So, to account for potential autocorrelation (i.e., temporal non-independence of the residuals from the model), we first ran the full model not accounting for autocorrelation and derived the residuals from it. In a subsequent step, we averaged, separately for each data point, the residuals of all other data points, whereby we weighted their contribution to the average by their distance to the respective data point of the same respective individual chimpanzee. We then included the resulting values as an "autocorrelation term" into the final model. The weighting function had the shape of a Gaussian distribution with a mean of zero and a standard deviation chosen such that the likelihood of the model with the autocorrelation term included was maximized.

To avoid pseudo-replication, we included the intercepts of the random-effects *chimpanzee individual, tree species* and *tree individual*. A recent study revealed that GLMMs that do not incorporate random slopes on top of random intercepts have a high chance of revealing type I errors, i.e., have a high probability of erroneously rejecting the null hypothesis (Barr et al. 2013). Hence, we also included random slopes in the model. In order to do this, we could only include the data of two females that were observed for longer time periods. For these two females, we had sufficient observations per level of the random-effect chimpanzee individual to avoid problems with separation of random effect's and residual variance. For example, to account for the possibility that the effect of food call presence on out-of-sight approach distance is strong for one female but weak or absent for the other female, one needs at least two recordings of presence and two of absence of a food call per chimpanzee individual. To keep type I error rates as low as possible, we included all random slopes possible for all predictor and control variables within chimpanzee individual (Barr et al. 2013). Since this procedure decreased our sample size from data on five females to data on only two, we also ran the model for all the data without random slopes. Since a decrease in sample size may increase type II errors, we decided to present and discuss the fit of both models.

Both models were fitted in R, version 3. 0.2 (R Core Development Team 2013) using the function "lmer" of the R-package "lme4" (Bates et al. 2012). To create stable models, we transformed the predictors in such a way that they resembled a roughly symmetric distribution, prior to running the models. For this, we transformed feeding duration and cumulative energy balance by taking the fourth root. After this, we z-transformed all covariates to establish comparable estimates. To establish normally distributed residuals, we transformed the response variable out-of-sight approach distance to the square root. We checked for whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting the qq plots and the residuals plotted against fitted values (both indicated no obvious deviations from these assumptions). We checked for model stability by excluding individual data points, chimpanzee individuals, species and tree individual, one by one, respectively. The results of these analyses indicated that the models were stable and no influential cases existed. Variance Inflation Factors (VIF, Field 2005) were derived using the function vif of the R-package car (Fox and Weisberg 2011) applied to a standard linear model excluding random effects and did not indicate collinearity to be an issue. To check the overall significance of the combined set of predictor variables, we ran likelihood ratio tests (Dobson 2002) to compare each full model with a respective null model containing only the random effects and control predictors. We only considered the effect of individual predictors if the initial full models reached significance (Forstmeier and Schielzeth 2011). Due to a recent discussion about the validity of p values of fixed effects in the framework of GLMMs, we provide p values derived by likelihood ratio test (Barr et al. 2013). To investigate the caloric differences between odiferous and non-odiferous fruit, we used the Welch's t test conducted on ranked data. These analyses were implemented in R using the packages "exactRankTests" (Hothorn and Hornik 2012).

Results

To investigate the nature of information that chimpanzees take into account when they revisit feeding trees, we designed a general linear mixed model (GLMM), which allowed us to estimate the combined effect of tree properties and feeding experience parameters on the distance that each female travelled between the last change point and the entry of the revisited tree's maximum detection field. This out-of-sight approach distance was on average 537.5 m ($SD = 499$ m; range 6.50–2,842 m) with a mean duration of 80 min ($SD = 81$ min; range 2–407 min; $N_{\text{approach distance}} = 180$; 27 trees species, $N_{\text{trees}} = 129$ fruit trees). The full model was significantly compared to the null model in which the five main predictors were excluded (GLMM: likelihood ratio test: $\chi^2 = 14.409$, $df = 5$, $p = 0.0132$, Table 1). The females travelled farther distances towards trees at which they had given food grunts during the previous visit, after controlling for the potential use of sensory cues provided by the current fruiting state and the female's relative energy balance (Table 1; Fig. 2). We also found a trend towards longer approach distance for trees at which females had rejected fewer fruits (Table 1; Fig. 2). Surprisingly, standardized estimated crown size and feeding duration did not influence approach distance. The control variables energy balance and the presence of other foragers in the tree did not influence approach distance either (Table 1). Our control variable for the potential use of visual and olfactory cues, the current fruit production class, had a significant positive impact on approach distance which suggests that the females either used visual cues from farther away than the estimated maximum detection distance or that they had anticipated the amount of fruit that they would find in the revisited trees (Fig. 3). Our other control for olfactory cues, whether or not the fruit had an obvious smell, had a negative effect on the approach distance (mean $\text{distance}_{\text{non-odiferous}} = 775.6$ m, mean $\text{distance}_{\text{odiferous}} = 469.5$ m), which makes it unlikely that longer approach distances were triggered by smell; otherwise, the effect would have been in opposite

Table 1 Influence of tree properties and feeding experiences on out-of-sight approach distance of Taï female chimpanzees

Predictors	Model without random slopes ($N_{\text{females}} = 5$)			Model including random slopes ($N_{\text{females}} = 2$)		
	Estimates	SE	p value	Estimates	SE	p value
(Intercept)	25.658	2.084		25.543	2.2	
Main predictors measured at previous feeding visit						
Fruit rejection ratio	−1.433	0.758	**0.060**	−1.882	0.871	**0.052**
Standardized estimated crown size	0.480	0.764	0.530	0.727	0.904	0.423
Feeding duration	−0.383	0.711	0.591	−0.518	0.854	0.535
Food grunt (no food grunt)	−3.165	1.481	**0.035***	−3.364	1.602	**0.055**
Previous fruit production class	−2.176	0.916	**0.020***	−1.319	1.040	0.212
Control predictors measured at current feeding visit						
Current fruit production class	3.288	0.927	**0.001*****	3.771	1.627	**0.087**
Smell of fruit (yes)	−3.880	1.868	**0.040***	−3.325	2.098	**0.051**
Other animals in tree (yes)	1.372	1.582	0.391	1.055	1.684	0.536
Relative energy balance at last change point	−0.257	0.696	0.713	−0.206	0.751	0.791
Temporal autocorrelation term individual	2.244	0.684	**0.001****	2.412	0.740	**0.001****

Bold values indicate that the p-value is significant or a trend (close to 0.05)

Single asterisk indicate significant; double asterisk indicate very significant; triple asterisk indicate very very significant direction (Table 1). Additionally, this negative effect could not be explained by the possibility that non-odiferous fruits had a higher value to the chimpanzees since these fruits typically had a lower caloric value (kJ) than odiferous fruit (Welsch *t* test: $t = -3.7561$, $df = 17.909$, $p = 0.0015$; $\text{mean}_{\text{odiferous fruit}} = 139.55$ kJ; $\text{mean}_{\text{non-odiferous fruit}} = 21.28$ kJ).

Initially, the previous fruit production class had a puzzling negative effect on approach distance (Table 1; see Fig. S2 in suppl. materials). To investigate this in more detail, we ran a second model that included all the random slopes for the random-effects chimpanzee individual. For this model, we could only include data from the two females that we had observed for longer periods (see methods for justification). The full model was again significant compared to the null model (likelihood ratio test: $\chi^2 = 11.149$, $df = 5$, $p = 0.04851$). The effect of previous fruit production class, however, disappeared completely. The effect of food grunt presence and fruit rejection ratio on approach distance remained a trend (Table 1). We therefore consider food grunt presence and fruit rejection ratio to be important factors influencing the out-of-sight approach distance of our focal chimpanzees (Fig. 2). The effects of standardized crown size and feeding duration and the control variables remained the same as in the first model except for the effect of the current fruit production class and whether or not the fruits had an obvious smell, which kept the same direction but changed into a trend (Table 1). The temporal autocorrelation had a strong significant effect in both models (Table 1). We argue it to be unlikely that the increase in *p* value for the effect of previous fruit production class on approach distance, in the second model, resulted from a decrease in sample size. The increase in *p* value was relatively large (from 0.02 in the first model to 0.2 in the second) compared to the increase in *p* values for the other predictors which all remained very close to 0.05 after adding in the effects of random slopes and even decreased for some (fruit rejection ratio; Table 1). We, therefore, conclude that the previous fruit production class did not affect the approach distance and that the significant negative effect of previous fruiting state in the first model was unreliable (Fig. S2; Table 1) and resulted from not considering the random slopes, i.e., the possibility that the slopes of the effect of the previous fruit production class on approach distance differed between females.

Discussion

To investigate the nature of information that foragers remember about their food resources in the natural habitat,

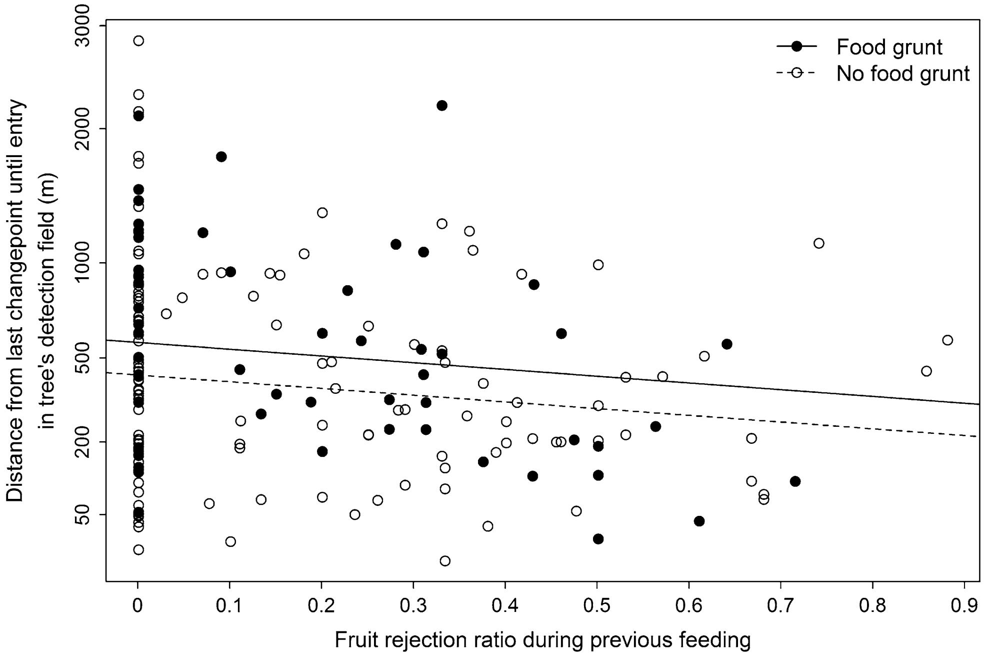

Fig. 2 Taï female chimpanzees revisited trees from farther away when they had given food grunts and had lower fruit rejection ratios on previous visits to the same tree. *Y*-values, shown on a square root scale, represent out-of-sight approach distances between last change point and their entry within the maximum detection field (Fig. 1). The *X*-values represent the proportion of fruits that were rejected at the revisited feeding tree during the previous visit. *Circles* represent observed distances depending on whether chimpanzee made a food grunt (*filled*) or not (*empty*). The *two lines* represent the out-of-sight approach distances predicted by the model when the chimpanzees emitted a food grunt (*straight line*) or not (*dashed line*)

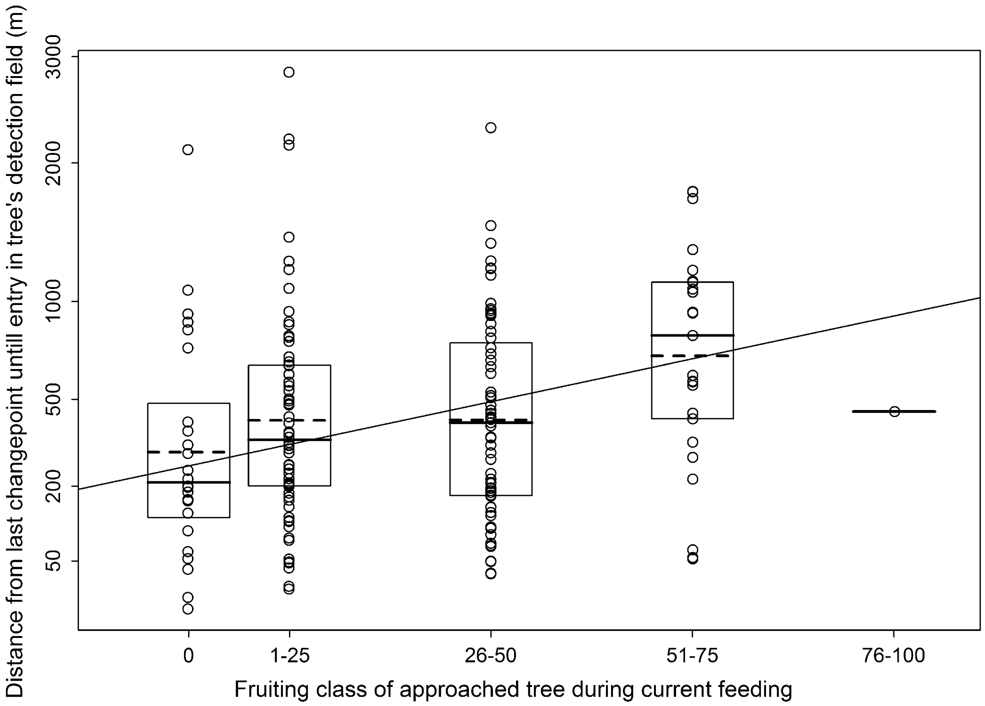

Fig. 3 Taï female chimpanzees revisited trees from farther away when they carried more fruits. *Y*-values, shown on a square root scale, represent out-of-sight approach distances between last change point until their entry within the maximum detection field (Fig. 1). *X*-values represent the current fruit production classes of the revisited trees. Class zero means that the trees were depleted during the revisit. The *circles* represent the out-of-sight approach distances for the respective fruit classes. The *oblique line* represents the out-of-sight approach distance predicted by the model. *Bars* in *straight* and *dash lines* represent respectively the median and mean values of the out-of-sight approach distances, and upper and lower boundaries of *boxes* represent the upper and lower quartiles

we examined from what distance adult chimpanzee females changed travel direction towards previous feeding trees. To exclude the possible use of visual and olfactory cues as an alternative explanation for their directional changes, we measured the distance from the last significant change point (Byrne et al. 2009) until the moment they entered the tree's detection field measured at ground level. We found that these out-of-sight approach distances were longer for trees at which they had made food grunts and had rejected a lower proportion of fruits compared to other previously visited feeding trees, even after we controlled for their relative energy balance and sounds from other foragers feeding in the revisited trees or sensory cues emitted from the tree that could potentially be detected from within tree crowns outside the estimated detection distance. These results are best explained by the possibility that the females remembered feeding experiences that occurred on average 3 days ago and used this information to direct their travels.

The out-of-sight approach distance was not affected by the previous feeding duration. This may appear surprising as earlier studies did show a clear effect of feeding duration on primates' approach behaviour towards fruit trees (Garber 1988; Janmaat et al. 2006; Normand et al. 2009). However, in contrast to our study, all these studies examined feeding duration after arrival instead of prior to arrival (measured during previous visits). It is possible that in these earlier studies, feeding duration did not reflect the value of the tree but simply the hunger levels of the approaching primates. Feeding durations could have simply been long after the primates had travelled for longer distances or at faster speed because they were hungrier at arrival or during approach, respectively (Janmaat et al. 2006).

Furthermore, we found that the out-of-sight approach distance was not significantly affected by the tree properties measured at the previous visit, such as the standardized crown size and previous fruit production class. It is possible that the variation in the standardized crown size of feeding trees was simply not large enough to be worth remembering (Janmaat et al. 2013a). The lack of a reliable effect of the previous fruit production class (Fig. S2; Table 1), and clear disappearance of its impact on the approach distance after including random slopes in the model, however, requires a more elaborate explanation. Previous studies on the same chimpanzee females did show a clear positive effect of the maximum of previous fruit production classes of feeding trees on re-inspection probability of the same trees the year after (Janmaat et al.

2013a). This difference could be explained by the possibility that the maximum productivity of individual trees is perhaps more relevant or reliable during fruit tree monitoring (where the risk of finding an empty tree is higher) than the intermediate and potentially changing production classes within fruiting seasons. Our results did indicate that the current fruit production class tends to affect the out-of-sight approach distance. This effect could have resulted from feeding events that took place inside a tree crown (as 33 % of the last change points coincided with arboreal feeding), from which the females could have ephemerally spotted the amount of fruit in the "to be revisited" tree. However, since the last change points were on average 537.5 meters from detection field of the revisited tree, it is more likely that the females were able to anticipate a change in fruit production class resulting from knowledge on the maturation or depletion rates of fruit, as was suggested to occur in other primate species (Janmaat et al. 2006). Whether chimpanzees can anticipate these changes is a topic for future study but results from captive studies do suggest that chimpanzees can indeed anticipate that particular food types disappear more quickly than others and know how long ago food was still edible (melting ice lollies vs. grapes; Martin-Ordas et al. 2010).

The contradicting effect of previous and current fruit production class could indicate that the females took into account that fruit amounts change over time. On the other hand, it could also imply that the proportion of fruit in the tree was an unreliable measure to estimate the value of the revisited trees. The latter explanation is important with regard to future studies on memory use and socio-ecology in the wild as it stresses the need for a careful approach when attempting to estimate the value of a food source. Although it is good to collect quality measurements of food that are independent from the forager's behaviour, such measurements are difficult to acquire. Simply counting or estimating the number of fruits in a tree may not be appropriate. Many fruit species do not change colour during maturation and need elasticity measurements to assess ripeness/sweetness (Janmaat et al. 2006), which is practically impossible to conduct for rainforest trees that can be up to 40 m high and contain more than a thousand fruits. Analysing the nutritional content of fallen fruit or feeding remains may not necessarily improve qualification either. For example, the nutritional value of fruits within a tree but also between trees of the same species can vary tremendously (Worman and Chapman 2005; 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). This knowledge should be considered in future studies that try to estimate the value of feeding trees. Our findings indicate that measures that use the animal's behaviour to estimate the value of food, such as fruit rejection ratios, should be incorporated in such studies.

A large part of the variation in the out-of-sight approach distance was influenced by the temporal autocorrelation term that was incorporated in our models to avoid a violation of the assumption of independence of residuals. This means that out-of-sight approach distances were somewhat clumped in time with some time periods with on average larger approach distances compared to other periods with shorter approach distances. We propose this reflects time periods during which individuals fed more frequently on scarcer or widely distributed fruit-bearing species, which would require longer approach distances, or time periods during which they fed on trees that were more abundant or clustered in space (Janmaat et al. 2013b).

Since none of the pairs of feeding trees and corresponding change points were the same during our observation period, our results are difficult to explain by the learning of specific time and place associations (Shettleworth 2010). We instead propose two distinct cognitive mechanisms as potential explanations of our findings that out-of-sight approach distances were longer for high-valued compared to low-valued trees. The first explanation is that the females knew their egocentric distance to the previously visited trees and optimized their foraging efficiency by only travelling long distances to sufficiently rewarding trees. Hence, they planned to travel further distances to reach high-valued trees and only aimed to travel to low-valued trees when they were nearby. This would be consistent with observations of planning behaviour in other wild primates like baboons (*Papio ursinus*) that bypass nearby food sources (that they feed on later in time) to reach out-of-sight resources (Noser and Byrne 2007) and in chimpanzees in other contexts (Mulcahy and Call 2006). An alternative and perhaps more parsimonious explanation, however, is that a memory of a high-valued tree is more salient and thus more easily retrieved outside the familiar area of a revisited feeding tree, which could cause changes in travel direction to occur more frequently from further distances than those of less-valued trees. In either case, our findings are best explained by the possibility that chimpanzees acted upon a retrieved memory of their last feeding experiences as if they were using memory in an anticipatory manner. The use of such a prospective memory has been observed in a variety of animals, such as rats, pigeons (Cook et al. 1985; Zentall et al. 1990; Thorpe et al. 2004) and hummingbirds (Gill 1988). Most remembered tasks that were "to be performed," however, occurred on rather short time scales such as 10 s to 15 min (Cook et al. 1985; Thorpe et al. 2004). In our study, the change of travel direction potentially caused by the memory retrieval occurred on average 80 min before the "to be performed act" of feeding, which would indicate a daily use of an exceptionally long-term prospective memory.

Chimpanzee females can feed on up to 21 trees per day (Janmaat et al. 2013b). Here, we show that trees can be revisited up to 26 days or more apart, making the potential amount of stored information on feeding visits substantial. Hence, it is worthwhile to discuss what could have triggered the retrieval of the previous feeding experiences that made the females change travel direction to revisit trees from far away. The puzzling finding that odiferous fruits that are of higher quality were approached from shorter distances than non-odiferous fruit could indicate that a gust of their smell (outside the olfactory detection distance), which is more likely to be encountered at close distance from a fruit tree, could have worked as a familiar cue that triggered the females' memory and prompted them to approach from shorter distances than non-odiferous fruits (note that the minimum out-of-sight approach distance for odiferous fruit was only 7 m). A high frequency of such occurrences could have decreased the average approach distance for trees that carried odiferous fruit. Similarly, fleeting distant visual cues could also have prompted memory retrieval. A fair percentage of the change points (33 %) occurred when the females were feeding in the crown of other feeding trees. Hence, a fleeting distant silhouette of the tree could have potentially prompted memory retrieval as well. Familiar olfactory or visual cues could thus have served as an event-based trigger, in a similar way that the smell of garlic can remind us humans that an Italian restaurant is nearby (Crystal 2013). The majority of change points, however, occurred on the ground and at a substantial distance (mean = 538 m) from the revisited trees. Knowing that Taï chimpanzees tend to not use the same paths and typically re-approach trees from variable directions (Normand and Boesch 2009; Porter et al. submitted), it is likely that many memory retrievals also occurred spontaneously without being triggered by familiar cues that are associated with the feeding tree or on routes towards them. The positive effect of the production of food grunts at previous feeding events on subsequent approach distances suggests that positive emotional experiences can help to trigger such spontaneous prospective memory retrievals when chimpanzees are further away from and have fewer familiar cues associated with respective feeding trees. We encourage cognitive scientists to find ways to further investigate the use of event-based and spontaneous retrieval in prospective memory and the role of emotional salience on memory retrieval in wild animals (Crystal 2013).

Acknowledgments We thank the Leakey Foundation (the Franklin Mosher Baldwin Memorial Fellowship), the Max Planck Institute for Evolutionary Anthropology (MPI), the Centre Suisse de Recherches Scientifiques (CSRS) and the Taï Chimpanzee Project (TCP) for providing funding for this study. We thank the Office Ivorien des Parcs et Réserves (OIPR), the Direction du Parc National de Taï and the Ministère de la Recherche Scientifique en Côte d'Ivoire and the Université Félix Houphouët Boigny for their permission to execute this research and logistical support. We thank C. Stephens and R. Mundry for statistical support and for writing programs in R to calculate the approach distances as well to determine the complete interval of revisits. We thank C. Stephens for proofreading. We are grateful to A. N'Guessan for sharing his data on the energy value of the chimpanzee foods. We are grateful also to J. Tahou, L.B. Bally, V. Gnagnon, R. Nabo and A. Siablo for assistance in field data collection. This study is based on non-invasive observations and complies with the laws of Côte d'Ivoire.

References

Baayen R (2008) Analyzing linguistic data. Cambridge University Press, Cambridge

Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. J Mem Lang 68:255–278

Bates D, Maechler M, Bolker B (2012) lme4: linear mixed-effects models using S4 classes. R package version 0.999999-0

Boesch C (2008) Why do chimpanzees die in the forest? The challenges of understanding and controlling for wild ape health. Am J Primatol 70:722–726

Boesch C, Boesch-Achermann H (2000) The Chimpanzees of the Taï Forest: behavioural ecology and evolution. Oxford University Press, Oxford

Boesch C, Crockford C, Herbinger I, Wittig R, Moebius Y, Normand E (2008) Intergroup conflicts among chimpanzees in Taï National Park: lethal violence and the female perspective. Am J Primatol 70:519–532

Byrne RW, Noser R, Bates LA, Jupp PE (2009) How did they get here from there? Detecting changes of direction in terrestrial ranging. Anim Behav 77:619–631

Carlson BA, Rothman JM, Mitani JC (2013) Diurnal variation in nutrients and chimpanzee foraging behavior. Am J Primatol 75:342–349

Cavonius CR, Robbins DO (1973) Relationships between luminance and visual acuity in the rhesus monkey. J Psychol 232:239–246

Chapman CA, Chapman LJ, Wrangham RW, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. Biotropica 24:527–531

Chapman CA, Chapman LJ, Rode KD, Hauck EM, McDowell LR (2003) Variation in the nutritional value of primate foods: among trees, time periods, and areas. Am J Primatol 24:317–333

Cook RG, Brown MF, Riley DA (1985) Flexible memory processing by rats: use of prospective and retrospective information in the radial maze. J Exp Psychol Anim Behav Process 11:453–469

Crystal JD (2013) Prospective memory. Curr Biol 23:750–751

Cunningham E, Janson C (2007) Integrating information about location and value of resources by white-faced saki monkeys (*Pithecia pithecia*). Anim Cogn 10:293–304

Dobson A (2002) An introduction to generalized linear models. Chapman, Hall/CRC, Boca Raton

Emlen JM (1966) The role of time and energy in food preference. Am Soc Nat 100:611–617

Fagan WF, Lewis MA, Auger-Méthé M et al (2013) Spatial memory and animal movement. Ecol Lett 16:1316–1329

Fedurek P, Slocombe KE (2013) The social function of food-associated calls in male chimpanzees. Am J Primatol 75:726–739

Field A (2005) Discovering statistics using spss. Sage, London

Forstmeier W, Schielzeth H (2011) Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol 65:47–55

Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. Sage, Thousand Oaks

Garber PA (1988) Foraging decisions during nectar feeding by tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*, callitrichidae, primates) in Amazonian Peru. Biotropica 20:100–106

Garber PA (1989) Role of spatial memory in primate foraging patterns *Saguinus mystax* and *Saguinus fuscicollis*. Am J Primatol 19:203–216

Gill FB (1988) Trapline foraging by hermit hummingbirds: competition for an undefended, renewable resource. Ecology 69:1933–1942

Glander K (1978) Howling monkey feeding behavior and plant secondary compounds: a study of strategies. In: Montgomery G (ed) The ecology of arboreal folivores. The symposia of the National Zoological Park, Smithsonian Institution, Washington, pp 561–574

Golla H, Ignashchenkova A, Haarmeier T, Thier P (2004) Improvement of visual acuity by spatial cueing: a comparative study in human and non-human primates. Vision Res 44:1589–1600

Goné Bi ZB (2007) Régime alimentaire des chimpanzés, distribution spatiale et phénologie des plantes dont les fruits sont consommés par les chimpanzés du Parc National de Taï, en Côte d'Ivoire. PhD Dissertation, Université de Cocody, Abidjan, Côte d'Ivoire

Goodall J (1986) The chimpanzees of Gombe: patterns of behavior. Cambridge University Press, Harvard

Guillaumet JL (1967) Recherches sur la végétation et la flore de la région du Bas-Cavally (Côte d'Ivoire). Mémoires ORSTOM, Paris, p 259

Hamann SB, Ely TD, Grafton ST, Kilts CD (1999) Amygdala activity related to enhanced memory for pleasant and aversive stimuli. Nat Am 2:289–293

Hauser DM (2000) The sound and the fury: primate vocalizations as reflections of emotion and thought. In: Nils L, Wallin BM, Steven B (eds) The origins of music. The MIT Press, Cambridge, pp 77–102

Hauser DM, Wrangham RW (1987) Manipulation of food calls in captive chimpanzees. A preliminary report. Folia Primatol 48:207–210

Hiramatsu C, Melin AD, Aureli F et al (2009) Interplay of olfaction and vision in fruit foraging of spider monkeys. Anim Behav 77:1421–1426

Hothorn T, Hornik K (2012) Exact distributions for rank and permutation tests. R package version 0.8-23

Houle A, Chapman CA, Vickery WL (2007) Intratree variation in fruit production and implications for primate foraging. Int J Primatol 28:1197–1217

Janmaat KRL, Chancellor RL (2010) Exploring new areas: how important is long-term spatial memory for mangabey (*Lophocebus albigena johnstonii*) foraging efficiency? Int J Primatol 31:863–886

Janmaat KRL, Byrne RW, Zuberbühler K (2006) Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. Anim Behav 72:797–807

Janmaat KRL, Ban SD, Boesch C (2013a) Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Anim Behav 86:1183–1205

Janmaat KRL, Ban SD, Boesch C (2013b) Taï chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. Anim Cogn 6:851–860

Janson C (1998) Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. Anim Behav 55:1229–1243

Janson CH, Chapman CA (1999) Resources and primate community structure. In: Fleagle JG, Janson C, Reed K (eds) Primate communities. Cambridge University Press, Cambridge, pp 237–267

Janson CH, DiBitetti MS (1997) Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. Behav Ecol Sociobiol 41:17–24

Kane MJ, Engle RW (2000) Working-memory capacity, proactive interference, and divided attention: limits on long-term memory retrieval. J Exp Psychol Learn Mem Cogn 26:336–358

Kano F, Tanaka M, Tomonaga M (2008) Enhanced recognition of emotional stimuli in the chimpanzee (*Pan troglodytes*). Anim Cogn 11:517–524

Laska M, Freyer D (1997) Olfactory discrimination ability for aliphatic esters in squirrel monkeys and humans. Chem Senses 22:457–465

Laska M, Liesen A, Teubner P (1999) Enantioselectivity of odor perception in squirrel monkeys and humans. Am J Physiol 277:1098–1103

Laska M, Seibt A, Weber A (2000) "Microsmatic" primates revisited: olfactory sensitivity in the squirrel monkey. Chem Senses 25:47–53

Laska M, Teresa L, Salazar H, Luna ER (2003) Food preferences and nutrient composition in captive spider monkeys, *Ateles geoffroyi*. Physiol Behav 78:321–329

Leighton M, Leighton DR (1982) The relationship of size of feeding aggregate to size of food patch: howler monkey (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. Biotropica 14:81–90

Marler P, Tenaza R (1977) Signalling behavior of apes with special reference to vocalization. In: Sebeok TA (ed) How animals communicate. Indiana University Press, Bloomington, pp 965–1033

Martin P, Bateson P (2007) Measuring behaviour. An introductory guide. Cambridge University Press, Cambridge

Martin-Ordas G, Haun D, Colmenares F, Call J (2010) Keeping track of time: evidence for episodic-like memory in great apes. Anim Cogn 13:331–340

McFarland Symington M (1988) Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behaviour 105:117–134

Merigan WH, Katz LM (1990) Spatial resolution across the macaque retina. Vis Res 30:985–991

Milton K (1981) Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. Am Anthropol Assoc 83:534–548

Mulcahy NJ, Call J (2006) Apes save tools for future use. Science 312:1038–1040

N'Goran PK, Boesch C, Mundry R, N'Goran EK, Herbinger I, Yapi FA, Kühl HS (2012) Hunting, law enforcement, and African primate conservation. Conserv Biol 26:565–571

N'Guessan AK, Ortmann S, Boesch C (2009) Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. Int J Primatol 30:481–496

Normand E, Boesch C (2009) Sophisticated Euclidean maps in forest chimpanzees. Anim Behav 77:1195–1201

Normand E, Ban SD, Boesch C (2009) Forest chimpanzees (*pan troglodytes verus*) remember the location of numerous fruit trees. Anim Cogn 12:797–807

Noser R, Byrne RW (2007) Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus*. Anim Behav 73:257–266

Parr LA (2001) Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). Anim Cogn 4:223–229

Peres CA (1991) Ecology of mixed-species groups of tamarins in Amazonian Terra Firme Forests. PhD Dissertation, Cambridge University, Cambridge

Porter LM, Garber PA (2013) Foraging and spatial memory in wild weddell's saddleback tamarins (*Saguinus fuscicollis weddelli*) when moving between distant and out-of-sight goals. Int J Primatol 34:30–48

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–154

R Core Development Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rosati AG, Hare B (2012) Chimpanzees and bonobos exhibit divergent spatial memory development. Dev Sci 15:840–853

Sayers K, Menzel CR (2012) Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. Anim Behav 84:795–803

Schel AM, Machanda Z, Townsend SW, Zuberbühler K, Slocombe KE (2013) Chimpanzee food calls are directed at specific individuals. Anim Behav 86:955–965

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Shettleworth SJ (2010) Cognition, evolution, and behavior. Oxford University Press, Oxford

Slocombe EK, Zuberbühler K (2006) Food-associated calls in chimpanzees: responses to food types or food preferences? Anim Behav 72:989–999

Thorpe CM, Jacova C, Wilkie DM (2004) Some pitfalls in measuring memory in animals. Neurosci Biobehav Rev 28:711–718

Van Schaik CP, Terborgh JW, Wright SJ (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377

Worman CO, Chapman CA (2005) Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. J Trop Ecol 21:689–697

Wrangham RW, Conklin-brittain NL, Hunt KD (1998) Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. Int J Primatol 19:949–970

Zentall TR, Steirn JN, Jackson-Smith P (1990) Memory strategies in pigeons' performance of a radial-arm-maze analog task. J Exp Psychol Anim Behav Process 16:358–371

Zuberbühler K, Janmaat KRL (2010) Foraging cognition in non-human primates. In: Platt ML, Ghazanfar AA (eds) Primate neuroethology. Oxford University Press, Oxford, pp 64–83