Wild chimpanzees plan their breakfast time, type, and location

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Not all tropical fruits are equally desired by rainforest foragers and some fruit trees get depleted more quickly and carry fruit for shorter periods than others. We investigated whether a ripe-fruit specialist, the chimpanzee (*Pan troglodytes verus*), arrived earlier at breakfast sites with very ephemeral and highly sought-after fruit, like figs, than sites with less ephemeral fruit that can be more predictably obtained throughout the entire day. We recorded when and where five adult female chimpanzees spent the night and acquired food for a total of 275 full days during three fruit-scarce periods in a West African tropical rainforest. We found that chimpanzees left their sleeping nests earlier (often before sunrise when the forest is still dark) when breakfasting on very ephemeral fruits, especially when they were farther away. Moreover, the females positioned their sleeping nests more in the direction of the next day's breakfast sites with ephemeral fruit compared with breakfast sites with other fruit. By analyzing departure times and nest positioning as a function of fruit type and location, while controlling for more parsimonious explanations, such as temperature, we found evidence that wild chimpanzees flexibly plan their breakfast time, type, and location after weighing multiple disparate pieces of information. Our study reveals a cognitive mechanism by which large-brained primates can buffer the effects of seasonal declines in food availability and increased interspecific competition to facilitate first access to nutritious food. We discuss the implications for theories on hominoid brain-size evolution.

prospective cognition | flexible planning | ecological intelligence | interspecific competition | foraging strategies

Three decades ago, Katharine Milton hypothesized that the diversity of food and the manner in which it is distributed in space and time have been major selective forces in the development of advanced cerebral complexity (the ecological intelligence hypothesis) (1, 2). Positive associations between a variety of brain size measures and levels of frugivory (i.e., the dietary proportion of patchily distributed and ephemeral food) were found in primates (3, 4), bats, and rodents (5). However, the idea that body size evolves more rapidly than brain size, meaning the small relative brain size of folivores could be a nonequilibrial situation, kept scientists from interpreting these associations as clear support for Milton's hypothesis (6; but see also ref. 7). The ecological intelligence hypothesis was, however, retained as one of the four components of the technical intelligence hypothesis, developed to find evolutionary explanations of great apes' representational skills (6). It was renamed the "cognitive map hypothesis," which unintentionally focused attention solely on the complexity of the spatial mapping of food and largely ignored the potential difficulty of anticipating the time and duration that food is present.

With recent comparative studies on brain size evolution, the role of the temporal availability of food sources has gained renewed attention (8, 9). These studies are built on the idea that additional neural tissue should not only be functional, but an animal must have sufficient energy to afford it (10, 11). Van Woerden et al. (9) found that relatively large-brained primate species showed less seasonality in their net energy intake, relative to that expected on the basis of

environmental seasonality of food, than smaller-brained species. Hence, large brains were proposed to provide cognitive behavioral flexibility that enables buffering against seasonal declines in food availability (the cognitive buffer hypothesis) (9). To date it remains unclear what this cognitive flexibility entails. Cognitive abilities needed to perform extractive foraging, such as tool use, were suggested to be potential candidates (9). However, not all large-brained primates use feeding tools or routinely rely on them (12). The aim of this study is to investigate an alternative mechanism by which large-brained primates can obtain extra energy in food-scarce periods, while focusing on the behavior of a ripe fruit specialist in a rainforest habitat.

In tropical rainforests, the principal habitat of most primate species (13), food availability can be extremely variable (e.g., refs. 14 and 15). Despite the persistent illusion of abundance created by giant fruit trees and lush foliage, ripe-fruit specialists in particular can face severe food shortages, such as for months, when only 0.2% of the trees carry ripe fruit (14, 15). The availability of nutritious rainforest food, like young leaves and ripe fruit, can be highly episodic and patchily distributed in time and space and very ephemeral in terms of optimal nutritional quality (e.g., refs. 1 and 16). For example, individual trees can bear ripe fruits for an average of 0.8 mo, with individual fruit or young leaves remaining edible for no more than 72 h per year (1). Rainforests are typically characterized by a large biomass of fruit-consuming foragers resulting in relatively high rates of fruit depletion, which further shortens periods of fruit presence in individual trees (15, 17).

Depending on the nutritional quality or handling time of the fruit, foragers prefer some fruits more than others (18, 19). For example, figs (*Ficus* spp.) are generally unprotected and

Significance

How do large-brained primates maintain high rates of energy intake when times are lean? By analyzing early-morning departure times and sleeping nest positioning of female chimpanzees as a function of the ephemerality of next day's breakfast fruit and its location, we found evidence that wild chimpanzees flexibly plan when and where they will have breakfast after weighing multiple factors, such as the time of day, their egocentric distance to, and the type of food to be eaten. To our knowledge, our findings reveal the first clear example of a future-oriented cognitive mechanism by which hominoids, like great apes, can buffer the effect of seasonal declines in food availability and increased interspecific competition to facilitate first access to nutritious food.

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accessible to frugivores, regardless of size, masticatory apparatus, or digestive abilities, and are typically fed on by a large number of animal species (18, 20). Even a single foraging visit can lead to the consumption of all available ripe fruit in a fig tree (17). Similarly, smaller fruit species are eaten by a significantly larger number of bird species than larger fruits (21, 22). These species can be swallowed more easily—for example, by small-gaped birds—and can also be eaten at a faster rate, especially when processing surfaces (e.g., teeth) are small (23).

We investigated whether a ripe-fruit specialist, the chimpanzee (24), uses prospective cognition to arrive earlier at breakfast sites with ephemeral and highly sought-after fruits (in particular figs and small fruits) than those with less ephemeral fruit that can be more predictably obtained throughout the entire day. To accomplish this, we recorded and analyzed (*i*) the nest (sleeping site) departure times and (*ii*) nest positioning relative to breakfast-site locations of five adult female chimpanzee all with young offspring (<7 y) during three fruit-scarce periods in the Taï National Park, Ivory Coast (25, 26).

Results

Nest Departure Time Model. To test if chimpanzees left their nest earlier when breakfast consisted of highly sought-after ephemeral fruit, we built a departure-time model (linear mixed model, LMM) (Table 1, Table S1, and *Supporting Information*). Our primary interest was to test the effects of the size (mm^3) and genus type (*Ficus* or other fruit) of breakfast fruit on the time that the females departed from their night nest in relation to the time of sunrise. We chose these two characterizations of breakfast fruit based on previous studies (18, 20–22) and our findings showing that chimpanzee feeding trees of the *Ficus* genus were rare within the target chimpanzee's territory, and were more often observed to be fed on by other foragers—such as monkeys, birds, and squirrels—than trees from other genera (proportion of times hetero-specific foragers were found feeding in a tree: Median$_{fig}$ = 0.45, Median$_{other\ fruit}$ = 0.35, Mann–Whitney U = 67.5, $N_{fig\ species}$ = 12, $N_{other\ fruit}$ = 29, P = 0.0016, density: 0.84 trees per ha^{-1}) (Fig. 1). Crucially, ripe figs and ripe small fruits were found present in trees for shorter periods than those of nonfig and large fruit species (ripe figs vs. other species: Mann–Whitney U = 160, $N_{other\ fruit\ species}$ = 74, $N_{fig\ species}$ = 8, P = 0.0322; fruit size: $r_{Spearman\ exact}$ = 0.33, P = 0.0025, $N_{fruit\ species}$ = 81) (see *Supporting Information* for ripe fruit presence duration calculations).
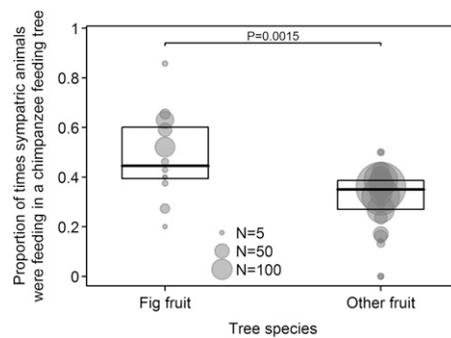

Fig. 1. Figs are more sought-after than other rainforest fruit. The difference in proportion of times that sympatric animals were observed feeding in a chimpanzee feeding tree. The circles show the proportion of trees per species. The area of the circles represents the number of measurements per tree species (n = 41). Bars represent median values of the proportions; upper and lower boundaries of boxes represent the upper and lower quartiles.

In addition to fruit size and genus type, the model included a collection of other covariates to account for more immediate spatiotemporal explanations of early departure times. To investigate the possibility that the chimpanzees' decisions were simply guided by sensory cues, we tested whether the females departed earlier in response to olfactory cues from figs, which typically have a stronger smell than other fruit species. We therefore included an interaction between the fruit genus type and the distance from the nest to the breakfast site in the model (Table 1), expecting the females to leave earlier when the figs were closer to the nest and when the smell could potentially be detected from within the nest. To disentangle the effect of competition for early access with other chimpanzees at the sleeping site from that with other foraging species at the breakfast site, we needed to control for the effect of intragroup competition on departure time. Hence, we included the number of males in the group and the duration of breakfast feeding as an estimate of the amount of edible fruit (27) at the breakfast site, and their interaction, as control predictors in the model (Table 1). We expected that departure time would be earlier when the estimated amount of food was small, especially when the number of males at the nest was larger, reflecting increased intragroup competition for breakfast fruit. Because the strong correlation ($r_{Spearman\ exact}$ = 0.88, n = 179, P = 0.0001) between the number of males and the total number of independent individuals that are not carried by the mother precluded inclusion of both covariates in the full model, we chose to include only the number of males as it was reported to influence departure time and also to decrease predation risk at dawn (28–30). Because nest departure time in primates is known to be delayed by a high energy balance (28, 31), high amounts of overnight rainfall, and low night temperatures (28, 32, 33), we also included these factors as control predictors in the model (Table 1).

We found that fruit size and fruit genus type significantly predicted departure time, with chimpanzee females departing earlier when they were going to breakfast on smaller fruit (Table 1 and Fig. S1). Females also departed earlier for figs than for other fruits, but—contrary to expectations from the sensory-stimulus hypothesis—only when the figs were far away from the nest (Fig. 2*A* and Table 1). Crucially, breakfast figs that were farther from the night nest were not fed on later than figs nearby ($r_{Spearman\ exact}$ = 0.0162, n = 46, P = 0.9148) (Fig. 2*B* and Table S2). Average approach speeds toward breakfast fig trees were significantly higher compared with other breakfast trees [median$_{fig}$ = 0.33 ms^{-1}, median$_{other\ fruit}$ = 0.16 ms^{-1}, Mann–Whitney U = 1,340, $N_{fig\ sites}$ = 32, $N_{other\ fruit\ sites}$ = 119, P = 0.0098 ($N_{fig\ breakfasts}$ = 46, $N_{other\ fruit\ breakfasts}$ = 133)]. When breakfast was obtained from other

Table 1. The influence of breakfast fruit size and other predictors on nest departure times (seconds from sunrise)

Predictor	Estimate	SE	*P* value
(Intercept)	779.1	293.7	
Target predictors			
Breakfast fruit size (mm^3)	316.3	136.9	0.0257
Breakfast genus type (no fig)	844.6	328.8	
Distance nest to breakfast site	−147.4	206.7	
Breakfast genus type × Distance nest to breakfast site	582.8	246	0.0254
Control predictors			
No. of adult males at nest	−242.3	116.2	
Feeding duration at breakfast site	−390.5	105.3	
Feeding duration at breakfast site × No. of adult males at nest	234.8	110.3	0.0433
Relative energy balance	−118.4	108	0.2759
Night temperature	−134.1	107.7	0.2490
Rain at nest (yes)	437.6	215.5	0.0435

Full model versus control model comparison: χ^2_4 = 22.67, $N_{females}$ = 5, N_{days} = 179, P = 0.0002.
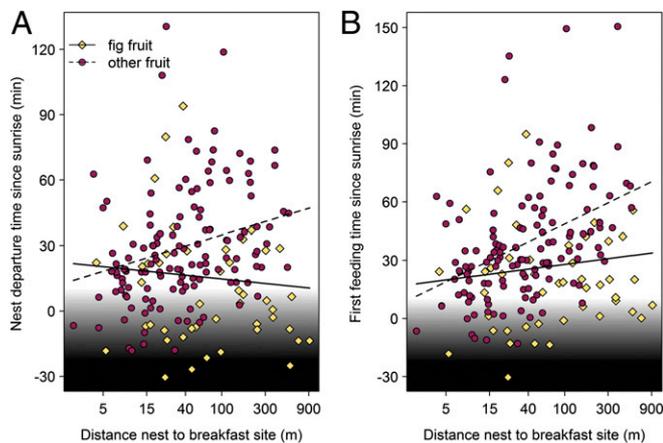
Fig. 2. Multifactorial planning of departure times. The interactive effects of fruit genus type and travel distance on the chimpanzees' (*A*) morning nest departure times and (*B*) breakfast arrival times. Zero on the *y* axis represents sunrise and the background shading reflects time since the beginning of the average dawn start time (black) to 10 min after sunrise (white). The datapoints ($n = 179$) show the observed departure times and starting times of breakfasting when the breakfast fruit was a fig (yellow diamonds) and a nonfig species (red circles). The lines illustrate expected departure (Table 1) and starting times of breakfasting (Table S2) predicted by the models (conditional on all other predictors being on its average and based on rainfall manually dummy coded and centered). They made their nest only 4 of 179 times in the breakfast tree and had breakfast outside the nest on all days.

fruit genera, the females left later rather than earlier when the site was far away as opposed to when it was close (Fig. 2*A* and Table 1). The random-effect variation for breakfast fruit species was not significant ($\chi^2_1 = 2.51$, P = 0.1134).

Nest-Positioning Models. To test if chimpanzees positioned their nest closer and more en route to breakfast that consisted of highly sought-after ephemeral fruit, to facilitate early arrival the next day, we built two nest-positioning models. Our primary interest was again to test the effects of the size (mm³) and genus type (*Ficus* or other fruit) of breakfast fruit on the positioning of the nest in relation to the breakfast site. A first model was designed to analyze nest proximity in relation to the breakfast tree (*Supporting Information* and Table S3). We found no indication that the females were able to make their nest closer to ephemeral breakfast sites than to other sites [the proximity model (LMM); genus type: estimate = −0.23, SE = 0.31, P = 0.4654; fruit size: estimate = 0.11, SE = 0.12, P = 0.3586) (see Table S3, Fig. S2, and *Supporting Information* for details on model design, results, and interpretation). In addition, the chimpanzees made very few nests inside breakfast trees (2%).

A second model was designed to investigate whether the females made their nest more en route to the breakfast site when breakfasting on highly sought-after fruit compared with other fruit (*Supporting Information* and Table S4). This model predicted the direction (α in Fig. 3*A*) along which the females built their nest (the difference between arrival and departure direction) (Fig. 3*A*). Because α takes on values between 0° and 180°, we assumed a β-distribution and used a generalized linear mixed model (GLMM) framework with a logit link to test the importance of fruit genus type and size on the direction (*Supporting Information*). To investigate whether a potential effect of fruit genus type and size on direction indicated planning for the next day and did not simply reflect a failed attempt to reach a late-night feeding site (e.g., because of a potential lower density of ephemeral fruits), we included the travel distance from the last feeding site to the subsequent breakfast site as a control predictor in the model (Table S4). Controlling for this travel distance, we found that the effect of fruit

size was not significant (Table S4). However, fruit genus had a significant effect on the direction in which the nest was built in relation to the breakfast site. The females were more likely to make their nests on the way to fig breakfast fruit compared with other breakfast fruit (Fig. 3*B* and Table S4).

Discussion

Multifactorial Planning by Departing Early. The complexity of the patterns of nest departure and nest positioning makes it difficult to explain our observations by the use of simple rules or different causal directions. For example, search by use of smell could not explain why the females departed earlier for distant figs. If the females had simply departed earlier in response to the olfactory cues, they should have left earlier when the figs were closer and when their smell was more salient. Such simpler foraging strategies furthermore fail to explain the opposite interactive effects of distance and fruit genus type on departure times (Fig. 2*A*). Nor is it likely that the females responded to visual cues, as they should then have breakfasted earlier on larger and easier to spot fruit. Differential preference by fruit type might also explain earlier departure times, but three lines of evidence suggest this is not the case. First, chimpanzees are known to experience higher caloric intake rates when feeding on large fruits (23), and hence might prefer species with larger fruits, yet we found the opposite
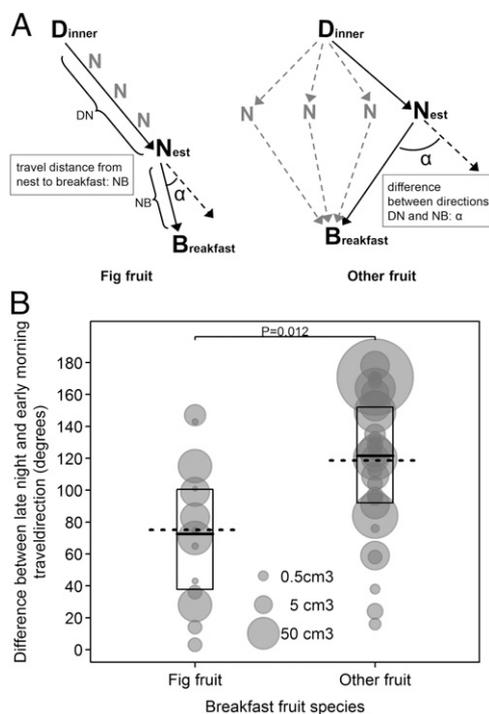
Fig. 3. Overnight planning of nest locations. (*A*) Schematic of direction of nest location and distance measurements. Whether or not the females built their nest on the way toward breakfast sites was determined by measuring the difference between late evening [from last feeding (dinner) to nest] and early morning (from nest to breakfast) travel direction. A small difference indicates that the nest was built in the direction of, and en route to the breakfast site. The gray *N* characters illustrate other potential nest locations. (*B*) The direction along which chimpanzees built their nest to the morning breakfast sites when breakfast was either fig or other fruit. The circles show the observed differences between late night and early morning travel direction toward and from the nest ($n = 44$). The area of the circles represents the size of the breakfast fruits. Bars represent median values of the differences in direction; upper and lower boundaries of boxes represent the upper and lower quartiles. The dotted lines represent the expected values for each fruit genus type as determined by the model.

effect of fruit size on departure times. Second, the lack of significance of the random-effect fruit species in explaining nest departure time variation further indicates that the females did not simply depart earlier to breakfast on particular fruit species that they preferred. Finally, if the females had departed earlier to breakfast on fig species simply because they preferred to feed on figs, departure times should have been approximately the same for all days for which breakfast consisted of figs, and should not have been later when the figs were nearby compared with when they were far away (i.e., there would not have been a significant interaction between breakfast fruit genus and distance). Early departures to distant figs also did not simply result from particular periods of low fruit availability (28, 31). Fig breakfasting occurred throughout the fruit-scarce periods, and was regularly alternated with breakfasting on other fruits (Fig. S3*A*).

Crucially, learned time–place associations of high rewards with particular nest and breakfast pair locations could not explain the observed pattern of results because the females typically slept at a different location each night (98% of the nights) and none of the sleep and breakfast pairs were the same within our observation period. (See *Supporting Information* for more detailed considerations of associative learning explanations.)

Because we controlled for the possible confounding variables night temperature, rainfall, and energy balance (see *Supporting Information* for extended discussion of the effects of these variables), we concluded that our findings are best explained by the idea that the females had left their nest earlier to make up for travel time when breakfasting on figs that were farther from the night nest. Because we controlled for the effect of intragroup competition (i.e., the interactive effect of the number of adult males and the estimated amount of fruit at the breakfast site on departure time) (Fig. S4), we propose that the females departed earlier to breakfast on more ephemeral fruit (i.e., figs and small fruit) compared with less-ephemeral fruit to arrive before sympatric hetero-specific foragers, such as birds, monkeys, and squirrels (see the *Supporting Information* for an expanded explanation of the results presented in Fig. S4).

When breakfast was obtained from fruit genera other than *Ficus*, the females left later rather than earlier when the site was far away as opposed to when it was close. It is feasible that fruit nearer to the nest provided more salient cues (social or sensory) and triggered earlier departure times when a nonfig breakfast was nearby. An alternative explanation is that when competition for early arrival is low, the females (all with small offspring) avoided traveling early when predation risk is greatest [forest leopards hunt diurnally with crepuscular peaks (30); see Fig. S5 regarding leopard attack rates], especially when the distance to be traveled was far and the breakfast tree could not be reached via arboreal travel.

We argue that the chimpanzees must have weighed disparate pieces of future information in their decisions (e.g., the time of arrival at the breakfast site, predation risk during travel, their egocentric distance to, and the type of fruit to be eaten), when considering alternative departure times. This theory is consistent with the possibility that they exhibited anticipatory planning and future-oriented reasoning (34). Chimpanzees are known to make decisions involving a single factor that affects them in future times, similar to what has been observed during goal-directed travel toward high-valued food sources in other primates (11, 32, 35, 36). Here, the interactive effect of distance and fruit type on departure time indicate that their decisions were conditional on the combined value of multiple factors that affected them in future times (defined here as multifactorial planning).

Planning for Tomorrow by en Route Nest Positioning Today. Our striking observation of chimpanzee females traveling with their young offspring during twilight hours (Fig. 2) (18% of all departures were before sunrise), when navigation is difficult and

predation risk is greatest, begs the question as to why they did not simply sleep closer to or inside the breakfast trees. Disturbed sleep by nocturnal frugivores or insects and a strong preference for particular nest locations, influenced by tree species (28, 37), particular leaf characteristics such as softness or insect repellent properties (38, 39), tree crown morphological features (38, 40), vegetation and landscape characteristics (40), and predation risk (38, 41), all explain why they did not (see Fig. S6 and *Supporting Information* for the females' preference scores). Long time and distance intervals between nest grunts (36) and nest building, and observations of inspections of multiple trees before nest building, indeed confirmed that suitable sleeping sites (for the target female or her party members) were not readily available at our study site [alone with offspring or orphans (<9 y): mean ± SD: 19 min ± 23, 980 m ± 685, n = 26; in party: 30 min ± 27, 1,194 m ± 1075, n = 82].

A restriction of suitable nest sites, however, did not stop the females from making their nest more en route to the breakfast site when breakfasting on very ephemeral fruit compared with other fruit. Despite the observation that the chimpanzees departed earlier for small fruit, we did not find any indication that they built their nest more en route to breakfast sites with small fruit. This finding could be because of variation in overall crop size of small-sized fruit and a smaller sample of nest positioning than departure time data (e.g., mornings at which breakfast was equal to the dinner site were excluded). For example, fruits of *Zanha golungensis* are small and eaten by many bird species, yet they tend to have extremely large ripe fruit crops, which likely delays depletion rates. Further investigations of a potential interactive effect of fruit and crop size are therefore needed.

Intriguingly, however, the females were more likely to make their nests on the way to fig breakfast fruit compared with other breakfast fruit. The females rarely nested at the territory boundary and nonfig breakfast sites were not clustered in the periphery (Fig. S3*B*), ruling out alternative noncognitive explanations, such as the possibility that a potential higher probability of measuring smaller α-values near the territory boundary (due to avoidance of entering neighboring territories) corresponded simply to a higher probability of breakfasting on nonfig trees in the periphery. In addition, as we controlled for the travel distance from the last feeding to the breakfast site, our results did not simply reflect failed attempts to reach a late-night feeding site triggered by a current motivation to feed.

Finally, the positioning models only included first visits to breakfast sites (*Supporting Information*) and each breakfast and nest location pair was unique. Hence, the chimpanzees performed a combination of arguably unique actions (nest departure and positioning), with the time of nest positioning being separated from the time of breakfasting (the target event) by a long period of other activities, including climbing, nest building, and sleeping, the latter of which is associated with a discontinuity of mental activity (42). We therefore conclude that the observed behavior is most consistent with future planning (42, 43).

Because all pairs of nest and breakfast sites analyzed here were unique, the question arises as to how the females could have anticipated the egocentric position of the nests in relation to the respective breakfast sites, as a large part of these breakfast sites were outside the visual detection distance (Fig. 2) (35) and 18% of the departures occurred in the dark. We propose that chimpanzees used personally retained facts on the location of fruit-bearing breakfast trees from foraging days preceding nest departure, which is consistent with earlier studies, indicating that the same target females were able to remember the location and fruiting state of individual trees (35, 36). The higher average approach speeds toward breakfast figs compared with other breakfast fruit support the idea that the females had previous knowledge on the trees and were not simply "stumbling upon" breakfast. The chimpanzee's breakfast fruit species belonged to 30 different (partly endemic) species, making the results difficult

to explain by a learned genetic predisposition for early departure and nesting on the way to very ephemeral breakfast species. Because revisit frequency to individual figs was on average only 1.9 (N_{trees} = 131), we argue that knowledge on species-specific ephemerality levels or depletion rates of fruit must have been learned during previous fruiting periods. Whether chimpanzees are able to generalize or learn to classify fruit trees to those having high or low levels of ephemerality in the same way as they are proposed to do for fruiting synchrony levels (44) is a topic for future studies.

In earlier studies of future planning in nonhuman animals, planning appeared restricted to particular domains. For example, scrub jays (*Aphelocoma californica*) are argued to singularly display "laser beam intelligence," implying that their intelligence is restricted as they are unable to plan outside the food-caching context (45). Notably our observations were outside the domain of tool use and social-exchange situations in which chimpanzees have been reported to plan (46–49), adding to the growing evidence that chimpanzee planning skills are not context-specific, a quintessential feature of human planning (45). Whether their decision making on departure times and nest-building locations was based on a human-like preexperiencing of future events [i.e., mental time travel (45)] or a generalized knowledge of personally acquired facts [semantic prospection (43)] remains elusive and a topic perhaps best investigated in language-trained chimpanzees.

Future-Oriented Behaviors in Other Foragers. There is increasing evidence for future-oriented behaviors that maximize food intake in foraging animals (32, 43, 46, 47, 50–52). Many of these behaviors are fixed-action patterns that are genetically hard-wired, such as migrations to better feeding grounds or food caching (43). Others can be explained by learned associations, such as the behavior of western honey bees (*Apis mellifera*) that arrived between 8:00 and 10:00 AM at jam pots located on outdoor breakfast tables (50). Behaviors, such as tool transport or tool making, by chimpanzees are argued to be guided by mental representations occurring a substantial time before the forager is confronted with a tool-use task, which is referred to as anticipatory planning (46, 47). Other behaviors, like that of chacma baboons (*Papio ursinus*) that first feed on figs after passing by edible seeds that they subsequently feed on later in the day (32, 43), suggest a perhaps more-advanced form of planning whereby animals evaluate and exclude alternative options and thereby show a level of self-control. Even more advanced cognitive behaviors are those that maximize the amount or variety of a forager's food intake on subsequent days, such as the experimentally induced caching activities of western scrub jays, or behaviors that maximize the next days' probability of foraging near conspecifics in orangutans (*Pongo abelii*) (42). These behaviors are argued to represent the only true form of planning, where the forager divorces itself from current motivation (51).

In humans, well-investigated forms of future-oriented behavior are route planning (52) and, on a smaller scale, the game of chess. Chess players continuously search and evaluate alternative choices to make their next move and plan subsequent steps. Extensive research clarified that despite the sophisticated forms of planning involved in the game, master chess players access the best moves by pattern-based retrieval and elaborate memory of chess positions acquired through years of experience (53). Learning theorists might argue that similar processes of pattern-based retrieval could explain observed travel decisions in wild chimpanzees (54). The foraging problems of chimpanzees would then perhaps be best compared with those faced in a game of chess in which the pieces do not only change position but also continuously change their state (e.g., from queen to pawn), with intervals that can last months for some yet only hours for others. For the sake of finding explanations of the chimpanzees' behavior that are computationally adequate to be used in

continuously changing tropical forest environments (47), we therefore focused here mainly on the higher cognitive instead of post hoc associative descriptions of our observations.

We propose that exploitation rates of sympatric foragers have a large impact on such continuous yet potentially predictable environmental changes (1), and that competition for food has been a crucial selective force in the evolution of many future-oriented behaviors. Few field studies address how future-oriented behaviors could minimize the negative effects of food competition. Langurs (*Presbytes potenziani*), for example, that were observed to leave their sleeping trees earlier than sympatric living gibbons (*Hylobates klossi*), were argued to achieve substantial food intake before eventually being supplanted from the breakfast trees by dominant gibbons (28). Similarly, chacma baboons that departed their sleeping cliffs earlier and in a more goal-directed manner to breakfast on sought-after figs compared with other fruit were proposed to outcompete other baboon groups in exploiting figs (32, 55). Studying rain forest chimpanzees enabled us to investigate whether foragers compensate for travel time by departing earlier conditional on the exploitation rate of and their egocentric distances to food, and whether they consider the degree of ephemerality of food sites on subsequent days. An exciting topic for future study is to examine to what extent such complex future-oriented behaviors can increase foraging efficiency more so than cognitively less-complex behaviors in environments where breakfast's market values vary in response to fluctuating weather conditions, foragers' preferences, and densities.

The Role of Ecological Complexity on Brain Size Evolution. Recent studies suggest that the costs of evolutionary brain enlargement were overcome by a permanent increase in net energy intake (8, 9), renewing interest in the role of ecological complexity in brain size evolution (1, 4, 6). To our knowledge, our study provides the first clear example of a future-oriented cognitive ability used in a food-scarce period within a highly competitive tropical forest environment that could enable all large-brained foragers to buffer drastic declines in food availability. We propose that large-brained foragers that need a reliable and steady intake of high-energy nutrition to maintain their large and costly brains (6, 11) could gain a clear evolutionary advantage by using flexible planning that reduces indirect interspecific competition. This attribute may have been particularly important for hominoids that specialized on stationary, energy-rich, and highly ephemeral food, such as ripe fruit (14, 17, 24), abandoned meat carcasses, or aquatic fauna trapped in receding waters (56). The proposed benefit of flexible planning skills, especially for hominids living in highly seasonal habitats like savannah, strongly encourages a more detailed focus on the temporal aspect of ecological complexity than has been done to date (1, 6), and a resumed investigation of its role in theories of primate and, in particular, hominid brain size evolution (11).

Materials and Methods

This study was based on noninvasive observations and complies with the laws of the Ivory Coast. The study site was located in primary lowland rainforest in the Taï National Park, Ivory Coast (35). A total of five adult habituated female chimpanzees were individually followed by K.R.L.J. and S.D.B. from April 16, 2009 to August 30, 2011 for continuous periods ranging from 4 to 8 wk, totaling 275 full days, during three fruit-scarce periods (25, 26) (Fig. S3A). A target female was followed from the point of waking until construction of an evening sleeping nest, and her activity recorded using continuous focal sampling (35). Duration and location of each activity (e.g., feeding duration and the number of males in the party) were recorded using a combination of a global positioning device (GPS; Garmin 60 CSx) and voice recorder. Each morning it was determined whether it had rained the previous night at the nest site by noting whether the nearby forest floor was wet or dry. We marked all feeding and nest sites, in which the target female fed and slept, with brightly colored spray paint and recorded their locations using the GPS device. The day after each focal observation day, trained

assistants relocated each marked tree, identified the species, recorded if other animal species were feeding in the tree, and took pictures of fallen ripe fruit with a reference label to measure their size using a SeaLife Dive & Sport Camera. See refs. 35 and 36 for more details on data collection and interobserver reliability tests for the scoring of activities and species determination. Each night, temperature was measured in the research camp. Astronomical sunrise times were retrieved from the website www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html. The energy balance was estimated using similar methods as described in ref. 57; see *Supporting Information* for details. We only analyzed data from days that followed complete observation days (from nest departure to nest building) so that the relative energy balance could be compared between mornings. Breakfast was defined as the first food item eaten after waking up. Only mornings where breakfast consisted of fruit were considered (74% of all mornings). To calculate the fruit volume, we combined the size calculations from the pictures of the fallen ripe fruit with botanical references (58, 59). We analyzed our results using Mann–Whitney U tests, a Spearman rank correlation test, and GLMM and LMM (60) in R (v3.0.3; R Development Core Team 2014). See *Supporting Information* for detailed information on data collection procedures, statistical model designs, diagnostics, inference, and analysis software.

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