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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-