# COMMENTARY

## Spatio-Temporal Complexity of Chimpanzee Food: How Cognitive Adaptations Can Counteract the Ephemeral Nature of Ripe Fruit

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Ecological complexity has been proposed to play a crucial role in primate brain-size evolution. However, detailed quantification of ecological complexity is still limited. Here we assess the spatio-temporal distribution of tropical fruits and young leaves, two primary chimpanzee (*Pan troglodytes*) foods, focusing on the predictability of their availability in individual trees. Using up to 20 years of information on monthly availability of young leaf, unripe and ripe fruit in plant species consumed by chimpanzees from tropical forests in East, Central, and West Africa, we estimated: (1) the forest-wide frequency of occurrence of each food type and (2) the predictability of finding ripe fruit-bearing trees, focusing on the timing, frequency, and amount of ripe fruit present. In all three forests, at least half of all encountered trees belonged to species that chimpanzees were known to feed on. However, the proportion of these trees bearing young leaves and fruit fluctuated widely between months. Ripe fruit was the most ephemeral food source, and trees that had more than half of their crown filled were at least nine times scarcer than other trees. In old growth forests only one large ripe fruit crop was on average encountered per 10 km. High levels of inter-individual variation in the number of months that fruit was present existed, and in some extreme cases individuals bore ripe fruit more than seven times as often as conspecifics. Some species showed substantially less variation in such ripe fruit production frequencies and fruit quantity than others. We hypothesize that chimpanzees employ a suite of cognitive mechanisms, including abilities to: (1) generalize or classify food trees; (2) remember the relative metrics of quantity and frequency of fruit production across years; and (3) flexibly plan return times to feeding trees to optimize high-energy food consumption in individual trees, and efficient travel between them. Am. J. Primatol.
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## INTRODUCTION

Tropical forest habitat and its distribution is thought to have a major impact on primate, and especially great ape evolution [e.g., Milton, 1981; Potts, 2004; Sussman, 1991; Sussman et al., 2013; Van Schaik et al., 1993; White et al., 2009]. One crucial argument for this supposition is that the majority of modern primate species, and all great apes, forage on foods produced by tropical forest trees [Doran-Sheehy et al., 2009; Fleagle, 1988; Fleagle & Reed, 1996; Knott, 2005; Potts, 2004; Robbins, 2008; Terborgh, 1986]. Given their lack of morphological and/or physiological dietary adaptations, great apes are, in contrast to old world monkeys, unable to digest chemically defended forest foods such as many mature leaves and certain seeds, and thereby must increase the consumption of energy-rich food, such as young leaves or ripe fruit, when more is available [reviewed in Doran-Sheehy et al., 2009]. A low percentage of ripe fruit in the diet has been shown to have a negative influence on female reproductive physiology and life history traits, such as waiting time to conception in great apes [Emory Thompson & Wrangham, 2008; Knott, 2005]. Any cognitive adaptation enabling the intake of more energy-rich food, ameliorating the competitive handicap of great apes would therefore seem highly advantageous. Detailed investigation of the temporal distribution of high-energy food in tropical forests thus has the potential to improve our understanding of great ape evolution and in particular that of their advanced representational skills and larger brain size [Byrne, 1997; Knott, 2005].

The availability of energy-rich plant food throughout the tropical forest is characterized by temporal fluctuations that result in periods of abundance, alternated by variably long periods of scarcity [e.g., Chapman et al., 1999a; Hladik, 1988; Knott, 2005; Polansky & Boesch, 2013; Polansky & Robbins, 2013; Van Schaik et al., 1993; Van Woerden et al., 2012]. Observations that necessary food resources could in fact be scarce but predictable led to the "ecological intelligence hypothesis" [Milton, 1981, 1988]—that primates, such as great apes, which rely on ephemeral and scattered fruits would need larger ranges and would have evolved advanced cognitive capacities that facilitate optimal food finding strategies [Milton & May, 1976; Milton, 1980]. The hypothesis found support in several comparative studies of primates as well as rodents and bats [Barton, 1996; Clutton-Brock & Harvey, 1980; Harvey & Krebs, 1990]. For example, sympatric primate species that differ considerably in relative brain size show clear dietary differences: with those that feed on energy rich ripe fruit for a larger percentage of feeding time exhibiting relatively larger brains or brain regions [Barks et al., 2015; Doran-Sheehy et al., 2006, 2009; Houle et al., 2010; Milton, 1981; Wrangham et al., 1991].

Other comparative studies found that larger-brained primate species, such as great apes, exhibit less seasonality in food consumption relative to that expected on the basis of environmental seasonality of food, than smaller-brained species [Van Woerden et al., 2012]. This finding led to the proposition that larger brains provide a cognitive flexibility in behavior which facilitates the buffering of periods of food scarcity ["the cognitive buffer hypothesis"; Allman et al., 1993; Van Woerden et al., 2012]. Proposed candidates for these flexible behaviors were extractive foraging or exploitation of dispersed food patches [Melin et al., 2014; Van Woerden et al., 2012]. Behaviors that facilitate early access, as well as an optimal timing of return to recently produced energy-rich and ephemeral food, such as ripe fruit, were not explicitly proposed, but are also promising candidates [Janmaat et al., 2014].

Such behaviors could entail a combined use of visual specializations [e.g., Barton, 1998, 2004; Changizi & Shimojo, 2008; Dominy & Lucas, 2004] and spatial memory [reviewed in Janson & Byrne, 2007; Zuberbühler and Janmaat, 2010] that have been shown to increase foraging efficiency [Janmaat & Chancellor, 2010; Riotte-Lambert et al., 2015]. To develop hypotheses about which other (flexible) cognitive abilities large-brained primates could use to optimize arrival time, it is necessary to first quantify metrics characterizing the complexity of food finding.

It has been argued that food finding becomes cognitively complex when the distribution of food has neither the lowest entropy (ordered), nor the highest entropy (random or chaotic), but rather has a certain pattern that is predictable without perfect knowledge [Fagan et al., 2013; Grassberger, 1986; Sambrook & Whiten, 1997]. Milton [1980] described predictability as an important feature that could work to the primate's advantage, proposing "once the location of a particular food tree is known, it becomes a dependable seasonal resource in terms of its location for the lifetime of the primate." Many rainforest tree species have reproductive strategies that cause different trees of the same species to bear fruit simultaneously within a clustered time period [i.e., fruiting season; Chapman et al., 1999b]. Hence, the time that the "known" tree will bear fruit could predictably be inferred from discoveries of fruit in conspecific trees [e.g., Janmaat et al., 2012; Menzel, 1991; Milton, 1980; Milton et al., 2005].

Yet, even granting perfect spatial memory that helps a primate to find a particular tree and knowledge of synchrony that helps it to predict when it bears food, we might ask how predictable a "known" food tree really is. Does it always produce food in the same month or simultaneously with all other conspecific trees? Will it bear fruits and grow edible leaves every fruiting or flushing season and, if so, will it always produce the same amount?

Botanical studies have revealed that primate food production is subject to complex selection processes involving both seasonally variable biotic (e.g., pollinator population dynamics) and abiotic factors [Herrera et al., 1998; Janson & Chapman, 1999; Milton et al., 2005; Rathcke & Lacey, 1985; Rothman et al., 2015; Sakai, 2001; Van Schaik et al., 1993; Wheelwright, 1986]. As a result, individual food plants show variation in the *timing*, *frequency*, and *amount* of food produced [Anderson et al., 2005; Chapman et al., 1999b; reviewed in Sakai, 2001; Van Schaik et al., 1993].

Decades after Milton [1980] developed the ecological intelligence hypothesis, very few studies have directly quantified these complex variations in food production. Instead, ecological complexity has been estimated using indirect measures such as the size of the species' ranging area [Clutton-Brock & Harvey, 1980; Dunbar, 1998], which is not necessarily related to increased complexity of resource distribution. Although some researchers [e.g., Janson & Chapman, 1999] have recognized this shortcoming and have proposed and analyzed quantitative measures of food abundance, the majority of botanical studies to date typically describe phenological patterns at the population level [Chapman et al., 1999b; Hladik, 1988; Janson & Chapman, 1999; Knott, 2005; Van Schaik et al., 1993]. Long-term data on the temporal fruiting patterns of *individual* trees, the actual food sources that primates need to find in daily life, is still limited [but see Janzen, 1978; Milton et al., 1982; Momose, 2004; Struhsaker, 1997; Wheelwright, 1986].

**THIS STUDY**

Here we use analyses of long-term data on the spatio-temporal food distribution of the chimpanzee to search for predictable patterns with the purpose to develop a number of cognitive hypotheses that explain how chimpanzees (*Pan troglodytes*) can buffer periods of food scarcity, ameliorate their proposed dietary handicap, and "counteract" the ephemeral nature of high-energy food. To do so, we expand earlier quantifications of ecological complexity [Milton 1980, 1981, 1988] by investigating the temporal distribution of the availability of tropical fruit and young leaves in individual trees [e.g., Goné Bi, 2007; Matsumoto-Oda & Hayashi, 1999; Medlicott & Thompson, 1985]. We focus on the availability of young leaves, unripe fruit, and ripe fruit because they are known to be important food sources for chimpanzees (and other sympatric large-brained primate species), used to fulfill basic energy and protein requirements [Doran-Sheehy et al., 2006, 2009; Head et al., 2011; Hladik, 1977; Janson & Chapman, 1999; Rogers et al., 1990; Vogel et al., 2012; Wrangham et al., 1991]. We concentrate on the availability of large ripe fruit crops because the high

energetic reward of large amounts of ripe fruit [Doran-Sheehy et al., 2009; Irwin et al., 2014; Woodward, 1972; Marriott et al., 1981; Matsumoto-Oda & Hayashi, 1999; Medlicott & Thompson, 1985] is expected to counterbalance the cost of travel and vertical climb [Goodall, 1986; Hanna et al., 2008; Jurmain, 1997; Kraft et al., 2014; Pontzer & Wrangham, 2006]. Chimpanzees are heavy, and despite the fact that heavier primates are equally and more efficient at climbing and locomotion, respectively, absolute costs of climbing as well as non-energetic costs caused by an increased risk of falling are higher for heavier primates than lighter ones [Goodall, 1986; Hanna et al., 2008; Jurmain, 1997; Kraft et al., 2014; Pontzer & Wrangham, 2006]. In addition, large ripe fruit crops are expected to provide social benefits as they enable chimpanzees traveling in parties to stay together and reduce feeding competition or engage in beneficial social behavior [Chapman et al., 1995; Emory Thompson et al., 2014; Isabirye-Basuta, 1988; Wakefield, 2008; Wrangham, 2000]. Lastly, and most importantly, we focus on the availability of chimpanzee food in individual trees instead of tree populations.

The phenology data analyzed here spans ∼5–20 years of individual trees sampled at monthly intervals, and were collected from three tropical forests located in East, Central, and West Africa. Using this unique collection of long-term datasets, we quantify the difficulty of finding relatively energy-rich young leaves, unripe fruit, ripe fruit and, in particular, large ripe fruit crops. We first describe the probabilities of encountering trees in each of these three plant phenophases forest wide. Second, we describe the predictability of the *timing*, *frequency*, and *quantity* of ripe fruit production in individual focal trees.

**METHODS**
**Phenology Data Collection**

Data were collected at three long-term research sites in tropical forests in East, Central, and West Africa: (1) East Africa- a moist evergreen tropical forest, transitional between lowland rainforest and montane forest in Kibale National Park, Uganda [Kanyawara; Chapman & Lambert, 2000; Struhsaker, 1997]; (2) Central Africa- a tropical lowland rainforest in Loango National Park, Gabon [Loango; Head et al., 2011]; and (3) West Africa- a lowland tropical moist forest in Taï National Park, Côte d'Ivoire [Taï; Anderson et al., 2005; Vooren, 1999]. Kanyawara, Loango, and Taï contain 11, 11, and 12 primate species, respectively, each including the chimpanzee [Janmaat, 2006; Head et al., 2011]. Chimpanzee diet composition was assessed through direct observations of feeding behavior of habituated

East and West African chimpanzees, *P. t. schweinfurthii*, *P. t. verus* by the Kibale Chimpanzee Project [Isabirye-Basuta, 1988; Wrangham et al., 1991] and the Taï Chimpanzee Project [Boesch & Boesch-Achermann, 2000], during periods of 35 and 33 years, respectively. The central African chimpanzees, *P. t. troglodytes* in Loango were not habituated and their diet was therefore assessed through analysis of fecal samples and feeding remains over 5 years [Head et al., 2011]. These studies adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

The phenology data collection at each site is based on monthly leaf and fruit production checks of individually marked plants within the territories of the respective chimpanzee communities of species known to be consumed by chimpanzees. In Kanyawara transects were located inside the territory of one chimpanzee community, while in Taï and Loango, transects were longer in order to represent fruit availability in territories of four and three different communities, respectively. In general, monitored trees were selected based on evidence of reproductive maturity and a species-specific diameter at breast height (DBH) threshold (>10 cm). Since the majority of the monitored species were trees, we will subsequently refer to them as trees (instead of trees, figs, and lianas). The details of tree selection and phenology data collection are provided in previous studies [Kanyawara: Chapman et al., 1999b; Loango: Head et al., 2011; Taï: Anderson et al., 2005; Polansky & Boesch, 2013]. Observations of the monthly production of the three phenophases in individually marked trees were made using binoculars. Ripeness of fruits was estimated based on a combination of fruit size and color and whether there was evidence of partially eaten fruit or olfactory cues (e.g., ripened fruit on the ground). Determining when a fruit is ripe is sometimes difficult since not all fruits change color during ripening. As a result, for each fleshy-fruited species we defined fruit as ripe when they were first eaten by frugivores after they had reached full size, or when olfactory cues of ripe fruit were detected under the tree. For wind dispersed species, we considered a tree to have ripe fruit when dehiscent fruits opened and seeds could be found under the focal tree. In all three forests, we evaluated the relative abundance of the three phenophases on a production scale of 0–4. For example, in Kanyawara and Taï, the score 0 for ripe fruit corresponded to no observed ripe fruit, and 1, 2, 3, and 4 corresponded to 1–25%, 26–50%, 51–75%, and 76–100% of tree crown filled with ripe fruit, respectively [see Anderson et al., 2005; Chapman et al., 1992 for details]. In Loango, 1, 2, 3, and 4 corresponded to the median of 1–10, 11–50, 51–100, >101 ripe or unripe fruits measured on three separate branches, respectively [Head et al., 2011]. No young leaf

status (old or young) measurements were collected in Loango.

The monitored trees in Kanyawara, Loango, and Taï, belonged to 45, 38, and 107 species, respectively. As chimpanzees in Kanyawara, Loango and Taï were observed to feed on a total of 79, 75, and 150 species, respectively, our data included 50–70% of all chimpanzee food species in each forest (Table I). The Taï forest is part of the Liberian quaternary refugium and has high species diversity and the highest tree density of all three forests [Table I; Maley, 2001]. Tropical forest in west Gabon is described as a biodiversity hot spot [Hladik, 1978; Maley, 2001]. However, the Loango forest is a heterogeneous tropical rainforest which includes savannah and lowland swamp habitat, and therefore has a relatively low tree density [Head et al., 2011]. The Kanyawara forest is thought to have appeared later than the Taï and Loango forests (around 12,000 B.P.) and had the lowest tree density, with relatively few endemic species [Hamilton et al., 2001; Olupot et al., 1994].

## Data Analyses

We analyzed data from Kanyawara, Loango, and Taï from April 1990 to May 2011, January 2007 to December 2011, and January 1989 to December 2010, respectively. The data concerned monthly phenology checks on 1,304, 741, and 3,422 trees representing 45, 38, and 107 chimpanzee food species, respectively. In Kanyawara the number of individuals decreased to 263 from 1997 onwards. Observation periods were not equal for all trees, since some of them fell down, died or their location got lost due to political unrest; however, the trees had an average total study duration from first to last observation of 94, 38, and 80 months per individual for Kanyawara, Loango and Taï, respectively. We only considered phenology data from trees which produced food items that were known to be fed on by the chimpanzees ranging in the respective forests. However, for

**TABLE I. Tree and Species Distribution in Three Tropical Forests**

|  | Kanyawara | Taï | Loango |
|---|---|---|---|
| # Trees/ha (DBH > 10 cm) | 406 | 507 | 321 |
| # Chimpanzee fruit trees/ha | 237 | 325 | 162* |
| # Average sized chimpanzee feeding trees/ha (DBH > 67 cm) | 9.81 | 11.00 | 8.18* |
| # Chimpanzee fruit species | 75 | 150 | 79* |
| # Monitored chimpanzee fruit species | 45 | 107 | 38 |

*These numbers may be underestimations as diet composition was based on 5 years of observation and dung analysis of non-habituated chimpanzees, compared to 30 and 25 years of feeding observations for the Taï and Kanyawara chimpanzee communities, respectively.

calculating the encounter probabilities per distance traveled conducted in the Kanyawara forest, we analyzed data from all mature trees (DBH>10 cm) and lianas that were tagged along a 5.2 km long and 10 m wide transect and checked for fruit availability on a monthly basis for a period of 6 years (1990–1996). Since the chimpanzee territory in the Kanyawara forest is a mix of old growth and recently logged forest we made additional calculations for the encounter probability of chimpanzee food trees in the old growth forest compartments (K30 area) only. We decided to make calculation for all transects and old growth forest separately, as the differences could provide future insight in the effects of habitat disturbance on primate evolution. To calculate the proportion of trees belonging to species that were known to be consumed by Kanyawara chimpanzees out of the total number of trees encountered (Table I) we included transects from both areas. To calculate comparable measures for Taï and Loango we used data from separate tree density transects for which the methods are described in [Goné Bi, 2007; Head et al., 2011; Janmaat et al., 2013a; (Table I)]. We managed and analyzed data in R version 3.1 (R Development Core Team, 2015).

*The challenge of finding a tree with ripe and unripe fruit and young leaves*

To obtain insight into the challenge faced when searching for trees with edible food, we first estimated the probability of encountering young leaves and unripe and ripe fruit at the forest community level. We did this in two ways: (1) by aggregating the data over all time, per site, to describe the percentage of individuals showing each phenophase through time and (2) reporting the minimum and maximum of these percentages at the monthly resolution. We also provide a detailed description of the temporal availability of large ripe fruit crops. By combining the particularly extensive and long-term dataset on tree density, crown size measures, and ripe fruit availability in individual fruit trees in the old growth forest compartments of Kanyawara, East Africa, with diet information based on long-term studies [Isabirye-Basuta, 1988; Wrangham et al., 1991], we also carried out additional calculations on the encounter rates of (large) ripe fruit-bearing trees per distance traveled in this forest to gain more accurate insight into the relative challenges faced.

*The timing of food production*

The *timing* of food production was assessed in two ways. First, to understand whether the onset of ripe fruiting periods was predictably linked to particular months of the year, we simply present graphics showing the monthly phenological state of each individual tree over the entire study. Second, we investigate whether and how the fruiting of

individual trees were synchronized in time between conspecific trees at given locales, to gain insight into the probability that a primate will find conspecific trees that fruit simultaneously. To estimate this probability we abstained from calculating traditional measures of synchrony, such as the average correlation coefficient of the fruiting states of all possible pairs of trees within a species [Bjørnstad et al., 1999; Janmaat et al., 2013b]. Instead we measured synchrony as the proportion of trees that carried fruit within a species when at least one tree of that species carried fruit and was presumably at the start of, at the end of, or in the middle of a fruiting period. This definition of synchrony most closely matches the aims of our study: to understand how the probability of finding fruit on a given tree, conditional on there being at least one tree with fruit, varies across species, and whether variation of this probability could indicate a value of species-level knowledge. For calculating these synchrony levels we only included species for which we had data from at least five individuals with at least 12 months of data to calculate a species level mean. We calculated synchrony values for each phenotype separately and visualized the variation in inter-individual fruiting synchrony of ripe and unripe fruit and inter-individual flushing synchrony of young leaves. Finally we compared how synchrony levels of ripe fruit varied among species in all three forests.

*The frequency and amount of ripe fruit*

When chimpanzees search for ripe fruit in tree species that have just started their fruiting season, do all trees within that species at that locale have a similar probability of bearing fruit and will they produce the same amount? To gain insight into the predictability of ripe fruit production frequencies and amount, we plot the histories of monthly ripe fruit production and amount in individual fruit. Furthermore, we investigate whether having tree specific knowledge on the probability of finding fruit is beneficial for all fruit species or only for some. For this, we visualized the variation in the total number of months that ripe fruit was found present in conspecific individuals and compare the amount of variation among species.

To calculate variation in the number of months that trees bore ripe fruits, we only included species that had data from at least five tree individuals. To investigate the variation in fruit production amount among individual trees we first determined the total number of months that each individual tree was observed to bear ripe fruit. We then calculated the percentage of these months that the tree had a fruit production class of two or more, as this corresponded to a crown that is more than half filled with fruit and was thus assumed to be particularly attractive for a chimpanzee and potential party members. To get a reasonable representation of the productive output of

trees and the variability across species, we only included trees that produced ripe fruit for a minimum of 5 months, and species that had data from a minimum of five trees. The analyses of fruiting frequency and amount were both restricted to a selection of three very long uninterrupted periods of data collection. These periods concerned 76, 67, and 144 months for Kanyawara, Loango, and Taï, respectively.

## RESULTS

### Availability of Young Leaves, Unripe and Ripe Fruit, and Full Crowns

We found substantial fluctuations in the availability of young leaves, unripe fruit and ripe fruit over time, with ripe fruit being the rarest food source of these phenophases in all three forests (Suppl. Tables S1–S3). Ripe fruit had the lowest probability of being present in trees at any moment in time (Fig. 1; Suppl. Tables S1–S3). Based on all phenology checks (425,836 observations), trees carried ripe fruit in 3.4%, 10.9%, and 8.6% of the observations in Kanyawara, Loango, and Taï, respectively. The lowest percentages of trees bearing ripe fruit were observed in August 1997 in Taï and April 2007 in Loango, when the percentages dropped to 0.3% and 1.1%, respectively (Suppl. Table S1). In Kanyawara the percentage of trees bearing ripe fruit was only 0.08% in April 1990 and dropped to zero several times after 1997 (partially resulting from the fact that the number of monthly checked chimpanzee food trees

dropped in 1997; Suppl. Table S1). While between-site comparisons could be influenced by differences in classifications, we found that trees with a ripe fruit production score larger than two were at least nine times as rare as trees bearing fewer fruits for all three forests (Fig. 1). In Kanyawara an abundance score of three or four for ripe fruit was only observed six and three times out of 4,064 observations of trees bearing ripe fruit, respectively, (Fig. 1).

### Encounter Rates of Ripe Fruit and Large Ripe Fruit Crops per Distance Traveled

In all three forests, more than 50% of all encountered trees belonged to a species that chimpanzees feed on (Table 1). For example, in Kanyawara 58% of mature trees (1,196 out of 2,070 trees with a DBH >10 cm) that were located along the 5.2 km long old growth and recently logged forest transects (all transects) belonged to chimpanzee food species (based on 25 years of feeding observations of the Kanyawara chimpanzees; $N_{\text{food species}} = 75$). The research assistants that walked these transects for 76 months, totaling 395 km, encountered on average one ripe fruit-bearing chimpanzee food tree every 97 m, while passing 37 other reproductively mature trees (of all species) along the transect. In the most fruit-scarce month they found one ripe fruit-bearing chimpanzee food tree every 1,730 m, while passing 687 mature trees. When we considered the availability of large ripe fruit crops (i.e., chimpanzee food trees with a DBH equal to or larger than the average size of a Kanyawara chimpanzee feeding tree (67 cm; [Potts, 2008] and a crown with at least 50% of the crown filled with ripe fruit), the observers found on average only one such tree every 21 km, while passing 7,992 mature trees. In the most fruit-scarce month no trees with large ripe fruit crops were encountered in the entire transect.

If only old growth forest compartments are considered, spanning 2.4 km long transects, encounter rates of ripe fruit-bearing trees increased slightly. Out of 1,156 trees, 62% belonged to species that were known chimpanzee fruit food. Furthermore, observers found on average one ripe fruit-bearing chimpanzee food tree every 79 m, passing 37 other mature trees (of all species), and one tree with a large ripe fruit crop every 10 km, passing 4,742 other mature trees. In the most fruit scarce month no trees with ripe fruit crop (small nor large) were encountered in the entire transect. The encounter rates fluctuated strongly in time and were substantially higher for unripe than for ripe fruit crops (Fig. 2; Suppl. Fig. S1).

### The Timing of Ripe Fruit Presence

We found some plant species produced ripe fruit at predictable months (Fig. 3a); however, a high level
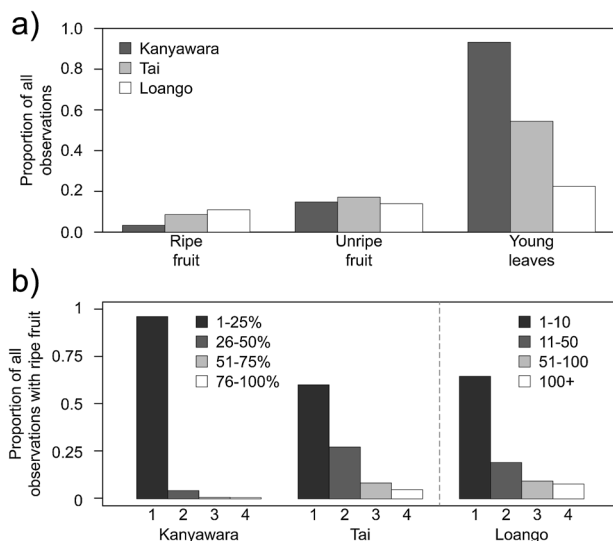


Fig. 1. The availability of young leaves, unripe fruit and ripe fruit in the focal phenology trees situated in three chimpanzee territories. (**a**) shows the proportion of all observations amongst trees that were found to bear ripe fruit, unripe fruit, young leaves, or none of the above (N = 425,836). (**b**) focuses on the ripe fruit phenophase, showing the proportion of observations in each of the four ripe fruit production scores given that ripe fruit was observed.
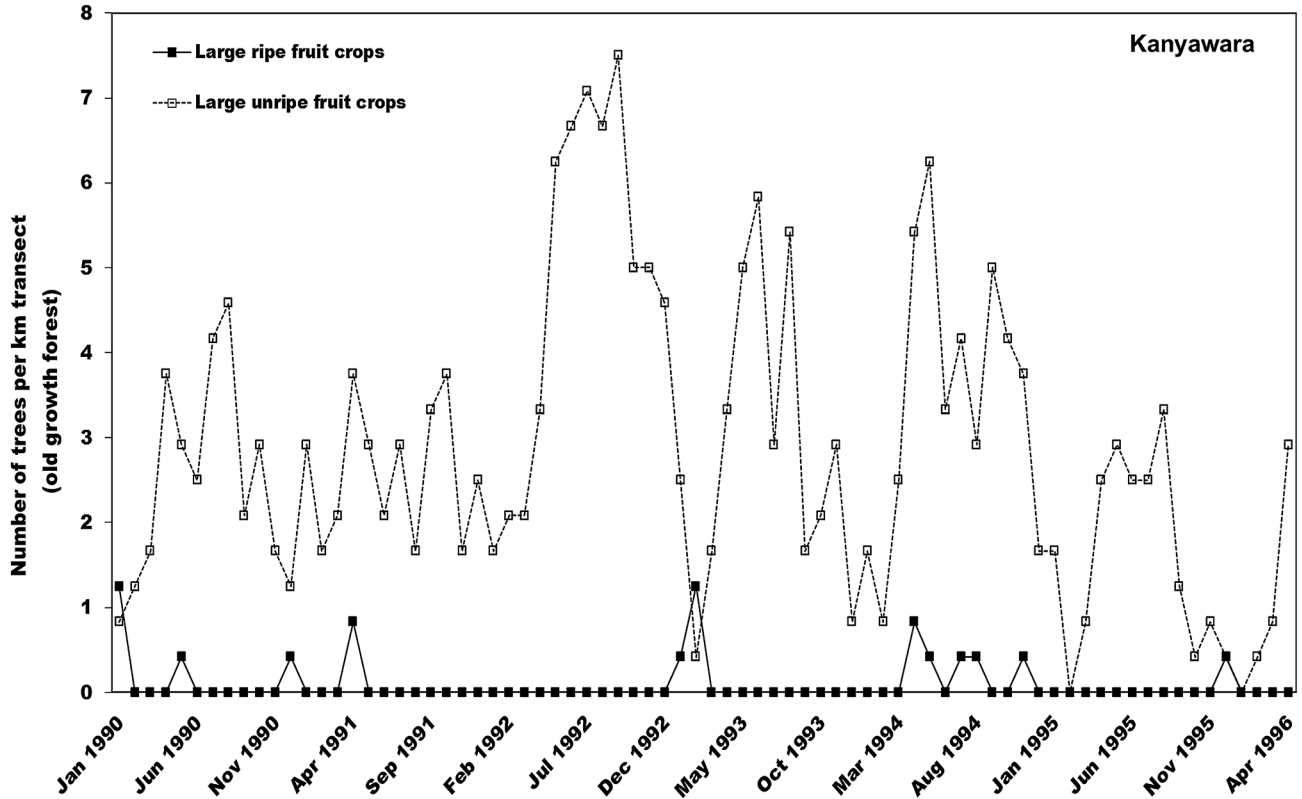
Fig. 2. The encounter rates of large ripe and unripe fruit crops in old growth Kanyawara rain forest. The open and filled squares represent the average number of trees found along 1 km of transect in the old growth forest of the Kanyawara chimpanzee community that bore a large unripe or ripe fruit crop, respectively. Trees with large fruit crops are defined as trees with a trunk size equal or larger than the average feeding tree of Kanyawara chimpanzees and a crown that is more than 50% filled (rank core >2) with ripe fruit.

of variation in the timing of fruit production was detected within species. For example, *Sacoglottis gabonensis* trees in Taï, which appear to bear ripe fruit predictably once a year in September, had a fruiting peak in April 2009 and in February 2010. Similarly *Uvariopsis congensis* trees in Kanyawara, which appear to bear ripe fruit once a year in June had a fruiting peak in December 1991 (Fig. 3b).

When we plotted the fruiting patterns over time of all monitored species, we observed species which produced ripe fruit in a highly synchronous manner, with a large proportion of individuals bearing ripe fruit in the same month (e.g., *Coula edulis* as shown in Fig. 3a). In other species, conspecific trees either produced fruit in different months or failed to produce during certain seasons or years, resulting in low levels of synchrony or asynchrony in fruit production (e.g., *Ficus sansibarica* as shown in Fig. 3c). To get an indication of how rewarding the use of the phenomenon of synchronous fruiting could be to the chimpanzees, we calculated synchrony levels across all species, phenotypes, and forest sites. These levels show large variation (Fig. 4; Suppl. Figs. S2 and S3). In all three forests, species had months in which the probability of finding ripe fruit in conspecific trees was extremely high and months in

which this probability was extremely low (Fig. 4). For example, *Vepris nobilis*, *Nauclea xanthoxylon*, and *Pycnanthus angolensis* had maximum and minimum probabilities of 1, 1, 1 and 0.01, 0.02, and 0.04, respectively. This suggests that ripe fruit presence in a single tree does not indicate the presence of ripe fruit in other conspecific trees at all times. It does so only in certain months. Other species had lower levels of variation, such as *Fagaropsis angolensis* in Kanyawara, for which levels ranged from 0.33 to 0.063 (Fig. 4). The median probabilities for all species were relatively low in all three forests. The maximum and minimum median species-specific probabilities at Kanyawara, Loango, and Tai were 0.6, 0.5, and 0.5 and 0.006, 0.09, and 0.08, respectively (Fig. 4), suggesting that the presence of ripe fruit in a single tree is a good indicator for the presence of ripe fruit in other conspecific trees in some species, but not in all. Comparisons of the range of this synchrony metric across species by forest indicated that each forest had a comparable range of intra-specific probabilities of finding ripe fruit (Fig. 4). However, median probabilities did differ between forests with Loango having on average the highest median probability of finding ripe fruits in conspecific trees in fruiting periods (Kruskal–Wallis $\chi^2 = 12.05$, $df = 2$, $P = 0.0024$,
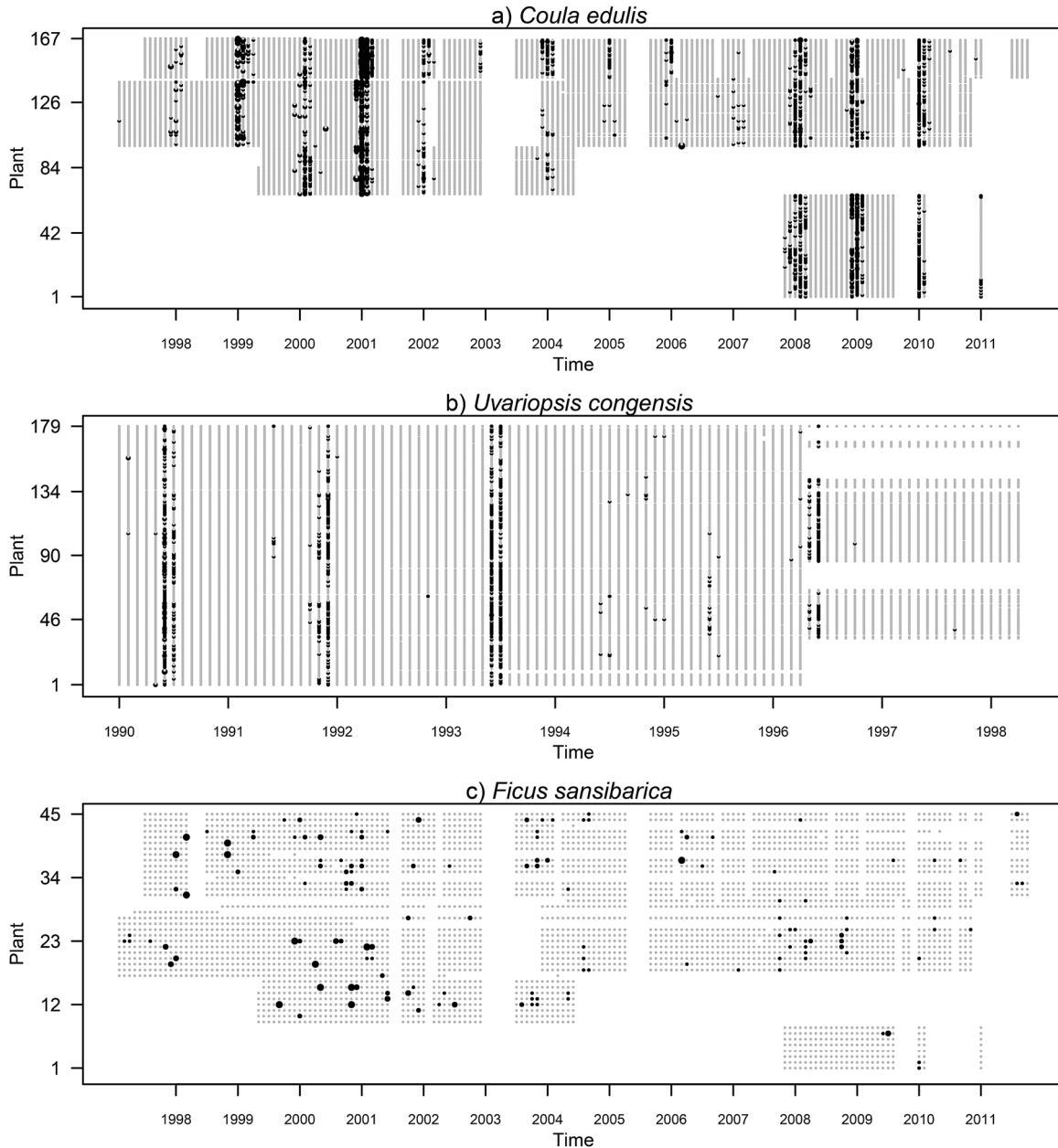
Fig. 3. The timing of ripe fruit availability in individual trees. Examples of frequency and intra-specific synchrony (see Fig. 4) of ripe fruit availability of individual trees. Black and gray dots represent ripe fruit presence and absence, respectively; no dot represents missing data. The size of the dots are propotional to the fruit production scores; blank white spaces denote no data collected. (**a**) shows the fruiting pattern for *Coula edulis* in Taï forest, for which it is relatively easy to predict which individual will bear fruit in season (high synchrony level) and in which month the season starts (fixed timing). (**b**) shows the pattern for *Uvariopsis congensis* in Kanyawara forest, for which it is relatively easy to predict which individual will bear fruit in the season (high synchrony level), but where the timing of the season is less predictable (fluctuating timing). (**c**) shows the pattern for *Ficus sansibarica* in Taï forest, in which it is difficult to predict which individuals will fruit in which month (asynchronous and fluctuating timing).

$N_{\text{species\_kanyawara}} = 24, N_{\text{species\_loango}} = 36, N_{\text{species\_tai}} = 74$, $\text{median}_{\text{kanyawara}} = 0.13$, $\text{median}_{\text{loango}} = 0.22$, $\text{median}_{\text{tai}} = 0.19$). Synchrony levels of some species occasionally changed through time and space, with proportions of trees bearing ripe fruit within fruiting periods being different across years (Suppl. Fig. S4) or between forests (Fig. 5).

## The Frequency of Ripe Fruit Presence

Fruiting periods of individual species on a population level vary in frequency. Some species bear fruit multiple times a year (continuous), twice a year (bi-annual), once a year (annual), or every other year or more (supra-annual; Suppl. Fig. S5). On an
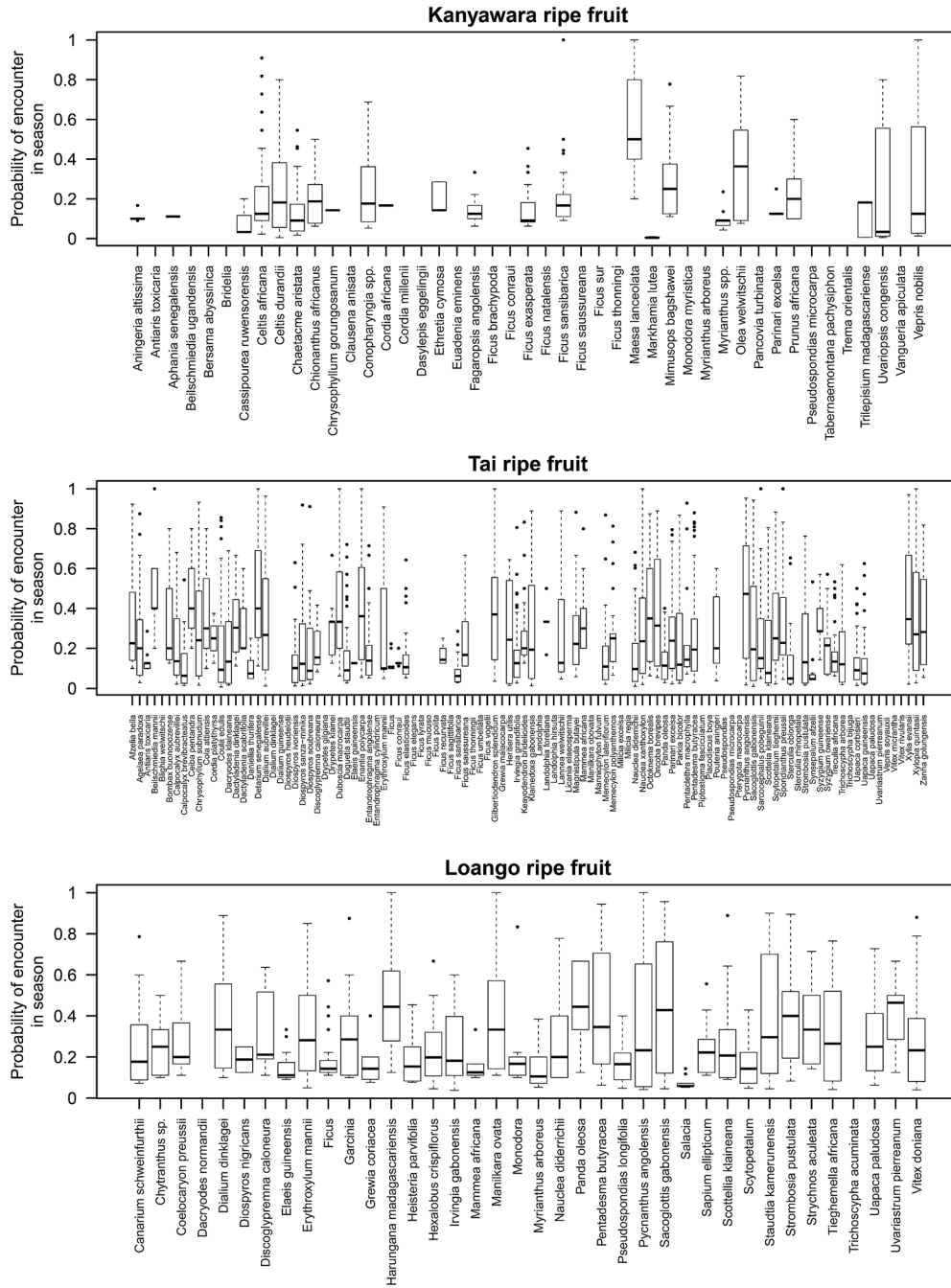
Fig. 4. Probability of encountering other ripe-fruit bearing trees in season (when at least one conspecific tree bears ripe fruit) by species at each of the three sites. At least five trees per species were monitored. Bars represent median values of the probabilities; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 times the interquartile range; Points represent outliers.

individual level, we found that ripe fruit production showed high levels of inter-individual variation in the number of times that fruit was produced and the number of months it persisted. For example, in Taï, one individual *Treculia africana* bore ripe fruit for 17 months out of 48 consecutive months, while another conspecific tree fruited only 3 months within the same period (Suppl. Fig. S6). Similarly, in

Kanyawara, in *Ficus sansibarica* one individual bore ripe fruit for 28 months out of 132 consecutive months, while another tree fruited only 4 months within that same period (Fig. S6). When we considered a large number of species with all trees monitored for similar time durations we found that for all three forests, some species had substantially more inter-individual variation in the number of
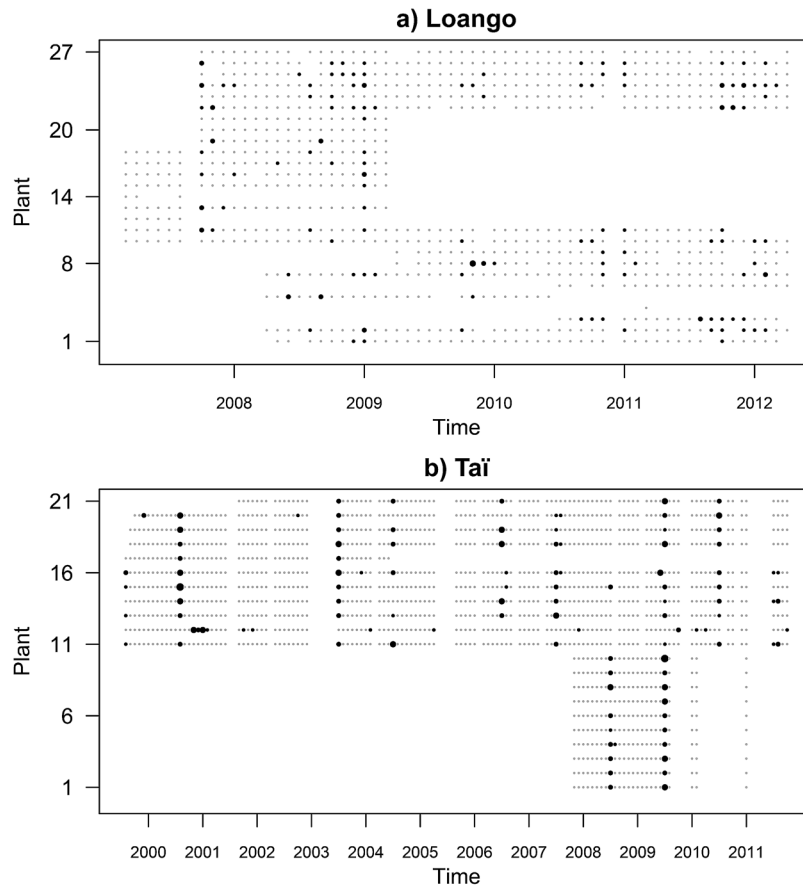
Fig. 5. Ripe fruit patterns for *Erythroxylum mannii* in two forests, (**a**) Loango and (**b**) Taï, illustrating that the same species can have contrasting levels of intra-specific synchrony. Black and gray dots represent ripe fruit presence and absence, respectively; no dot represents missing data. The size of the dots are proportional to the fruit production scores; blank white spaces denote no data collected.

months that ripe fruits were produced than other species (Fig. 6).

### The amount of ripe fruit

The number of months that individual trees were scored as having more than 50% of their crown full of ripe fruit (production score >2) varied between years (e.g., *Xylia evansii* in Fig. S5b). The proportion of months in which the ripe fruit production score was larger than two, out of all the months that a tree was observed to bear ripe fruit, also varied between individual trees (Fig. 7). For example, in *Sarcocephalus pobeguinii* in Taï, one individual produced more than half of what it maximally could (production score >2) 4 out of 53 months, while another tree only produced small amounts of fruit (all scores ≤2) within that same period. However, very few tree individuals produced only large or small amounts of fruit for the entire period (Figs. 3 and 5; S4–S6). In Loango and Taï, some species had substantially more inter-individual variation in the proportion of months with a high productive output (score >2) than other species (Fig. 7). For Kanyawara, variation across species was low as trees rarely had more than

50% of their crown filled, even in the old growth forest compartments (Fig. 7).

## DISCUSSION

### The Challenge of Finding a Tree With Ripe and Unripe Fruit and Young Leaves

Due to a combination of fruit size, physical protection, taste, toxicity, and inaccessibility, primates only feed on a fraction of the many hundreds of fruit species in a tropical forest [Janson & Chapman, 1999]. The Taï forest, for example, harbors an estimated 1,300 plant species [Guillaumet, 1967] from which only 150 species produce fruits that are known to be consumed by three neighboring chimpanzee communities [Goné Bi, 1999; KJ unpublished data]. Our study, however, reveals that plant species fed on by chimpanzees are surprisingly abundant in space. In all three forests more than half of all encountered trees belonged to a fruiting species that chimpanzees were known to consume. A chimpanzee's challenge is therefore not so much to find plants that belong to an edible species, but to find
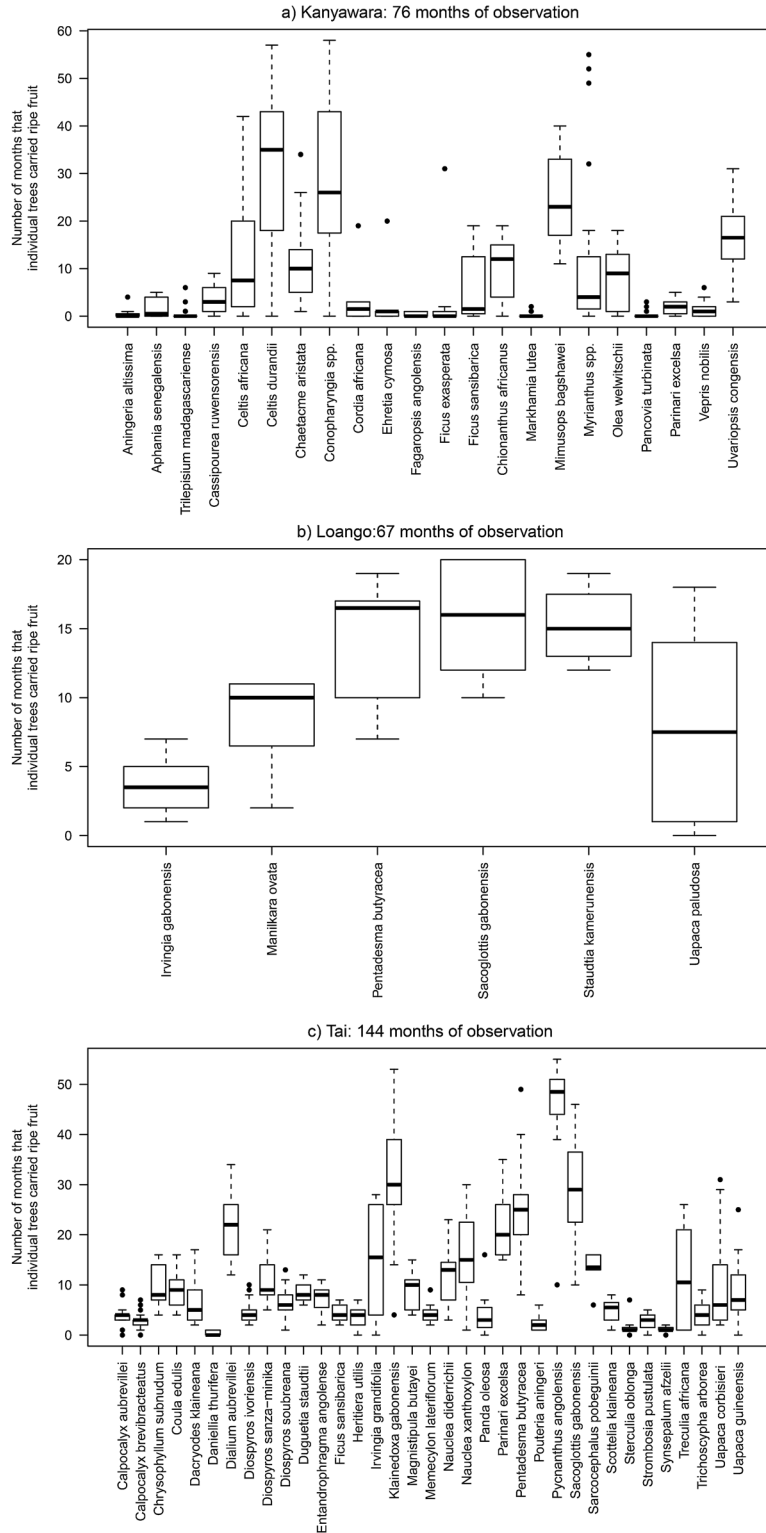
Fig. 6. Inter-individual variation in ripe fruit production frequencies in individual trees. The number of months that individual trees bore ripe fruit within a consecutive uninterrupted observation period of (**a**) 76 months in Kanyawara, (**b**) 67 months in Loango, and (**c**) 144 months in Taï forest. At least five trees per species were monitored. Bars represent median values of the proportions; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 times the interquartile range; Points represent outliers.
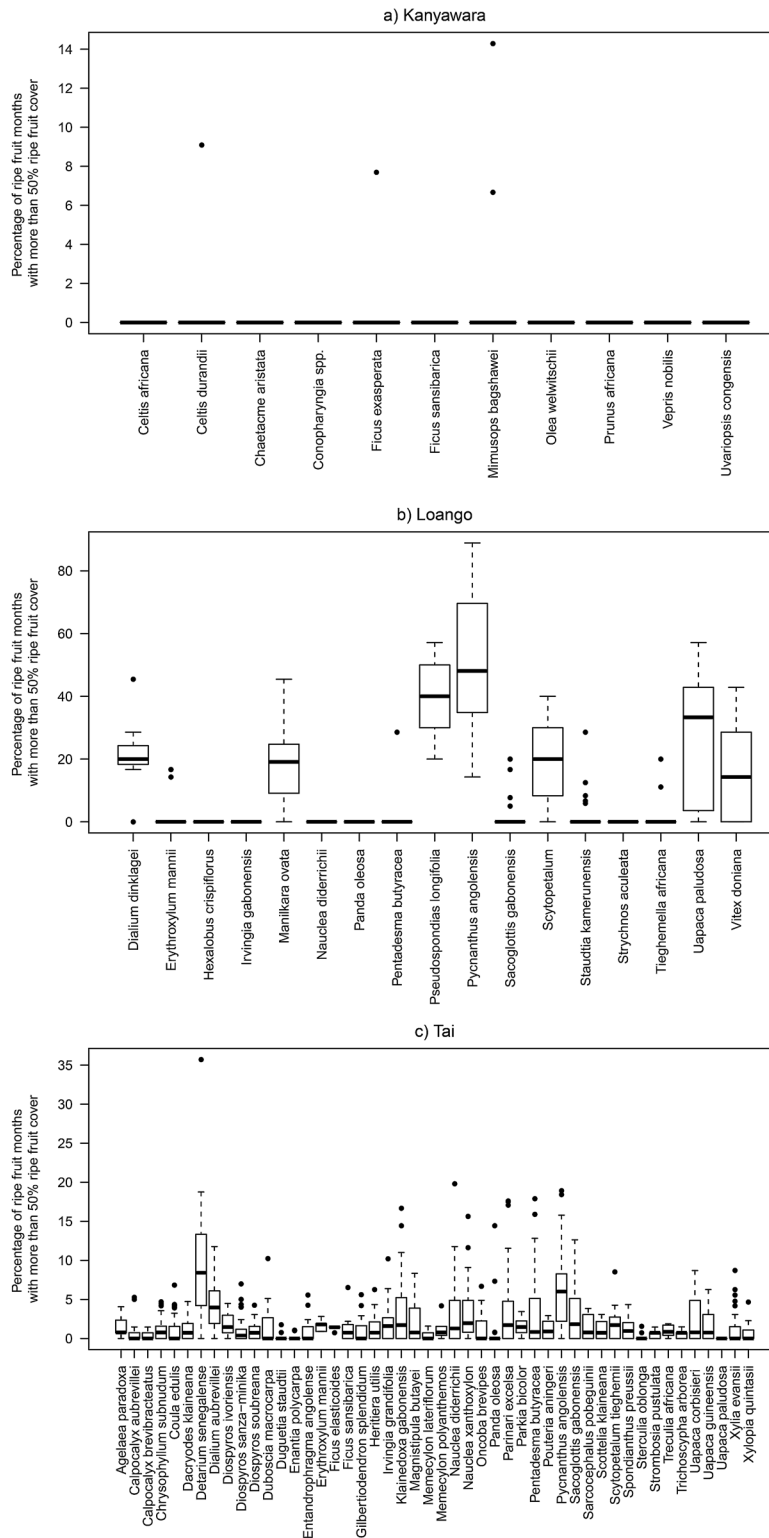
Fig. 7. Inter-individual variation in the amount of ripe fruit produced during ripe fruiting bouts. The percentage of months individual trees had a fruit production score larger than two out of all the months individual trees bore ripe fruit. Each species includes data on at least five individuals that bore fruit for at least 5 months. Bars represent median values of the proportions; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 times the interquartile range; Points represent outliers.

those that actually produce food, in particular those that produce ripe fruit at the relevant time. Similar to Milton's [1980] observations in the neo-tropical forest in Panama, ripe fruit in the forest ecosystems observed here was the most ephemeral food source, with the lowest encounter rates, compared to young leaves and unripe fruit. Finding ripe fruit can be inferred to be the most challenging, absent of the chimpanzee's use of any sensory cues. Observations of trees with more than half of their crown filled with ripe fruit were particularly rare, being at least nine times as rare as trees with lower productive outputs.

The encounter rates observed when travelling on the straight-line Kanyawara transects allow us to better understand the difference between the challenges of finding ripe fruit when a chimpanzee would have no knowledge compared to perfect knowledge. As a baseline, we can calculate the encounter rate when a chimpanzee lacks any knowledge and simply walks in straight lines through the forest until it spots a tree. Search by straight-line movement has been shown to be the optimal search strategy when food patches are randomly distributed in space and their locations are not memorized [Bartumeus et al., 2005; Riotte-Lambert et al., 2015]; the long straight-line segments of a Lévy walk have been argued to be the optimal search strategy when food is heterogeneously distributed and difficult to detect [Edwards et al., 2007; Viswanathan et al., 1999; but see Benhamou & Collet, 2015]. If we assume that the chimpanzees have no knowledge and use such a straight-line search strategy with a 5 m detection distance (i.e., the distance from the middle of a transect line to its edge), we find that encounter rates of trees with ripe fruit crops were substantially lower than that of trees with unripe fruit crops. During the whole year, a chimpanzee would on average only have had to travel 97 m to find one tree bearing ripe fruit; however, in fruit scarce months this average distance increased nearly 20 times (to 1,730 m), with hundreds of trees passed before encountering one single ripe fruit-bearing chimpanzee food tree in the territory, while none were encountered in the old growth forest compartments. When we considered only trees with ripe fruit crops that were large (meaning a tree that was at least as large as an average chimpanzee feeding tree, with a crown that was half or more filled with fruit), encounter rates were extremely low, reaching zero in certain months. Chimpanzees traversing transects located in old growth forest compartments would encounter such a large fruit crop on average only once every 10 km, or as little as once every 21 km if they traverse all transects (in old growth and logged forest). Considering that the average day journey length of chimpanzees in the Kanyawara forest is 2.1 km [Pontzer & Wrangham, 2004], this encounter rate can be translated into an average rate as low as one tree with a large crop of ripe fruit per 10 days.

Unfortunately, we were unable to make similarly detailed calculations for the Taï and Loango forests, since phenology trees at these sites were selected and did not represent all food trees on a transect as was the case in Kanyawara between 1990 and 1996. However, transect data revealed that trees larger than the average feeding tree size of Kanyawara chimpanzees (67 cm) were of similar density [9.8, 8.2, and 11.0 trees ha$^{-1}$, in Kanyawara, Loango, and Taï, respectively; Potts et al., 2011]. In addition, the overall proportion of phenology trees carrying ripe fruit and its variation was comparable, although slightly higher in Taï and Loango compared to Kanyawara (Fig. 1; Suppl. Table S1). Observations of high fruit production scores were rare in all three forests (Fig. 1).

Based on these similarities we hypothesize that chimpanzees in West, Central, and East Africa are all considerably more challenged in finding ripe fruit crops during certain months of the year compared to unripe fruit. For Kanyawara this difference can be 17 times more. In addition, we hypothesize that they are more challenged in discovering large ripe fruit crops—those which are sizeable enough to feed an average sized chimpanzee party—compared to trees with any amount of ripe fruit. For Kanyawara this difference can be 216 times more. Indeed, both challenges appeared considerably larger for the Kanyawara chimpanzees, having several periods of ripe fruit absence (Fig. 2; Table S1), which could potentially explain the lower levels of dyadic associations reported in Kanyawara female chimpanzees compared to those in Taï [Wittiger & Boesch, 2013]. On the other hand, the lower diversity of tree species in Kanyawara compared to Taï (the Liberia refugium; Booth, 1957) should make it easier to identify and locate trees belonging to food species, which could potentially limit the complexity and decrease the cognitive challenge [Janson & Chapman, 1999].

If we assume that a chimpanzee has perfect knowledge the following challenge estimation can be made. For this we consider the encounter rate of one ripe fruit crop per 21 km $^{*}$10 m (the width of a transect) found at Kanyawara, which translates into ca. 5 large ripe fruit crops/km$^2$. A simple simulation study distributing five trees randomly within 1 km$^2$ 1,000 times, and calculating the mean inter-individual separation distance for each replicate, shows that the average nearest neighbor distance given this ripe fruit tree density is approximately 281 m. Thus a chimpanzee who travels 2.1 km per day [Pontzer & Wrangham, 2004] and has perfect knowledge of the locations of all fruit bearing trees can visit approximately seven trees with a large fruit crop per day, dramatically more than approximately one per every 10 days without this knowledge. How this encounter rate differs when trees are clustered (patchily distributed) remains to be investigated, but will

depend on within and between patch distance variation.

Despite prior research that revealed that wild chimpanzees do use advanced cognitive abilities during foraging, and have spatio-temporal knowledge on which trees have produced fruit at the moment of travel [e.g., Ban et al., 2014; Janmaat et al., 2013b; Sayers & Menzel, 2012], a chimpanzee's knowledge is however, unlikely to be perfect, as fruiting states change continuously. To fully estimate the chimpanzee's challenge we therefore need detailed information on the chimpanzee's knowledge about: (1) how many tree locations are remembered exactly and for how long; (2) how accurate chimpanzees are in predicting the first day of edibility and the last day before depletion [Van Roosmalen, 1985]; (3) what their sensory detection distances are and how sensory cues and memory are integrated. Unfortunately, this information is still lacking, which makes it currently impossible to estimate the chimpanzee's absolute challenge. However, the encounter rates presented in this study do provide a clear idea of the substantial gains in foraging efficiency that can be obtained by cognitive movement and the relative difficulty that chimpanzees face in comparison to primates that can also feed on less ephemeral unripe fruit and trees with small crops The study also indicates the severity of fruit scarce periods in which not one single tree with ripe fruit was found in a 5.2 km transect. In such times, even a chimpanzee with perfect knowledge will not find fruit unless it explores larger areas, or a larger variety of food species than investigated in this study.

## Once a Tree Is "Known" to Produce Fruit, When Will it Produce Ripe Fruit Again?

In all three forests, we detected conspecific trees that produced ripe fruit during predictable months of the year. However, substantial variations in fruiting months were found, making it difficult for chimpanzees to rely on monitoring of photoperiods, climatic variables, or particular orders in fruiting seasons.

Earlier studies [Janmaat et al., 2012, 2013b] in Taï and Kanyawara forest suggest that chimpanzees and gray-cheeked mangabeys (*Lophocebus albigena*), make use of the phenomenon of synchronous fruiting to predict the moment in time that a "known" tree bears ripe fruit. They used the detection of a ripe fruit bearing tree to predict ripe fruit availability in a large number of conspecific trees. Comparable levels of ripe fruit synchrony across the three forests, found in this study, suggest that Taï and Kanyawara are not exceptional and that the use of the phenomenon of synchronous fruiting could be employed by primates from Loango forest as well as those in other African rainforests.

The substantial variation in synchrony levels across species in each forest suggests a possible benefit to chimpanzees in learning species-specific differences in synchrony levels. Evidence for such learning abilities has been shown in Taï chimpanzees [Janmaat et al., 2013b]. The probability that the chimpanzee inspected a tree, that is, raised the head and gazed in the direction of a tree crown, was significantly higher for species with higher mean intra-specific synchrony values, having a larger proportion of trees bearing fruit, even when controlling for fruit availability [Janmaat et al., 2013b]. These findings were supported by a captive study that showed that chimpanzees are able to discriminate between relative frequency distributions (ratios) of two different food types [Rakoczy et al., 2014]. It remains to be investigated what other primate species have the cognitive abilities to learn differences in synchrony levels, and whether they are aided by an ability to generalize or classify trees in species with high versus low levels of synchrony.

It is difficult to judge which species are worthwhile for primates to inspect once one or several fruit-bearing tree are found within that species. What can be said is that gray-cheeked mangabeys were shown to use fruiting synchrony to find fruits of *Uvariopsis guienensis* [Janmaat et al., 2012] which in this study has a median and maximum synchrony probability of only 0.034 and 0.8, respectively. We found that 88%, 100%, and 100% and 13%, 31%, and 49% of the species have a similar or higher median and maximum synchrony probability than *U. guienensis* in Kanyawara, Loango, and Taï, respectively. This suggests that the number of species that can be found by a synchrony-based search strategy could be substantial.

However, we observed strong fluctuations in the monthly percentage of trees that bore fruit within the same species across years and between forests. These findings are congruent with results from earlier studies [Chapman et al., 1999b; Janmaat et al., 2012; MacKinnon, 1974], which indicated that synchrony levels differed between separate parts of a home range or a forest. MacKinnon [1974] suggested that these spatial differences in synchrony levels could be attributable to heavy local rains, which kill both the flowers and pollinators responsible for fertilizing them, inhibiting fruit production locally. Similarly, we found fluctuations in the monthly percentages of trees that bore fruit within species within years depending on whether observations occurred in the beginning, middle or end of the season.

Considering these spatio-temporal fluctuations, we argue that it is unlikely that chimpanzees rely on a synchronicity-based search strategy that is genetically "hardwired," but that these strategies need to be learned to lead to efficient foraging. We hypothesize that such learning is flexible, enabling primates to update themselves on synchrony levels by "sampling" the encounter rates of fruit-bearing trees at the start of each season, rather than remembering

species-specific levels from previous seasons or feeding locations [Janmaat et al., 2012].

## Once a Tree Is "Known" to Produce Ripe Fruit, How Often Will it Produce and How Much?

Considering the large variation in fruiting frequencies by individual trees during the fruiting time period of the species, we hypothesize that chimpanzees remember fruit production histories of individual trees to avoid travel towards trees that are likely to be empty. However, since some species showed substantially higher levels of inter-individual variation than others, it is unlikely that the advantages of such information will be similar for all tree species. Some species show such small variation in fruiting frequencies that remembering the histories of individual trees may not be worth the effort. Another factor that could result in a low benefit of remembering fruiting histories of individual trees is the species' spatial distribution. If trees are spatially clustered, it could be as efficient to simply remember the fruiting history of a forest patch [Normand et al., 2009]. Such advantages could potentially explain the higher performance of human and non-human primates in short-term memory tasks when locations are clustered in space, compared to when they are not [De Lillo et al., 1997; De Lillo & James, 2012].

We found that within years certain trees had full crowns for a substantially larger proportion of ripe fruit bearing months than others. The inter-individual variation was however weaker than expected, with very few individuals producing only large or only small fruit crops. Moreover, the number of months that the same trees had high fruit production scores differed between years. This can be explained by the possibility that crop size is not only determined by the age of the plant and its micro-habitat conditions (e.g., soil quality), but also by temporal changes in weather conditions and fruit foragers' densities [e.g., Houle, 2004; Van Schaik et al., 1993].

It is difficult to predict what frequencies and amounts of fruit production make it worthwhile to remember and revisit a "known" tree to check whether fruits have been produced. Is a tree that produced a large fruit crop five out of ten fruiting seasons worth a targeted approach or does the tree need to have had a full crown at least eight out of ten seasons before the chimpanzee should invest time in approaching a tree? The answer to these questions lays in the design of quantitative models that predict optimal inspection frequencies of particular trees and the data to test them. The first step for such designs lays in knowledge of the natural range of fruit production frequencies, such as provided here. We argue that testing such models can be promising as behavioral data already suggest that chimpanzees do not just approach and inspect any tree, but especially the large trees that are known to grow more fruit for longer time periods [Anderson et al., 2005; Janmaat et al., 2013b] and thus have an increased chance of bearing fruit at any moment in time.

Extensive observations of habituated chimpanzee females in the Taï forest, however, indicate that inter-annual revisiting and goal-directed monitoring of feeding trees is extremely rare when territories are large and tree density and diversity is high [Janmaat et al., 2013a,b]. Out of 268 trees that were fed on by one female chimpanzee in Taï in 2009, only 20 and 18 trees were fed on in the same months and fruiting seasons in 2010 and 2011, respectively [Janmaat et al., 2013b]. Out of 118 trees that were fed on by a second focal female in 2009, none were fed on in the same months of 2010, while other trees of the same species were producing fruit. In addition, most trees were inspected for fruit en route, and only 13% were approached in a goal-directed manner [Janmaat et al., 2013a]. This suggests that targeted inspections by use of an across-seasonal memory of fruiting histories is likely restricted to a very small number of trees that reliably produce large fruit crops. Evidence for an across-seasonal memory was found in Taï chimpanzees [Janmaat et al., 2013a]. Chimpanzee females were more likely to inspect trees that had large fruit crops and were revisited repeatedly within the fruiting season of the previous year [Janmaat et al., 2013a]. In captive studies chimpanzees have been shown to remember the locations of tools over a period of 3 years, after only four exposures to the respective location [Martin-Ordas et al., 2013].

Based on this combination of empirical evidence for the chimpanzees' use of distant past information and the large variation in fruit production histories observed in this study, we hypothesize that chimpanzees will target their travels to monitor a small number of trees that have a high probability of producing large fruit crops compared to other conspecific trees, yet only for those species that show a relatively high inter-individual variation in fruit production. In other words, we do not expect the chimpanzees to remember the fruiting histories of individual trees in all species and expect an interactive effect of species-specific variation in fruit production and the tree-specific fruit production history on the inspection probability. To select promising trees, chimpanzees should store and retrieve information on fruiting histories over a large number of years, especially when we consider that some inter-fruiting intervals are greater than 6 years (e.g., *Parinari excelsa* in Kanyawara, within 132 months of consecutive observation).

## What Cognitive Abilities Could Facilitate the Localization of Ephemeral Food and Maximize Energy Intake When Times Are Lean?

One of the proposed energy rewarding behaviors that could help large-brained primates, like great

apes, to buffer periods of food scarcity is extractive foraging with tool use [Melin et al., 2014; Van Woerden et al., 2010, 2012]. Our extensive assessment of the spatio-temporal complexity and predictability of chimpanzee plant foods allows us to propose an additional important set of flexible behaviors that large-brained primates can use to maximize their energy intake when times are lean. Using chimpanzees as a model species, we propose that large-brained primates can use behavioral strategies to outcompete sympatric animals in exploiting easily accessible energy-rich and ephemeral foods, such as ripe fruit, by optimizing their arrival and return time. It could be argued that for chimpanzees the timing of arrival is of little importance, as they can simply chase away competitors from ripe fruit sources through direct (contest) competition, likely facilitated by a larger body size [Anderson, 1984; Houle, 2004; Houle et al., 2010; Milton, 2003; but see Zuberbühler & Janmaat, 2010]. However, such chases will not stop competitors from consuming all ripe fruit prior to the arrival of chimpanzees. Hence, we hypothesize that chimpanzees can still benefit by actively reducing indirect (scramble) competition for dispersed and ephemeral foods through adjusting their timing of arrival. Chimpanzees could employ cognitive strategies that enable them to forage more efficiently, either by facilitating early discoveries of large amounts of energy-rich foods, or by optimizing return times to previous feeding locations.

A variety of studies have found evidence that primates use spatial memory to relocate ephemeral food sources and can even keep track of changes in fruit availability [Ban et al., 2014; Janmaat et al., 2006a,b; reviewed in Janson & Byrne, 2007; Janson & Chapman, 1999; Martin-Ordas et al., 2010; Noser & Byrne, 2015; Sayers & Menzel, 2012; Zuberbühler & Janmaat, 2010]. Barton [1998, 2004] furthermore suggested that the advanced visual specialization of primates, despite short average detection distances within dense forest vegetation, facilitates ripe fruit discovery [Janmaat et al., 2013a; Janson & Di Bitetti, 1997]. However, knowledge on what other cognitive strategies are used to discover newly produced and ephemeral food, and optimize the time of return to this food, is limited and in need of further investigation.

Based on the results of this study, we hypothesize that to improve the efficiency of fruit discovery, chimpanzees continuously update their knowledge regarding both the synchrony levels of their food in time and space and the species-specific differences of these levels, as well as the fruiting histories of individual trees belonging to species with high levels of inter-individual variation or patches of trees. We further hypothesize that chimpanzees have an ability to use the following suite of cognitive mechanisms in combination with search by use of spatial memory of "known" trees: (1) an ability to learn to generalize or classify food plants as belonging to a species (with or without the presence of food), or a class with high and low levels of synchrony, food persistence duration (ephemerality levels) or food production frequencies; (2) an ability to flexibly learn to acquire, store, integrate, order, and retrieve information on (a) the frequency of phenophase occurrences; (b) the relative amounts of fruit and young leaves and variables that influence changes in these amounts in individual plants; as well as (c) sensory information emitted by plants (e.g., the smell of ripe fruits) and other sympatric foragers, including group members that indicate the availability of food; and (3) an ability to flexibly plan or anticipate efficient return times to last season's and recent feeding trees, and efficient travel between them.

We expect that chimpanzees will use a combination of these cognitive abilities to reach their goals. For example, once a chimpanzee discovers the first fruit in a highly synchronous plant species that has high variation in fruiting frequencies, it could plan its approach towards a specific tree of the same species—a tree for which its long-term memory informs the chimpanzee that it had a good fruiting history and a high probability of bearing a large amount of fruit within season. The chimpanzee could then use this information in combination with the sounds of other foragers and smell of the fruit to confirm whether the tree has not been depleted or occupied by a certain number of competitors from neighboring chimpanzee communities [Wilson et al., 2012], and spatial memory (using a variety of cognitive maps or orientation skills) to efficiently travel towards or avoid the respective tree.

In short, ecological intelligence involves much more than solely remembering the spatial location of a number of food trees within a large home range. We conjecture that successful foraging depends on a combination of cognitive skills, especially an ability to obtain, store and retrieve knowledge on temporal availability of food in individual trees. Here, we hypothesized on the existence of a suite of cognitive strategies that chimpanzees can employ to maximize food finding efficiency in periods of scarcity by using individual and species-specific information on the predictability of their food in individual trees. We challenge cognitive scientists to test whether chimpanzees and other large-brained primates indeed employ the proposed strategies and whether primates with smaller brains are able to do the same. Lastly, we hope that our quantification of the temporal complexity of primate food in the three African tropical forests will provide new insight and ideas for the comparative studies that further test the role of ecological complexity in the evolution of primate brain size and cognition.

## ACKNOWLEDGMENTS

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.