Taï chimpanzees change their travel direction for rare feeding trees providing fatty fruits

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The production of edible rainforest fruits is characterized by fluctuating and seasonal patterns that require frugivores to flexibly adjust their ranging behaviour. We investigated whether significant changes in a forager's travel direction can inform us about the importance of the nutritional and energetic aspects of different food sources for a wild animal's diet. We recorded the ranging patterns of five adult female chimpanzees, *Pan troglodytes verus*, for a total of 275 full days in the Taï National Park in Côte d'Ivoire and designed two models that predicted their directional changes at, and on the way to, fruit-bearing feeding trees. In both models, directional change was significantly influenced by the density of the feeding tree species and the crude fat content of that species' fruit. Female chimpanzees were more likely to change their travel direction for rarer trees, at which they fed on fruits that contained higher amounts of fat. In addition, directional changes tended to be positively influenced by the content of nonstructural ('easy energy') and structural carbohydrates (NDF) in that species' fruit. We did not detect any effect of sensory cues or social factors on the directional changes, in either model. The amount of fruit available and the time since the start of the fruiting season positively influenced directional change in the second model, which suggests that chimpanzees were updating their knowledge of the fruit availability in individual trees over time. Our results indicate that the nutrient content of fruit and its abundance exerted a significant impact on the shape of chimpanzee female travel paths, which opens up a new avenue for investigation of food preferences in wild animals through analyses of their ranging patterns.

Tropical rainforests are characterized by a diversity of food resources (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999; Milton, 1977, 1981). Animals living in such environments can choose among a large variety of plant food species as well as types, such as fruit pulp, seeds, leaves, flower buds, bark, pith and gum (Chivers, 1998; Conklin-Brittain, Wrangham, & Hunt, 1998; Milton, 1981; Myers, 1980; Richard, 1985; Wrangham, Conklin-Brittain, & Hunt, 1998). The food type that is eaten by most rainforest foragers is palatable fruit (Dew & Boubli, 2005; Fleagle, 1988; Fleagle & Reed, 1996; Terborgh, 1986).

Some foragers rely on these fruits only temporarily, for example western lowland gorillas, *Gorilla gorilla gorilla*, which can switch their diet from predominantly fruit to foods such as fibrous herbs, leaves and bark (Kuroda, Nishihara, Suzuki, & Oko, 1996; Remis, 1997; Tutin, Fernandez, Rogers, Williamson, & McGrew, 1991). Other foragers are able to maintain a highly frugivorous diet throughout the year (saki monkey, *Pithecia pithecia*: Cunningham & Janson, 2007; Pallas's long-tongued bat, *Glossophaga soricina*: Kalko, Herre, & Handley Jr, 1996; black-casqued hornbill, *Ceratogymna atrata*: Poulsen, Clark, Connor, & Smith, 2002; maned wolf, *Chrysocyon brachyurus*: Motta-Junior & Martins, 2002; chimpanzee, *Pan troglodytes*: Goodall, 1986; Nishida, 1990; Wrangham et al., 1998). Chimpanzees in the Taï National Park, the focus of this study, feed on ripe fruit for 85% of their feeding time and this percentage fluctuates little throughout the year (Goné Bi, 2007; Porter, Garber, Boesch, & Janmaat, in press).

Palatable fruits are produced by many different tree species (Frankie, Baker, & Opler, 1974; Gentry, 1983) and are all of high caloric value compared to other food types (Matsumoto-Oda &

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Hayashi, 1999; Rogers, Maisels, Williamson, Fernandez, & Tutin, 1990); however, not all are equally desired (Newton-Fisher, 1999; Vellayan, 1981; Wrangham, Chapman, Clark-Arcadi, & Isabirye-Basuta, 1996; Wrangham, Gittleman, & Chapman, 1993). For instance, recordings of the presence of foraging animals in tree crowns in a West African rainforest revealed a higher probability of finding them in fig trees, Ficus spp., than in trees of other genera (Janmaat, Polansky, Ban, & Boesch, 2014). Differences in preference could be related to intake rates, facilitated by low handling times or large fruit crops (e.g. Shanahan, So, Compton, & Corlett, 2001). However, nutritional and energetic requirements that are vital for reproduction, fitness and survival (Altmann, 1991, 1998; Janson & Chapman, 1999; Schoener, 1983) are likely to play an important role in food selection as well. For example, chimpanzees, which have a larger body, as well as a larger, energy-demanding brain, spend three times as much of their feeding time eating sugar-rich ripe fruit as do sympatric monkey species (Conklin-Brittain et al., 1998; Laska, Sanchez, & Ernesto, 1998; Wrangham et al., 1998). In contrast, sympatric monkeys eat relatively more protein than chimpanzees, which is consistent with their smaller body mass and greater detoxification needs (Conklin-Brittain et al., 1998). Consequently, many studies have linked preferences for food sources, food choice and selectivity for particular fruit species to animals' nutritional and energetic needs (Ganas, Ortmann, & Robbins, 2008; Hladik & Simmen, 1996; Remis, 2002; Rogers et al., 1990), which affect reproduction, health and survival (Altmann, 1991, 1998; Janson & Chapman, 1999). Increased knowledge of food preferences should therefore help to explain variation in foraging strategies as well as the abundance of wild animals in their natural habitat (Altmann, 1991; Ganas et al., 2008; Janson & Chapman, 1999; Rothmann, Chapman, & van Soest, 2012).

Since individuals of the same species frequently prefer the same food (Remis, 2002; Simmen & Hladik, 1998), species-specific food preferences have been established by choice tests (Benz, Leger, & French, 1992; Nunnally, 1978; Simmen, 1994). For instance, choice tests with captive chimpanzees have indicated that they prefer fruit high in nonstarch sugars and low in total dietary fibre (Remis, 2002). Such studies are valuable; however, as patterns of food acceptance and aversion are also shaped by past experiences and exposure to conspecifics (Barker, Best, & Domijan, 1977; Remis, 2002; Rozin & Kennel, 1983; Steiner & Glaser, 1984; Watts, 1985), it is unclear to what extent the observed preferences may have been influenced by exposure to a limited set of captive conspecifics as well as to human behaviour. In addition, it is unclear to what extent the preferences were influenced by protracted exposure to cultivated fruit, which contains much lower levels of fibre and higher levels of sucrose than wild rainforest fruit (Milton, 1999).

Fruit preference in wild foragers is traditionally estimated by recording feeding durations, sometimes in combination with an estimate of food availability (Barrett, 1995; Boesch, Goné Bi, Anderson, & Stahl, 2006; Doran-Sheehy, Mongo, Lodwick, & Conklin-Brittain, 2009; Ganas et al., 2008; Janmaat, Chapman, Meijer, & Zuberbühler, 2012; Matsumoto-Oda & Hayashi, 1999). The preference rank lists that result from such studies are often difficult to interpret as many other factors, such as social factors and food handling time (i.e. the time it takes to process and consume the food), can influence feeding duration. In addition, search strategies, such as the use of a synchrony-based inspection strategy whereby animals actively search for a particular fruit species because it is temporarily more efficient to feed on that species, can influence feeding duration (Janmaat et al., 2012). Lastly, it is unclear how exactly one should control for food availability. As a consequence, rare species such as fig species often end up at the top of preference lists (Janmaat, Byrne, & Zuberbühler, 2006).

In this study, we explored an alternative means of gaining insight into which nutritional and energetic values of food are important to wild animals. We tested for a relationship between the characteristics of a fruit-bearing tree, such as the nutritional content of the fruit on which wild chimpanzees chose to feed, and adjustments in their ranging patterns. A plethora of studies have revealed that primates adjust their ranging patterns according to the seasonal distribution of high-energy rich food, such as fruit (Garber, 1992; Hashimoto et al., 2004; Lehmann & Boesch, 2004; Nunes, 1995; Robinson, 1986; Terborgh, 1983; Waser, 1984; Waser & Floody, 1974). Studies that analysed adjustments in the shape of primate travel paths in more detail by applying a change point test (Byrne, Noser, Bates, & Jupp, 2009) have revealed that many directional changes were associated with the locations of important biologically relevant activities. For instance, change points, a straight line of travel followed by travel in a significantly different direction, were found at locations where feeding activities took place in gibbons, Hylobates lar (Asensio, Brockelman, Malaivijitnond, & Reichard, 2011), mouse lemurs, Microcebus murinus (Joly, Scheumann, & Zimmermann, 2008) and baboons, Papio ursinus (Byrne et al., 2009; Noser & Byrne, 2013), or monitoring locations in chimpanzees (Janmaat, Ban, & Boesch, 2013). Intriguingly, most mouse lemur change points occurred at the locations of keystone food resources such as gum or honeydew, during scarce food periods, and those of gibbons and baboons occurred at locations where they had been observed to feed on particular fruits (Asensio et al., 2011; Noser & Byrne, 2013). In baboons, fruit finding was found to occur twice as often at change points, compared with other randomly selected points on their route (Noser & Byrne, 2013). Furthermore, when change points occurred during travel, the next change point took place at a fruit feeding location more than 40% of the time (Noser & Byrne, 2013). In short, the results of these studies suggest that an analysis of changes in travel direction can inform us about the location of potential goals such as important (high-caloric) food types like gum, honeydew or fruit.

To investigate this possibility in more detail, we recorded the ranging patterns of five adult female chimpanzees and the location of all fruit-bearing feeding trees for a total of 275 full days in the Taï National Park in Côte d'Ivoire. We then analysed these records in combination with existing data on the nutritional content of the consumed fruit (Hohmann et al., 2010; N'Guessan, Ortmann, & Boesch, 2009). The ultimate aim of our study was to gain insight into which fruit tree species might be of high value in terms of nutritional content, and which nutritional and energetic aspects of a fruit species and characteristics of feeding trees were preferred by chimpanzees. For this we utilized two statistical models that predicted two different types of directional change that potentially could indicate whether a fruit-bearing feeding tree was a travel goal.

It is notoriously difficult to know what the goal of a foraging animal is (discussed in Sigg & Stolba, 1981) and we therefore stress that our approach is exploratory. The first type of directional change (used as the response in our first model) that we expected to indicate whether a tree was a travel goal was the occurrence of a change point at a fruit-bearing feeding tree. The second type of change was defined as a change point that occurred before (on the way to a fruit-bearing feeding tree) and at the same feeding tree (see Methods for justification).

We predicted that each of our proxies for a goal-directed approach was more likely to occur for fruit trees belonging to species containing high amounts of fructose, glucose, saccharose or starch, here summed into one component termed 'easy energy'. We also expected an effect of neutral detergent fibre (NDF), although the predicted direction of its effect is not straightforward. NDF in-

cludes cellulose and hemicellulose which can be partially transformed into energy by the microbes that live in the hindgut of chimpanzees (Conklin-Brittain, Knott, Anderson, & Wrangham, 2006; Holloway, Tasman-Jones, & Lee, 1978; Milton & Demment, 1988), yet it also includes indigestible lignin and is regarded as a feeding deterrent for herbivores (Milton, 1979; Remis, 2002). Chimpanzees, like other primates, have been reported to be more likely to eat fibrous and protein-rich food such as leaves later in the day (Wrangham, 1977), to fill up their gut before resting as fibre is reported to be more difficult to digest (Chapman & Chapman, 1991; Janson & Chapman, 1999; but see Carlson, Rothman, & Mitani, 2013 for an alternative explanation). We therefore expected chimpanzees to be less likely to change direction for fruits that contain high levels of NDF in the early morning than in the evening, and included an interactive effect of NDF with time of day.

Earlier studies of diet composition in wild primates revealed a relatively high percentage of fat content in fruits compared to herbaceous leaves (mountain gorillas, *Gorilla beringei beringei*: Reiner, Petzinger, Power, Hyeroba, & Rothman, 2014; wild howler monkeys, *Alouatta palliata*: Chamberlain, Nelson, & Milton, 1993). Fat contains a large amount of energy and is involved in physiological mechanisms such as neural, retinal and brain growth, tissue, cellular and cardiovascular development and the maintenance and function of the immune system (Conner, 2000; Crawford, 1992; Reiner et al., 2014; Wainwright & Ward, 1997). Hence we also investigated the role of fat in fruit, and expected that a directional change in travel was more likely to occur if the fruit species at a feeding tree contained a higher average amount of fat.

In addition, we predicted that the probability of occurrence of both types of directional change would be positively influenced by characteristics of the feeding tree, such as its crown size and the amount of fruit in the tree crown, and was more likely to occur when the tree belonged to the genus *Ficus* (Janmaat et al., 2014; Wrangham et al., 1993). The nutritional value of figs is highly debated (Shanahan et al., 2001; Wrangham et al., 1993), yet primates' ranging behaviour has been shown to be influenced by the location of fig trees (Janmaat et al., 2014; Noser & Byrne, 2007). We therefore investigated whether chimpanzees were more likely to travel in a goal-directed way towards figs than trees of other genera.

We furthermore predicted that chimpanzees would be more likely to perform a goal-directed approach to trees of rare species, either because they remember their location (Janmaat et al., 2013; Normand, Ban, & Boesch, 2009) and target these trees from a distance (prospective memory: Ban, Boesch, & Janmaat, 2014), or simply because they prefer to eat the fruit of trees that are not commonly available and therefore are more likely to change their travel direction for rare species.

Moreover, we predicted that the probability that each type of change would occur would be positively influenced by the presence of other chimpanzees at a feeding tree, either because their presence indicates the availability of food or for social reasons. Finally, we expected an effect of the time elapsed since the first day that any individual in the study group had been observed feeding on the respective fruit species. On the one hand, we expected that the chimpanzees would be more likely to direct their travel towards trees of a given species at the beginning of the season, as they may prefer to feed on newly emerged foods rather than types they have been feeding on for months, due to a phenomenon called taste fatigue (Carlson et al., 2013). This variety-seeking feeding behaviour has been observed in humans, who most likely have similar taste bud physiology to chimpanzees (Rolls, 1985; Wisniewski, Epstein, & Caggiula, 1992). On the other hand, we expected that as the season progressed, the chimpanzees' knowledge of which trees had produced fruit would become more advanced. As

primates, including chimpanzees, have been reported to remember the fruiting states of trees (e.g. Ban et al., 2014; Janmaat et al., 2013, 2006; Cunningham & Janson, 2007), we expected that the chimpanzees would be more likely to perform a goal-directed approach to fruit-bearing trees at the end of their season than at the beginning.

METHODS

Study Site and Subjects

Our study site (26.5 km^2) is located on the western side of the Taï National Park (TNP) at 15 km east of the Taï village. At the time of the study the chimpanzee, *P. t. verus*, community included on average four adult males and six adult females and an average total number of 28 individuals (South group). Located in southwest Côte d'Ivoire, TNP harbours approximately 1300 tree species (Guillaumet, 1967), and represents the largest remaining protected area of old growth lowland rainforest in West Africa (5050″20″N, 7019″16″W) covering 5360 km^2 (Boesch et al., 2008; Kouakou, Boesch, & Kuehl, 2011; N'Goran et al., 2012). We followed five adult female chimpanzees habituated to human presence by the Taï Chimpanzee Project (Boesch & Boesch-Achermann, 2000; Boesch et al., 2008). Data were collected from 16 April 2009 to 30 August 2011, for successive continuous periods ranging from 4 to 8 weeks, totalling 275 full days.

Data Collection

Five adult female chimpanzees were followed every day from dawn (when they were still in their sleeping nest) until dusk (when they made a new sleeping nest). The locations of all trees in which females ate fruit were recorded with a GPS 60CsX (Global Positioning System) and marked with brightly coloured spray paint. We used a GPS and voice recorder to record the duration and location of each feeding activity via continuous focal sampling (Martin & Bateson, 2007). Two observers (K.J. and S.B.) followed a given female on alternate days (results of interobserver reliability tests for the scoring of activities are provided in Janmaat et al., 2013). In addition, we recorded the number of adults present in the group (party size) and the number of males and females to determine the sex ratio (ratio of males to females). These two social measures were recorded to control for the possibility that they influenced the shape of the travel path and the probability of a directional change occurring. Animals that forage in a large group have been shown to perform a 'pushing forward' behaviour whereby competing members keep searching for food in the same direction, which can make it more difficult for individuals within the group to change travel direction (also referred to as 'group inertia'; Janson, 2007; van Schaik, van Noordwijk, De Boer & Den Tonkelaar, 1983). In addition, chimpanzee males were observed to back-track less (Bates & Byrne, 2009) than female chimpanzees, making sex ratio an important control predictor. We furthermore recorded whether other chimpanzees were in the tree at the moment of the focal female's arrival. This was done to control for the possibility that females directed their travel towards a feeding tree because they had heard (auditory cues) or seen (visual cues) other chimpanzee individuals already at the tree and hence approached those trees for social reasons.

To test the effect of tree characteristics on changes in female travel direction, trained field assistants relocated each marked feeding tree the day after each focal observation, estimated the tree crown size and measured the amount of fruit in its crown (see Ban et al., 2014 for detailed explanations). With the use of binoculars, the amount of fruit was estimated by checking the tree crown from

all four cardinal directions and ranking the amount in classes of 0%, 1–25%, 26–50%, 51–75% and 76–100% of the crown being covered in fruit (Chapman et al., 1992; Goné Bi, 2007; Peres, 1991). For tree density, we used the density measures collected by Goné Bi (2007).

Data Analyses

To record the focal chimpanzee's travel path we used the GPS's track log function (see Janmaat et al., 2013 for information on settings, accuracy measurements and data cleaning procedures). To gain insight into what factors influenced the probability that the chimpanzees approached feeding trees in a goal-directed way, we determined for the daily travel path of each female the point at which the female changed her travel direction significantly by use of the 'change point test' (Byrne et al., 2009; Janmaat et al., 2013). We used a significance criterion of 0.05, step interval = 5 min and $q = 4$, which has been argued to be optimal for chimpanzees in rainforest habitat (Byrne et al., 2009). In order not to disturb the feeding chimpanzees, we did not always follow them underneath the crown of feeding trees. We therefore combined all cases where a change point occurred within a tree's detection field (mean = 33.90; SD = 12.32) and cases that occurred in the fruit fall area (mean = 6.51 m; SD = 175.76), and defined such cases as a

'directional change at the feeding tree' (Fig. 1a). The probability that such a directional change occurred or not was used as the binomial response in our first statistical model. This choice was inspired by previous studies discussed above (Asensio et al., 2011; Byrne et al., 2009; Janmaat et al., 2013; Joly & Zimmermann, 2011; Noser & Byrne, 2013). However, to some this choice may not be straightforward. One may argue that when a change in travel direction occurs after feeding it provides little indication that the tree was in fact targeted earlier in time. However, we argue that a change point is only detected when it is preceded by a relatively straight-line approach (in our case four travel segments each separated by a 5 min interval) and followed by a significant change in direction (often back towards the area from where the forager came; Fig. 1a; Byrne et al., 2009; Janmaat et al., 2013). This could, therefore, indicate a goal-directed approach of the location at which the change point occurred (see Janmaat et al., 2013).

For the second response measure, we selected all cases that had a directional change before the chimpanzee's arrival (between the previous feeding tree and the detection field of the feeding tree and a second change point occurring at the feeding tree; Fig. 1b). This first change point could be regarded as a potential 'decision point' after which the forager reaches a goal (see Byrne et al., 2009). To exclude cases in which the change points occurred because the
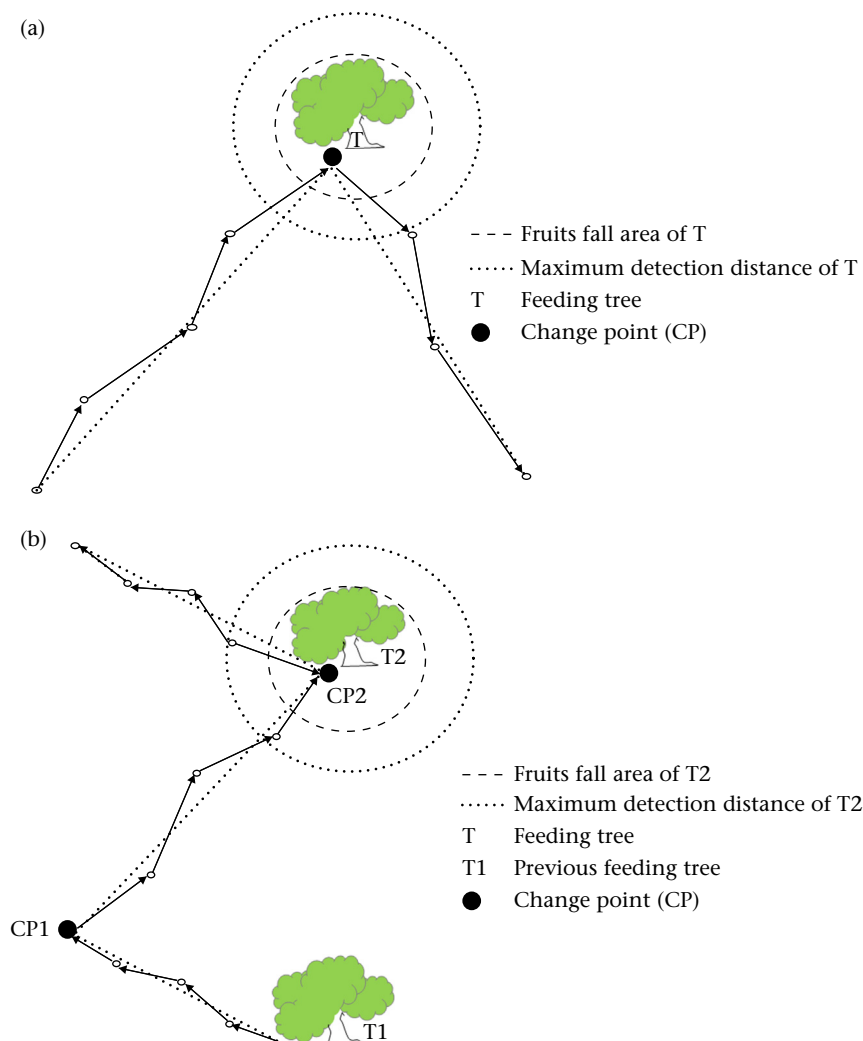
Figure 1. Schematic representation of changes in travel direction made by a female chimpanzee. (a) A directional change (CP) at a feeding tree. (b) Changes in travel direction before reaching (CP1) and then at a feeding tree (CP2).

chimpanzee was in fact aiming to approach a different tree, we included the requirement that the first change point had to be located between the previous feeding tree (T1; Fig. 1b) and the feeding tree of interest (T2; Fig. 1b). To make it even more likely that the tree of interest (T2) was indeed a goal and not simply fed upon 'en passant' we included a second condition, which was that the chimpanzee also had to change direction at tree T2. Hence, our second response incorporated two consecutive directional changes (as in Noser & Byrne, 2013): (1) a change point (CP1) occurring on the way from a previous feeding tree (T1) to the feeding tree of interest (T2), and (2) a second change point (CP2) taking place at the feeding tree (T2). The probability of the occurrence of these two consecutive directional changes was thus the binomial response in our second model. We used two types of response instead of only one to gain a better insight into which directional changes might best indicate a goal-directed approach.

We estimated the nutritional content of the fruit in each feeding tree using the average values calculated per species from a previous study conducted at the same study site (Hohmann et al., 2010; N'Guessan, 2012; N'Guessan et al., 2009; see Table 1 showing nutritional values of the fruit species). Fruit samples were collected by N'Guessan from the trees in which the chimpanzees were feeding at the time of sample collection (N'Guessan et al., 2009). The fruit items collected were either ripe or midripe since chimpanzees are known to specialize on ripe and midripe fruits (Houle, Conklin-Brittain, & Wrangham, 2014; Wrangham et al., 1998). In most fruit species the chimpanzees ate the pulp, but in some they ate the seeds or the kernel inside the cracked nuts (Table 1). Nutritional analyses were only conducted on parts of the fruit that were observed to be eaten.

The first predictor in each model, defined as 'easy energy', was the sum of the average percentages in each fruit species of four nonstructural carbohydrates, namely glucose, fructose, saccharose and starch (Table 1). These were determined using commercial enzymatic tests (R-Biopharm, Darmstadt, Germany; UV method, Hohmann et al., 2010). The second predictor was the average percentage of NDF (structural carbohydrate; Table 1), for which levels were measured using the analysis system of van Soest (1994) as in N'Guessan et al. (2009) and Hohmann et al. (2010). These nutritional values were calculated per fruit species. Hence, fruit items from trees of the same species were assumed to possess a similar nutritional value. The third predictor was the average percentage of

crude fat (Table 1). This was extracted with ethyl ether via a fully automatic Soxhlet-system (Gerhardt Laboratory Systems, Königswinter, Germany; Hohmann et al., 2010). Some of the high fat levels in fruit pulp, for example in *Chrysophyllum taiensis* (Table 1), may be due to the latex found in the fruit (Houle et al., 2014).

Since we predicted that the time since the start of the feeding season would influence the probability of a directed approach, we included a variable to represent 'day since the season started'. This was defined as the number of days that had elapsed since the first day on which a chimpanzee from our study group had been observed eating fruit of the respective species. To calculate this measure for tree approaches that occurred within the first few weeks of our data collection, we used prior feeding data collected by assistants of the Taï Chimpanzee Project before the start of our study period.

To control for a potential effect of energy balance we calculated the focal female's relative cumulative energy balance, in each case estimated at the immediately previous change point. The cumulative energy balance was defined as the cumulative sum of the energy intake and energy expenditure in kilocalories and was estimated as follows. We started calculations at value zero at the moment when the female left her nest in the morning. We then added the values of energy intake and deducted energy expenditure throughout the day, until the moment the female reached the last change point after which she visited a feeding tree (see Ban et al., 2014 for details of the calculations).

Ethical Note

This study is based on noninvasive observations. We followed the ASAB/ABS Guidelines for conducting research on the chimpanzees and obtained official approvals for the research in the country in which our study was conducted (Permit number: 208/MESRS/DGRSIT/KYS/sac and authorization 2008/08_922 from the Ministère de l'enseignement supérieur et de la recherche scientifique, Côte d'Ivoire). To minimize the chance of disease transmission from humans to chimpanzees, the five adult females were typically followed by one observer at a time and observers took care to remain at a distance of at least 7 m at all times (Boesch, 2008; Leendertz et al., 2006).

Table 1
Nutritional contents of the parts of the fruit that were eaten by the five adult female chimpanzees (percentage dry matter)

Fruit species	Part of the fruit analysed	Easy energy	NDF	Fat
Chrysophyllum taiensis	Pulp	48.12	23.94	21.33
Dialium aubrevillei	Pulp	50.65	12.53	0.2
Drypetes aubrevillei	Pulp	53.57	20	0
Duboscia macrocarpa	Pulp	13.62	48.4	1.7
Ficus elasticoides	Pulp	1.11	47.49	10.44
Ficus eriobotryoides	Pulp	4.37	57.46	3.91
Ficus macrosperma	Pulp	17.9	30.13	5.27
Ficus mucuso	Pulp	24.69	25.33	4.86
Irvingia grandifolia	Pulp	46.38	25.51	0.26
Klainedoxa gabonensis	Pulp	34.85	50.07	1.51
Nauclea diderrichii	Pulp	41.64	35.46	1.28
Nauclea xanthoxylon	Pulp	24.91	20.12	2.89
Pachypodanthium staudtii	Pulp	23.83	48.83	7.82
Panda oleosa	Kernel	3.52	40.78	51.73
Parinari excelsa	Pulp	43.53	15.91	0.65
Parinari excelsa	Kernel	0.12	14.46	78.05
Sacoglottis gabonensis	Pulp	38.23	26.96	0.7
Scottelia klaineana	Pulp	4.53	49.65	38.06
Sterculia oblonga	Pulp	3.78	36.58	2.76
Treculia africana	Pulp+seed	14.25	47.39	2.33

Statistical Analyses

To investigate which factors influenced the probability that a female chimpanzee changed her travel direction at a feeding tree (first response; Fig. 1a), as well as at a feeding tree and on the way to that feeding tree (second response; Fig. 1b), we used two generalized linear mixed models (GLMM; Baayen, 2008) with binomial error structure and logit link function. In both models we included as main predictors the fruit nutrient contents of the tree species: namely easy energy, fat and the interaction between NDF and time of day; feeding tree characteristics: total fruit amount, standardized crown size, species density and whether the tree belonged to the genus *Ficus* (yes or no); day since the season started for the respective tree species; and whether other chimpanzees were already at the feeding tree (yes or no). Sex ratio, party size, relative cumulative energy balance measured at the last change point before an approach and a temporal autocorrelation term were included as control predictors. Chimpanzee individual, tree species and tree individual were included as random effects to avoid pseudoreplication and to investigate the effect of tree species. To investigate the possibility that chimpanzees had an individual preference for particular species and whether this varied among individuals, for example due to differences in past experience or dental wear (one female was lacking the teeth needed to eat tough fruit), we included the random effect chimpanzee individual preference (which was the combination of focal individual and tree species). To keep type I error rate at the nominal level of 5% (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) we included random slope components for all the main predictors within chimpanzee individual that showed sufficient variation within the levels of the random effect of chimpanzee. We considered variation to be sufficient for quantitative predictors when there were at least three different values for at least half of the chimpanzees and for factors when they had at least two levels with each having at least two observations per chimpanzee. Note that such random slopes account for possible individual differences in the effects of these predictors on the response.

To create stable models, we transformed predictors so as to achieve roughly symmetric distributions. We square-root transformed days since the season started and log transformed relative energy balance, tree density, party size and fat. After this, we z-transformed all covariates to establish comparable estimates and enable us to interpret interaction terms more easily (Schielzeth, 2010).

To derive the temporal autocorrelation term (i.e. temporal nonindependence of the residuals from the model), we first ran the full model without accounting for autocorrelation and derived the residuals. In a subsequent step we averaged, separately for each data point, the residuals of all other data points of the same respective individual chimpanzee, whereby we weighted their contribution to the average by their distance to each respective data point. We then included the resulting values as an 'autocorrelation term' in each final model (Fürtbauer, Mundry, Heistermann, Schülke, & Ostner, 2011). The weighting function had a Gaussian distribution with a mean of zero and a standard deviation chosen such that the likelihood of the model with the autocorrelation term included was maximized.

Since the occurrence of two successive change points (Fig. 1b) was rare, our second model did not initially converge. To decrease model complexity and increase stability we therefore removed subsequent visits to the same feeding trees from the data, so that the random effect of tree individual could be removed from the model. We assessed model stability by visually comparing the estimates derived from a model based on all data with those obtained from models in which each level of a random effect (such as

chimpanzee individual and tree species) was excluded one at a time. This revealed that the final models were stable with regard to the effects of all main, control and random predictors, with the exception of the predictor fig (*Ficus*, yes or no) in the first model. To rule out multicollinearity, we determined variance inflation factors (VIF; Field, 2005; Quinn & Keough, 2002) for a standard linear model excluding the random effects and the interaction term for all the predictors (main and control). Multicollinearity was only an issue for the predictors easy energy and fat, which revealed rather high VIF values in both models (easy energy: 6.24 and 6.01; fat: 5.35 and 5.56; for the first and second models, respectively). However, as both predictors showed a significant effect in the first and a trend in the second model, and multicollinearity tends to influence standard errors and hence *P* values, we decided to present and interpret the results from the models including both easy energy and fat values.

We first assessed the overall significance of the main predictors (Forstmeier & Schielzeth, 2011) by comparing the full model comprising all predictors with a null model which omitted the main predictors but comprised the control predictors (relative cumulative energy balance, sex ratio, party size and autocorrelation terms) and the same random effects structure, using a likelihood ratio test (Dobson, 2002). Since the interaction between NDF and time of day was not significant in the second model, we removed it from the model and re-ran it without the interaction term (Table 3).

Given that a GLMM with a binomial outcome was used, change in the odds ratios was calculated. To calculate the 95% confidence intervals of the estimates we used a parametric bootstrap simulation based on a custom-written function (Mundry, 2015) as follows. Parametric bootstraps were derived by generating a new response based on the model output. More specifically, we sampled estimates for the fixed effects from normal distributions with means and standard deviations being the estimates and their standard errors, and estimates for the random effects (intercepts and slopes) from normal distributions with means of zero and standard deviations, all as specified in the model output. In this way, we derived a bootstrapped response for which we then fitted the same model as for the original data. We repeated these steps 1000 times and derived confidence intervals by cutting off 2.5% at either edge of the derived distributions of the estimates (Mundry, 2015).

Overdispersion did not appear to be an issue (dispersion parameter: 0.74 and 0.97, respectively, for the first and second

Table 2
Factors influencing the probability that female chimpanzees changed their travel direction at a feeding tree (Fig. 1a; $N_{females}$ = 5; $N_{feeding\ visits}$ = 1510)

	Estimate	SE	P
Intercept	−1.193	0.084	
Main predictors			
Nutritional values of fruit in feeding tree			
Easy energy	0.270	0.154	0.080
NDF: Time of day	−0.141	0.063	**0.024**
Fat	0.375	0.143	**0.011**
Other feeding tree characteristics			
Standardized crown size	0.021	0.063	0.739
Total fruit amount	0.101	0.070	0.151
Tree density	−0.363	0.103	**0.003**
Fig tree* (yes)	0.606	0.287	**0.047**
Days since the season started	0.134	0.069	0.106
Chimpanzee at arrival tree (yes)	−0.309	0.431	0.426
Control predictors			
Sex ratio	−0.082	0.074	0.271
Party size	−0.002	0.076	0.979
Relative energy balance	−0.155	0.138	0.225
Temporal autocorrelation term	0.179	0.060	**0.004**

Significant *P* values are in bold.
* This effect was unstable.

Table 3
Factors influencing the probability that female chimpanzees changed their travel direction before (on the way to the feeding tree) and at a fruit-bearing feeding tree (Fig. 1b; $N_{females} = 5$; $N_{feeding\ visits} = 982$)

	Estimate	SE	P
Intercept	−2.589	0.159	
Main predictors			
Nutritional values of fruit in the feeding tree			
Easy energy	0.635	0.304	0.055
NDF	0.384	0.168	0.056
Fat	0.688	0.302	**0.034**
Other feeding tree characteristics			
Standardized crown size	−0.011	0.125	0.929
Total fruit amount	0.445	0.142	**0.011**
Tree density	−0.772	0.202	**0.004**
Fig tree (yes)	−0.694	0.603	0.246
Chimpanzee at arrival tree (yes)	−0.652	0.637	0.271
Days since the season started	0.284	0.141	0.086
Time of day	−0.157	0.175	0.366
Control predictors			
Sex ratio	0.018	0.163	0.923
Party size	−0.057	0.150	0.703
Relative energy balance	−0.405	0.291	0.160
Temporal autocorrelation term	0.167	0.105	0.143

Significant P values are in bold.

Figure 2. Change in the odds ratios (that the female changed direction at the food tree) per unit increase of the test predictors. Indicated are odds ratios, their 95% confidence intervals and respective P values. *This effect disappeared when we removed data on one female (Julia).

models). Total sample size was 1510 and 982 feeding tree visits in the first and second models, respectively, observed on 982 tree individuals belonging to 19 fruit species consumed by five female chimpanzees. Models were implemented in R (R Core Team., 2014) using the function glmer of the R package lme4 (Bates, Maechler, & Bolker, 2013). Model diagnostics were calculated using the functions 'vif' (R package 'car', Fox & Weisberg, 2011). To investigate whether rare trees have larger trunks, we used Spearman exact test. These analyses were implemented in R using the packages 'gtools'.

RESULTS

To investigate what factors influenced the probability that chimpanzee females approached a feeding tree in a goal-directed manner we designed two statistical models that allowed us to estimate the combined effect of the nutritional content of the fruit, the amount of fruit, indicators of the chimpanzees' knowledge of the fruiting states of different trees, and social factors, on the probability that a chimpanzee female made a directional change at the feeding tree (response 1; Fig. 1a), and at the feeding tree as well as on her way to the feeding tree (response 2; Fig. 1b).

The first model was significant compared to the null model (likelihood ratio test: $X^2 = 19.04$, $P = 0.039$; $N_{females} = 5$; $N_{feeding\ visits} = 1510$). After controlling for party size, sex ratio, relative energy balance and temporal autocorrelation, we found that the greater the percentage of fat in the fruit species and the lower the tree density in the territory, the more likely females were to change direction at the feeding tree (Table 2, Fig. 2). Moreover, we found a significant interactive effect of the percentage of NDF and the time of day on the probability that a directional change occurred at a feeding tree. However, contrary to our expectations, the females were more likely to direct travel towards fruit species containing high levels of NDF earlier rather than later in the day (Table 2, Figs. 2 and 3). We also found a trend towards a higher likelihood of a directional change when the fruit species contained a higher percentage of easy energy (nonstructural carbohydrates such as sugars and starch; Table 2, Fig. 2). The temporal autocorrelation term had a positive impact on the response (Table 2). However, crown size, total fruit amount, presence of other chimpanzees at the tree, the number of days since the season started and the control predictors
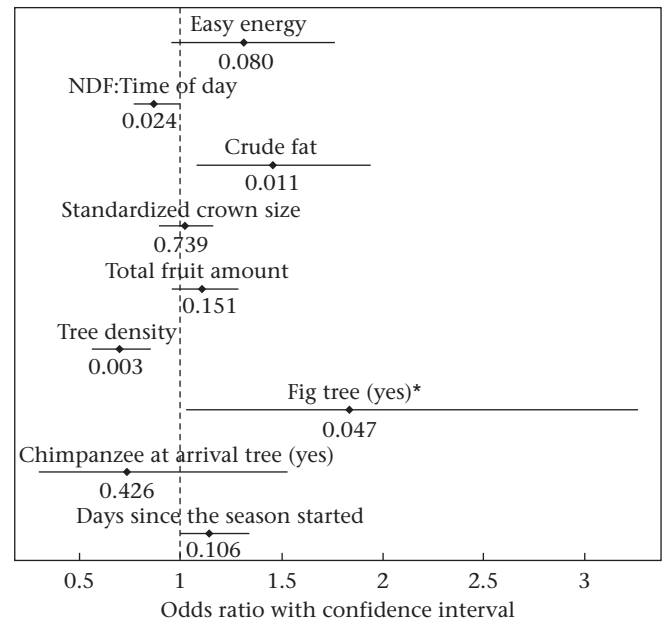
(sex ratio, party size and relative energy balance) had no significant effect on the probability that chimpanzee females changed their travel direction at feeding trees (Table 2). No effect was found of the random effects individual preference ($X^2 = 0.000$ (when rounded), $P = 1.000$ (when rounded) and tree species ($X^2 = 0.000$, $P = 1.000$)). The model results initially indicated that females were more likely to change travel direction at fig trees than trees belonging to other genera (Table 2, Fig. 2). However, detailed model diagnostics revealed that this result was unstable and was strongly influenced by the behaviour of one of the five females (the female, Julia, that lacked a certain number of teeth and had difficulty eating tough food).
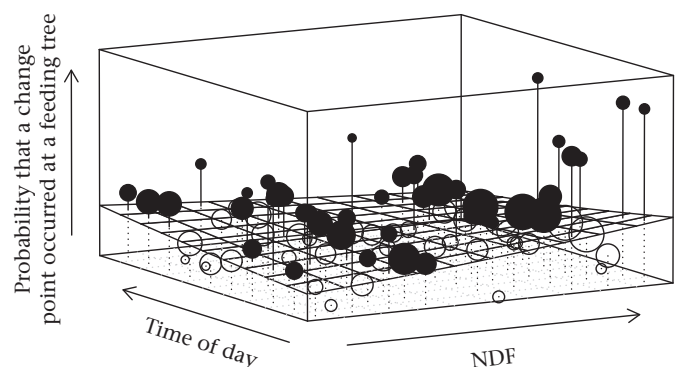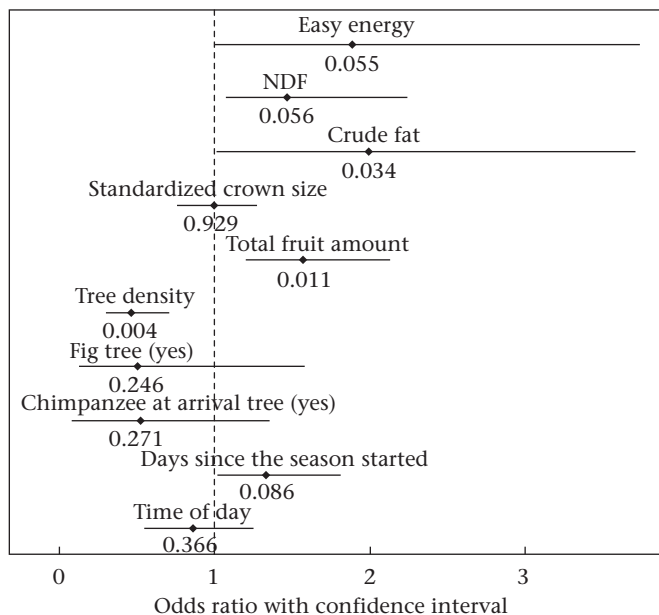

Figure 3. Probability of female chimpanzees changing their travel direction in relation to level of fibrous energy (NDF) and time of day. The height of spheres represents the probability that a change point occurred at the feeding tree, per combination of NDF content and time of day. Each surface (i.e. square) represents the expected probability of a change in travel direction at the feeding tree according to the model (conditional on all other predictors being set at their average value, with the predictors 'fig tree' and 'chimpanzees at arrival' manually dummy coded and centred). Sphere size corresponds to the relative number of observations, with closed circles being above the model surface and open circles below.

The second model was also significant compared to the null model (likelihood ratio test: $X^2 = 19.59$, $P = 0.033$; $N_{females} = 5$; $N_{feeding visits} = 982$; Table 3). As in the first model, females were more likely to change travel direction before and at the feeding tree (response 2; Fig. 1b) when the fruit species contained a higher percentage of fat (Table 3, Figs 4 and 5) and when the tree species was at lower density in the territory (Table 3, Figs. 4 and 6), after controlling for party size, sex ratio, relative energy balance and temporal autocorrelation. When the fat content of fruit ranged between 0 and 4% the probability of changing travel direction increased steadily with increasing fat concentrations, while from 4% onwards the probability increased in a more exponential way (Fig. 5). We found a trend towards a higher likelihood of a directional change when the fruit species contained a higher percentage of easy energy (Table 3, Fig. 4). No significant interactive effect of NDF and time of day was detected; however, an unexpected and marginally significant positive effect of NDF was found. Total fruit amount had a significant positive impact (Table 3, Figs. 4 and 7), and there was a trend for an effect of the number of days since the season started for a given tree species (Table 3, Fig. 4). Females were more likely to change travel direction before and at the feeding tree later in the season. Standardized crown size, time of day, whether another chimpanzee was at the feeding tree and whether the tree was a fig tree, as well as the control predictors (sex ratio, party size, relative energy balance and the temporal autocorrelation term), had no significant effect on the probability that the chimpanzee females changed their travel direction at and on the way to feeding trees (Table 3). The random effect tree species did not have a significant effect on the second response measure ($X^2 = 0.000$, $P = 1.000$).
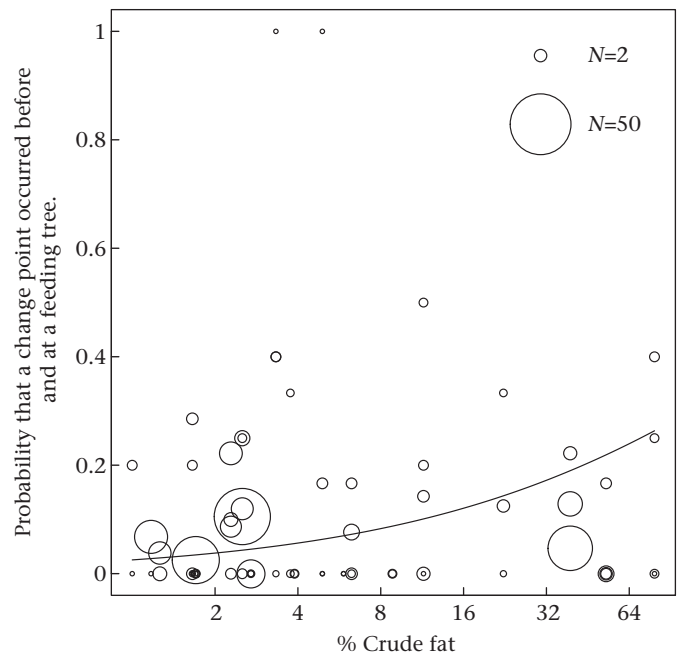
DISCUSSION

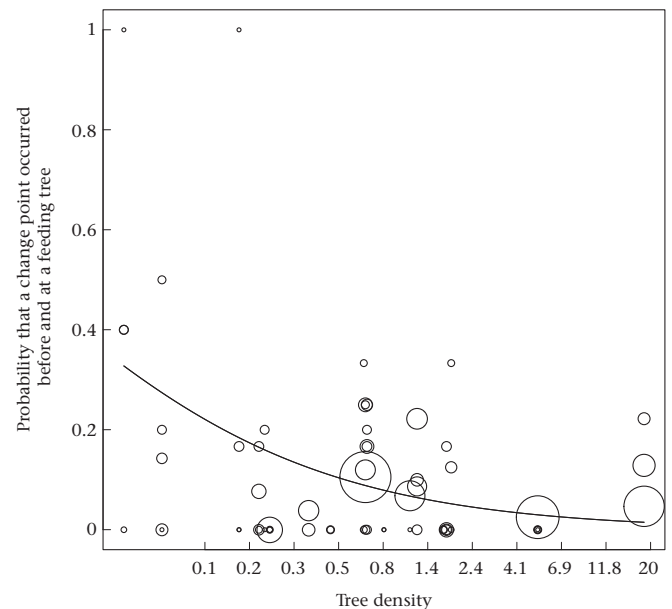### Do Chimpanzees Change Travel Direction for Particular Nutrients?

To gain insight into how chimpanzees value their feeding trees and hence explore an alternative way to gain insight into the food
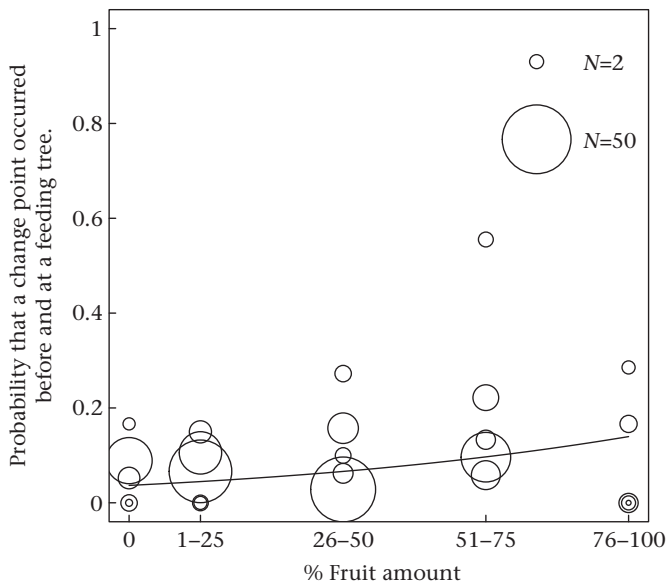

Figure 5. Probability of female chimpanzees changing travel direction in relation to the fat content of fruit on a tree. The Y-axis represents the probability that a change point occurred before and at the feeding tree (Fig. 1b) and the X-axis represents the percentage of fat found in the consumed fruit species. The area of circles represents sample size per combination of binned predictor and response. The line represents the expected probability that individuals change travel direction before and at a feeding tree predicted by the model (conditional on all other predictors being set to their average values, with the predictors 'fig tree' and 'chimpanzees at arrival' manually dummy coded and centred).

Figure 6. Probability of female chimpanzees changing travel direction in relation to tree density. The Y-axis represents the probability that a change point occurred before and at the feeding trees (Fig. 1b) and the X-axis represents the tree density of the consumed fruit species. The line illustrates the expected probability that individuals change their travel direction at a feeding tree predicted by the model (conditional on all other predictors being set to their average values, with the predictors 'fig tree' and 'chimpanzees at arrival' manually dummy coded and centred). The area of the circles represents the sample size per combination of binned predictor and response.

Figure 4. Change in the odds ratios (that the female changed direction before reaching, and then at, the food tree) per unit increase of the test predictors. Indicated are odds ratios, their 95% confidence intervals and respective *P* values. For example, for one unit of increase in the fat content of the fruit at the feeding tree, the odds of changing direction before and at the food tree increase by two.

Figure 7. Probability of female chimpanzees changing travel direction before and at feeding trees in relation to the amount of fruit on the tree. The Y-axis represents the probability that a change point occurred before and at a feeding tree (Fig. 1b) and the X-axis represents the fruit amount ranked in classes of 0%, 1–25%, 26–50%, 51–75% and 76–100%. The area of the circles represents the sample size per combination of binned predictor and response. The line illustrates the expected probability that individuals change their travel direction before and at a feeding tree predicted by the model (conditional on all other predictors being set to their average values, with the predictors 'fig tree' and 'chimpanzees at arrival' manually dummy coded and centred).

was only a trend, while in the first model chimpanzee females were more likely to change direction at feeding trees with high levels of NDF but, contrary to our predictions, more so in the morning than the evening. It is possible that fruit with high levels of NDF also contain other chemical components (e.g. a low level of antifeedants, such as bitter tannins or low levels of lignin) that we were unable to analyse, since this information was unavailable for the selected fruit species. This possibility requires further investigation using a larger number of samples to allow these components to be assessed. However, even if that were the case it would still be difficult to explain why females would only feed on fruit containing low levels of antifeedants or lignin early in the day. As chimpanzees and humans show a similar kinetic response to different fibre levels in the diet (i.e. more rapid turnover of ingesta with increased fibre level), as well as a similarity in their respective abilities to degrade (via gut flora) the cellulose and hemicelluloses (Milton, 2003; Milton & Demment, 1988), we searched the human literature in an effort to explain our findings. In humans, chewing highly fibrous food produces saliva and gastric secretions that fill the stomach and increase satiety. Satiety further increases owing to the bulk of the fibre in the stomach (Papagiannidou, Tsipis, Athanassiadou, Petrou, & Athanassiadou, 2013). It is possible that eating fibrous fruit in the morning provides both energy and a feeling of satiety after a relatively long (overnight) period of not feeding. In addition, eating a highly fibrous food in the morning may help individuals feel satiated for longer, as energy is released at a slower rate than that from sugars (Jenkins et al., 1993; Slavin, 2005). The consumption of fibrous food at any time of the day may also improve fat oxidation (release energy) and fat storage (Slavin, 2005), which is useful for brain development and maintenance (Crawford, 1992).

Do Chimpanzees Change Travel Direction for Particular Trees?

Both models revealed a significant negative effect of tree density on the probability of a directional change at or on the way to a feeding tree. This could be explained by the possibility that females were better able to remember the location of each of the lower number of a rare tree type and were therefore more likely to direct their travel towards such trees from a greater distance (Janmaat et al., 2013; Normand et al., 2009). These memories may be more salient as rare trees are known to have larger trunks (diameter at breast height; Spearman exact test for trees in the females' territory: $r = 0.68$, $N_{species} = 33$, $P < 0.0001$) and are more productive (Anderson, Nordheim, & Moermond, 2002). Crown size (standardized using the average crown size of the species) did not have a significant impact in either model, which may be because all the trees considered were feeding trees and thus did not vary greatly in standardized crown size (Janmaat et al., 2013). The lack of any significant impact of the random effect tree species in both models might be because some species were only rarely visited during our observation period (Tables A1 and A2 in the Appendix). Hence, we propose that future studies that aim to reveal which fruit species are preferred by chimpanzees should exclude from their analyses species that are rarely visited. A large part of the variation in the probability of a directional change was explained by the autocorrelation terms that considered the time lags between tree visits. The positive impact of temporal autocorrelation on change probability may have many explanations. One of them could be that the effect is a reflection of temporal clustering, if chimpanzees were feeding on trees containing fruit of similar fat levels or densities within the species' respective fruiting seasons.

Evidence for effects of other tree characteristics upon the probability of a directional change occurring was found, but these

preferences of wild foragers, we investigated which feeding trees were approached in a goal-directed manner by chimpanzees and which ones were not. Our results indicated that female chimpanzees were more likely to change their travel direction for trees that bore fruit containing a higher amount of fat. Fat contains more energy (9 kcal/g) than sugars and protein (4 kcal/g, each; FAO, 2003; Slavin, 2005) and aids in vitamin absorption (Maynard, Loosli, Hintz, & Warner, 1979; Calvert, 1985). This is especially true when it is associated with a high fibre intake (Slavin, 2005). Considering that rainforest fruits overall possess a relatively high amount of fibre (Milton, 1999) compared with cultivated fruits, it may be particularly important for the absorption of vitamins to select fruits that have relatively high amounts of fat. In humans it has been shown that fats such as olive oil are essential for the body to absorb provitamin A carotenoids in salads (Brown et al., 2004). In addition, directional changes by females tended to be more likely when fruit in the feeding tree contained a greater amount of easy energy, i.e. sugars. This supports the findings of wild and captive studies on primate food choice, preferences and selection (Remis, 2002; Reynolds, Plumptre, Greenham, & Harborne, 1998; Wrangham et al., 1998). The lack of a significant effect of easy energy in both models was surprising, but might be explained by low variation in average sugar levels among the different fruit species. Alternatively, it is possible that the sugar levels of fruit in females' feeding trees were different from the average levels measured for the species, due to differences in the microhabitat of the tree, height of the collected fruit in the tree, day of season, time of day at which samples were collected (Carlson et al., 2013; Houle et al., 2014; Reynolds et al., 1998; Rothman et al., 2012) or the fruit's ripening stage, and that this obscures an overall effect of easy energy.

In addition to fat and easy energy, NDF appeared to be an important predictor in both models. In the second model its effect

effects differed between models. For example, the amount of fruit did not have any significant effect in the first model, but had a positive effect in the second. We argue that the second response measure is potentially a better indicator of a long-distance goal-directed approach (the mean distance between the first change point (CP1; Fig. 1b) and the detection field of a target feeding tree was 369.11 m), in which fruit amount was an important factor in the decision to direct long-distance travel to a particular tree. The first response measure may also have included cases where females simply directed their travel to a tree after spotting it along the way. Our suggestion that the second response is a better indicator of a long-distance goal-directed approach could also explain why we did not find an effect of time since the start of the fruiting season in the first model, but did so in the second. Towards the end of the season, the chimpanzees probably had more knowledge of the availability and amount of fruit in feeding trees than at the beginning, and hence might have been more likely to target feeding trees from greater distances and invest in a long-distance approach. Our results suggest that foragers have more updated knowledge of the fruiting state of trees at the end of a season than early in the season and adjust their ranging behaviour accordingly.

Our study clearly indicates that the nutrient content of fruit has a significant impact upon the shape of a chimpanzee female's travel path. These findings pave the way for future investigations of food preference in wild animals through the analysis of their ranging patterns. We would like to stress that our study was exploratory and we encourage continued investigations of different types, or sequences, of directional changes that might be used as a proxy for goal-directed approach. One type could be a true detour, in which the animal 'deviates' from a current travel route. Future effort should focus on how we may best define and quantify such deviations. In addition, changes in speed, and not only in direction, should be considered as a potential indicator of travel decisions and goals (Polansky, Werner, & George, 2015). Future investigations should also focus on other parameters influencing the occurrence of directional changes on foragers' travel routes. One such parameter could be the nutrient content of fruit samples obtained from individual trees at the same time as, or even prior to, the point when primates were feeding there, rather than estimates of content based on analyses conducted at a species level as in this study (Houle et al., 2014) especially because nutritional values can differ dramatically between plant individuals (e.g. Rothman et al., 2012). Such analyses should, in addition, include other nutritional variables such as secondary metabolites, protein, minerals and vitamins to gain further insight into the importance of the nutritional content of fruit in a wild forager's diet.

Acknowledgments

References

Altmann, S. A. (1991). Diets of yearling female primates (*Papio cynocephalus*) predict lifetime fitness. *Proceedings of the National Academy of Sciences United States of America, 88*(2), 420–423.

Altmann, S. A. (1998). *Foraging for survival: Yearling baboons in Africa.* Chicago, IL: University of Chicago Press.

Anderson, D. P., Nordheim, E. V., & Moermond, T. C. (2002). Factors influencing fission–fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In C. Boesch, G. Hohmann, & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 90–101). Cambridge: Cambridge University Press.

Asensio, N., Brockelman, W., Malaivijitnond, S., & Reichard, U. (2011). Gibbon travel paths are goal oriented. *Animal Cognition, 14*, 395–405. http://dx.doi.org/10.1007/s10071-010-0374-1.

Baayen, R. (2008). *Analyzing linguistic data.* Cambridge, U.K.: Cambridge University Press.

Ban, D. S., Boesch, C., & Janmaat, R. L. K. (2014). Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition, 17*, 1353–1364. http://dx.doi.org/10.1007/s10071-014-0771-y.

Barker, L. M., Best, M. R., & Domijan, M. (1977). *Learning mechanisms in food selection.* Cambridge, MA: Baylor University Press.

Barrett, L. (1995). *Foraging strategies, ranging patterns and territoriality among grey-cheeked mangabeys in Kibale forest, Western Uganda* (Unpublished Ph.D. thesis). London, U.K.: University College London.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language, 68*, 255–278. http://dx.doi.org/10.1016/j.jml.2012.11.001.

Bates, L. A., & Byrne, R. W. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): foraging and border checking. *Behavioral Ecology and Sociobiology, 64*(2), 247–255. http://dx.doi.org/10.1007/s00265-009-0841-3.

Bates, D., Maechler, M., & Bolker, B. (2013). *lme4: Linear mixed-effects models using S4 classes.* R package version 0.999999-2 http://CRAN.R-project.org/package/lme4.

Benz, J. J., Leger, D. W., & French, J. A. (1992). Relation between food preference and food-elicited vocalizations in golden lion tamarins (*Leontopithecus rosalia*). *Journal of Comparative Psychology, 106*, 142–149.

Boesch, C. (2008). Why do chimpanzees die in the forest? The challenges of understanding and controlling for wild ape health. *American Journal of Primatology, 70*, 722–726. http://dx.doi.org/10.1002/ajp.20571.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution.* Oxford, U.K.: Oxford University Press.

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. *American Journal of Primatology, 70*, 519–532. http://dx.doi.org/10.1002/ajp.20524.

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

Brown, M. J., Ferruzzi, M. G., Nguyen, M. L., Cooper, D. A., Eldridge, A. L., Schwartz, S. J., et al. (2004). Carotenoid bioavailability is higher from salads ingested with full-fat than with fat-reduced salad dressings as measured with electrochemical detection. *American Society for Clinical Nutrition, 8*, 396–403.

Byrne, R. W., Noser, R., Bates, L. A., & Jupp, P. E. (2009). How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour, 77*, 1–13. http://dx.doi.org/10.1016/j.anbehav.2008.11.014.

Calvert, J. J. (1985). Food selection by Western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia, 65*, 236–246.

Carlson, B. A., Rothman, J. M., & Mitani, J. C. (2013). Diurnal variation in nutrients and chimpanzee foraging behavior. *American Journal of Primatology, 75*, 342–349.

Chamberlain, J., Nelson, G., & Milton, K. (1993). Fatty-acid profiles of major food sources of howler monkeys (*Alouatta palliata*) in the Neotropics. *Experientia, 49*, 820–824.

Chapman, C. A., & Chapman, L. J. (1991). The foraging itinerary of spider monkeys: when to eat leaves? *Folia Primatologica, 56*, 162–166.

Chapman, C. A., Chapman, L. J., Wrangham, R. W., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica, 24*, 527–531.

Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., & Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology, 15*, 189–211.

Chivers, J. D. (1998). Measuring food intake in wild animals: primates. *Proceedings of the Nutrition Society, 57*, 321–332.

Conklin-Brittain, N. L., Knott, C. D., Anderson, D., & Wrangham, R. W. (2006). Energy intake by wild chimpanzees and orangutans: methodological considerations and preliminary comparison. In G. Hohmann, M. Robbins, & C. Boesch (Eds.), *Feeding ecology in apes and other primates* (pp. 445–465). Cambridge, U.K.: Cambridge University Press.

Conklin-Brittain, N. L., Wrangham, R. W., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. II. Macronutrients. *International Journal of Primatology, 19*, 971–998.

Conner, W. E. (2000). Importance of n-3 fatty acids in health and disease. *American Journal of Clinical Nutrition, 71*, 171S–175S.

Crawford, M. A. (1992). The role of dietary fatty acids in biology: their place in the evolution of the human brain. *Nutrition Reviews, 50*, 3–11.

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

Dew, J. L., & Boubli, J. P. (2005). *Tropical fruits and frugivores: The search for strong interactors.* Dordrecht, The Netherlands: Springer.

Dobson, A. J. (2002). *An introduction to generalized linear models.* Boca Raton, FL: Chapman & Hall/CRC.

Doran-Sheehy, D. M., Mongo, P., Lodwick, J., & Conklin-Brittain, N. L. (2009). Male and female western gorilla diet: preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. *American Journal of Physical Anthropology, 140*, 727–738.

FAO (2003). Food energy − methods of analysis and conversion factors. *Food and agriculture organization of the United Nations: Roma. Report of a technical workshop.* Food and Nutrition paper 77. Rome, Italy: FAO.

Field, A. (2005). *Discovering statistics using SPSS.* London, U.K.: Sage.

Fleagle, J. G. (1988). *Primates: Adaptation and evolution.* San Diego, CA: Academic Press.

Fleagle, J. G., & Reed, K. E. (1996). Comparing primate communities: a multivariate approach. *Journal of Human Evolution, 30*, 489–510.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*, 47–55.

Fox, J., & Weisberg, S. (2011). *An R companion to applied regression.* London, U.K.: Sage.

Frankie, G. W., Baker, H. G., & Opler, P. A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology, 62*, 881–919.

Fürtbauer, I., Mundry, R., Heistermann, M., Schülke, O., & Ostner, J. (2011). You mate, I mate: macaque females synchronize sex not cycles. *PLoS one, 6*(10), e26144. http://dx.doi.org/10.1371/journal.pone.0026144.

Ganas, J., Ortmann, S., & Robbins, M. M. (2008). Food preferences of wild mountain gorillas. *American Journal of Primatology, 70*, 927–938.

Garber, A. P. (1992). Vertical clinging, small body size, and the evolution of feeding adaptations in the *Callitrichinae. American Journal of Physical Anthropology, 88*, 469–482.

Gentry, A. H. (1983). Dispersal ecology and diversity in neotropical forest communities. In K. Kubitzki (Ed.), *Dispersal and distribution* (pp. 303–314). Berlin, Germany: Verlag Paul Parey.

Goné Bi, Z. B. (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* (Unpublished Ph.D. dissertation). Abidjan, Côte d'Ivoire: Université de Cocody.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior.* Harvard, MA: Harvard University Press.

Guillaumet, J. L. (1967). *Recherches sur la végétation et la flore de la région du Bas-Cavally (Côte d'Ivoire).* Paris, France: Mémoires ORSTOM.

Hashimoto, C., Suzuki, S., Takenoshita, Y., Yamagiwa, J., Basabose, A. K., & Furuichi, T. (2004). How fruit abundance affects the chimpanzee party size: a comparison between four study sites. *Primates, 44*, 77–81.

Hladik, C. M., & Simmen, B. (1996). Taste perception and feeding behavior in nonhuman primates and human populations. *Evolutionary Anthropology, 5*, 58–71.

Hohmann, G., Potts, K., N'Guessan, A., Fowler, A., Mundry, R., Ganzhorn, J. U., et al. (2010). Plant foods consumed by *Pan*: exploring the variation of nutritional ecology across Africa. *American Journal of Physical Anthropology, 141*, 476–485.

Holloway, W. D., Tasman-Jones, C., & Lee, S. P. (1978). Digestion of certain fractions of dietary fiber in humans. *The American Journal of Clinical Nutrition, 31*(6), 927–930.

Houle, A., Conklin-Brittain, N. L., & Wrangham, R. W. (2014). Vertical stratification of the nutritional value of fruit: macronutrients and condensed tannins. *American Journal of Primatology, 76*, 1207–1232.

Janmaat, K. R. L., Ban, S. D., & Boesch, C. (2013). Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. *Animal Behaviour, 86*, 1183–1205.

Janmaat, K. R. L., Byrne, R. W., & Zuberbühler, K. (2006). Evidence for a spatial memory of fruiting states of rainforest trees in wild mangabeys. *Animal Behaviour, 72*, 797–807.

Janmaat, K. R. L., Chapman, C. A., Meijer, R., & Zuberbühler, K. (2012). The use of fruiting synchrony by foraging mangabey monkeys: a 'simple tool' to find fruit. *Animal Cognition, 15*, 83–96.

Janmaat, K. R. L., Polansky, L., Ban, S. D., & Boesch, C. (2014). Wild chimpanzees plan their breakfast time, type, and location. *Proceedings of the National Academy of Sciences of United States of America, 111*, 16343–16348.

Janson, C. H. (2007). Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition, 10*, 341–356.

Janson, C. H., & Chapman, C. A. (1999). Primate resources and the determination of primate community structure. In J. G. Fleagle, C. Janson, & K. Reed (Eds.), *Primate communities* (pp. 237–267). Cambridge, U.K.: Cambridge University Press.

Jenkins, D. J., Wolever, T. M., Rao, A. V., Hegele, R. A., Mitchell, S. J., Ranson, T. P., et al. (1993). Effect on blood lipids of very high intakes of fiber in diets low in saturated fat and cholesterol. *New England Journal of Medicine, 329*, 21–26.

Joly, M., Scheumann, M., & Zimmermann, E. (2008). Wild mouse lemurs revisit artificial feeding platforms: implications for field experiments on sensory and cognitive abilities in small primates. *American Journal of Primatology, 70*, 892–896.

Kalko, E. K. V., Herre, E. A., & Handley, C. O., Jr. (1996). Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography, 23*, 565–576.

Kouakou, C. Y., Boesch, C., & Kuehl, H. (2011). Identifying hotspots of chimpanzee group activity from transect surveys in Taï National Park, Côte d'Ivoire. *Journal of Tropical Ecology, 27*, 621–630.

Kuroda, S., Nishihara, T., Suzuki, S., & Oko, R. A. (1996). Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 71–81). Cambridge, U.K.: Cambridge University Press.

Laska, M., Sanchez, E. C., & Ernesto, R. (1998). Relative taste preferences for food-associated sugars in the spider monkey (*Ateles geoffroyi*). *Primates, 39*, 91–96.

Leendertz, F., Pauli, G., Maetz-Rensing, K., Boardman, W., Nunn, C., Ellerbrok, H., et al. (2006). Pathogens as drivers of population declines: the importance of systematic monitoring in great apes and other threatened mammals. *Biological Conservation, 131*, 325–337.

Lehmann, J., & Boesch, C. (2004). Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Taï National Park, Côte d'Ivoire. *Behavioral Ecology, 14*, 642–649.

Martin, P., & Bateson, P. (2007). *Measuring behaviour: An introductory guide.* Cambridge, U.K.: Cambridge University Press.

Matsumoto-Oda, A., & Hayashi, Y. (1999). Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica, 70*, 154–162.

Maynard, L. A., Loosli, J. K., Hintz, H. F., & Warner, R. G. (1979). *Animal nutrition* (7th ed.). New York, NY: McGraw Hill.

Milton, K. (1977). *The foraging strategy of the howler monkey in the tropical forest of Barro Colorado Island, Panama* (Unpublished Ph.D. thesis). New York, NY: New York University.

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *American Naturalist, 114*, 362–378.

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropologist, 83*, 534–548.

Milton, K. (1999). Nutritional characteristics of wild primate foods: do the diets of our closest living relatives have lessons for us? *Nutrition, 15*, 488–498.

Milton, K. (2003). The critical role played by animal source foods in human (*Homo*) evolution. *Journal of Nutrition, 133*, 3886S–3892S.

Milton, K., & Demment, M. W. (1988). Digestion and passage kinetics of chimpanzees fed high and low fiber diets: comparison with human diets. *Journal of Nutrition, 118*, 1082–1088.

Motta-Junior, J. C., & Martins, K. (2002). The frugivorous diet of the maned wolf, *Chrysocyon brachyurus* in Brazil: ecology and conservation. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution, and conservation* (pp. 291–303). Oxford, U.K.: CABI Publishing.

Mundry, R. (2015). *boot.lme.mr.2: An R function to calculate confidence intervals for (Generalized) linear mixed models fitted with lme4.* Leipzig, Germany: Max Planck Institute for Evolutionary Anthropology.

Myers, N. (1980). *Conversion of tropical moist forests.* Washington, DC: National Academy of Sciences.

N'Goran, P. K., Boesch, C., Mundry, R., N'Goran, E. K., Herbinger, I., Yapi, F. A., et al. (2012). Hunting, law enforcement, and African primate conservation. *Conservation Biology, 26*, 565–571.

Newton-Fisher, E. N. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. *African Journal of Ecology, 37*, 344–354.

Nishida, T. (1990). A quarter century of research in the Mahale Mountains: an overview. In T. Nishida (Ed.), *The chimpanzees of the Mahale Mountains: sexual and life history strategies.* Tokyo, Japan: University of Tokyo Press.

Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (*Pan troglodytes verus*) remember the location of numerous fruit trees. *Animal Cognition, 12*, 797–807.

Noser, R., & Byrne, R. W. (2007). Travel routes and planning of visits to out-of-sight resources in wild chacma baboons, *Papio ursinus. Animal Behaviour, 73*, 257–266.

Noser, R., & Byrne, R. W. (2013). Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology, 76*, 399–409.

Nunes, A. (1995). Foraging and ranging patterns in white-bellied spider monkeys. *Folia Primatologica, 65*, 85–99.

Nunnally, J. C. (1978). *Psychometric theory* (2nd ed.). New York, NY: McGraw-Hill.

N'Guessan, A. K. (2012). *Aspects quantitatifs et qualitatifs du régime alimentaire des chimpanzés (*Pan troglodytes verus, *Blumenbach 1779) au Parc National de Taï, Côte d'ivoire* (Unpublished Ph.D. dissertation). Abidjan, Côte d'Ivoire: Université de Cocody.

N'Guessan, A. K., Ortmann, S., & Boesch, C. (2009). Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology, 30*, 481–496.

Papagiannidou, E., Tsipis, A., Athanassiadou, A. M., Petrou, E., & Athanassiadou, P. (2013). Dietary energy density, satiety and weight management. *Journal of Allergy and Therapy, 2*, 585. http://dx.doi.org/10.4172/scientificreports.585.

Peres, C. A. (1991). *Ecology of mixed-species groups of tamarins in Amazonian Terra Firme Forests* (Unpublished Ph.D. dissertation). Cambridge, U.K.: Cambridge University.

Polansky, L., Werner, K., & George, W. (2015). Elucidating the significance of spatial memory on movement decisions by African savannah elephants using state–-space models. *Proceedings of the Royal Society of B: Biological Sciences, 282,* 20143042. http://dx.doi.org/10.1098/rspb.2014.3042.

Porter, L., Garber, P., Boesch, C., & Janmaat, K. R. L. (2016). Using GIS to examine long-term foraging strategies in tamarins and chimpanzees. In C. Shaffer, F. Dolins, J. Hickey, N. Nibbelink, & L. Porter (Eds.), *GPS and GIS for primatologists: A practical guide to spatial analysis.* Cambridge, U.K.: Cambridge University Press (in press).

Poulsen, J. R., Clark, C. J., Connor, E. F., & Smith, T. B. (2002). Differential resource use by primates and hornbills: implications for seed dispersal. *Ecological Society of America, 83,* 228–240.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists.* New York, NY: Cambridge University Press.

R Core Team. (2014). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Reiner, W. B., Petzinger, C., Power, M. L., Hyeroba, D., & Rothman, J. M. (2014). Fatty acids in mountain gorilla diets: implications for primate nutrition and health. *American Journal of Primatology, 76,* 281–288. http://dx.doi.org/10.1002/ajp.22232.

Remis, M. J. (1997). Gorillas as seasonal frugivores: use of resources that vary. *American Journal of Primatology, 43,* 87–109.

Remis, M. J. (2002). Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *International Journal of Primatology, 23,* 231–249.

Reynolds, V., Plumptre, A. J., Greenham, J., & Harborne, J. (1998). Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. *Oecologia, 115*(3), 331–336.

Richard, A. F. (1985). Primate diets: patterns and principles. In A. F. Richard (Ed.), *Primates in nature* (pp. 163–205). New York, NY: W. H. Freeman.

Robinson, J. G. (1986). Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. *Smithsonian Contributions to Zoology, 431.*

Rogers, M. E., Maisels, F., Williamson, E., Fernandez, M., & Tutin, C. E. G. (1990). Gorilla diet in the Lope Reserve, Gabon: a nutritional analysis. *Oecologia, 84,* 326–339.

Rolls, B. J. (1985). Experimental analyses of the effects of variety in a meal on human feeding. *American Journal of Nutrition, 42,* 932–939.

Rothman, J. M., Chapman, C. A., & van Soest, P. J. (2012). Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology, 33,* 542–566.

Rozin, P., & Kennel, K. (1983). Acquired preferences for piquant foods by chimpanzees. *Appetite, 4,* 69–77.

van Schaik, C. P., van Noordwijk, M. A., De Boer, R. J., & Den Tonkelaar, I. (1983). The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology, 13,* 173–181.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1,* 103–111.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology, 20,* 416–420.

Schoener, T. W. (1983). Simple models of optimal feeding territory size: a reconciliation. *American Naturalist, 121,* 608–629.

Shanahan, M., So, S., Compton, S. G., & Corlett, R. (2001). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews of the Cambridge Philosophical Society, 76,* 529–572.

Sigg, J., & Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia Primatologica, 36,* 40–75.

Simmen, B. (1994). Taste discrimination and diet differentiation in New World primates. In D. J. Chivers, & P. Langer (Eds.), *The digestive system in mammals* (pp. 150–165). Cambridge, U.K.: Cambridge University Press.

Simmen, B., & Hladik, C. M. (1998). Sweet and bitter taste discrimination in primates: scaling effects across species. *Folia Primatologica, 69,* 129–138.

Slavin, J. L. (2005). Dietary fiber and body weight. *Nutrition, 21,* 411–418.

van Soest, P. J. (1994). *Nutritional ecology of the ruminant.* Ithaca, NY: Cornell University Press.

Steiner, J., & Glaser, D. (1984). Differential behavioral responses to taste stimuli in primates. *Journal of Human Evolution, 13,* 709–723.

Terborgh, J. (1983). *Five new world primates.* Princeton, NJ: Princeton University Press.

Terborgh, J. (1986). Community aspects of frugivory in tropical forests. In A. Estrada, & T. H. Fleming (Eds.), *Frugivores and seed dispersal* (pp. 371–386). Dordrecht, The Netherlands: Dr W. Junk Publishers.

Tutin, C. E. G., Fernandez, M., Rogers, M. E., Williamson, E. A., & McGrew, W. C. (1991). Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. *Philosophical Transactions of The Royal Society of London B Biological Sciences, 334,* 179–186.

Vellayan, S. (1981). The nutritive value of *Ficus* in the diet of lar gibbon (*Hylobates lar*). *Malaysian Applied Biology, 10,* 177–182.

Wainwright, P., & Ward, G. (1997). Early nutrition and behavior: a conceptual framework for critical analysis of research. In J. Dobbing (Ed.), *Developing brain and behaviour: The role of lipids in infant formula* (pp. 387–414). San Diego, CA: Academic Press.

Waser, M. P. (1984). Ecological differences and behavioral contrasts between two mangabey species. In P. S. Rodman, & J. G. H. Cant (Eds.), *Adaptations for foraging in nonhuman primates: Contributions to an Organismal biology of prosimians, monkeys, and apes* (pp. 195–216). New York, NY: Columbia University Press.

Waser, M. P., & Floody, O. (1974). Ranging patterns of the mangabey, *Cercocebus albigena*, in the Kibale Forest, Uganda. *Zeitschrift für Tierpsychologie, 35,* 85–101.

Watts, D. P. (1985). Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla beringei*). *American Journal of Primatology, 8,* 1–10.

Wisniewski, L., Epstein, L. H., & Caggiula, A. R. (1992). Effect of food change on consumption, hedonics, and salivation. *Physiology and Behavior, 52,* 21–26.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In T. H. Clutton-Brock (Ed.), *Primate ecology* (pp. 504–538). London, U.K.: Academic Press.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Socio-ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 45–57). Cambridge, U.K.: Cambridge University Press.

Wrangham, R. W., Conklin-Brittain, N. L., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *International Journal of Primatology, 19,* 949–970.

Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology, 32,* 199–210.

Appendix

Table A1
Number of trees that coincided with a change point occurring at the feeding tree per species (Fig.1a)

Tree species	Number of trees where no change point occurred	Number of trees where a change point occurred at least once	% Trees at which change point(s) occurred
Chrysophyllum taiensis	11	8	42
Dialium aubrevillei	70	23	24
Drypetes aubrevillei	8	7	46
Duboscia macrocarpa	66	14	17
Ficus elasticoides	33	28	45
Ficus eriobotryoides	8	13	61
Ficus macrosperma	36	31	46
Ficus mucuso	3	0	0
Irvingia grandifolia	67	28	29
Klainedoxa gabonensis	294	103	25
Nauclea diderrichii	94	24	20
Nauclea xanthoxylon	6	1	14
Pachypodanthium staudtii	8	1	11
Panda oleosa	31	8	20
Parinari excelsa (fruit)	23	10	30
Parinari excelsa (nut)	18	8	30
Sacoglottis gabonensis	182	31	14
Scottelia klaineana	142	47	24
Sterculia oblonga	4	2	33
Treculia africana	10	9	47

Table A2
Number of trees that coincided with a change point occurring before and at the feeding tree per species (Fig.1b)

Tree species	Number of trees where no change point occurred	Number of trees where change point occurred at least once	% Trees at which change point(s) occurred
Chrysophyllum taiensis	11	2	15
Dialium aubrevillei	56	4	6
Drypetes aubrevillei	5	1	16
Duboscia macrocarpa	48	0	0
Ficus elasticoides	22	4	15
Ficus eriobotryoides	7	2	22
Ficus macrosperma	27	2	6
Ficus mucuso	2	0	0
Irvingia grandifolia	35	1	2
Klainedoxa gabonensis	192	25	11
Nauclea diderrichii	57	9	13
Nauclea xanthoxylon	7	0	0
Pachypodanthium staudtii	7	0	0
Panda oleosa	32	1	30
Parinari excelsa (fruit)	18	3	14
Parinari excelsa (nut)	12	3	20
Sacoglottis gabonensis	128	3	2
Scottelia klaineana	136	11	7
Sterculia oblonga	5	1	16
Treculia africana	8	5	38