



Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons



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We studied the nature of information that frugivorous foragers take into account to increase their chances of discovering bountiful fruit crops. We recorded the foraging behaviour of five adult female chimpanzees, *Pan troglodytes verus*, for continuous periods of 4–8 weeks, totalling 275 full days, throughout multiple fruiting seasons in the Taï National Park, Côte d'Ivoire. We found that chimpanzees fed on individual trees that were significantly larger than other available and reproductively mature trees of the same species, especially if their fruit emitted an obvious smell. Trees that were merely checked for edible fruit, but where monitoring could not have been triggered by olfactory or auditory cues because the tree did not carry fruit, were also significantly larger. Most trees were monitored along the way during travel, but 13% were approached in a goal-directed manner (assessed using a 'change point test'). These approaches were unlikely to have been initiated by visual cues and occurred more often when females foraged solitarily and when trees were large as opposed to small. Our results suggest that goal-directed monitoring is guided by a long-term 'what–where' memory of the location of large potential food sources. These findings were confirmed in a quasiexperiment that tested which of 15 876 potential food trees with different crown sizes were approached in a goal-directed manner. Observations on one female who was followed intensively over 3 consecutive years indicated that monitoring probability was highest for trees with which she had become more familiar through frequent previous visits and that had carried more fruit, suggesting that she was able to remember this information across fruiting seasons. Long-term phenological data on individual trees indicated that the interval between successive fruiting seasons, and hence the 'memory window' of chimpanzees required for effective monitoring activities, could be up to 3 years.

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Previous studies indicate that frugivores use spatial memory to relocate fruit-bearing trees (fruit bats: Holland et al. 2005; primates: reviewed in Janson & Byrne 2007; Zuberbühler & Janmaat 2010). However, it is less clear what strategies frugivores employ to find fruit in the first place. Fruit discovery can be especially challenging for species living in rainforest habitat in which individual trees show complex reproduction patterns, often with unpredictable timing (Milton 1980, 1991; van Schaik et al. 1993; Sakai 2001; Janmaat et al. 2012). To deal with this challenge, frugivores are known to complement search using sensory cues with other strategies that facilitate fruit discovery. For example, trees of a large number of rainforest species fruit simultaneously with other members of the same species (Hladik 1975; van Schaik et al. 1993; Chapman et al. 1999). Such species do not all fruit regularly and can

skip between 1 and 4 years (Wheelwright 1985; van Schaik et al. 1993; Sakai 2001; Chapman et al. 2005); however, animals can use the discovery of fruit in one tree as an indicator for its presence in others of the same species (spider monkeys, *Ateles geoffroyi*: Milton 1981; Japanese macaques, *Macaca fuscata*: Menzel 1991; grey-cheeked mangabeys, *Lophocebus albigena*: Janmaat et al. 2012; chimpanzees, *Pan troglodytes*: Janmaat et al. 2013).

To date, it is unknown whether the discovery of fruit-bearing trees simply triggers inspections of conspecific trees that are encountered along the way (Janmaat et al. 2013), or whether frugivores direct their travel towards these trees in order to monitor all or particular specimens and update themselves on the availability of edible fruit. As some individual trees produce consistently larger quantities of fruit or reproduce at more reliable rates than others, frugivores are expected to discriminate between the output of individual trees and be selective in the trees that they approach to check for fruit (Struhsaker 1997; Sakai 2001; Koenig et al. 2003; Janmaat 2006; Appendix Table A1). In this study, we examined whether chimpanzees, *P. t. verus*, in the Taï National Park, Côte

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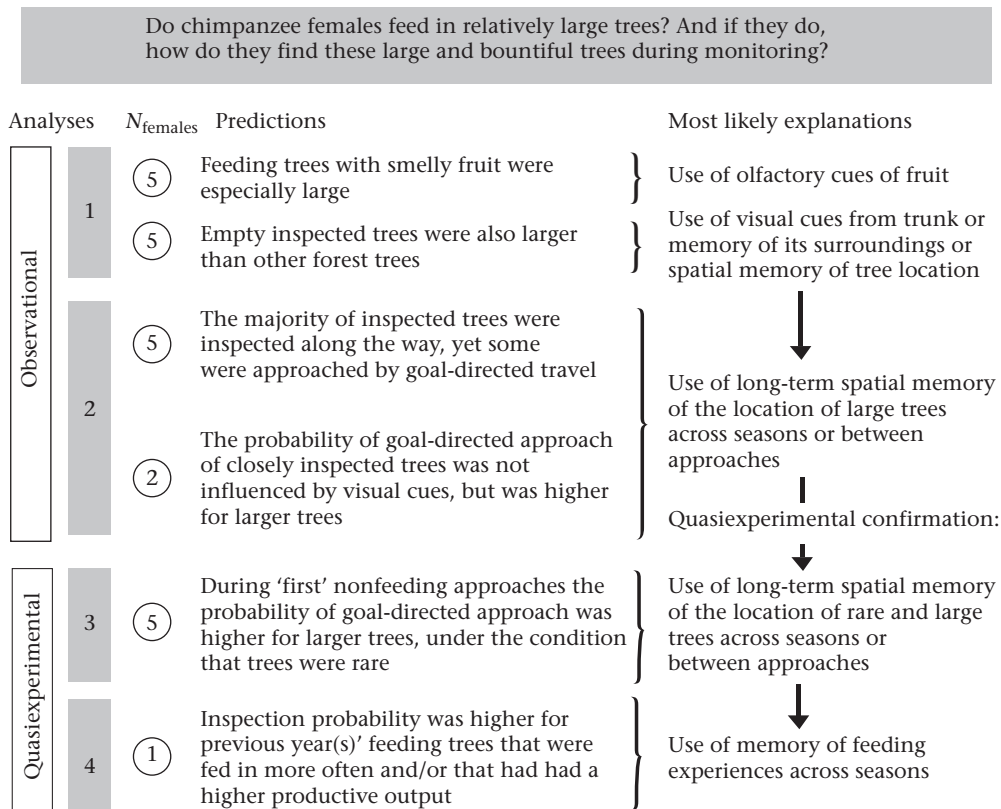


Figure 1. Diagram summarizing predictions and the sequence of steps in analyses.

d'Ivoire, discriminate between potential feeding trees and we investigated which cues (e.g. the smell of ripe fruit) and previous information (e.g. memory of feeding experiences) are taken into account during monitoring activities.

For the majority of trees in a chimpanzee's territory, reproductive history is typically unknown. However, we do know that trees with a large trunk diameter are likely to have carried large quantities of fruit (McFarland Symington 1987; Chapman et al. 1992) and produce fruit for longer periods once they fruit (Anderson et al. 2005). Feeding in trees with large trunks and crown sizes, furthermore, provides social benefits as it enables individuals to travel in parties and feed together (Isabirye-Basuta 1988; Wakefield 2008). Moreover, high absolute costs of travel and the cost and risk of climbing associated with large body size in chimpanzees (e.g. Risser et al. 1996; Jurmain 1997; Hanna et al. 2008) are likely to be traded off against the benefits of feeding in tree crowns with large fruit crops. We therefore predicted that chimpanzees would preferentially monitor larger trees, to increase the success rate of discovering large crops that can be exploited for longer periods. But what strategies do they employ to find these large trees?

Experimental studies indicate that captive chimpanzees are able to remember the quality, quantity and location of food items and the time elapsed before provisioning (i.e. 'what, where and when' memory), for up to 1 h (Martin-Ordas et al. 2010; Sayers & Menzel 2012). Observational studies in the wild also suggest that chimpanzees are able to remember their feeding durations at trees from previous visits (Normand et al. 2009). How long they remember these feeding events is unclear, but the average revisit interval was 5 days in the latter study. Are chimpanzees' 'memory windows', however, long enough to remember food characteristics across

seasons, long after food has been depleted, until trees restart their reproductive cycles and new food can be discovered?

We conducted 28–56 day-long focal follows of five adult chimpanzee females throughout multiple fruiting seasons and recorded their foraging behaviour. To investigate whether individuals discriminated between large and small trees we first tested whether the size of trees in which females fed was larger than that of alternative forest trees of the same species and reproductive size. Using a variety of data sets, we then investigated how the individuals had located the large trees (Fig. 1). In analysis 1, we tested whether feeding trees from species possessing smelly fruit (in which large crops can be more easily discovered using olfactory cues) were larger than trees with nonsmelly fruit. In addition, we tested whether trees that were monitored but were not currently bearing fruit (and therefore could not be located using olfactory or auditory cues such as the sound of other frugivores feeding on fruit) were also larger than the alternative conspecifics available. In analysis 2, we tested whether monitored trees were simply those passed along the way or whether they were potential travel goals. We also tested whether goal-directed travel towards such trees was initiated or guided by visual cues or long-term memory of the locations of large trees. Building on the results, we conducted two quasiexperiments (sensu Janson 2012) that used systematic observations of tree properties to measure their effect on the presence or absence of specific measures of monitoring behaviour. In analysis 3, for a set of 15 876 potential feeding trees of known location and size, we examined whether each was approached and, if so, whether goal-directed monitoring (i.e. the first targeted nonfeeding approach of a tree in the respective fruiting period) was more likely to occur if the trees were large

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