Anim Cogn (2013) 16:851–860
DOI 10.1007/s10071-013-0617-z

ORIGINAL PAPER

Taï chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes

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

Received: 30 August 2012 / Revised: 28 December 2012 / Accepted: 18 February 2013 / Published online: 11 April 2013

Abstract Fruit foragers are known to use spatial memory to relocate fruit, yet it is unclear how they manage to find fruit in the first place. In this study, we investigated whether chimpanzees (*Pan troglodytes verus*) in the Taï National Park make use of fruiting synchrony, the simultaneous emergence of fruit in trees of the same species, which can be used together with sensory cues, such as sight and smell, to discover fruit. We conducted observations of inspections, the visual checking of fruit availability in trees, and focused our analyses on inspections of empty trees, so to say "mistakes". Learning from their "mistakes", we found that chimpanzees had expectations of finding fruit days before feeding on it and significantly increased inspection activity after tasting the first fruit. Neither the duration of feeding nor density of fruit-bearing trees in the territory could account for the variation in inspection activity, which suggests chimpanzees did not simply develop a taste for specific fruit on which they had fed frequently. Instead, inspection activity was predicted by a botanical feature—the level of synchrony in fruit production of encountered trees. We conclude that chimpanzees make use of the synchronous emergence of rainforest fruits during daily foraging and base their expectations of finding fruit on a combination of botanical knowledge founded on the success rates of fruit discovery, and a categorization of fruit species. Our results provide new insights into the variety of food-finding strategies employed by primates and the adaptive value of categorization capacities.

Keywords Foraging strategies · Fruiting synchrony · Frugivores · Categorization · *Pan troglodytes*

Introduction

Ripe fruits are ephemeral. They only appear at certain times in the year, and when they do, many animals compete over this sweet and energy-rich food (Marriott et al. 1981; Diaz-Perez et al. 2000; Houle et al. 2006). Ripe fruit availability fluctuates in time, and the percentage of rainforest trees carrying ripe fruit can be as low as 0.2 % (Chapman et al. 2005). A low percentage of (ripe) fruit in a diet, during such fruit-scarce periods, is shown to influence life history traits such as waiting time to conception and breeding activity (primates: Thompson and Wrangham 2008, rodents: Glanz et al. 1982; Milton et al. 2005). These studies suggest that it would pay to discover newly emerged fruit earlier than other foragers and to be the first to feed on it. Fruit-dependent foragers (frugivores), such as primates, use spatial memory to relocate fruit-bearing trees (primates: reviewed in Janson and Byrne 2007; Zuberbühler and Janmaat 2010, fruit bats: Holland et al. 2005). However, it is unclear how they discover it in the first place. Fruit trees become depleted and new fruiting seasons begin, meaning frugivores must continuously update their knowledge of the locations of edible fruit. Since not all rainforest trees carry fruit every year, and sometimes skip one or more years (Chapman et al. 1999; Koenig et al. 2003; Struhsaker 1997; Polansky and Boesch in press), frugivores have to learn, every year, which individuals produced fruit and which ones did not. The relatively short duration of fruiting seasons, which can be

---

Electronic supplementary material The online version of this article (doi:10.1007/s10071-013-0617-z) contains supplementary material, which is available to authorized users.

K. R. L. Janmaat (✉) · S. D. Ban · C. Boesch
Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
e-mail: karline_janmaat@eva.mpg.de; kjanmaat@hotmail.com

S. D. Ban
Université de Félix Houphouët Boigny, Abidjan, Côte d'Ivoire

as short as 2 weeks, in combination with the low density and wide distribution of trees of many primate fruit species, increases the challenge of discovering newly emerged fruit (Anderson et al. 2005; Chapman et al. 1999; Milton 1981; Milton et al. 2005 (pg.19); Vooren 1999).

Primates could complement their use of sensory cues with other search strategies that facilitate the discovery of newly emerged fruit. Since many rainforest tree species have a reproductive strategy that causes different trees of the same species to fruit simultaneously within a clustered time period (i.e. fruiting season; Chapman et al. 1999; Koenig et al. 2003), primates could use this phenomenon to increase their fruit-finding efficiency (Milton 1980). We expected primates to use the discovery of fruit in one tree as an indicator for the presence of fruit in other trees of the same species. After discovering fruit in one tree, they can switch to an “inspect all strategy” and start approaching and inspecting other trees of the same species. Indications for the use of such a synchronicity-based inspection strategy were first found in Japanese macaques and later in grey-cheeked mangabeys (*Macaca fuscata*, Menzel 1991; *Lophocebus albigena*, Janmaat et al. 2012). In this study, we investigated whether chimpanzees follow a similar strategy and what type of botanical information they use while doing so. Not all tree species in the chimpanzee’s territory emerge fruit simultaneously (Boesch et al. 2006; Goné Bi 1999, 2007). The probability that other rainforest trees carry fruit at the time of fruit discovery can vary extensively and depends on each species’ reproductive strategy, for example, whether individual trees produce each year or at variable times of the year, such as most fig trees (Koenig et al. 2003; Van Schaik et al. 1993). We predicted that chimpanzees will increase their success rate of inspections by knowing these differences and by especially activating an “inspect all” strategy for those species that have high compared to low synchrony levels.

We recorded feeding and tree inspection behaviour of adult chimpanzee females in the rainforest of the Taï National Park, Côte d’Ivoire. We analysed the females’ inspections of empty trees that did not carry fruit, so to say “mistakes”. This innovative approach in field research enabled us to exclude the possibility that inspections were guided by the use of sensory cues emitted by the fruit themselves and provided us with unique insights into the botanical parameters that influenced the females’ expectations about fruit finding.

Methods

Data collection and analyses

We followed five adult chimpanzee females from 16 April 2009 to 30 August 2011 for continuous periods ranging from 4 to 8 weeks, totalling 330 days, within the fruit-scarce period of April–August (Anderson et al. 2005). Their territory (south community) was located in the largest remaining tract (5,363 km^2) of primary lowland rainforest in West Africa: Taï National Park, Côte d’Ivoire (5°50′20″N, 7°19′16″W; territory size: 26.5 km^2; Boesch et al. 2008; Kouakou et al. 2011; N’Goran et al. 2012). K. Janmaat and S. Ban alternated days following each female from the moment the target female woke up to the evening sleeping nest. They recorded the duration and location of each activity using a combination of a G.P.S. (Garmin 60 CSx) and voice recorder. Activities were recorded using continuous focal sampling (Martin and Bateson 2007). We marked all trees in which the target female fed, or for which the crown was inspected, with brightly coloured paint spray. Inspection was defined as a movement of the target female’s head combined with a fixed gaze in the direction of a tree crown (see supplementary materials for video-recordings of inspections). The majority of recorded inspections occurred after the female came to a halt (95 %). We tested for potential observer differences in the recording of inspections (Kappa = 0.7–0.8; Martin and Bateson 2007) and controlled for this in the final statistical model. The next day trained assistants relocated the marked tree, identified the species and measured whether fruit was present, by checking its crown from all wind directions using binoculars. Kappa coefficients for agreements on species identity ranged between 1 and 0.99 ($N = 81$). Observers were unaware of the synchrony level of the inspected trees at the moment of data collection. From the analyses we excluded inspections (1) for which the gaze was not clearly directed at one single tree crown (e.g. distant inspections), (2) of trees belonging to species for which the fruit was only eaten on the ground, (3) for sleeping locations, which occurred after the females had emitted a nest grunt (Nishida et al. 2010), (4) during which monkeys or other chimpanzees were present in the tree (e.g. during hunting) and (5) that occurred prior to feeding on food that grew in the inspected tree.

To exclude the use of sensory cues as an alternative explanation for the observed behavioural patterns, we ran our comparative tests using inspections of empty trees only (trees that were not carrying ripe nor unripe fruit). Even in highly synchronous species, individual trees can fail to produce (Polansky and Boesch in press; supplementary materials). We therefore expected chimpanzees to make “mistakes”, that is, to inspect trees that had in fact an empty crown. To avoid pseudo-replication, we only considered first observed inspections to the marked trees in our analyses. To calculate the synchrony level of each food species, we used phenology (tree life cycle) data collected monthly on 173 individual trees of 16 species from January 2001 and February 2008 (see Anderson et al. 2005 and Boesch et al. 2006 for a detailed description of the data collection). All trees were located within the female's territory. Synchrony, defined as the simultaneous production of fruit in tree individuals of the same species within clustered time periods (fruiting seasons), was measured as the average of all Spearman rank correlation coefficients that could be calculated for the fruiting state of all possible pairs of trees within a species (Bjørnstad et al. 1999; Buonaccorsi et al. 2001; Koenig et al. 2003). When all tree individuals had the same fruiting state in each month, mean rho Spearman rank correlation coefficients were equal to 1 and a species was defined as having the highest synchrony level. Low synchrony levels were calculated if, for example, not all trees carried fruit within a fruiting season or when some trees emerged fruit in other months (e.g. *Ficus sansibarica*). Rho was calculated by comparing in pairs of trees the (1) absence/presence of ripe fruit (synchrony level A) and (2) amount of ripe fruit scored using the relative ranks: 0, 1, 2, 3 or 4 (synchrony level B). Rank 1, 2, 3 and 4 corresponded to 1–25 %, 26–50 %, 51–75 % and 76–100 % of the branches observed to bear fruit, respectively (see Chapman et al. 1992; Anderson et al. 2005). Since chimpanzees were suggested to also consider the amount of fruit in trees (Normand et al. 2009), we tested the effect of both synchrony values in the final model. Calculations of both types of synchrony levels were conducted by Leo Polansky (unpublished data). To estimate the density of fruit-bearing trees in the territory, we multiplied the proportion of trees in the phenology transect that carried fruit within the month of observation with the tree density of each respective species in the territory. Tree density was measured by Zorro Goné Bi placing five long parallel belt transects of 4,000 × 10 m and 3,000 × 10 m, in the north–south and east–west direction, respectively, within the females' territory. Each transect was placed 500 m apart and contained 200 and 150 quadrants of 10 × 20 m for north–south and east–west transects, respectively, in which the density of all trees with a diameter at breast height $\geq$10 cm was recorded (Anderson et al. 2002; Goné Bi 2007).

Statistical analyses

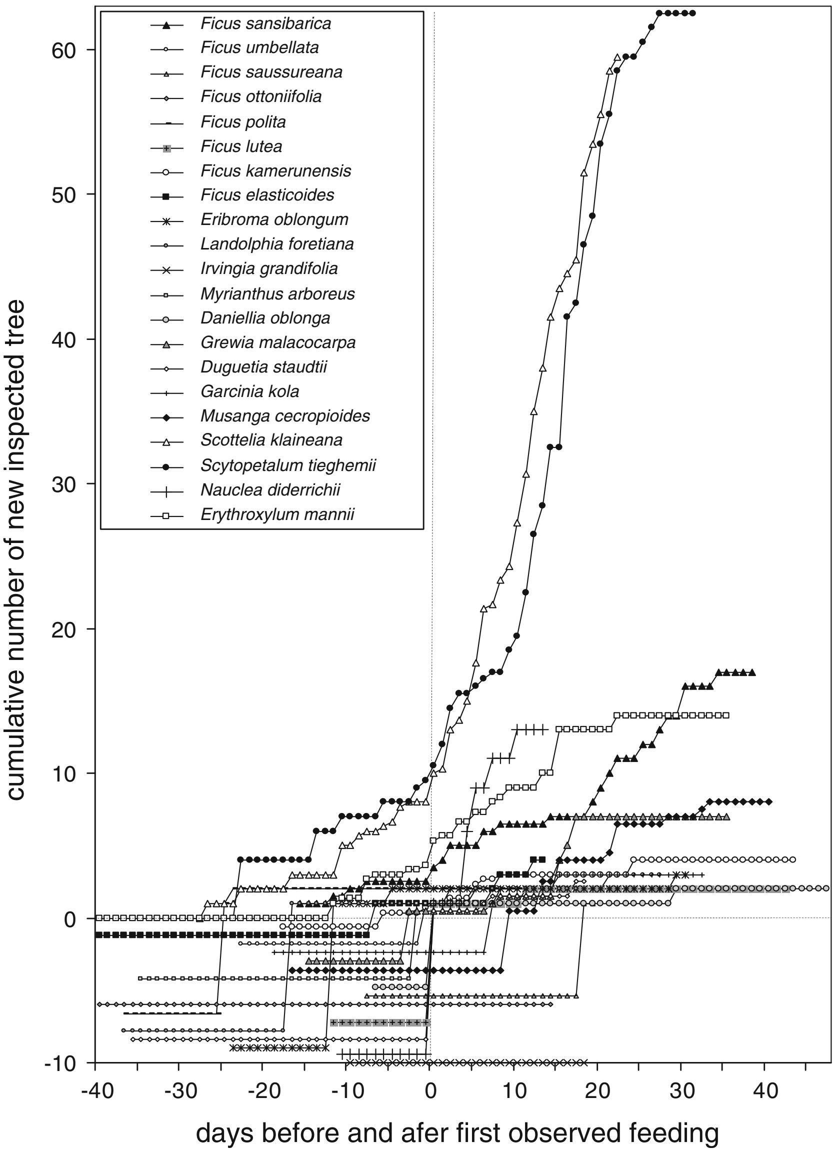
We analysed our results by running Wilcoxon matched pairs tests and generalized linear mixed models (GLMM; Baayen 2008) in R (version 2.12.2, R Development Core Team 2012) using the function lmer provided by the R package lme4 (Bates et al. 2011). For the Poisson model, we checked for absence of over-dispersion and found no deviation from the assumption that the residuals were Poisson distributed ($\chi^2 = 125.16, df = 39$, $P = 0.96$, dispersion parameter = 0.65). To check the overall significance of all predictor variables, we ran likelihood ratio tests comparing the full models with the respective null models. We only considered the effect of the individual predictors if the full model reached the significance (Forstmeier and Schielzeth 2011). 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 log transformed the feeding duration and transformed the number of inspected fruit-bearing trees and the estimated density of fruit-bearing trees to the third and fourth root, respectively. After this we z-transformed all main predictors to establish comparable estimates. We checked for co-linearity by inspecting variance inflation factors (VIF) derived from a multiple regression with the random effects excluded (using the function "vif" of the R package "car" (Fox and Weisberg 2011)). This did not indicate any co-linearity problems with the largest VIF = 1.17 in all models. We assessed the models' validity by comparing the estimates derived by a model based on all data with those obtained from a model with data points dropped one by one, which indicated that both models were stable. In the final model we included two autocorrelation terms to test for temporal autocorrelation of the inspections. To derive the autocorrelation terms, we first calculated the residuals of the full model and second, separately for each data point, averaged the residuals of all other data points from either the same respective individual (term individual) or the same respective species (term species). The contribution of the residuals to these averages was weighted by the time lag between the particular data point and the others. We modelled the weight functions as a Gaussian distribution with a mean of zero (maximum weight at time lag = 0). Its standard deviation was obtained by maximizing the likelihood of the full model with both autocorrelation terms included. Since there is some uncertainty about the validity of *P* values of fixed effects in the framework of GLMMs (Bolker et al. 2008), we additionally tested the effect of (1) the number of fruit-bearing inspected trees on the number of empty inspected trees, controlling for feeding duration and (2) the synchrony level on the inspection probability, controlling for the estimated density of fruit-bearing trees in the territory, using a partial rank correlation permutation test, programmed by R. Mundry in Visual Basic. We controlled for multiple testing (three likelihood tests and two Wilcoxon matched paired tests) by using the Fisher's Omnibus test (Haccou and Meelis 1994) which revealed an overall significant *P* value ($\chi^2 = 111.32$, $df = 10$ and $P = <0.0001$). All tests were two tailed.

Results

Is fruit discovery followed by increased inspection?

To investigate whether chimpanzees use fruiting synchrony, we first recorded the frequencies of the females' feeding and inspection behaviour and tested whether the

Fig. 1 Chimpanzee females increased inspection of trees (full or empty) after feeding on trees of the same species. Day zero represents the day of first observed feeding on each fruit species. To make data from each species visible, we summarized the cumulative number of inspections per species and averaged the number of new inspections performed by the different females when the days after or before first feeding overlapped. To show at which point in time each fruit observation period started and ended, we extended the *Y*-axis below zero. However, all *Y*-values lower than zero should be considered equal to zero



discovery of edible fruit at the start of a season was followed by increased inspection of trees of that same species. The target females fed on an average of 7.14 trees (SD = 3.89, range: 1–21) and 4.03 species (SD = 1.66, range: 1–9) each day, of which 4.63 trees (SD = 2.88, range: 0–16) and 0.57 species (SD = 1.15, range: 0–7) were not revisited and were new within each observation period. They inspected 4.97 trees (SD = 4.75, range: 0–24) and 3.31 species (SD = 2.65, range: 0–14) per day, of which 4.42 trees (SD = 3.97, range: 0–22) and 0.47 species (SD = 0.94, range: 0–5) were new. Although target females already started inspecting trees before we saw them eat fruit of that same species, they increased inspection after the first observed moment of feeding (Fig. 1). When we excluded the use of sensory cues by only considering inspections of empty trees, females inspected trees significantly more after than before they were first observed to feed on fruit of the same species (Wilcoxon paired signed rank (exact): $T^+ = 140$, $P = 0.0013$, Nb of species inspected = 17 (4 ties)). To make a valid comparison, we only considered fruit species for which the first feeding observation took place at least 1 week before the end and at least 1 week after the start of the observation period ($N = 17$). To verify whether the females indeed already started inspecting trees before they had been feeding on fruit from the same species, and to see what could have triggered this, we separately analysed female follows consisting of 16–44 consecutive days. Within these unique consecutive follows, the observers were able to follow the females without interruption and we were thus certain that the females had not yet fed on the concerned fruit species. We confirmed that females were indeed inspecting the fruiting state of trees days before they fed on fruit of that same species (Fig. 2). In addition, the

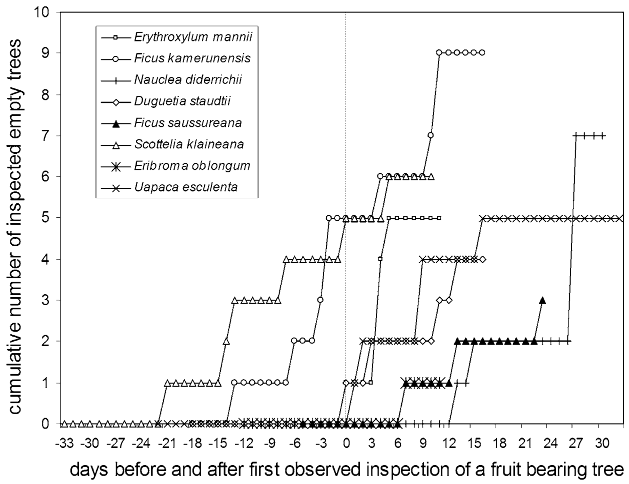


Fig. 2 Chimpanzee females inspected (empty) trees before feeding. Day zero represents the day of first observed inspection of a fruit-bearing tree. The species-specific differences in the number of the last analyzed day are determined by either the day at which the females started feeding or the day at which observers lost contact with the target females

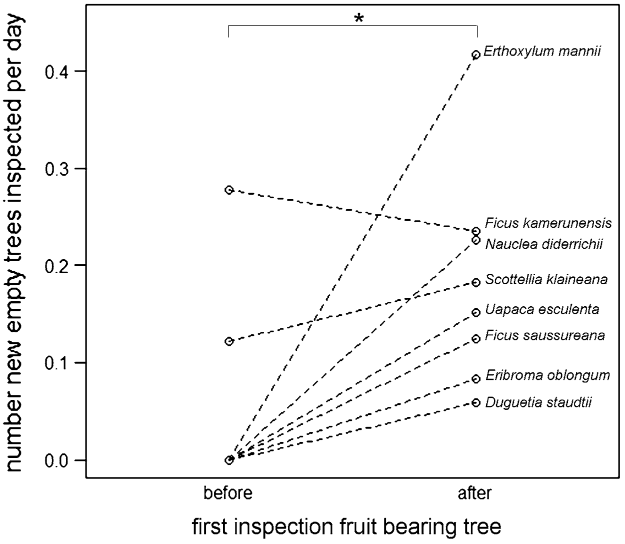


Fig. 3 Chimpanzee females also inspected more trees after than before they were first observed to see fruit. *Each circle* represents the mean number of new empty trees inspected per day of a fruit species. The *lines* in between represent the differences between the means of before and after the first time the females were observed to see (inspect) the fruit belonging to the same fruit species

number of new empty trees inspected per day was significantly higher after than before they were first observed to inspect fruit-bearing trees (i.e. to see fruit of the same species), suggesting that it is not only the taste of fruit that triggered the chimpanzee's expectations but also the observation of the fruit itself ($T^+ = 35$, $P = 0.015$, Nb of inspected species = 8; Fig. 3). In these analyses, we only considered fruit species for which we recorded inspections of fruit-bearing trees but no feeding within the consecutive following periods (Nb = 8).

Table 1 Effect of the number of inspected fruit-bearing trees and feeding duration on the number of empty trees that the chimpanzees inspected

Predictors	Estimate	Std. error	*Z*-value	*P* value
Intercept	−2.41	0.30	−8.14	<0.0001
# Inspected fruit-bearing trees per day	0.54	0.15	3.93	<0.0001
Feeding duration per day	0.21	0.11	1.81	0.0704

Do chimpanzees act on feeding experience or the number of fruit-bearing trees?

We now investigated whether it was just the duration of feeding that triggered inspection, or whether inspection behaviour was influenced by a botanical feature, namely the number of fruit-bearing trees that they had encountered for each of the concerned species. We designed a generalized linear mixed model (GLMM) with Poisson error function and log link to measure the combined effect of both covariates on the number of empty inspected trees within a season, defined as a fruit observation period. This period ranged from the first to the last day in which fruits of the respective species were observed (through feeding or inspection) by the respective females. Because feeding duration and the encountered number of feeding trees per species were, as expected, correlated ($r_s = 0.54$) and thus were likely to cause co-linearity issues, we compared the effect of feeding duration per day with the number of inspected fruit-bearing trees per day instead and included them as main predictors in the model. We also included two random factors, chimpanzee individual and fruit species, to avoid pseudo-replication and two offset variables to control for tree density and the duration of the fruit observation period (since Poisson models require that the response is a count variable (Crawley 2007)). The full model was significant compared to the null model in which both main predictors were excluded (GLMM: likelihood ratio test: $\chi^2 = 210.4$, $df = 1$, $P < 0.0001$). The number of inspected fruit-bearing trees significantly predicted the number of inspected empty trees of the same species, while only a trend was found for feeding duration (Table 1). The effect of the number of inspected fruit-bearing trees was confirmed with a partial rank correlation permutation test, correlating the mean number of inspected empty trees per day with the mean number of inspected fruit-bearing trees per day, while controlling for the mean feeding duration per day (Kendall's Tau = 0.4347, Nb of inspected species for which tree density values were available = 18,

Table 2 Effect of synchrony level and other predictor variables on chimpanzee inspection probability

Predictors	Estimate	Std. Error	*Z*-value	*P* value
Intercept	−1.37	0.19	−7.07	<0.001
Synchrony level B (r_s)	0.41	0.16	2.60	0.009
Density fruit-bearing trees	0.23	0.14	1.67	0.095
Autocorrelation term individual	0.39	0.15	2.54	0.011
Autocorrelation term species	0.87	0.14	6.21	<0.001

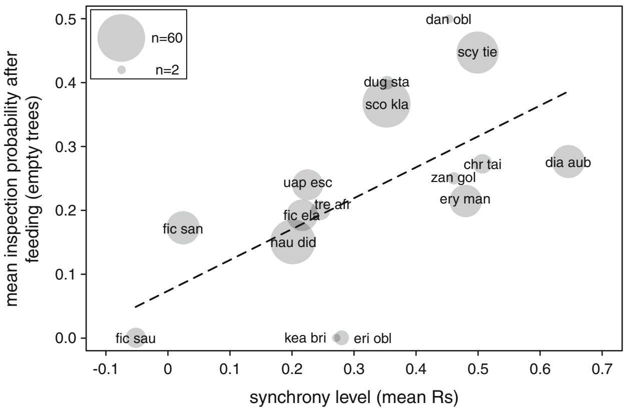


Fig. 4 Synchrony levels (B) significantly influenced inspection probability by chimpanzee females, when controlled for the estimated number of fruit-bearing trees in the territory during observations. The *circle size* represents the sample size for each species. The *dotted line* represents a trend line. The *codes* represent the first three letters of the generic and specific name of the fruit species, respectively

$P = 0.0108$, N permutations = 10,000). A comparison of the estimates of the GLMM suggests that it was not so much the duration that the females had spent feeding on a fruit species that had a positive impact on the inspection rate of conspecific trees. Yet, the females' expectations on fruit availability in individual trees were more strongly guided by the encountered number of trees that produced fruit in the same species. In the next section, we continued to investigate the effect of two botanical variables that are unrelated to the animal's behaviour itself, on inspection probability.

Discrimination between trees of highly and less synchronous fruit species

To investigate whether the chimpanzees have knowledge on the different synchrony levels of fruit species, we tested the effect of the botanical variable synchrony on the females' inspection probability. Building on the finding that inspection rate increased after feeding (Fig. 1), we analysed whether or not the females inspected a tree soon after (that day or the day after) they had fed on a tree of the same species. We tested whether the females were more likely to inspect trees when the concerned fruit species had a high compared to a low synchrony level. Since we did not want to make assumptions on the females' spatial knowledge on tree locations and goal-directed travel towards trees, we included inspections made the day after because some feeding events took place in the afternoon. In this way, the females had sufficient time to encounter a tree of a conspecific species along the way. We only considered absence/presence of inspections recorded within the same day or the day after feeding, instead of the total number, to limit the influence of the clumpedness or the density of trees of the inspected species on inspection probability. To exclude the use of sensory cues, we again only considered the inspections of empty trees. We designed a GLMM with a binomial error function and a logit link and as main predictor one of the two measures of synchrony (synchrony A or B; see methods). We included two temporal autocorrelation terms for chimpanzee individual and fruit species. We controlled for the effect of individual, fruit species and observer by including them as random effects. To gain insight into the cognition behind the inspection activities, we included a second botanical variable, the density of fruit-bearing trees estimated for the female's territory (see methods), as a fourth predictor in both models. This allowed us to test the most parsimonious null hypothesis that assumed the least complex cognitive explanation, namely that inspection probability was simply predicted by the encounter rate of fruit, that is low-level associations created between the fruit and visual features of the tree in which the fruits were eaten. Independent of the type of synchrony measure included, the model was significant compared to the null model that included only the random factors and the autocorrelation terms (including synchrony A: $\chi^2 = 7.47$, $df = 2$, $P = 0.024$; including synchrony B: $\chi^2 = 10.049$, $df = 2$, $P = 0.007$). Both synchrony levels had a positive impact in each respective model (synchrony A: Estimate = 0.32, St. Error = 0.15, $P = 0.039$; synchrony B: Estimate = 0.41, St. Error = 0.16, $P = 0.009$). Yet, the model that explained the variation in inspection probability best was the one that included the predictor synchrony B, which also considered the fruit amount classes (Akaike values: model B: 319.7; model A: 321.9; evidence ratio based on Akaike weights: 0.328; Table 2). For this model fruit-bearing tree density showed only a trend (Table 2). The result regarding the effect of synchrony B was confirmed using a partial rank correlation permutation test, correlating the mean probability of inspections per species with their synchrony level while controlling for fruit-bearing tree density of the concerned species (Kendall's Tau = 0.4478, Nb of inspected species for which synchrony levels could be calculated = 16, $P = 0.013$, N permutations = 10,000; Fig. 4).

Discussion

Innovative approach to detect an alternative fruit-finding strategy

Newly ripened fruit can be discovered by use of visual and olfactory cues emitted by the fruit or sounds produced by other frugivores feeding on them (Bicca-Marques and Garber 2004; Dominy et al. 2001; Olupot et al. 1998; but see Zuberbühler and Janmaat 2010). By adopting an innovative field methodology that analyses the chimpanzee "mistakes", namely their inspections of trees that had empty crowns, we found support for an alternative or complementary fruit-finding strategy to one purely based on sensory cues and association. The results indicate that females developed expectations of finding fruit by inspecting trees, days before feeding on them, and increased inspection activity after tasting the first fruit. Inspection rate especially increased for the two species that had a high synchrony level and high tree density (*Scytopetalum tieghemii* and *Scottelia klaineana*; Fig. 1). The target females did not simply react to the duration of feeding, which potentially triggered a taste for specific fruit, but took into account the number of fruit-bearing trees that they had encountered. When controlling for the fruit-bearing tree density in the territory, inspection probability especially increased as a function of the botanical feature synchrony level of the inspected fruit species. The chimpanzee females differentiated between trees from species that produced fruit in a high versus low proportion of trees in season, had higher expectations to find fruit and acted upon this by inspecting especially those trees with high synchrony levels. The inspection probability was best predicted by the synchrony measure that also considered the fruit amount classes. This could be caused by a preference to inspect species for which a large proportion of trees carry similar high amounts of fruit during the season. Our results indicate that chimpanzees used this synchronicity-based fruit-finding strategy on a regular basis in their daily foraging (they inspected an average of five (and two empty) trees per day). A large part of the variation in the probability of inspection was explained by the autocorrelation terms that considered the time lags between inspections of the same fruit species or inspections by the same individual. The impact of temporal autocorrelation on inspection probability can have many explanations. It could be a reflection of (1) the temporal clustering of fruit production in trees within the same species (fruiting seasons), (2) a temporal preference for a particular fruit species or (3) periods in time (e.g. late in the season) in which the females were less likely to inspect trees, because they already knew the fruiting state of most trees in the territory. The impact of the autocorrelation term for individual could be explained by "inspection moods" possibly triggered by an individual's lack of knowledge of trees' fruiting states in the respective area of observation. The latter explanation is consistent with the high observed variation in daily inspection rate (0–24) and our impression that inspection rate was particularly high in areas that the target female had not recently visited. To fully understand the chimpanzees' inspection behaviour, we encourage field scientists to study how inspection activity relates to detailed measurements on the availability of fruit-bearing trees over time (e.g. early/late in season) and space (e.g. areas in the territory with high/low proportions of fruit-bearing trees) for one highly synchronous fruit species (sensu Janmaat et al. 2012). In addition, recordings of inspections of empty trees could be combined with measurements of the duration of such inspections. Long durations could indicate the so-called surprise reactions, previously used to measure object individuation in captive animals (e.g. Tinklepauh 1928; Brauer and Call 2011).

The underlying cognition

To generate expectations about trees of particular species, and to preferentially inspect those trees, we argue that the females must have integrated (1) information on the success rate of finding fruit in trees for each species (the synchrony level) and (2) knowledge of botanical (perceptual and polymorphous) features to identify to what species the empty trees belong.

Information on high/low success rates

It could be argued that the effect of synchrony level on inspection probability is a simple result of a low-level process of positive association formation. Throughout fruiting seasons and across years, stronger associations could have been created and maintained between familiar spatially separated trees of highly synchronous species, in which a higher proportion of trees produce fruit, than for less synchronous species. For example, when a chimpanzee female discovers fruit in a tree of a highly synchronous species and she subsequently encounters another tree of that same species, inspection of the second tree could simply be activated just because both trees fruited and were fed on in the previous year, and a positive association had been created. We consider this explanation to be unlikely for two reasons. First, we argue that positive associations made in the previous fruiting seasons are unlikely to be useful for the simple reason that the rate at which chimpanzees revisit trees across years is extremely low. We base this conclusion on unique follows of one target female in the three subsequent years of our study. The first year we followed and marked all the feeding trees visited by the target female during a period of 28 consecutive days (Nb of trees = 268). The second and third year we followed her within continuous periods of 8 weeks, attempting to cover the same fruiting seasons, starting from 4 and 2 weeks, respectively, before the starting date of the 2009 period. This unique data collection design revealed that only 20 and 18 trees were fed on again in 2010 and 2011, respectively. Despite the temporal variability in the starting of fruiting seasons, the small amount of revisits could not be explained by a low overlap in fruiting periods as 25 out of 30 species fed on in 2009 were also fed on in 2010, and 22 out of 32 species fed on in 2009 were also fed on in 2011. Hence, they were feeding on the same fruit but not the same trees. A low revisit rate across years is perhaps not surprising because (1) ranging areas within similar fruiting seasons vary between years (see supplementary materials) and (2) not all trees fruit every year (Koenig et al. 2003; Struhsaker 1997). From the eight inspected most synchronous species ($r_s > 0.35$) that produced fruit once a year, individuals on the average bore ripe fruit only 49 % of all years (range: 0–86 %). Hence, the probability that any tree will bear ripe fruit two subsequent years in a row is low, and the majority of inspected trees were unlikely to be fed on in the previous fruiting seasons. Therefore, associative revisiting of previously rewarding locations would be a poor foraging strategy. Second, if the females had been solely relying on positive associations made in earlier years, they would have been equally likely to approach and inspect trees of species with a high fruit-bearing tree density that likely had a similar density in previous years, yet the effect of this predictor was insignificant (Table 1).

A more parsimonious explanation for the observed behaviour is that the chimpanzees recognized individual trees as belonging to a specific species with either a low or high synchrony level and relied on that botanical knowledge to make their decision to inspect. They likely categorized newly encountered trees into the class of a specific species to infer a relationship between the synchrony level of that species and the fruit availability of those individual trees to predict whether inspection would pay off. Learned rules of more/less, above/below and same/different relationships are considered to be crucial ingredients of concepts (Chittka and Jensen 2012). Indications for the use of such rules were found in a variety of animal species ranging from great apes to insects (same/different: e.g. Thompson et al. 1997; Giurfa et al. 2001; Zentall et al. 2008, above/below: e.g. Avarguès-Weber et al. 2011; Depy et al. 1999; Spinozzi et al. 2004, more/less: e.g. Boysen and Hallberg 2000; Vlaming et al. 2006). Whether the chimpanzees in this study inferred high/low success rates of fruit finding in a tree species by a hierarchical or relational rule requires further investigation by means of experimental studies.

Food plant identification

We argue that the females' expectations of finding fruit in trees of synchronously fruiting species were triggered by botanical cues that were unrelated to the visual availability of the fruit, as both full and empty trees were inspected. Chimpanzees are not unique among primates in their ability to use detailed knowledge on the perceptual features of associated plant items to anticipate food finding prior to seeing it. Baboons (*Papio ursinus*) and mangabeys (*Cercocebus atys*) have been regularly observed to dig for underground corms (*Eulophia foliosa, Watsonia lepida*) or seeds (*Anthonota fragans*), respectively, when the only available visual (and olfactory when seeds were experimentally removed) cue was a stem or tree sapling above the ground (Byrne 1995; unpublished data KJ). In a complex and changing food environment, the capacity to recognize different foods remotely may arguably be at a premium in many animal species. Darwin suggested that even bees, with their miniscule brains (Avarguès-Weber et al. 2011), are able to recognize plants when the associated food is absent. On page 224 of "Cross and self-fertilization of plants", Darwin (1876) describes a bee flying in a straight line from one larkspur (*Delphinium spp.*) to another larkspur, which did not as yet have a single flower open. The observation inspired and preceded numerous studies on the perceptual cues that animals use to identify potential food (e.g. Manning 1956; Edwards et al. 1997; Vogels 1999; Santos et al. 2001; Inoue et al. 2008). Experimental studies revealed that bumble bees (*Bombus terrestris*), dependent on the flower species, became conditioned to either the perceptive features of the flower or the general form of a plant, but were unable to recognize the species (e.g. Manning 1956). Foraging bumblebees that were specialized on Hound's-tongue flowers (*Cynoglossum officinale*), in fact, made numerous errors. Bees inspected (here defined as flying to the base of the stem and hovering up and down from it without subsequent feeding) up to 13 other plant species with similar visual features (upright stem, bearing leaves along most of the plant's length), yet none of them flowered within the observation period (Manning 1956). In contrast, our target chimpanzees rarely inspected empty trees that belonged to species that did not carry ripe or unripe fruit within the observation period. Only 13 out of 1,433 inspections concerned plant species that did not carry fruit in the observation period or between the same dates in previous years, which suggests that they were able to identify fruitless trees of potential food species.

To learn to distinguish between fruitless trees of different rainforest tree species is no trivial task and can take human botanists years of training (Zuberbühler and Janmaat 2010). The chimpanzee females fed on an average of one "new" species every 2 days and at least 152 in their lifetime (this study; Goné Bi 1999). Bees instead show flower constancy and forage on very few flower species at a time (e.g. Plateau 1901; Waser 1986). Flower constancy increases with increasing differences among available flower types (Waser 1986), and bees that focus on one flower species only find other flower individuals more quickly (Chittka et al. 1997), which has led researchers to suggest that food choices in bees are limited by memory capacities (e.g. Chittka et al. 1997; Chittka and Thomson 1997).

Comparative studies on animals' capacities to learn to accurately identify large numbers of food species and to remember and use that information quickly and comparisons of the botanical features that animals use to recognize or classify food will help us to quantify and qualify memory capacities and understand the frequencies with which different species generate new behavioural solutions (Chittka and Niven 2009). We, therefore, encourage cognitive scientists to further investigate the cognition behind the synchronicity-based fruit-finding strategy as it will improve our knowledge of information processing and may well elucidate the evolutionary origins of categorization abilities and abstract thinking in humans (Shettleworth 2010).

Acknowledgments Financial support for this research was provided by the Max Planck Institute for Evolutionary Anthropology. In Côte d'Ivoire we thank the Ministère de la Recherches Scientifiques, the Ministère de l'Environnement et des Eaux et Forêts, the Office Ivoirien des Parcs et Réserves, the directorship of the Taï National Park, the Centre Suisse de Recherche Scientifique, L.Wittiger, D. Dowd, A. Diarrassouba, I. Kone and S. Kone for logistic support and permission to conduct our studies. We are indebted to J. Tahou, R. Nabo, L. B. Bally and V. Gnagnon for invaluable assistance in the field. We are grateful to L. Polansky for sharing his calculations on synchrony values. We happily acknowledge R. Mundry for training K. Janmaat to model in R and for programming the permutation test and the autocorrelation function. We thank R. Moore, J. Call, A. Kalan and C. Hicks for helpful comments. This study is based on non-invasive observations and complies with the laws of Côte d'Ivoire.

References

Anderson DP, Nordheim EV, Moermond TC (2002) Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch B, Hohmann G, Marchant LF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, pp 90–101

Anderson DP, Nordheim EV, Moermond TC, Goné Bi ZB, Boesch C (2005) Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. Biotropica 37:631–640

Avarguès-Weber A, Deisig N, Giurfa M (2011) Visual cognition in social insects. Annu Rev Entomol 56:423–443

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

Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.R-project.org/package=lme4

Bicca-Marques JC, Garber PA (2004) Use of spatial, visual, and olfactory information during foraging in wild nocturnal and diurnal anthropoids: a field experiment comparing *Aotus*, *Callicebus*, and *Saguinus*. Am J Primatol 62:171–187

Bjørnstad ON, Ims RA, Lambin X (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends Ecol Evol 14:427–432

Boesch C, Goné Bi Z, Anderson D, Stahl D (2006) Food choice in Taï chimpanzees: are cultural differences present? In: Hohmann G, Robbins M, Boesch C (eds) Feeding ecology in apes and other primates. Cambridge University Press, Cambridge, pp 365–399

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

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2008) Generalized linear mixed models: a practical guide for ecology. Am J Physic Anthropol 135:171–181

Boysen ST, Hallberg KI (2000) Primate numerical competence: contributions toward understanding nonhuman cognition. Cognitive Sci 24:423–443

Brauer J, Call J (2011) The magic cup: great apes and domestic dogs (*Canis familiaris*) individuate objects according to properties. J Comp Psychol 125:353–361

Buonaccorsi JP, Elkinton JS, Evans SR, Liebhold AM (2001) Measuring and testing for spatial synchrony. Ecology 82:1668–1679

Byrne RW (1995) The thinking ape. Evolutionary origins of intelligence. Oxford University Press, Oxford

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, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE (1999) Fruit and flower phenology at two sites in Kibale National Park, Uganda. J Trop Ecol 15:189–211

Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulsen JR (2005) A long-term evaluation of fruiting phenology: importance of climate change. J Trop Ecol 21:31–45

Chittka L, Jensen K (2012) Animal cognition: concepts from apes to bees. Curr Biol 21:116–119

Chittka L, Niven J (2009) Are bigger brains better? Curr Biol 19:995–1008

Chittka L, Thomson JD (1997) Sensori-motor learning and its relevance for task specialization in bumble bees. Behav Ecol Sociobiol 41:385–398

Chittka L, Gumbert A, Kunze J (1997) Foraging dynamics of bumble bees: correlates of movements within and between plant species. Behav Ecol 8:239–249

Crawley MJ (2007) The R book. Wiley, Chichester

Darwin C (1876) The effects of cross and self fertilisation in the vegetable kingdom. Murray, London

Depy D, Fagot J, Vauclair J (1999) Processing of above/below categorical spatial relations by baboons (*Papio papio*). Behav Process 48:1–9

Diaz-Perez JC, Bautista S, Villanueva R (2000) Quality changes in sapote mamey fruit during ripening and storage. Postharv Biol Technol 18:67–73

Dominy NJ, Lucas PW, Osoria D, Yamashita N (2001) The sensory ecology of primate food perception. Evol Anthropol 10:171–186

Edwards GR, Newman JA, Parson AJ, Krebs JR (1997) Use of cues by grazing animals to locate food patches: and example with sheep. Appl Anim Behav Sci 51:59–68

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, CA. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Giurfa M, Zhang S, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933

Glanz WE, Thorington R, Giacalone-Madden J, Heaney LR (1982) Seasonal food use and demographic trends in *Sciurus granatensis*. In: Leigh EG, Rand AS, Windsor DM (eds) Ecology of a tropical forest. Smithsonian Press, Washington, DC, pp 239–252

Goné Bi ZB (1999) Phénologie et distribution des plantes dont divers organes (principalement les fruits) sont consommés par les chimpanzés, dans le Parc national de Taï, Côte d'Ivoire. Mémoire DEA, University of Cocody, Abijdan, Côte d'Ivoire

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. Dissertation, University of Cocody, Abidjan, Côte d'Ivoire

Haccou P, Meelis E (1994) Statistical analyses of behavioural data. Oxford University Press, Oxford

Holland RA, Winter P, Waters DA (2005) Sensory systems and spatial memory in the fruit bat *Rousettus aegyptiacus*. Ethology 111:715–725

Houle A, Vickery WL, Chapman CA (2006) Mechanisms of coexistence among two species of frugivorous primates. J Anim Ecol 75:1034–1044

Inoue T, Hasegawa T, Takara S, Lukáts B, Mizuno M, Aou S (2008) Categorization of biologically significant objects, food and gender, in rhesus monkeys I. Behavioral study. Neurosci Res 61:70–78

Janmaat KRL, Chapman CA, Meijer R, Züberbuehler K (2012) The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit. Anim Cogn 15:83–96

Janson C, Byrne RW (2007) Resource cognition in wild primates-opening up the black box. Anim Cogn 10:357–367

Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD (2003) Dissecting components of population-level variation in seed production and the evolution of masting behavior. Oikos 102:581–591

Kouakou CY, Boesch C, Kuehl H (2011) Identifying hotspots of chimpanzee group activity from transect surveys in Taï National Park, Côte d'Ivoire. J Tropic Ecol 27:621–630

Manning A (1956) Some aspects of the foraging behaviour of bumble-bees. Behaviour 9:164–201

Marriott J, Robinson M, Karikari SK (1981) Starch and sugar transformation during the ripening of plantains and bananas. J Sci Food Agric 32:1021–1026

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

Menzel CR (1991) Cognitive aspects of foraging in Japanese monkeys. Anim Behav 41:397–402

Milton K (1980) The foraging strategy of howler monkeys. A study of primate economics. Columbia University Press, New York, p 138

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

Milton K, Giacalone S, Wright SJ, Stockmayer G (2005) Do frugivore population fluctuations reflect fruit production? Evidence from Panama. In: Dew JL, Boubli JP (eds) Tropical fruits and frugivores. The search for strong interactors. Springer, The Netherlands, pp 5–35

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

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

Olupot W, Waser PN, Chapman CA (1998) Fruit finding by mangabeys (*Lophocebus albigena*): are monitoring of fig trees and use of sympatric frugivore calls possible strategies? Int J Primatol 19:339–353

Plateau F (1901) Observations sur le phénomène de la constance chez quelques hyménoptères. Ann Soc Entomol Belg 45:56–83

Polansky L, Boesch C (in press) Long-term fruit phenology and rainfall trends conflict in a West African lowland tropical rainforest. J Tropic Ecol. Supplementary materials

Santos LR, Hauser MD, Spelke ES (2001) Recognition and categorization of biologically significant objects by rhesus monkeys (*Macaca mulatta*): the domain of food. Cognition 82:127–155

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

Spinozzi G, Lubrano G, Truppa V (2004) Categorization of above and below spatial relations by tufted capuchin monkeys (*Cebus apella*). J Comp Psychol 118:403–412

Struhsaker TT (1997) Ecology of an African rainforest. University Press of Florida, Gainesville

Thompson ME, Wrangham RW (2008) Diet and Reproductive Function in Wild Female Chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda and evolution. Trends Ecol Evol 24:127–135

Thompson RKR, Oden DL, Boysen ST (1997) Language-naïve chimpanzees (*Pan troglodytes*) judge relations between relations in a conceptual matching to sample task. J Exp Psychol Anim Behav 23:31–43

Tinklepauh OL (1928) An experimental study of representative factors in monkeys. Comp Psychol 8:197–236

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

Vlaming PHJM, Uher J, Call J (2006) How the great apes (Pan troglodytes, Pongo pygmaeus, Pan paniscus, and Gorilla gorilla) perform on the reversed contingency task: the effects of food quantity and food visibility. J Exp Psychol Anim Behav 32:60–70

Vogels R (1999) Categorization of complex visual images by rhesus monkeys. Part 1: behavioural study. Eur J Neurosci 11:1223–1238

Vooren AP (1999) Introduction de la bionomie dans la gestion des forêts tropicales denses humides. Dissertation. Wageningen University, The Netherlands

Waser NM (1986) Flower constancy: definition, cause and measurement. Am Nat 127:593–603

Nishida T, Zamma, K, Matsusaka T, Inaba A, McGrew WC (2010) Chimpanzee behavior in the wild: an audio-visual encyclopedia. Springer, Tokyo

Zentall TR, Wasserman EA, Lazereva OF, Thompson RKR, Rattermann MJ (2008) Concept learning in animals. Comp Cogn Behav Rev 3:13–45

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