Animal Behaviour 86 (2013) 1183–1205

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Karline R. L. Janmaat [a,*], Simone D. Ban [a,b], Christophe Boesch [a]

[a] *Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*
[b] *Université de Félix Houphouët Boigny, Côte d'Ivoire*

ARTICLE INFO

Article history:
Received 1 December 2012
Initial acceptance 27 February 2013
Final acceptance 3 September 2013
Available online 25 October 2013
MS. number: 12-00902R

Keywords:
chimpanzee
foraging cognition
frugivore
long-term spatial memory
monitoring
Pan troglodytes verus
phenology
search strategy
sensory cues

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.

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

---

[*] Correspondence: K. R. L. Janmaat, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
E-mail addresses: karline_janmaat@eva.mpg.de, kjanmaat@hotmail.com (K. R. L. Janmaat).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.09.021

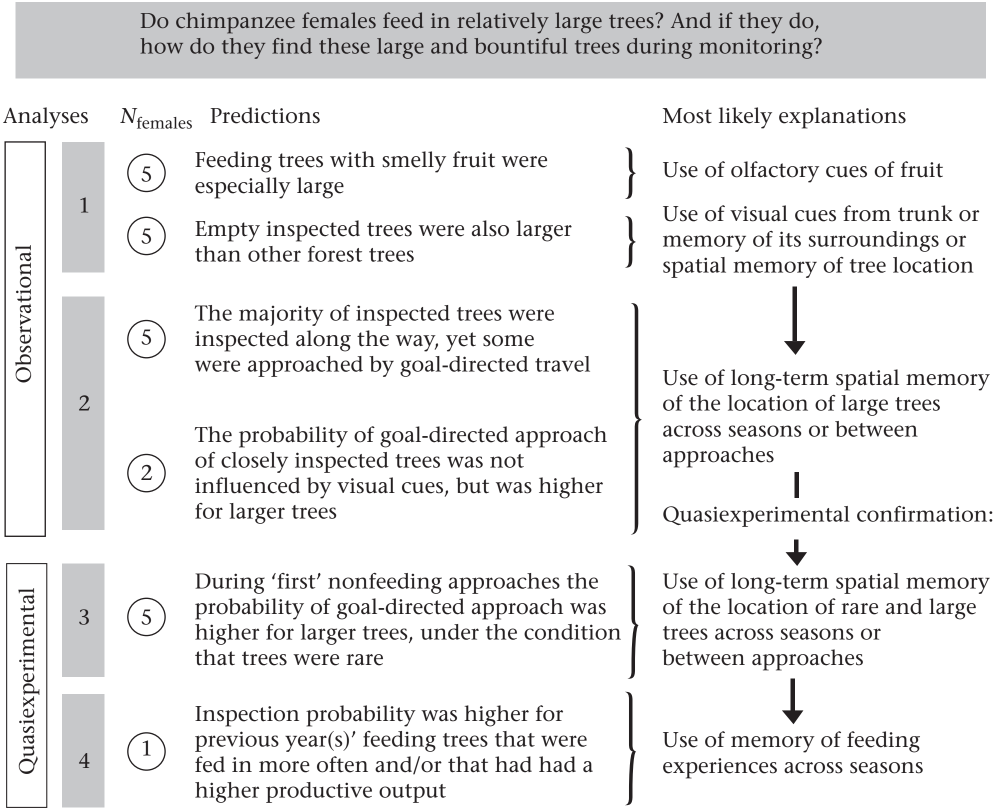

Figure 1. Diagram summarizing predictions and the sequence of steps in analyses.

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

Table 1
Maximum olfactory or visual detection distance (MDD) of tree species in which chimpanzees fed (mean = 37 m)

Species	MDD (m)	No. of observations	Species	MDD (m)	No. of observations
Agelaea paradoxa	24	3	*Irvingia grandifolia*	46	250
Alstonia boonei	33	3	*Keayodendron bridelioides*	37	22
Anthonotha fragrans	27	12	*Klainedoxa gabonensis*	68	1226
Celtis mildbraedii	37	2	*Landolphia dulcis*	28	12
Chrysophyllum taiense	46	107	*Landolphia foretiana*	36	59
Cordia platythyrsa	52	113	*Lannea welwitchii*	20	3
Coula edulis	50	47	*Leptaulus daphnoides*	13	3
Daniellia thurifera	28	6	*Mammea africana*	36	3
Dialium aubrevillei	41	421	*Maranthes aubrevillei*	24	6
Diospyros mannii	31	6	*Musanga cercopioides*	55	261
Diospyros sanza-minika	19	6	*Myrianthus arboreus*	40	12
Diospyros soubreana	29	3	*Myrianthus libericus*	38	10
Discoglypremna caloneura	21	3	*Nauclea diderrichii*	70	517
Drypetes aframensis	16	3	*Nauclea xanthoxylon*	40	32
Drypetes aubrevillei	36	25	*Oldfieldia africana*	24	3
Drypetes klainei	29	21	*Panda oleosa*	47	152
Duboscia macrocarpa	54	229	*Parkia bicolor*	40	11
Duguetia staudtii	37	44	*Parinari excelsa*	47	183
Entandrophragma cylindricum	21	3	*Pentaclethra macrophylla*	33	7
Erythrophleum ivorense	36	3	*Pouteria aningeri*	41	2
Erythroxylum mannii	61	102	*Pycnanthus angolensis*	38	19
Ficus artocarpoides	24	32	*Rhodognaphalon brevicuspe*	28	6
Ficus elasticoides	43	292	*Sacoglottis gabonensis*	48	760
Ficus conraui	70	28	*Scottelia klaineana*	59	1037
Ficus kamerunensis	50	143	*Scytopetalum tieghemii*	42	638
Ficus lyrata	42	27	*Spondianthus preussii*	16	6
Ficus mucuso	37	15	*Sterculia oblonga*	43	48
Ficus ottoniifolia	24	12	*Strombosia pustulata*	21	7
Ficus polita	100	73	*Tabernaemontana crassa*	18	3
Ficus pseudomangifera	24	16	*Treculia africana*	48	102
Ficus recurvata	70	14	*Trichoscypha arborea*	22	4
Ficus sansibarica	70	389	*Triplochiton scleroxylon*	40	5
Ficus saussureana	46	92	*Uapaca corbisieri*	41	178
Ficus thonningii	25	6	*Uapaca guineensis*	42	41
Ficus umbellata	45	30	*Vepris soyauxii*	43	6
Ficus vogeliana	30	19	*Vitex micrantha*	27	3
Garcinia kola	36	37	*Vitex rivularis*	39	3
Grewia carpinifolia	55	11	*Xylia evansii*	50	193
Grewia malacocarpa	50	121	*Zanha golungensis*	43	37
Hirtella butayei	30	14	Total		8418
Irvingia gabonensis	40	15			

rather than small. Finally, in analysis 4, we used the behaviour of one female who was observed over 3 consecutive years to test whether her monitoring of a set of 514 previous feeding trees was influenced by the frequency with which she had been feeding on these trees during the preceding year(s) and the trees' fruit output during these feeding events. Importantly, none of the monitoring behaviour we analysed was followed by a feeding bout. This enabled us to decrease the likelihood that approaches and subsequent monitoring had been guided by the smell of ripe fruit or the sounds of other chimpanzees or heterospecific foragers eating ripe fruit in that tree.

METHODS

Study Subjects and Data Collection

We followed five adult chimpanzee females during fruit-scarce periods, from 16 April 2009 to 30 August 2011, for successive continuous periods ranging from 4 to 8 weeks (total full days = 275). Their territory (South Group; 26.5 km^2) was located in the largest remaining tract (5363 km^2) of primary lowland rainforest in West Africa: Taï National Park, Côte d'Ivoire (Boesch et al. 2008; Kouakou et al. 2011; N'Goran et al. 2012). A target female was followed from the point of waking until construction of an evening sleeping nest, and her activity noted using continuous focal sampling (Martin & Bateson 2007). Duration and location of each activity were recorded using a combination of a GPS (Garmin 60 CSx) and voice recorder. To estimate the focal animal's location at all times, we used the GPS's track log function (see Appendix for accuracy measurements and data cleaning procedures). All trees in which she fed, or in which the crown was closely inspected (see below), were recorded with the GPS and marked with brightly coloured paint spray. To decrease the chance of disease transmission from humans to chimpanzees, females were typically followed by one observer at a time (Leendertz et al. 2006). 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 the Appendix). Potential observer differences in the recording of inspections were, in addition, controlled for in the third statistical model (analysis 4). The day after each focal observation day, trained assistants relocated each marked tree, identified the species, estimated crown size and fruit production class (see below) by checking its crown from all wind directions using binoculars, and obtained an accurate GPS measure of its location. The visual and olfactory detection distance of the tree trunk and crown were estimated by tape measuring the distance at which the human observers could smell the fruit and see the trunk and crown when walking away from the tree trunk in the arrival direction of

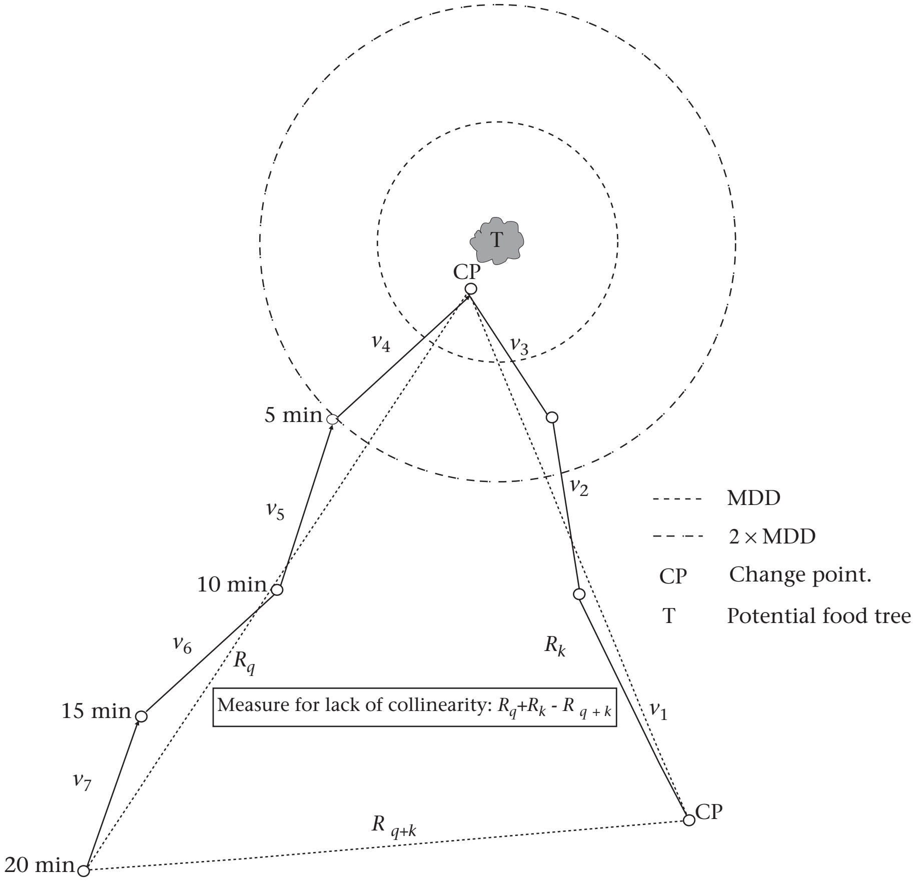

Figure 2. Illustration of a goal-directed approach towards a potential food tree. The route is viewed as a series of vectors v_7–v_1, each separated by 5 min (intervals without movement are discarded). This approach is considered to be goal-directed because a significant change point (CP) occurred within the maximum detection distance (MDD). The likelihood of a change point occurring between v_3 and v_4 within the detection distance of the potential food tree, i.e. a lack of collinearity between the arrival and departure routes, was examined by comparing the distances R_q ($q = 4$) and R_k (number of vectors from the last CP) with the length of the resultant R_{q+k} (see Byrne et al. 2009 for further details). In our analyses, all significant change points are typically preceded by 20 min of relatively straight-line travel.

the chimpanzee (which was uploaded in the assistant's GPS the previous night). Interpretation of these measurements was based on studies demonstrating that (1) visual acuity thresholds are lower for human than for nonhuman primates, since the latter typically possess smaller eyes and hence smaller retinal image size (e.g. Cavonius & Robbins 1973; Merigan & Katz 1990; Golla et al. 2004), and (2) nonhuman and human primates fall within the same range of olfactory performance with regard to sensitivity to isoamyl acetate, the major component in a large variety of fruit odours (Laska & Freyer 1997; Laska et al. 1999, 2000, 2003). As only 3% of travel bouts occurred within trees (*N* travel bouts = 1 523 961) we measured detection distances only from ground level (Table 1). The maximum estimated visual detection distances of the trunk and crown, and olfactory distance in the forest, were 62 m, 50 m and 100 m, respectively (*N* measures = 8418). Since human observers can easily spot fruit on branches (fruit diameter of 5 cm) in unobstructed forest view at 150 m, we assumed that chimpanzees travelling within these maximum detection distances of trees were able to update themselves on the presence or absence of fruit in these trees (Janmaat et al. 2006).

Measures of Monitoring Behaviour

In this study we used two measures to investigate monitoring behaviour, defined as updating of information on the ripening state or merely presence or absence of fruit in potential food trees. We only analysed monitoring behaviour towards trees of species that had been approached within a species' specific fruit observation period. This period ranged from the first to the last day that the females had observed fruit in a given species (via feeding or inspection of a fruit-bearing tree).

Distant versus close inspections

Our first measure of monitoring behaviour was visual inspection that occurred within the detection distance of a tree. Inspection was defined as a movement of the target female's head combined with a fixed gaze in the direction of a tree crown (Janmaat et al. 2013). The majority of recorded inspections occurred after the female came to a halt (95%). This measure has the advantage that it concerns a body movement that can be performed at all times and is least influenced by the ranging decisions of other party members. Close inspections were defined as inspections of trees that were then marked using the GPS and paint and for which the fruiting state could therefore be checked the next day by our assistants. Distant inspections were defined as inspections in which the tree concerned was at such a distance from the human observer that tree identity could not be assured by the observer and/or the tree was too far away to walk and mark the tree (owing to the risk of losing the target individual). The locations of these distant inspections were marked in the GPS only. (See the Supplementary material for video recordings of the two types of inspection.) Distant inspections were used only for analysis 4 and were collected consistently only in 2011, after data collection in 2010 revealed that our recordings of close inspections of the previous year's feeding trees (see below) were rare. To exclude the possibility that monitoring was guided by the sensory cues emitted by edible fruit we excluded all inspections that were directly followed by feeding at that tree. Inspections for sleeping locations, which occurred after the females had uttered a nest grunt (Nishida et al. 2010) and inspections during which monkeys or other chimpanzees were present in the tree (e.g. during hunting) were also excluded from the analyses.

Goal-directed monitoring: an indirect measure

As inspection is a fleeting behaviour, which one can easily fail to observe when following chimpanzees in a dense forest, we knew that we had not captured all monitoring events. Hence, we also used a second, indirect, measure termed goal-directed monitoring. This was defined as the first observed goal-directed approach towards a tree within its detection field and during the relevant fruit observation period in which the individual could potentially have checked the fruiting state of the tree (presence/absence of fruit), but after which no feeding occurred either on the tree or in its detection field. To determine whether the tree constituted a travel goal, we built on previous studies that found associations between significant changes in travel direction (change points) and biologically relevant 'goals', such as feeding trees (Byrne et al. 2009; Asensio et al. 2011; Noser & Byrne 2013). A goal-directed approach was defined as a relatively straight-line approach to within the maximum olfactory or visual detection distance of the tree, followed by a significant change in travel direction (change point; Fig. 2). To determine change points we used the 'change point test', a statistical method that objectively determines directional changes in animal travel routes. We used a significance criterion of 0.05, step interval = 5 min and $q = 4$, which has been argued to be best for chimpanzees in rainforest habitat (Byrne et al. 2009). Figure 2 illustrates that the change points in this study corresponded to a minimum (if the chimpanzee continued travel) of 20 min (4 × 5 min) of relatively straight travel, followed by a significant change in direction and subsequent straight-line travel away from the tree. We used a combination of R (R Development Core Team 2011), ARCGIS ArcMap version 9.2 (Esri, Redlands, CA, U.S.A.) and C# (Microsoft Visual Studio version 11.0.50727.1 RTMREL, http://www.microsoft.com/visualstudio/eng/products/visual-studio-ultimate-2012) to determine the change points, entries into and feeding occurring within the detection distances of potential food trees.

Investigating How Chimpanzees Discover Large Fruit Crops

Below we discuss how and why we collected and analysed four separate data sets to test our predictions. The four steps in the analysis are summarized in Fig. 1.

Data set for analysis 1

Did chimpanzees discriminate between large and small trees using sensory cues?. To investigate whether chimpanzees discriminate between individual fruit trees of different size, we first compared the trunk sizes of trees on which females chose to feed or inspect with those of other trees of the same species (control trees) in the females' territory. These control trees were encountered on botanical transects designed to measure the densities of reproductive trees with a diameter of the trunk at breast height (DBH) that was larger than 10 cm (Goné Bi 1999, 2007). Trunk size was measured as the DBH at 1.2 m above ground using a tape measure (Chapman et al. 1992). DBH is an indicator of crown size and is the best known predictor of biomass and fruit number (McFarland Symington 1987; Chapman et al. 1992; see Appendix for methodological details).

Since large feeding trees generally carry more fruit and so emit a stronger smell, any size difference between feeding and control trees might simply be explained by the greater probability of discovering larger trees when using olfactory cues. The geographical distance between consecutive fruit-bearing feeding trees was large (mean: 269 m), yet the range of distances was such that females could theoretically have smelled fruit-bearing trees from within a previous feeding tree (range 1–2796 m; N females = 5, N trees = 2100). To investigate this possibility we tested whether the size difference between feeding and control trees was especially large for species in which the fruit emitted an obvious smell, detectable by human observers, as compared to nonsmelly species. A species was defined to be nonsmelly if the fruit odour could not be detected at 10 cm from the human nose.

Data set for analysis 2

Was monitoring preceded by goal-directed travel?. Here we investigated whether close inspections were only triggered along the way, by positive associations made between previous feeding events and perceptual features that surrounded the inspected tree, or whether females also located large fruit-bearing trees by aiming their travel in the direction of these trees, by goal-directed approach (using the change point test mentioned above; Fig. 2).

Was targeted approach of inspected trees guided by visual cues or spatial memory?. We subsequently investigated whether the closely inspected trees that were approached in a goal-directed manner were larger than those that were not, and whether the probability of such an approach was influenced by visual cues (fruit availability) and search potential (the number of independent individuals in the female's party) or long-term spatial memory. To control for the possibility that goal-directed approach was caused by the presence of other food items close to the inspected tree, we recorded the location of all feeding events within the maximum olfactory and visual detection distance of the

Table 2

Number of productive trees of the 17 fruit species eaten by chimpanzees in the botanical map

Fed in*	Species	Species code	No. of trees in botanical map (17.8 km^2)	Estimated no. of trees in territory (26.5 km^2)
No	*Afzelia bella*	afzbel	64	95
Yes	*Treculia africana*	treafr	80	120
Yes	*Ficus elasticoides*	ficela	114	169
Yes	*Irvingia grandifolia*	irvgra	121	180
No	*Pouteria aningeri*	pouani	148	220
No	*Dacryodes klaineana*	dackla	344	512
No	*Zanha golungensis*	zangol	352	526
Yes	*Parinari excelsa*	parexc	655	974
Yes	*Sterculia oblonga*	steobl	658	977
Yes	*Klainedoxa gabonensis*	klagab	746	1,108
Yes	*Nauclea diderrichii*	naudid	785	1,169
No	*Trichoscypha arborea*	triarb	924	1,374
Yes	*Panda oleosa*	panole	1,280	1,904
Yes	*Dialium aubrevillei*	diaaub	1,499	2,231
Yes	*Sacoglottis gabonensis*	sacgab	1,929	2,871
Yes	*Chrysophyllum taiense*	chrtai	2,248	3,339
No	*Xylia evansii*	xyleva	3,907	5,811
	Total		15,854	23,583

* Some species were not observed to be consumed during the data collection period, indicated in this column by 'No'.

inspected tree. Since fruits eaten by chimpanzees grow not only in trees but also in strangler figs and lianas, we estimated and standardized these plants' crown sizes in three separate ways and refer to each as the estimated crown size (see Appendix for details of how these values were made comparable). Since the majority of chimpanzee fruit species are trees, we refer to them as trees (rather than trees, figs and lianas) in the remainder of the text. We only included species on which the females fed and excluded those for which the females consumed both leaves and fruit as in the latter case it was unclear whether monitoring was prompted by an interest in fruit.

Data set for analysis 3

Was goal-directed monitoring guided by spatial memory of large trees?. After finding that females not only inspected along the way, but also aimed their travel towards especially large potential food trees to check for edible fruit at close range, we decided to use the second indirect measure of monitoring (goal-directed monitoring, see above) to investigate further the use of long-term spatial memory using a larger data set and a quasiexperimental approach (sensu Janson 2012). For this, we first created a botanical map with the location and trunk size of all the potential feeding trees of 17 fruit species within a 17.8 km^2 area, overlaying the females' core area (Table 2). Subsequently, we used this set of trees to test whether females were indeed more likely to perform goal-directed monitoring towards large compared to small trees.

We selected all cases in which one of the five target females entered the vicinity (defined as twice the maximum detection distance) of a tree on the botanical map and analysed whether or not the female performed goal-directed monitoring towards the tree. We predicted that an effect of trunk size on probability of goal-directed monitoring would be significant only for rare, but not for common, species. This was based on our expectation that a memory of the size and location of individual trees is acquired through previous feeding experiences at those trees. Since the number of large trees on which our target females had fed was limited in comparison with the total number of available trees in their territory, we expected females to perform goal-directed monitoring towards only a proportion of the available trees. For this reason, many large-trunked trees belonging to common species were expected to be passed along the way, making it likely that an effect of trunk size on the probability of goal-directed monitoring would not be apparent in common species (see Fig. A10 in the Appendix). We therefore hypothesized that the effect of tree size on the probability of goal-directed monitoring would be significant only for species that had an equal or lower estimated number of trees in the territory (Table 2) than the estimated number of trees of that species in which the target female had fed (and thus could remember) through its own feeding experience. The latter was estimated using extremely long continuous following periods that provided us with uniquely detailed information on the number of individual trees in which females fed (Table 3).

Table 3
Estimation of the maximum number of trees per species in which a target female could have fed, assuming that all species are equally utilized and using the generous assumption that each season females feed upon and learn the sizes and locations of a set of uniquely new trees

Mean no. of new trees fed in per day (N=5 females, 275 days)	4.63
Total no. of new trees fed in per year	1690
Estimated age of oldest target female, in years	39
Likely age of dispersion, in years (Goodall 1986; Boesch and Boesch-Achermann 2000)	11
No. of years of memory building	28
No. of trees fed in during a female's entire stay in the territory	47318
No. of fruit species eaten by Tai chimpanzees (Goné Bi 1999; C. Boesch, unpublished data)	152
Max. no. of trees per species that a target female could remember through feeding experience	311

To ascertain that the botanical map trees (for which no measurements of individual detection distances were conducted) could not be detected at the moment that the target female entered within their vicinity, we defined detection distance as the maximum detection distance of all the measured trees of each respective species. Our 'vicinity' definition (twice the maximum detection distance) was based on the reasoning that it was sufficiently close to the tree for the target female not to lose contact with other party members during approach, but sufficiently far to ensure that the female could not see the tree (Table 1). To improve our chances of capturing monitoring events, we analysed only the first time that the target female entered within the vicinity of an individual tree during its species- and year-specific fruit observation period, so that we decreased the probability that the entry occurred when the tree was already depleted. In addition, we selected only cases in which the target female did not feed on any food within the detection distance. Furthermore, we excluded *Zanha golungensis* trees as we analysed travel only towards tree species for which the fruit observation period lasted at least 1 week, again to avoid including trees that were at the end of their season and likely to have been approached previously. Finally, we included only species from the botanical map on which females fed within the observation period of the entire study and excluded those for which the females foraged on both leaves and fruit (*Sterculia oblonga*) as it was unclear whether the monitoring event involved an interest in fruit (N species selected for analysis = 10). The botanical map was established by walking line transects located 15 m apart, using a handheld GPS displaying a virtual transect created in MapSource software. In total we mapped 15 876 trees in an area of 3.9 km (east–west) by 4.6 km (north–south) between November 2008 and November 2011 (see Appendix for details on methodology).

Data set for analysis 4

What did chimpanzees remember about large trees?. If chimpanzees remembered the locations of large trees, for what length of time did they remember and on what information was this memory based? Did they remember large trees because they had become more familiar with them because of a higher frequency of feeding there in the past, as large trees produce fruit for longer periods and probably for more years? Or did females specifically remember the bountiful crop that these trees had produced the previous season? To address these questions we followed one target female continuously for 4, 8 and 8 weeks in 2009, 2010 and 2011, respectively. In the second and third years we attempted to cover the same fruiting seasons, by commencing 4 and 2 weeks, respectively, before the starting date of the 2009 period. We recorded the location and productive output of all trees she fed on in 2009 and 2010, and conducted a second quasiexperiment to determine which tree properties influenced the probability that this female would monitor these same trees in 2011 (see Fig. A9 in the Appendix for a map of the locations of trees and ranging). The target female fed in a total of 514 trees in 2009 and 2010. Of these trees, 505 belonged to a species for which sufficient trees were measured to standardize the crown size estimations. Of these 505 trees, 180 were approached to within detection distance in 2011. All 180 trees belonged to species on which this female also fed in 2011 (N species = 18). On her first approach within a respective fruit observation period 32 trees were fed on and 148 were not. We analysed the female's monitoring behaviour (close and distant inspections) on

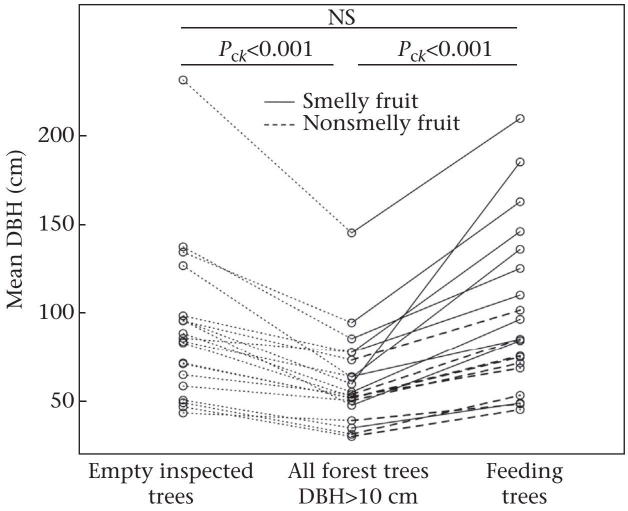

Figure 3. A comparison of the mean trunk size (DBH) of closely inspected trees that were not carrying fruit (empty), feeding trees and control trees that were of productive size (all forest trees with DBH >10 cm). Each circle represents the mean DBH value of a fruit tree species and the lines in between represent the differences between the means of the different tree types belonging to the same fruit species.

these first approaches towards the 148 trees in which she did not feed.

The productive output of feeding trees during the 2009 and 2010 visits was measured as the proportion of fruit (both ripe and unripe) observed out of the estimated total that can be produced, ranked on a relative scale from zero to four. Ranks 1, 2, 3 and 4 corresponded to 1–25%, 26–50%, 51–75% and 76–100% of the branches being observed to bear fruit, respectively (see Chapman et al. 1994; Anderson et al. 2005 and the Appendix for details of these measurements and results of interobserver tests). We calculated the maximum of all productive outputs observed in 2009 and 2010 and defined this as the maximum fruit production class.

Statistical Analyses

For analysis 1 we used Welch's *t* test and a repeated measures ANOVA with paired *t* tests as post hoc tests. The analyses were implemented in R using the packages 'exactRankTests' and 'ez' (Hothorn & Hornik 2011; Lawrence 2011). After log-transformation of the mean DBH, visual inspection of the residuals from the standard linear model revealed no obvious deviation from the assumptions of normally distributed and homogeneous residuals (Zuur et al. 2010). The sphericity assumption was not violated ($P > 0.59$). We adjusted alpha levels for the post hoc *t* tests using a conversion of the Dunn–Šidák method (Sokal & Rohlf 1995; Kipper et al. 2006) to control for multiple testing. We denote these corrected *P* values as P_{ck}, with *k* indicating the number of tests controlled for. For analyses 2, 3 and 4 we ran three generalized linear mixed models with binomial error structure and a logit link function (GLMM; Baayen 2008) using the function lmer provided by the R package lme4 (Bates et al. 2011). To check the overall significance of the combined set of predictor variables, we ran likelihood ratio tests (Dobson 2002) to compare each full model with a respective null model containing only the random effects and control predictors. We considered the effect of individual predictors only if the initial full model reached significance (Forstmeier & Schielzeth 2011). To create stable models certain predictors were log-transformed to produce roughly symmetric distributions prior to running models: the number of independent individuals present in a female's party during inspection (analysis 2) and the number of feeding visits in the previous year(s) (analysis 4; see Appendix for further details on model stability and collinearity testing). To avoid pseudoreplication we considered only the first close inspection observed (analysis 2), and the first observed entries to within (1) the vicinity of botanical map trees (analysis 3) and (2) the maximum detection distance of the previous year(s) feeding trees (analysis 4). Since fruiting trees get depleted and females were followed consecutively, we assumed that the monitoring behaviour of a target female is not influenced by the recorded monitoring behaviour of the other target females that came within the vicinity of the same trees at different time periods. We controlled for multiple testing by using Fisher's omnibus test, combining the *P* values from the different tests (three likelihood ratio tests, one ANOVA and one Welch's *t* test; Haccou & Meelis 1994; Quinn & Keough 2002). The overall H_0 is that all the H_0s in the set of tests are true. The test revealed an overall significant *P* value ($\chi^2_{10} = 98.13$, $P < 0.0001$). All tests were two tailed.

RESULTS

Did Chimpanzees Use Sensory Cues?

To investigate whether both feeding and closely inspected trees were larger than control trees, we tested the effect of the type of tree (as a within-subject factor) on trunk size. Overall, we found a significant difference between the trunk sizes of trees that were of the same species but different types (control trees, feeding trees and closely inspected trees that had an empty crown; RM-ANOVA: $F_{2,38} = 64.31$, $P < 0.001$; Fig. 3). The trunk sizes of trees in which chimpanzees fed were larger than those of control trees (first post hoc *t* test: $t_{19} = 9.90$, $P_{c3} < 0.001$; Fig. 3).

The difference between the mean trunk sizes of feeding trees versus control trees was higher for species with smelly fruit than for species that did not emit an obvious odour, suggesting that females used olfactory cues to find large fruit-bearing trees (Welch's *t* test conducted on ranked data: $t_{17.5} = -3.76$, $P_{c3} = 0.002$; mean difference in mean trunk sizes (in cm): smelly fruit = 53.36, *N* species = 11; nonsmelly fruit = 19.77, *N* species = 10).

To investigate whether females also took information from previous tree visits into account during their search for fruit-bearing trees, we conducted a second post hoc test and compared the sizes of trees that were inspected but did not contain any fruit with that of the control trees. We found that these empty trees (which obviously could not have emitted any olfactory or auditory cues, e.g. the sound of fruit falling) were also larger than control trees ($t_{19} = 9.66$, $P_{c3} < 0.001$; Fig. 3). Moreover, feeding trees and inspected empty trees did not differ significantly in size ($t_{19} = -2.19$, $P_{c3} = 0.119$). These results strongly suggest that the chimpanzees did not rely solely on olfactory or auditory cues to find large fruit trees. Either their monitoring activities were guided by (1) visual search for trees with large trunks or crowns, (2) formation of long-lasting positive associations from previous feeding visits with features in the area surrounding large trees, or (3) long-term memory of the location of large trees. To distinguish between the latter two possibilities we conducted the following analysis.

Was Monitoring Preceded by Goal-directed Travel?

We found that the majority of close inspections occurred 'along the way', either being triggered by visual cues or positive associations from previous feeding events once the female was in the area

Table 4
Effect of crown size and other predictor variables on the probability of goal-directed approach towards inspected trees

Predictor	Estimate	SE	*Z*	*P*
Intercept	−2.38	0.18		
Estimated crown size	0.25	0.09	2.75	0.006
Number of party members	−0.20	0.10	−1.95	0.051
Fruit in crown (yes)	-0.04	0.19	-0.20	0.845
Feeding close to inspected tree (yes)	0.93	0.19	4.93	<0.001

surrounding the inspected tree (*N* trees = 1292, *N* species = 29, *N* females = 5). However, 13% of these close inspections were preceded by a goal-directed approach, suggesting that some inspections were anticipated from further away.

Did Chimpanzees Use Visual Cues or Spatial Memory?

We continued to investigate whether goal-directed approaches of inspected trees were more likely to occur for large than small trees and whether these approaches were guided by distant visual cues or long-term spatial memory. Hence, we designed a GLMM (see Methods) to measure the effect of the covariate estimated crown size and the categorical factor fruiting state (fruits: yes or no) on the probability of goal-directed approach to closely inspected trees. If chimpanzees mainly use visual cues to find large fruit crops we expected them to aim travel not only towards large trees, but especially towards trees that contain fruit, in order to inspect and check at closer range whether and how many fruits are ripe. In addition, we expected that if goal-directed approach was guided by sight the probability of such approaches would increase when chimpanzees were accompanied by others, since a larger party size increases search swath and the probability that at least one party member will spot the potential fruit-bearing tree from far away. For this reason, we included the number of independent individuals (all party members) present during inspections as a third predictor. For 8% of the inspected trees, females were observed to feed on other food items within the detection distance of the inspected tree. Hence, we also included the occurrence of feeding close (i.e. within the maximum detection distance) to the inspected tree (yes or no) as a control predictor in the model. Finally we included two random effects, chimpanzee individual and fruit species, to avoid pseudoreplication. To achieve a stable model we tested data only from the two target females that were followed for substantially longer periods (totalling 12 and 20 weeks) and for which we had sufficient recordings of goal-directed inspections. Overall, the full model was significant as compared to the null model (likelihood ratio test: $\chi^2_3 = 10.70$, $P = 0.013$, *N* inspected trees = 1078). Estimated crown size positively influenced the probability of goal-directed approach, also when we controlled for the (positive) effect of feeding activities close to the inspected tree (Table 4). However, fruiting state did not, and the number of party members had an unexpected negative influence on the probability of goal-directed approach (Table 4). The lack of influence of the presence/absence of any fruit crop and the negative impact of party size on goal-directed approach suggest that targeted approaches of inspected feeding trees were initiated or guided not by visual cues, but by a long-term spatial memory of the locations of large trees.

Did Chimpanzees Use Spatial Memory of Larger Trees?

Here, we verified the findings of the observational data collection in analysis 2 by means of a quasiexperiment combining data from a botanical map of all potential feeding tree locations with the

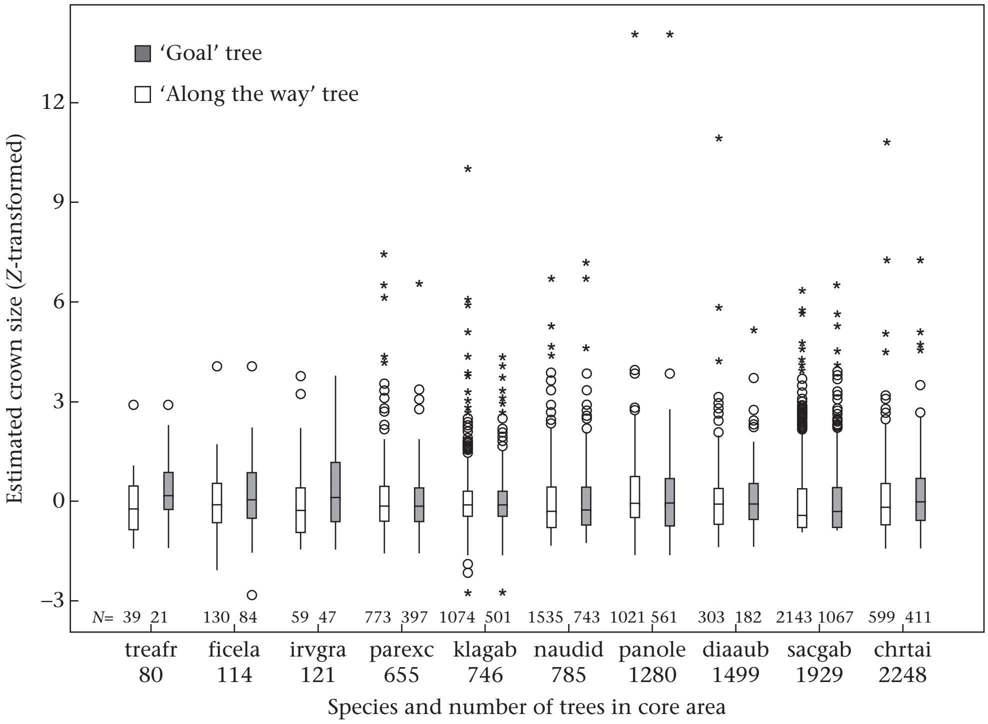

Figure 4. Estimated crown sizes of 'goal' and 'along the way' trees in 10 fruiting species ('goal' versus 'along the way' refers to trees that were or were not approached in a goal-directed manner, respectively). For species codes see Table 2. *N* represents the total number of times that the five females came within the vicinity of one of the mapped trees, for each species (using only the first entry without feeding in detection distance). Bars represent median values of estimated crown sizes; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 × the interquartile range; circles and asterisks represent outliers and extreme outliers, respectively.

ranging and feeding behaviour of all five females. We designed a GLMM (see Methods) that tested for an interaction between estimated crown size and the categorical factor density class (common or rare) on the probability of goal-directed monitoring of the (quasiexperimentally) preselected food trees when the females approached to within the vicinity (5824 of 15 876 trees) within their respective fruit observation periods. We expected an effect of tree size only on the probability of goal-directed monitoring for rare species, namely those possessing a lower estimated number of trees in the territory (Table 2) than the estimated total on which a female was likely to have fed in the past and thus remember (Table 3; N feeding trees per species = 311). Three species met this definition: *Irvingia grandiflora*, *Ficus elasticoides* and *Treculia africana* (Table 2). We included two random effects, chimpanzee individual and fruit species, to avoid pseudoreplication. The full model was significant compared to the null model ($\chi^2_3 = 8.91$, $P = 0.030$). A significant interaction was found between estimated crown size and density class (estimate $= -0.25 \pm 0.10$, $z = -2.48$, $P = 0.013$). Crown size had a positive impact on the probability of goal-directed monitoring, under the condition that the tree density was low (Fig. 4). The random effect ‘species’ had a significant effect, suggesting that females had a preference for checking the fruiting state of particular species more than others ($\chi^2_1 = 11.38$, $P = 0.001$). The results again suggest that females used a long-term spatial memory of the location of large potential feeding trees.

What did Chimpanzees Remember about Large Trees?

Using observations on one female that was followed in 3 subsequent years, we investigated what features of large trees are remembered and for how long. We designed a GLMM (see Methods) to measure the effect of the maximum fruit production class of the feeding trees used in 2009 and 2010, and the total number of times that the previous year(s)’ trees were fed in, upon the probability that a close or distant inspection (see Methods) occurred on the first occasion that the female entered within the species-specific maximum detection distance of a previous year(s)’ tree. Since the fruit production categories possess a true order we included this effect as a covariate by using the mean value for each fruit production category, so as not to discard information on the magnitude of the levels. We controlled for the effect of observer and tree species by including these as random effects. To control for the possibility that inspections were triggered by trees that possessed larger crown and trunk sizes, and so were more easily spotted, we included estimated crown size as a control predictor. Overall, the full model was significant compared to the null model (likelihood ratio test: $\chi^2_2 = 13.07$, $P = 0.001$). When we controlled for crown size both the number of feeding visits in previous year(s) and the maximum fruit production class had a significant impact on inspection probability (Table 5, Fig. 5; N approached = 148, N close inspections = 16, N distant inspections = 14). Of the closely inspected trees, 70% had a different fruit production class from that of the previous feeding year, which was on average higher.

Table 5
Effect of number of feeding visits in previous year(s) and other predictor variables on inspection probability

Predictor	Estimate	SE	Z	P
Intercept	−1.74	0.70		
Maximum fruit production class	0.47	0.23	2.02	0.043
Estimated crown size	0.13	0.23	0.55	0.581
No. of feeding visits in previous year(s)	0.58	0.22	2.62	0.009

DISCUSSION

By analysing the monitoring behaviour of five chimpanzee females, followed on foot for continuous periods of up to 8 weeks, we investigated chimpanzees’ abilities to discriminate between small and large rainforest trees and the underlying cognition used to discover large fruit crops. We found that the focal animals preferentially fed on larger trees, compared to alternative conspecific trees of reproductive size encountered on control transects. The difference in trunk size between trees used for feeding and controls was particularly marked in species that produced smelly as opposed to nonsmelly fruits. This is consistent with the possibility that chimpanzees use the smell of ripe fruit in their search for trees with large fruit crops. To investigate whether females also integrated information from previous tree visits in their search and to exclude the use of olfactory cues or the sounds produced by other frugivores foraging in a tree, we also compared the size of control trees with trees that were monitored but had no fruit. We found that trees that were monitored when they did not carry fruit were also significantly larger than the control trees. Moreover, they did not differ significantly in size from the feeding trees. This suggests that monitoring activities were prompted by (1) visual cues, given that trees with large trunks or crowns are easier to spot than smaller trees, (2) long-lasting positive associations from previous feeding visits and (perceptual) features in the area surrounding specific large trees or (3) a long-term memory of the location and size of these trees (Fig. 1).

To distinguish between the latter two possibilities we first investigated whether close inspections were preceded by targeted approaches or whether females only checked a tree’s fruiting state along their way, once they entered the area surrounding the tree. Even though most monitoring seemed to occur along the way, we found that 13% of the trees monitored were approached in a goal-directed manner. When controlling for the effect of other feeding activities in the area surrounding an inspected tree, we found that the probability of goal-directed approach was higher for trees possessing relatively larger crowns, yet it was not influenced by the presence of visual cues of a fruit crop. Furthermore, the effect of chimpanzee party size was negative, implying that the wider visual search swath potentially achieved by a larger number of individuals did not influence the probability of goal-directed approach. These results suggest that for at least a small percentage of trees, monitoring was not triggered by visual cues, but rather by a long-term memory of their size and location. By combining data on the location and size of 15 876 potential food trees in the females’ core area with the ranging locations of each of the five target females, we confirmed that chimpanzees were more likely to perform goal-directed monitoring (i.e. a first targeted approach early in a tree species’ respective fruit observation period, in which the chimpanzees had not yet fed on either the tree approached or in the area surrounding it) towards large than small trees. The measurements for this quasiexperiment started as soon as females entered the vicinity of a tree, defined as twice the maximum detection distance. We argue that from this distance the females were unable to detect the tree from ground level. The possibility that goal-directed approaches were initiated from a smaller distance (within the estimated visual detection field) was unlikely, as goal-directed approaches involved a minimum of 20 min of relatively straight-line travel (Fig. 2) yet it takes only 90 s of travel at average speed to reach a tree from the edge of the maximum visual detection field (maximum estimated detection distance of trunk and crown: 62 m and 50 m, respectively; N measurements = 2272; speed: mean = 0.69 m/s, median = 0.57 m/s, N females = 5). Hence, we argue that goal-directed approaches were most likely to be initiated before the females were able to spot the trees. It is always possible that females had observed the existence and direction of

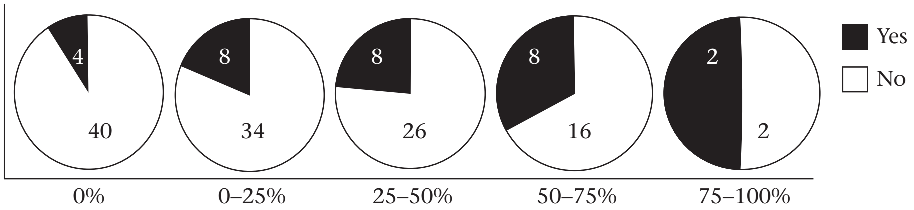

Figure 5. Proportion of inspections that occurred following the target female's first approach in 2011 to within the detection distances of trees in which she had fed during the previous year(s), according to the fruit production history of these trees. Only approaches that were not subsequently followed by feeding are included. Pie sections represent the proportion of first approaches followed by an inspection (shaded black) versus no inspection (white). Numerals indicate the number of trees involved. Percentages beneath the chart show the maximum fruit production class measured across 2009 and 2010.

large trees from within the crown of a previous feeding tree, while outside the detection field of those trees (not within, because trees for which entries coincided with feeding inside the detection field were excluded from the analysis). Yet, since 97% of all travel bouts concerned travel on the forest floor and none of the target females were observed to travel long distances in the canopy, females would need to have retained knowledge of the location of the spotted tree after their descent in order to travel directly towards it. Given that the Taï forest is flat, the view from the forest floor changes rapidly with every step owing to the high tree density (507 tree/ha for trees of DBH >10 cm; C. Chatelain, unpublished data), and we think it unlikely that females would be able to keep travelling straight towards such a tree without the use of a long-term memory of its location.

Combining this knowledge with the finding that the probability of goal-directed approach of inspected trees was not influenced by visual cues of the presence of fruit or the visual search potential of party members, we conclude that our results are best explained by the possibility that targeted monitoring was guided by a long-term 'what–where' memory of the location and size of potential food trees. Tree size influenced the probability of goal-directed monitoring only in rare species, which suggests that females either (1) specifically remember the sizes of rare trees, which seems adaptive as these can less easily be found using visual cues or (2) also remember the sizes of trees of more common species, but that the proportion of large 'goal trees' out of the total number of large trees in the population was too low for us to detect the use of memory where common species were concerned. Variation in the probability of goal-directed monitoring was only partly explained by the interaction between tree size and tree density. It is possible that monitoring probability was also influenced by the presence of other 'goals' that fell within the maximum detection distance of a tree, such as the presence of forest gaps suitable for grooming. Variation in monitoring probability might also be explained by incorrect assignment of significant changes in direction in the change point test (Byrne et al. 2009). Yet we see no reason why such 'goals' or errors would occur more often near large than small trees, and thus do not consider these possibilities as likely alternative explanations for our findings.

Our study was conducted during a period of fruit scarcity, in which all fruit species were considered to be important; however, we found a significant effect of the random factor fruit species on the probability of goal-directed monitoring. Whether fruit with particular nutritional content (e.g. high sugar content) is more likely to be monitored in a goal-directed manner is an interesting topic for future analysis. In addition, we suggest it is worth focusing on species that have just commenced their fruiting season, such as *Chrysophyllum taiense* and *Sacoglottis gabonensis* in our study (Fig. 4).

To investigate further whether females remembered the location of large trees from previous approaches or from feeding events in the previous fruiting season (cross-seasonal memory), and on what this memory might be based, we analysed the monitoring behaviour of one target female towards trees in which she had fed in the preceding 1 and/or 2 years. This revealed that both the number of feeding visits in previous year(s) and the maximum fruit production class of a tree had a significant impact on the probability that monitoring occurred. Since we controlled for crown size, we could exclude the alternative explanation that inspection was simply triggered by spotting the larger trunks of large-crowned trees along the way. It is puzzling that estimated crown size did not influence monitoring probability here. However, it is possible that in this case the variation in crown size was insufficient to reveal any effect because all trees in this sample had been feeding trees.

Since the analysis was based solely on the target female's initial entry to within a tree's detection distance during the species' fruit observation period, and the female did not continue to approach and feed on the fruit, it is unlikely that she was prompted to look up and inspect by obvious cues from the fruit. In addition, we found that in 70% of the closely inspected trees for which fruiting state was checked by our assistants, the maximum fruit production rating differed and was on the average lower than that of the year(s) before, making it more likely that inspections were guided by the previous rather than current fruit production class. The female particularly inspected when in the detection field of trees with which she had become more familiar, through frequent visiting in previous seasons (long-term temporal weighting; Devenport et al. 1997). We therefore conclude that our results are best explained by the possibility that she was able to remember this information across feeding visits and fruiting seasons. We encourage cognitive scientists to conduct follow-up studies on chimpanzees possessing smaller territories in forests with lower tree densities, which probably rely upon a smaller number of feeding trees. Such conditions are expected to increase the inspection rate across seasons and offer opportunities for more elaborate investigations of the effect of past versus current fruit production classes on monitoring behaviour and hence provide more detailed insights into the content of the stored (semantic or episodic-like) information (e.g. territory size in Kanyawara community is 14.9 km^2, Chapman & Wrangham 1993; with 406 trees/ha of DBH >10 cm, Chapman & Chapman 1997).

The Length of the Memory Window

It is difficult to pinpoint for how long the target female must have remembered these feeding experiences. In some species in the set of 514 feeding trees, individuals typically fruit once a year (e.g. *Scottelia klaineana*). In other species (e.g. *Ficus sansibarica*) individuals are, however, known to fruit twice per year (subannual) or more often (irregular; Goné Bi 2007; Polansky & Boesch 2013). So it is possible that some monitoring activities were based on feeding experiences that had occurred less than 1 year ago. If we consider our longest continuous period of phenological data collection (without interruption in monthly data collection; 41 consecutive months), we find that the fruit production intervals for tree species consumed by chimpanzees in the Taï forest range between 2 and 37 months (the greatest observed intervals were 37, 36 and 35 months for single trees of *Dialium aubrevillei*, *Diospyros sanza-minika* and *Pouteria aningeri* respectively; see Appendix). This suggests that the female's memory window had been at least 2 months and the effective window (the duration over which information needs to be remembered from previous feeding experiences to achieve successful monitoring) is expected to vary from 2 months to 3 years. Long-term phenology studies that have examined variation in the reproductive intervals of individual rainforest trees demonstrate that a wide range of intervals exists. Even *Ficus* fruit, which is often referred to as a fallback food with continuous fruiting patterns, reproduces at intervals of 47 weeks on average, with certain specimens observed to fruit only once in 16 years (Milton 1991; Janmaat 2006). Studies on pollinator stratification suggest that flowering frequency is lower in canopy species (large) than subcanopy species (small), but with higher amplitude (quantity of flowers) in canopy species (Sakai 2001). Similarly, associations were found with species density, with rare species exhibiting longer lags in flower emergence but more explosive production (Momose 2004). These studies suggest that particularly rare and large rainforest trees are worth making a detour for to see whether they have grown fruit, which is consistent with our findings. We found that such detours were less frequent when the females were more gregarious, as party size negatively influenced the probability of goal-directed approaches towards inspected trees. This implies that gregarious females have less need to make detours to monitor fruit trees, because they can find sufficient fruit in the presence of others (using their 'reservoir of knowledge on fruiting states'), and/or that being social constrains them from goal-directed updating on fruiting states of trees. The latter possibility concerns the difficulty of influencing group movement for single individuals, and suggests a new aspect of what the costs of a gregarious life may be.

The Adaptive Value of Long Memory Windows

Keeping memories accurate for long periods is argued to be costly for neural circuits and genetic machinery in terms of the maintenance and repair they require (Dukas 1999). Keeping memories for too long may, in addition, result in inappropriate behaviour when conditions change (James 1890; Shettleworth 2010). Based on studies of optimal foraging strategies in great tits, *Parus major*, Cowie (1977) therefore predicted that frequent changes in the environment should favour a short-term memory window, whereas stability should favour long-term storing of experiences. Theoretical models, in addition, predict that long-term memory becomes especially beneficial when stable food sources vary in productive output or spatial distribution (Barraquand et al. 2009; E. Normand, D. Caillaud, D. S. Ban & C. Boesch, unpublished data). Perhaps because such conditions are common in nature we find evidence for the use of long-term memory windows of days or weeks in a wide variety of animal taxa ranging from apes to insects (e.g. rats, *Rattus norvegicus*: Tolman 1948; chimpanzees: Menzel 1973; honeybees, *Apis mellifera*: Dyer 1996; capuchin monkeys, *Cebus apella nigritus*: Janson 1998; three-spined sticklebacks, *Gasterosteus aculeatus*: Girvan & Braithwaite 1998; nutcrackers, *Nucifraga columbiana*: Balda & Kamil 1998; sooty mangabeys, *Cercocebus atys atys*: Janmaat et al. 2006).

Memory windows differ in length, dependent on the demands of the natural environment. Animals that return annually to the same breeding or feeding grounds should arguably retain spatial information that they have not needed for many months or even years, rather than pay the costs of relearning locations. For example, in a comparison of the migratory garden warbler, *Sylvia borin*, and closely related nonmigratory Sardinian warbler, *Sylvia melanocephala momus*, the migrating species could remember spatial information about a vegetation type associated with food (artificial geranium plants versus artificial ivy) over longer periods than the nonmigratory species (2 weeks compared to 1 year; Mettke-Hoffmann & Gwinner 2003). In a similar way, frugivorous rainforest primates are expected to retain 'what' and 'where' information (production frequency, amplitude, duration and location) about fruit production sites (trees) over much longer time periods than a single fruiting season, since production is ephemeral and fruit may be absent for many years (Struhsaker 1997; Chapman et al. 1999; Sakai 2001; Koenig et al. 2003; Janmaat 2006).

The present study on chimpanzees is the first to provide evidence that rainforest primates use long-term spatial memory to monitor food sources and remember feeding experiences across feeding seasons, long after food has been depleted and new food can be discovered. Chimpanzee females were typically observed to monitor trees when they encountered them along the way; however, their territory was large (26.5 km^2; Kouakou et al. 2011) and compared to primate species with smaller ranges only a small percentage of their potential food trees were encountered on a regular basis (Milton 2000; Di Fiore & Suarez 2007). Perhaps as a result, chimpanzees were also found to aim travel actively towards specific trees to check for the availability of new fruit. Whether chimpanzees are unique among frugivores in having sufficient neural capacity to combine a long-term spatial memory of current fruiting trees with a longer-lasting memory of feeding trees from previous seasons, to facilitate the discovery of large bountiful crops, is a topic for future studies.

Acknowledgments

Financial support for this research was provided by the Max Planck Institute for Evolutionary Anthropology. In Côte d'Ivoire, we thank the Ministère de la Recherches Scientifiques, the Ministère de l'Environnement et des Eaux et Forêts, the Office Ivoirien des Parcs et Réserves, the directorship of the Taï National Park, the Centre Suisse de Recherche Scientifique, L. Wittiger, D. Dowd, A. Diarrassouba, I. Kone and S. Kone for logistic support and permission to conduct our studies. We are indebted to J. Tahou, R. Nabo, L. B. Bally and V. Gnagnon for invaluable assistance in the field. We thank L. Wittiger for the idea to compare the size of chimpanzee feeding trees with that of trees on transects. We kindly thank C. Chatelain for sharing his botanical data and L. Polansky for creating Fig. A11. We gratefully acknowledge R. Mundry for training K.J. to model in R, and for writing programs that cleaned the GPS tracking data (Appendix) and calculated the times at which females entered within detection distances of mapped trees. We thank O.A.K. Idrissou for writing programs in C# and R to calculate the occurrence of change points and feeding within those detection distances and P. Jupp for automating the change point test. We thank J. Call, P. Gratton, F. Mafessoni, R. Mundry, S. Held and two anonymous referees for helpful comments and A.J.N. Kazem for proofreading. This study is based on noninvasive observations and complies with the laws of Côte d'Ivoire and the ASAB Guidelines.

Supplementary Material

Supplementary material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2013.09.021.

References

Anderson, D. P., Nordheim, E. V., Moermond, T. C., Goné Bi, Z. B. & Boesch, C. 2005. Factors influencing tree phenology in Taï National Park, Côte d'Ivoire. *Biotropica*, **37**, 631–640.

Asensio, N., Brockelman, W. Y., Malaivijitnond, S. & Reichard, U. H. 2011. Gibbon travel paths are goal oriented. *Animal Cognition*, **14**, 395–405.

Baayen, R. H. 2008. *Analyzing Linguistic Data*. Cambridge: Cambridge University Press.

Balda, R. P. & Kamil, A. C. 1998. The ecology and evolution of spatial memory in corvids of the Southwestern USA: the perplexing pinyon jay. In: *Animal Cognition in Nature: The Convergence of Psychology and Biology in Laboratory and Field* (Ed. by R. O. Balda, I. M. Pepperberg & A. C. Kamil), pp. 29–64. San Diego: Academic Press.

Barraquand, F., Inchausti, P. & Bretagnolle, V. 2009. Cognitive abilities of a central place forager interact with prey spatial aggregation in their effect on intake rate. *Animal Behaviour*, **78**, 505–514.

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

Boesch, C. & Boesch-Achermann, H. 2000. *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. Oxford: 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.

Byrne, R. W., Noser, R. N., Bates, L. A. & Jupp, P. E. 2009. How did they get here from there? Detecting changes of direction in terrestrial ranging. *Animal Behaviour*, **77**, 619–631.

Cavonius, C. R. & Robbins, D. O. 1973. Relationships between luminance and visual acuity in the rhesus monkey. *Journal of Psychology*, **232**, 239–246.

Chapman, C. A. & Chapman, L. J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica*, **29**, 396–412.

Chapman, C. A. & Wrangham, R. W. 1993. Range use of the forest chimpanzees of Kibale: implications for the evolution of chimpanzee social organization. *American Journal of Primatology*, **31**, 263–273.

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. & Chapman, L. J. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*, **26**, 160–171.

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.

Chapman, C. A., Chapman, L. J., Struhsaker, T. T., Zanne, A. E., Clark, C. J. & Poulsen, J. R. 2005. A long-term evaluation of fruit phenology: importance of climate change. *Journal of Tropical Ecology*, **21**, 1–14.

Cowie, R. C. 1977. Optimal foraging in great tits (*Parus major*). *Nature*, **268**, 137–139.

Devenport, L. D., Hill, T., Wilson, M. & Ogden, E. 1997. Tracking and averaging in variable environments: a transition rule. *Animal Behaviour*, **47**, 787–802.

Coyne, M. S. & Godley, B. J. 2005. Satellite tracking and analysis tool (stat): an integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology Progress Series*, **301**, 1–7.

Di Fiore, A. & Suarez, S. A. 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: cognitive and evolutionary implications. *Animal Cognition*, **10**, 317–329.

Dukas, R. 1999. Costs of memory: ideas and predictions. *Journal of Theoretical Biology*, **197**, 41–50.

Dobson, A. J. 2002. *An Introduction to Generalized Linear Models*. Boca Raton: Chapman & Hall/CRC.

Dyer, F. C. 1996. Spatial memory and navigation by honeybees on the scale of the foraging range. *Journal of Experimental Biology*, **199**, 147–154.

Field, A. 2005. *Discovering Statistics using SPSS*. London: Sage.

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*. 2nd edn. Thousand Oaks, California: Sage.

Gamer, M., Lemon, J., Fellows, I. & Singh, P. 2010. *Irr: various coefficients of interrater reliability and agreement*. R package version 0.83. http://CRAN.R-project.org/package=irr.

Girvan, J. R. & Braithwaite, V. A. 1998. Population differences in spatial learning and memory in three-spined sticklebacks. *Proceedings of the Royal Society B*, **265**, 913–918.

Golla, H., Ignashchenkova, A., Haarmeier, T. & Thrier, P. 2004. Improvement of visual acuity by spatial cueing: a comparative study in human and non-human primates. *Vision Research*, **44**, 1589–1600.

Goné Bi, Z. B. 1999. *Phénologie et distribution des plantes dont divers organes (principalement les fruits) sont consommés par les chimpanzés, dans le Parc National de Taï, Côte d'Ivoire*. M.Sc. thesis. Côte d'Ivoire: University of Cocody.

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*. Ph.D. thesis. Côte d'Ivoire: University of Cocody.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Massachusetts: Harvard University Press.

Haccou, P. & Meelis, E. 1994. *Statistical Analyses of Behavioural Data*. Oxford: Oxford University Press.

Hanna, J. B., Schmit, D. & Griffin, T. M. 2008. The energetic cost of climbing in primates. *Science*, **320**, 898.

Holland, R. A., Winter, P. & Waters, D. A. 2005. Sensory systems and spatial memory in the fruit bat *Rousettus aegyptiacus*. *Ethology*, **111**, 715–725.

Hothorn, S. & Hornik, K. 2011. *Exact distributions for rank and permutation tests*. R package version 0.8-22. http://CRAN.R-project.org/package=exactRankTests.

Hladik, C. M. 1975. Ecology, diet and social patterning in Old and New World monkeys. In: *Socioecology and Psychology of Primates* (Ed. by R. H. Tuttle), pp. 3–35. Paris: Mouton de Gruyter.

Isabirye-Basuta, G. 1988. Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. *Behaviour*, **105**, 135–147.

James, W. 1890. *The Principles of Psychology*. New York: Henry Holt.

Janmaat, K. R. L. 2006. *Fruits of enlightenment: fruit localization strategies in wild mangabey monkeys*. Ph.D. thesis. University of St. Andrews.

Janmaat, K. R. L., Byrne, R. W. & Zuberbühler, K. 2006. Evidence for spatial memory of fruiting states of rainforest fruit in wild ranging mangabeys. *Animal Behaviour*, **71**, 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., Ban, S. D. & Boesch, C. 2013. Tai chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. *Animal Cognition*, http://dx.doi.org/10.1007/s10071-013-0617-z, published online 11 April 2013.

Janson, C. H. 1998. Experimental evidence for spatial memory in foraging wild capuchin monkeys *Cebus apella*. *Animal Behaviour*, **55**, 1229–1243.

Janson, C. H. 2012. Reconciling rigor and range: observations, experiments, and quasi-experiments in field primatology. *International Journal of Primatology*, **33**, 520–541.

Janson, C. H. & Byrne, R. W. 2007. Resource cognition in wild primates: opening up the black box. *Animal Cognition*, **10**, 357–367.

Jurmain, R. 1997. Skeletal evidence of trauma in African apes, with special reference to the Gombe chimpanzees. *Primates*, **38**, 1–14.

Kipper, S., Mundry, R., Sommer, C., Hultsch, H. & Todt, D. 2006. Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Animal Behaviour*, **71**, 211–217.

Koenig, W. D., Kelly, D., Sork, V. L., Duncan, R. P., Elkinton, J. S., Peltonen, M. S. & Westfall, R. D. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos*, **102**, 581–591.

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.

Laska, M. & Freyer, D. 1997. Olfactory discrimination ability for aliphatic esters in squirrel monkeys and humans. *Chemical Senses*, **22**, 457–465.

Laska, M., Liesen, A. & Teuber, P. 1999. Enantioselectivity of odor perception in squirrel monkeys and humans. *American Journal of Physiology*, **277**, 1098–1103.

Laska, M., Seibt, A. & Weber, A. 2000. 'Microsomatic' primates revisited: olfactory sensitivity in the squirrel monkey. *Chemical Senses*, **25**, 47–53.

Laska, M., Hernandez Salazar, L. T. & Luna, E. R. 2003. Successful acquisition of an olfactory discrimination paradigm by spider monkeys, *Ateles geoffroyi*. *Physiology & Behavior*, **78**, 321–329.

Lawrence, M. A. 2011. *ez: Easy analysis and visualization of factorial experiments*. R package version 3.0-0. http://CRAN.R-project.org/package=ez.

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

McFarland Symington, M. 1987. Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, **105**, 117–134.

Martin, P. & Bateson, P. 2007. *Measuring Behaviour*. Cambridge: Cambridge University Press.

Martin-Ordas, G., Haun, D., Colmenares, F. & Call, J. 2010. Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition*, **13**, 331–340.

Menzel, E. W. 1973. Chimpanzee spatial memory organization. *Science*, **182**, 943–945.

Menzel, C. R. 1991. Cognitive aspects of foraging in Japanese monkeys. *Animal Behaviour*, **41**, 397–402.

Merigan, W. H. & Katz, L. M. 1990. Spatial resolutions across the macaque retina. *Vision Research*, **30**, 985–991.

Mettke-Hoffmann, C. & Gwinner, E. 2003. Long-term memory for a life on the move. *Proceedings of the National Academy of Sciences, U.S.A.*, **100**, 5863–5866.

Milton, K. 1980. *The Foraging Strategy of Howler Monkeys: a Study in Primate Economics*. New York: Columbia University Press.

Milton, K. 1981. Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. *American Anthropology*, **83**, 535–643.

Milton, K. 1991. Leaf change and fruit production in six neotropical *Moraceae* species. *Journal of Ecology*, **79**, 1–26.

Milton, K. 2000. Quo vadis? Tactics of food search and group movement in primates and other animals. In: *On the Move: How and Why Animals Travel in Groups* (Ed. by S. Boinski & P. A. Garber), pp. 375–417. Chicago: University of Chicago Press.

Momose, K. 2004. Plant reproductive interval and population density in aseasonal tropics. *Ecological Research*, **19**, 245–253.

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

Nishida, T., Zamma, K., Matsusaka, T., Inaba, A. & McGrew, W. C. 2010. *Chimpanzee Behavior in the Wild: an Audio-visual Encyclopedia.* Tokyo: Springer–Verlag.

Normand, E. 2010. *Spatial abilities of wild chimpanzees (*Pan troglodytes verus*).* Ph.D. thesis. University of Leipzig.

Normand, E., Ban, D. S. & 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. 2013. Change point analysis of travel routes reveals novel insights into foraging strategies and cognitive maps of wild baboons. *American Journal of Primatology*, published online 14 August 2013. http://dx.doi.org/10.1002/ajp.22181.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. & Matthiopoulos, J. 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution*, **23**, 87–94.

Polansky, L. & Boesch, C. 2013. Long-term fruit phenology and rainfall trends conflict in a West African lowland tropical rainforest. *Journal of Tropical Ecology*, **45**, 409–535.

Quinn, G. P. & Keough, M. J. 2002. *Experimental Designs and Data Analysis for Biologists.* Cambridge: Cambridge University Press.

Risser, D., Bönsch, A., Schneider, B. & Bauer, G. 1996. Risk of dying after a free fall from height. *Forensic Science International*, **78**, 187–191.

R Development Core Team 2011. *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing.

Sakai, S. 2001. Phenological diversity in tropical forests. *Population Ecology*, **43**, 77–86.

Sayers, K. & Menzel, C. R. 2012. Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. *Animal Behaviour*, **84**, 795–803.

van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**, 353–377.

Shettleworth, S. J. 2010. *Cognition, Evolution, and Behavior.* Oxford: Oxford University Press.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry. The Principles and Practice of Statistics in Biological Research.* 3rd edn. New York: W. H. Freeman.

Struhsaker, T. T. 1997. *Ecology of an African Rainforest.* Gainesville: University Press of Florida.

Tolman, E. C. 1948. Cognitive maps in rats and men. *Psychological Review*, **55**, 189–208.

Tremblay, Y., Robinson, P. W. & Costa, D. P. 2009. A parsimonious approach to modelling animal movement data. *PLoS One*, **4**, 4711.

Wakefield, M. 2008. *Socioecology of female chimpanzees (*Pan troglodytes schweinfurthii*) in the Kibale National Park, Uganda: social relationships, association patterns, and costs and benefits of gregariousness in a fission–fusion society.* Ph.D. thesis. Yale University.

Warnes, G. R. 2010. *Includes R source code and/or documentation contributed by Ben Bolker and Thomas Lumley. gtools: various R programming tools.* R package version 2.6.2. http://CRAN.R-project.org/package=gtools.

Wheelwright, N. T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos*, **44**, 465–477.

Zuberbühler, K. & Janmaat, K. R. L. 2010. Foraging cognition in non-human primates. In: *Primate Neuroethology* (Ed. by M. L. Platt & A. A. Ghazanfar), pp. 64–83. Oxford: Oxford University Press.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology & Evolution*, **1**, 3–14.

Appendix

Statistical Analyses

To establish comparable estimates in the GLM models we z-transformed all covariates prior to running the models. We checked for collinearity by inspecting variance inflation factors (VIF; Quinn & Keough 2002; Field 2005) derived from a multiple regression with the random effects excluded (using the function 'vif' of the R package 'car', Fox & Weisberg 2011). There was no indication of collinearity (largest VIF = 1.69 in all models). We assessed model stability by comparing the estimates derived from a model based on all data with those obtained from a model in which (1) the individual data points or (2) the data points from a given individual had been dropped one by one, which indicated that all models were stable.

Behavioural Data

The majority of follows were conducted by K.J. and S.B., with the exception of sick leave days, on which local assistants who were trained in continuous focal sampling of chimpanzees took over. Interobserver reliability tests based on simultaneous follows of 1173–2086 sampling minutes, for which observations were tested against observer K.J., revealed acceptable correlation coefficients for party size ($r_s = 0.82–0.99$) and acceptable kappa coefficients for the occurrence of inspections within sampling minutes ($k = 0.7–0.8$; Martin & Bateson 2007). Interobserver tests were implemented in R using the packages 'gtools' (Warnes 2010) and 'irr' (Gamer et al. 2010).

Tree Data

Since fruits eaten by chimpanzees grow not only in trees but also in strangler figs and lianas, we estimated the plants' crown sizes in three separate ways and refer to each one as the estimated crown size. For trees the estimated crown size was equal to the DBH. For strangler figs, we measured the distance from the trunk to the point at which the crown ended in all four wind directions and defined estimated crown size as the surface of the crown as if it was projected perpendicularly on the forest floor. For lianas, we measured the diameter of up to four liana roots that reached the forest floor and defined estimated crown size as the sum of the surface area of a cross-section of each root. We made the estimated crown sizes of trees, figs and lianas from different species comparable by z-transforming them (subtracting the mean crown size of the species concerned and dividing the result by the standard deviation of these same crown sizes). We only included species for which we had size measurements for at least five plant individuals in the analyses, to get reliable means and standard deviations.

Interobserver tests were conducted by measuring characteristics of the same trees. All assistants were tested against our local botanist J. Tahou. Trees with buttresses represented a difficulty since the buttress increases the diameter at the base but this inflated diameter is unlikely to reflect the tree's ability to produce fruit. To estimate trunk diameters for trees with buttresses we took a picture of the entire trunk, when vegetation cover allowed it. We then estimated the diameter from the picture of the tree and a reference marker pinned on the trunk, using Universal Desktop Ruler software (http://www.avpsoft.com). Otherwise, the DBH was estimated using a tape measure and elongated sticks. Correlation coefficients for estimated DBH values of the same trees ($N = 15$) by assistants ranged between 0.85 and 0.92.

The productive output of feeding trees during visits in 2009 and 2010 was measured as proportion of fruit (ripe and unripe) observed out of the estimated total that can be produced ranked on a relative scale from zero to four. Ranks 1, 2, 3 and 4 corresponded to 1–25%, 26–50%, 51–75% and 76–100% of the branches being observed to bear fruit, respectively. Trace quantities of fruit and leaves were scored 0 (see Chapman et al. 1994; Anderson et al. 2005). For fruit species that were exclusively eaten on the ground we used ranks calculated for the fruit fall area instead. Here rank 4 corresponded to the maximum estimated density of fruit observed in the fruit fall area for the species. We chose this option as we were unsure whether the target female had observed the amount of fruit in the tree when she had only been feeding on the ground. Obviously, this method required comparative observations of several fruit trees. Hence, phenology data were collected by trained assistants who had worked in the forest for several fruiting seasons before the start of our study. Kappa coefficients for agreement on species identity and fruit production class ranged between 1 and 0.99 ($N = 81$) and between 0.71 and 0.78 ($N = 112$), respectively.

Collection of Botanical Map Data

Along the line transects that were used to establish the botanical map we mapped all trees of reproductive size for 17 fruit species encountered within 7.5 m north and 7.5 m south of the middle of the line transect. The set of fruit species selected consisted of species that were fed on a large proportion of the time and provided a good representation of rare, common, dispersed and clumped species (see Normand 2010). Our botanical map is slightly bigger than the map created by Normand (2010), owing to an extension of the females' territory to the south. For each tree we estimated the crown size using the method described above and marked it with an aluminium tag and the GPS using the option 'averaging waypoint'.

Collection of Long-term Phenology Data

To analyse the individual variation in fruit production rate and consistency of productive output over years for chimpanzee fruit trees in general (Table A1), we determined the maximum fruit production classes per year for 729 trees. These trees were located on phenology transects within the females' territory and were monitored monthly from January 2001 to February 2008 (N species = 89; Anderson et al. 2005).

Accuracy Measurements, Cleaning and Smoothing of GPS Tracking Data

A recommended way to measure the location of an animal that cannot be collared and needs to be followed on foot with a handheld GPS is to remain at a given location until the GPS has made a number of estimations of its location and to save the average value manually. However, if study subjects travel rapidly and for long continuous periods, as chimpanzees do, observers often do not have time to mark such averaged locations at regular intervals. We therefore used the track log function of our GPS, which automatically recorded locations in time. We chose a setting that recorded locations 'as often as possible', meaning that the GPS automatically stored a location whenever sufficient satellites were available to calculate it. However, we found that certain intervals between recorded locations corresponded to exceptionally high travel speeds. After checking the maximum speed of one of our observers (K.J.; by running a 50 m track in an open area) we discovered that some of the speeds estimated were unrealistic (e.g. 120 km/h) and the GPS was making severe errors that needed to be corrected for (maximum speed of K.J.: 18.4 km/h running; 11.16 km/h walking).

Several other issues also arose, which we list below.

(1) At moments when we were with the target chimpanzee and not moving (e.g. sitting under a tree in which the chimpanzee was feeding) the GPS recorded continuous movement. For example, distances between the locations estimated by a GPS that was left to record at the same location for 11 days summed up to 52 km of travel.

(2) The GPS would sporadically record a nest location outside observation hours, when we were downloading data in camp.

(3) The GPS would give exactly the same location for a large number of consecutive time points, as if it became stuck.

Comparison of the track data with behavioural observations suggested that accuracy during nontravel was lower than during travel (Fig. A1). Extreme outliers (>100 m) occurred only when the chimpanzees were stationary. In addition, the track route sometimes exhibited a zigzag shape when we had in fact travelled in a relatively straight line. This seemed to occur more often when the animal was travelling slowly.

GPS Accuracy during Travel versus Nontravel

To investigate whether there was a difference between the accuracy of locations recorded during travel and nontravel (as suggested in Fig. A1) we first measured accuracy during nontravel. During our data collection period, we therefore let one of our GPS devices record 5456 locations at the same place (under forest canopy) for 11 days. The average distance of all recorded locations to their mean was 11.77 m ($N = 5456$, SD = 7.32 m, range 0–65.30 m). To determine accuracy during travel we marked 64 locations with tags on research trails and passed and marked them in the GPS twice each during travelling. The accuracy during travelling had a mean of 4.79 m ($N = 64$ pairs of measurements, SD = 3.14 m, range 0.37–4.72 m), suggesting that GPS estimations were more accurate during travel. We do not know the exact reason for this, as the software algorithms used by Garmin are not known. We presume the increased accuracy during travel is caused by internal software corrections that also use the previous location(s) and movement for estimation of new locations. If this is correct, accuracy may be further increased by the possibility that any temporary failures to receive satellite signals last for shorter periods during travel.

GPS Accuracy during Slow versus Fast Travel

To investigate our impression that the GPS was less accurate during slow travel and caused straight-line routes to appear as zigzag routes, we conducted the following measurements. We walked eight forest routes, once rapidly and once slowly, and compared the distances and linearity of each pair of routes estimated by the GPS. Each route was approximately 2–3 km long and contained both travel and a stopping location lasting 10 min (Fig. A2). The routes were walked along forest trails that meandered because of tree falls and obstructions. We found no significant difference between the distance and linearity (Fig. A3a) estimated by the GPS when moving fast as compared to slowly along the eight forest routes (distance: $T^+ = 20$, $N = 8$, $P = 0.84$; Fig. A3b; linearity: $T^+ = 5$; $N = 8$, $P = 0.66$; Fig. A3c; slow travel: 352 min; fast travel: 212 min). In addition, we walked 20 short travel routes (without stopping points) that contained high variation in linearity (Fig. A4). For these routes we had measured the distance and linearity with a tape measure and compass and therefore knew the exact distance (100 m) and linearity of the routes. We then expressed the difference between the distances estimated by the GPS and true distances measured with tape (100 m) as a percentage of the true distance and defined this percentage as the 'GPS error'. We found that despite the large differences, the GPS error did not differ significantly between routes travelled rapidly and slowly ($T^+ = 107$, $N = 20$, $P = 0.96$; Fig. A5a). Nor did we find a significant difference in linearity ($T^+ = 145$, $N = 20$, $P = 0.14$; Fig. A5b; slow travel: mean ± SD = 0.69 ± 0.22 m/s; fast travel: 1.50 ± 0.29 m/s).

Developing a Cleaning and Smoothing Method

To deal with these issues we developed an automated method to clean and smoothen our track data (325 000 track locations). Many studies that have addressed the handling process of GPS track data concern animals for which there can be uncertainty about the animal's location for considerable time periods (e.g. marine animals that would disappear under water for up to half an hour; Coyne & Godley 2005). Methods such as state space modelling were developed to estimate where the animals could have been (Coyne & Godley 2005; Patterson et al. 2008; Tremblay et al. 2009). In contrast, our data did not have long time lags between recorded locations. Our GPS device had recorded a sufficient number of locations, even under dense canopy, yet it was unclear to what extent these could be trusted. We therefore decided to create the following options to clean and smoothen our data:

Cleaning Track Data

We first filtered out points, identified as: (1) speed $>$ maximum speed of our observers (using the value 18.4 km/h) as determined from the previous location (points were omitted iteratively if a single deletion did not lead to a speed lower than or equal to the maximum speed); (2) multiple consecutive locations recorded at exactly the same location; and (3) locations recorded at times outside observation hours.

Smoothing Track Data

Second, we created the option to smoothen the data for nontravel and slow travel as described below.

Nontravel

Primatologists are privileged in being able to follow target animals on foot and know from observation whether an animal has moved or not (e.g. during resting). We therefore decided to use this behavioural information to smoothen the GPS data. We identified a nontravel bout in the track data by linking the time of behavioural observations that indicated nontravel with the time of track locations. We then created the option to replace and summarize all locations in these nontravel bouts with the median of the track locations within the respective bout. We used the median location instead of the mean since the track locations did not have a normal distribution and included large outliers of up to 100 m (Fig. A6; this method is similar to what a GPS does when the user stands still for some time to average their location manually).

Slow Travel

Dealing with errors made during travel was less straightforward. Despite our finding that the distances and linearity indices estimated during fast versus slow travel did not differ significantly we decided to create an option to summarize ‘slow travel bouts’ (Fig. A6). We first defined these as time periods in which all successive locations were less than 2 × mean GPS accuracy (measured during travel) to the subsequent location in the bout. In other words, these were periods in which the GPS locations were so close to each other that the GPS ‘failed’ to detect travelling (when GPS accuracy is taken into account; Fig. A6). We then replaced all locations in these slow travel bouts with a single location (the median or first location, see below). As soon as the next location was further than 2 × mean GPS accuracy from the first location in a bout, it was excluded from the bout and a new slow travel bout was defined. Hence, long periods of slow travel were ‘summarized’ step by step and were replaced by several locations.

Choice of Smoothing Methods

To find out how best to smoothen the track data and what options to choose we investigated the following three approaches (Fig. A6): (1) replace all points in nontravel bouts with the median location; (2) use approach 1 plus replace all points in slow travel bouts with the first location; and (3) use approach 1 plus replace all points in slow travel bouts with the median location.

Testing the Smoothing Methods

We tested the effect of such summarizing by comparing the performance of each of the three smoothing methods. We checked which method gave the best estimates of the real distance and linearity and how these estimates related to raw GPS data that had not been cleaned or smoothened. To measure true distances and linearity we again walked eight different trajectories (Fig. A7). Each trajectory again resembled part of a chimpanzee route by commencing with a stopping point of 10 min, then continuing with travel, yet this time we had measured the exact distance and linearity with tape and compass. For each trajectory we calculated the difference between the distance measured with tape and the distance estimated by the GPS when travelling at slow speed and calculated the GPS error as above.

The results indicated that for raw track data collected with the option ‘as often as possible’, the GPS distance estimation was approximately twice that of the true distance (Fig. A8a). Hence we concluded that cleaning and smoothing was necessary and continued to investigate which smoothing method was best by comparing their effect on the GPS error (Fig. A8b). The best estimate of the real travel distance, with a GPS error of only 2.7%, was achieved by summarizing the locations of both the nontravel and slow travel bouts and replacing them by the median of all locations within each bout. For linearity the GPS error was a little higher (4.9%; Fig. A8c, d). Here too the third smoothing method (see above), which summarized the locations of both nontravel and slow travel bouts and replaced them by the median of all locations within each bout, provided the best results. Hence, we improved the accuracy of our track data using the third smoothing method.

R Functions, Programs and Manuals

All programs, functions (and manuals) for cleaning and smoothing of track data were written in R (R Development Core Team 2011) by Roger Mundry and K.J. These programs are especially interesting if behavioural data have been recorded simultaneously. There are different program functions and one can choose between various options for data handling (e.g. only clean for certain bugs or also smoothen) using the manuals as a guide. If, for example, the recording interval is small and GPS inaccuracy is high one may want to summarize only the nontravel bouts. Since our setting of the GPS was such that it collected locations as often as possible we also wrote a program that allowed us to extract the location at regular intervals, which is required to calculate daily path lengths. When a particular time is not in the data, the program estimates the location at that time, assuming that the animal was walking with a constant speed and in a straight line from the location immediately preceding the one immediately following the unknown location. We argue that this is a reasonable assumption since the time interval between known locations was very short (for our data: mean $=$ 20 s, range 5–97 s) and the chimpanzees are not expected to show much variation in speed and linearity within such short intervals. The functions, programs and manuals explaining their use can be obtained by contacting the corresponding author.

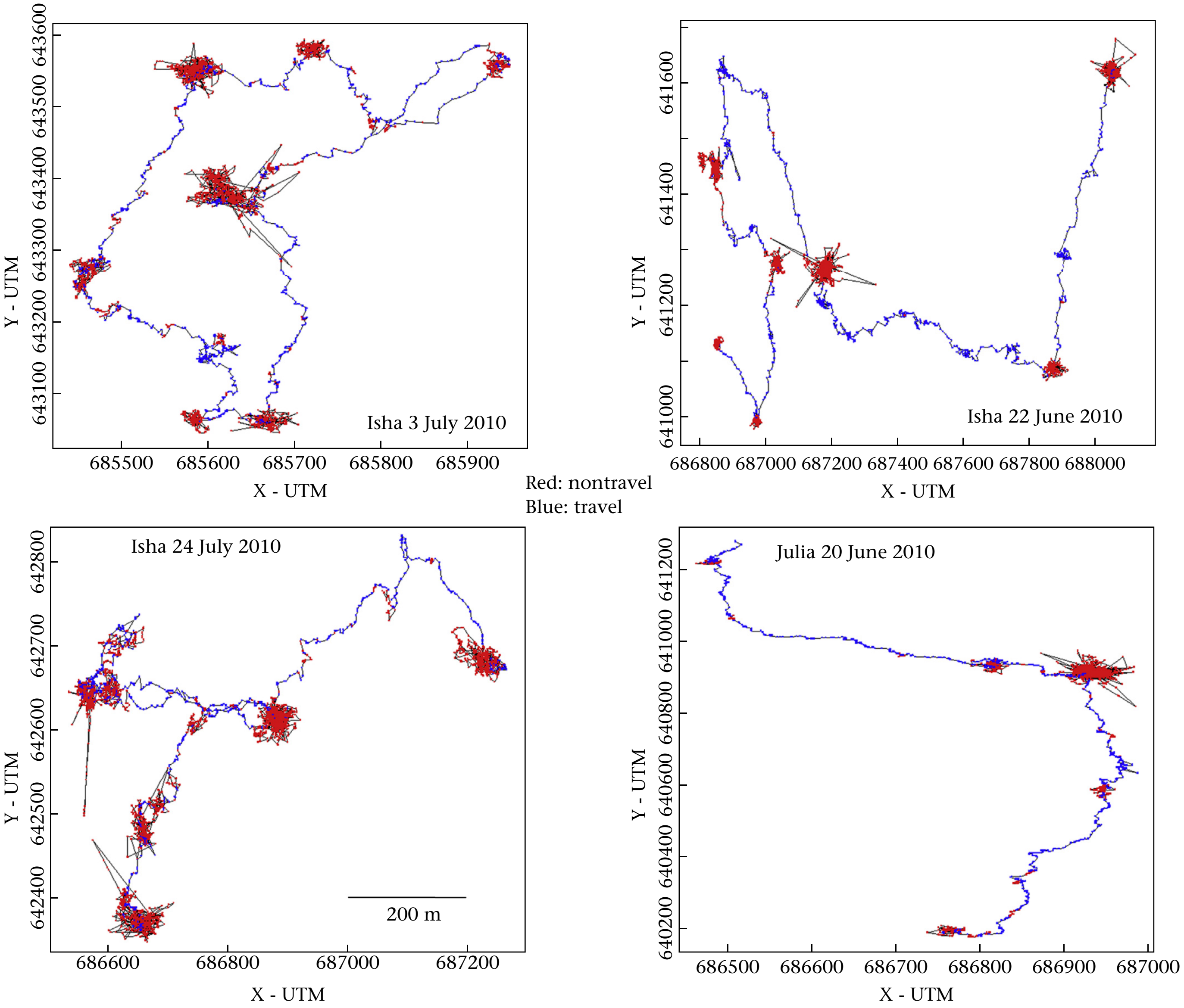

Figure A1. Raw track data of four daily travel paths from two chimpanzees recorded when we followed them with our handheld GPS. The blue and red colours represent the track data for the times that the chimpanzees were and were not travelling (e.g. during periods when they were grooming), respectively.

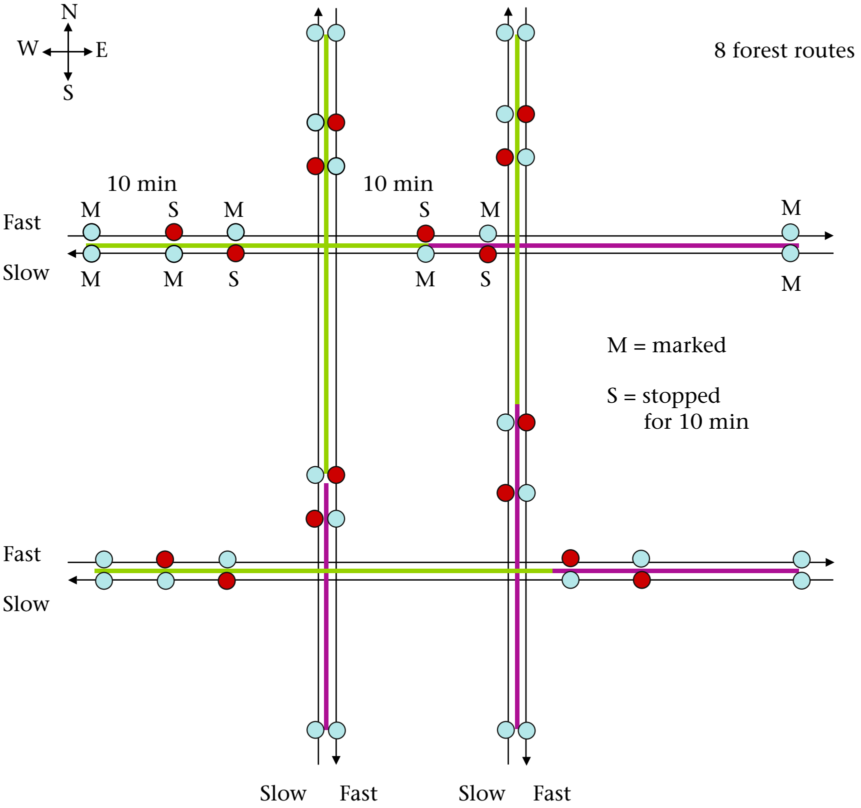

Figure A2. Schematic illustration of eight forest routes (four purple and four green lines) of about 2–3 km each. Each route was walked once fast and once slowly in opposite directions and each included a 10 min stopping point (red dot) and three points (blue dots) at which the route was marked. The points corresponded to the beginning and end of a route and the beginning and end of a trajectory.

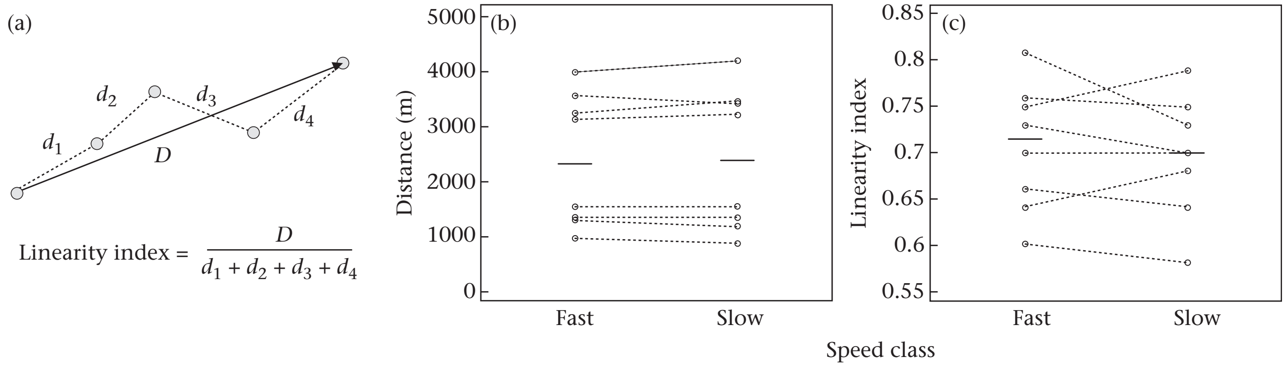

Figure A3. (a) Calculation of linearity: the sum of the distances of the different steps (d_i) that created the animal's route divided by the straight-line distance between the start and end point of the same route (D). (b, c) Differences between GPS measurements of the same eight forest routes as in Fig. A2 with unknown (b) length and (c) linearity walked at fast and slow speeds. Circles represent the estimated measurements (distance or linearity) for each route and the dotted lines in between represent the differences between the measurements at fast or slow speed for the same routes. The thick lines represent the median values.

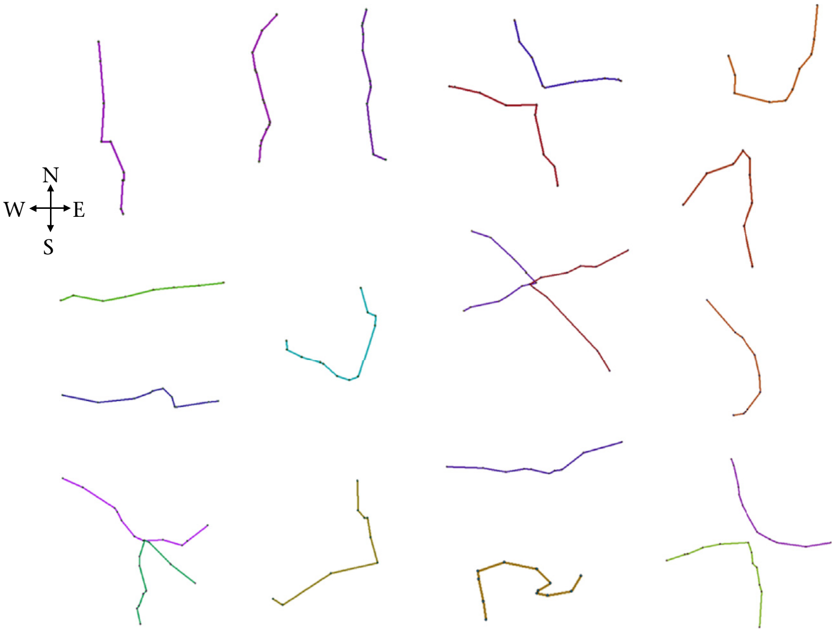

Figure A4. Shapes of 20 travel routes (100 m each) with variable linearity.

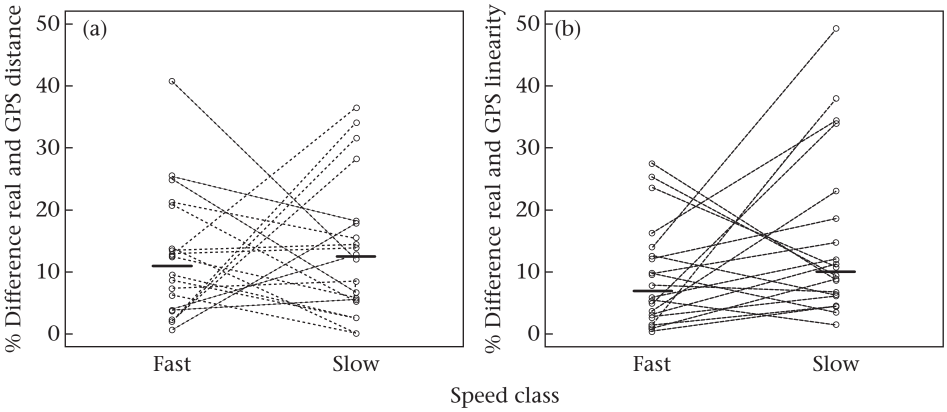

Figure A5. GPS errors (% difference to (a) the real distance or (b) the linearity) made estimating the same 20 travel routes as in Fig. A4 walked fast and slow. Circles represent the GPS errors for each route and the dotted lines in between represent the differences between the errors at fast or slow speed for the same routes. The thick lines represent the median values.

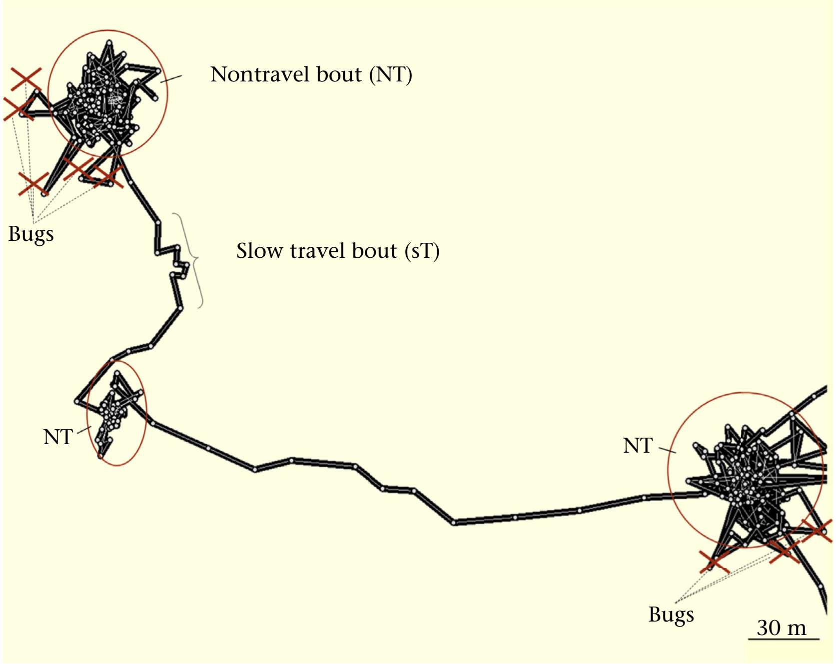

Figure A6. Illustration of the cleaning and smoothing options for the track data recorded while following a chimpanzee. The first option is to remove the bugs (red crosses) corresponding to, for example, locations that indicated impossible travel speeds. The second option is to summarize nontravel bouts (all locations within the red circles; NT) and replacing all locations within with the median value. Lastly, there is the option to summarize slow travel bouts illustrated by a short zigzag route and to replace all locations within a slow travel bout with one location.

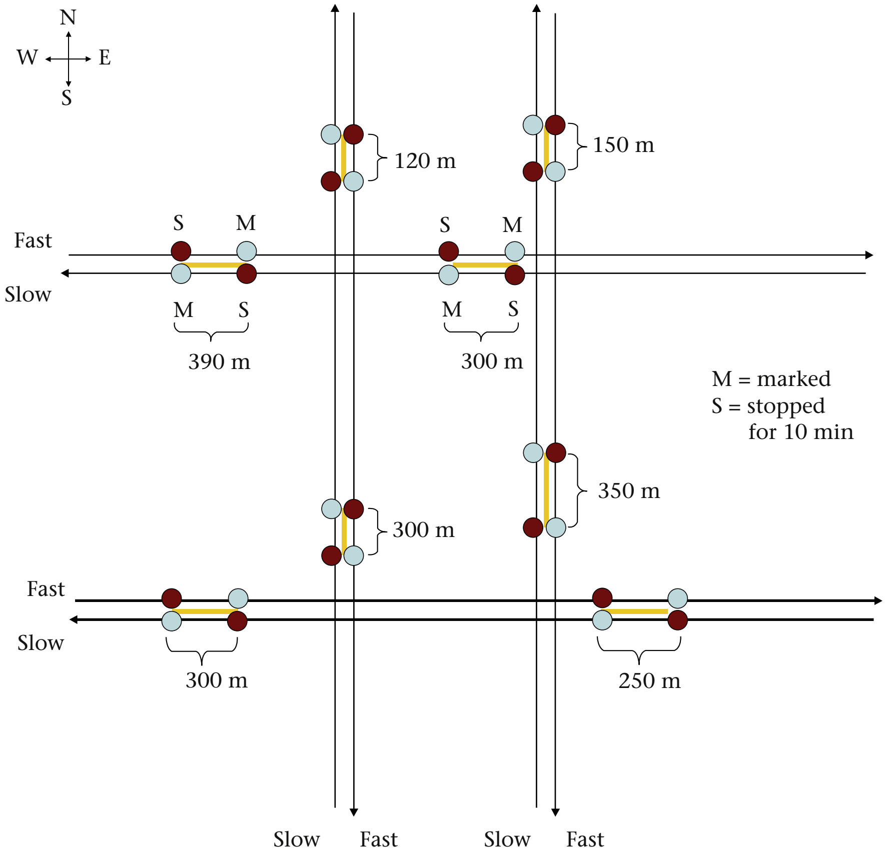

Figure A7. Schematic illustration of eight trajectories (yellow lines) of known length and linearity. Each trajectory was walked once fast and once slow in opposite directions and included a 10 min stopping point at its beginning (red dot). We used only the measurements during slow travel to test the different methods. The blue dots represent the markings of the location of the end of each trajectory.

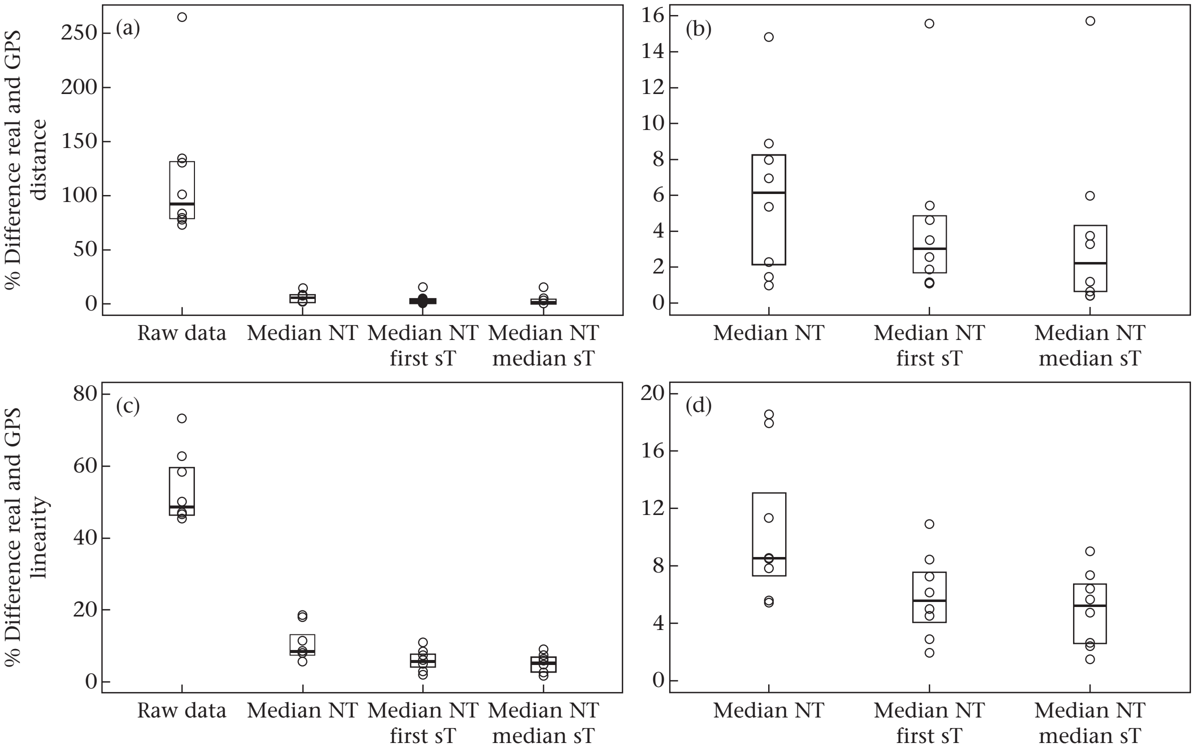

Figure A8. The effect of three smoothing methods on GPS errors made during (a, b) distance and (c, d) linearity estimation. GPS errors were calculated as the percentage of the differences between the distance (or linearity) estimated by the GPS and the real distance (or linearity) out of the real distance (or linearity) of eight trajectories. We used the data collected during slow travel. Raw data indicate that no cleaning or smoothing had taken place. Median NT indicates the smoothing method whereby only the nontravel data were summarized with the median. First sT and median sT indicate that slow travel bouts were summarized by the first value in the bout or the median value, respectively. (a, c) Raw data compared with median NT, first sT and median sT. (b, d) Results for median NT, first sT and median sT expanded to show more detail. Bars represent median values; upper and lower boundaries of boxes represent the upper and lower quartiles and circles represent the range.

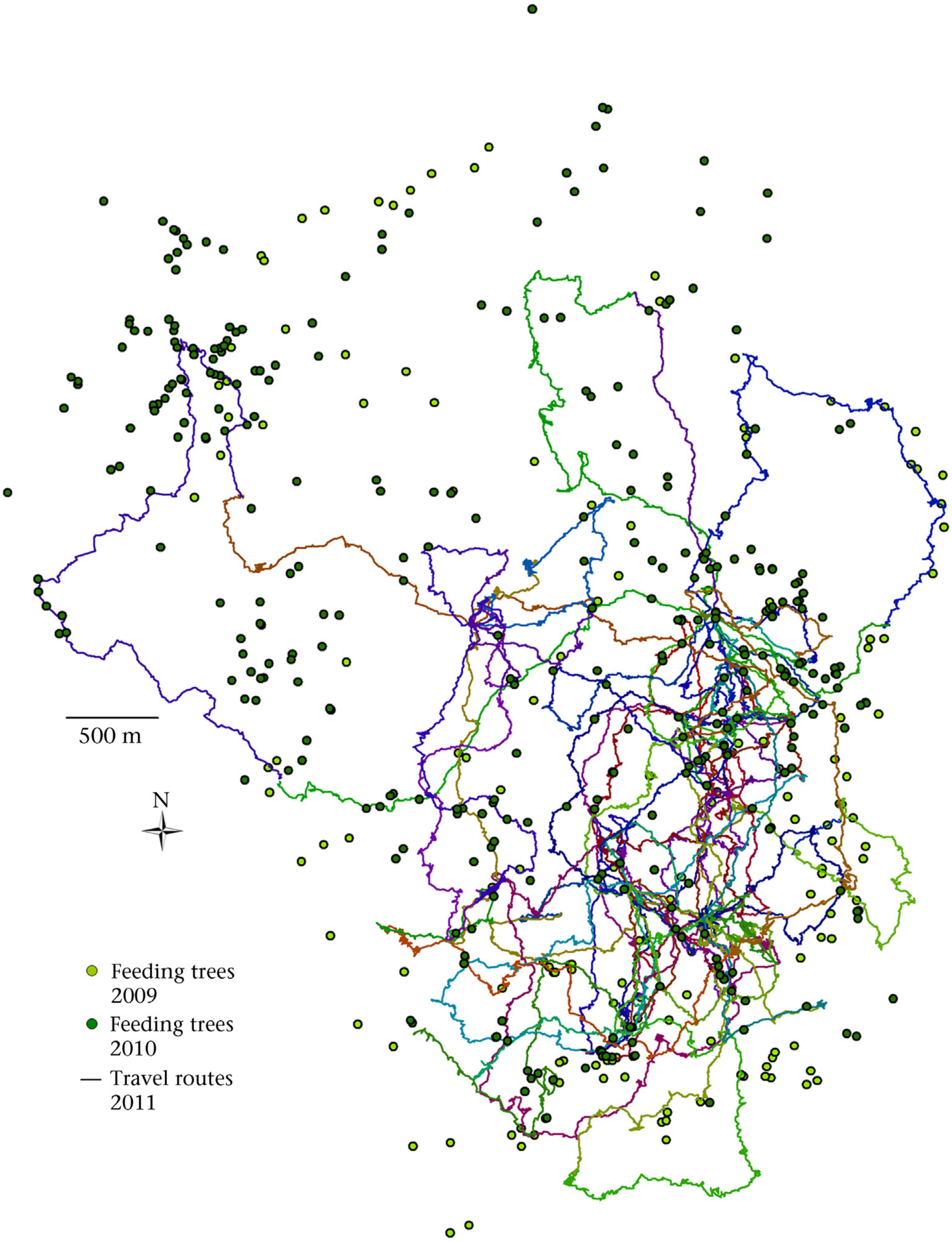

Figure A9. Travel route and last year(s)' feeding tree locations of target female Isha followed for 50 full days in 2011 (30 consecutive days).

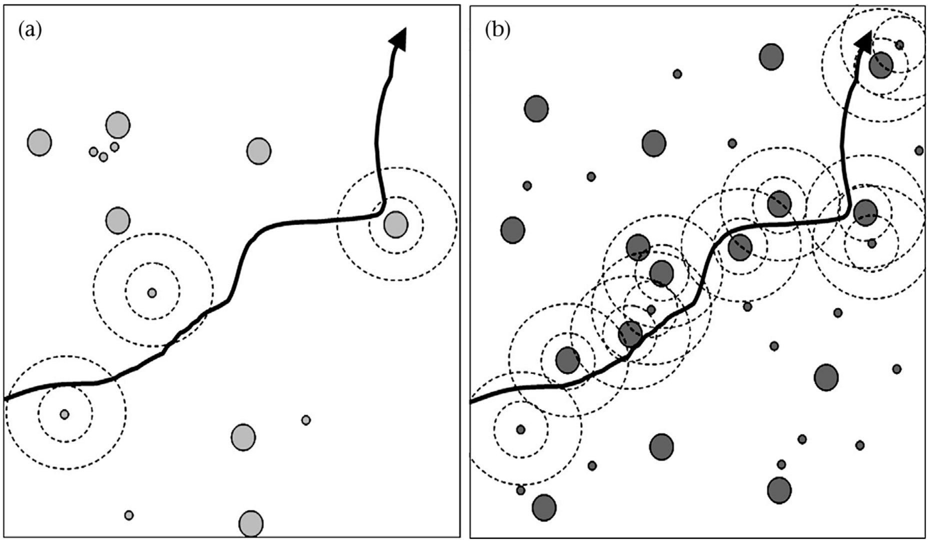

Figure A10. Schematic illustration of a chimpanzee travel route among trees of (a) low-density (rare) and (b) high-density (common) species. Large and small dots and the black line represent large trees, small trees and the travel route, respectively. The outer and inner circles represent two and one times the maximum detection distance, respectively. If density is high (b), females are likely to pass within the detection distance of many large trees along the way. A significant effect of size on probability of goal-directed approach is therefore only expected for species with low densities (a), for which females can perform goal-directed monitoring to a substantial proportion of large trees within the species' population.

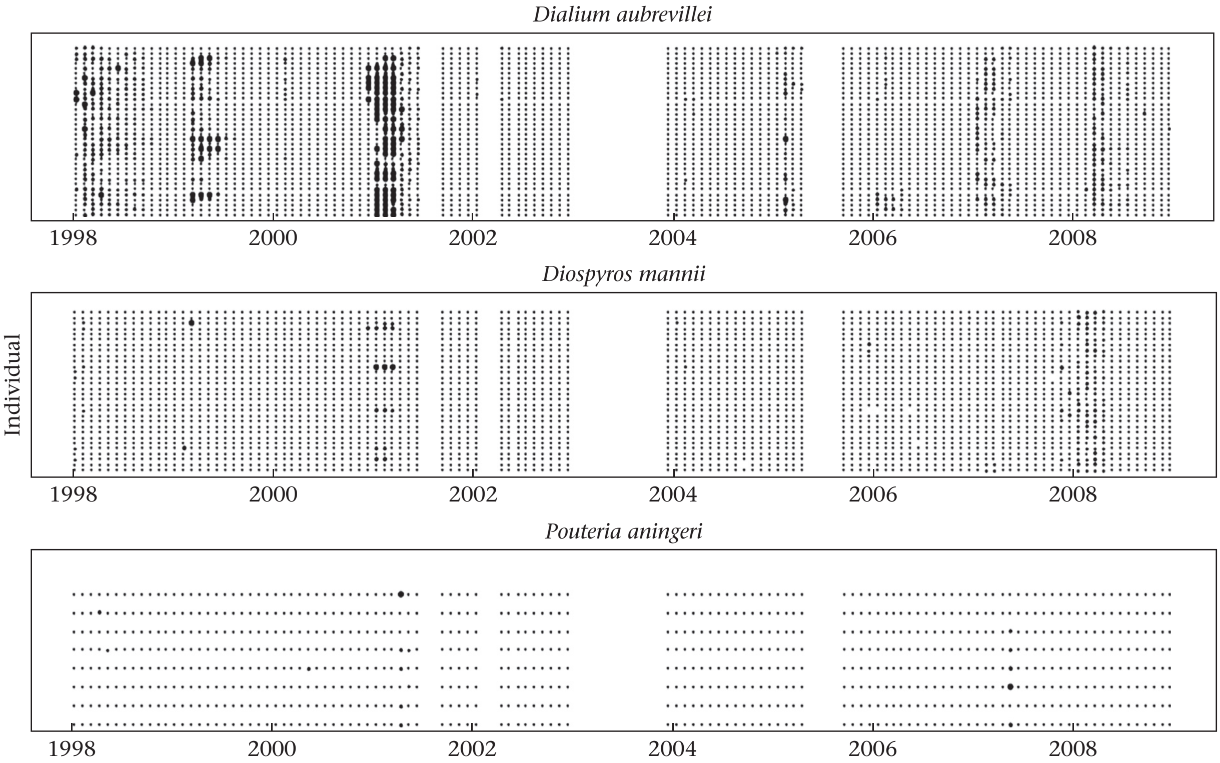

Figure A11. Examples of ripe fruit availability in individual trees in the phenology transect of three chimpanzee fruit species. Each dot represents a phenology check (monthly). The size of the dot represents the fruit production class ranging from 0 to 4. Figures are made by Leo Polansky.

Table A1

Consistency of the productive output of fruit trees in the Taï forest

Maximum production class*	No. of individual trees	Mean % of years with same production class
1 (1–25%)	126	58
2 (26–50%)	207	56
3 (51–75%)	95	52
4 (76–100%)	39	51

* To estimate a tree's maximum reproductive output we first calculated for each tree the maximum of all ripe production classes recorded within each year (yearly maximum class: 1, 2, 3 or 4). We subsequently classified each tree by the yearly maximum class that was recorded for the majority of years in which the tree carried fruit and assigned this class to be the maximum production class. We only included trees that produced fruit for at least 5 years in the 11 years of observation.

Table A2

Duration of consecutive intervals between ripe fruit production over 11 years for *Treculia africana*, *Irvingia grandifolia* and *Ficus elasticoides*

Tree individual	Fruiting bout interval duration (months)			
	N intervals	Minimum	Maximum	Mean
treculia_1	3	3	20	14
treculia_2	4	8	24	13
treculia_3	4	7	27	13
treculia_4	5	4	13	9
treculia_5	1	10	10	10
treculia_6	2	7	10	9
irvingia_1	8	4	12	8
irvingia_2	2	9	21	15
irvingia_3	2	8	21	15
irvingia_4	4	7	14	10
irvingia_5	2	8	14	11
irvingia_6	6	2	14	8
irvingia_7	4	3	8	6
irvingia_8	1	3	3	3
irvingia_9	4	3	17	9
irvingia_10	3	2	12	8
irvingia_11	2	4	5	5
irvingia_12	2	2	4	3
ficus_1	1	19	19	19
ficus_2	2	4	24	14
ficus_3	1	11	11	11
ficus_4	1	17	17	17
ficus_5	1	7	7	7

The range of fruiting intervals for the three species for which the large trees were monitored in a goal-directed manner and for which we argue that the location of large trees could have been remembered was 3 to 27 months for *Treculia africana*, 2 to 21 for *Irvingia grandifolia* and 4 to 24 for *Ficus elasticoides*. The maximum durations could potentially have been even longer; however, our longest uninterrupted period of data collection is unfortunately limited to 41 months.