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Seasonal Change in Terrestriality of Chimpanzees in Relation to Microclimate in the Tropical Forest

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KEY WORDS chimpanzee; food distribution; microclimate; terrestrial behavior; thermoregulation

ABSTRACT Seasonal change in time spent for terrestrial behavior of chimpanzees was investigated from the viewpoint of the distribution of food and microclimate in the forest at Bossou, Guinea, West Africa. Daily and monthly data for activity budgets of three focal animals, climatic variables in the forest, and indices of fruit availability and distribution of fruit-bearing trees were estimated and analyzed. Mean activity budgets calculated by monthly means were 23.4% for terrestrial behavior (range, 2.9% in August to 42.1% in November) and 76.6% for arboreal behavior. Chimpanzees spent more time on the ground in warm or dry months. Chimpanzees also spent less time in trees in months with high fruit production (trees of diameter at breast height ≥10 cm). The daily percentage of terrestrial behavior showed a positive correlation with maximum temperature and a negative correlation with the minimum humidity of the day. Only maximum temperature of the observation day influenced time spent on the ground significantly, as analyzed by generalized linear models (GLZ), which included all variables (fruit production, distribution of fruit-bearing trees, and climatic variables). It was concluded that the reason why arboreal behavior increased in the rainy season was not owing to the vertical distribution of food, but rather in order to reduce thermoregulation costs by resting in trees during cool periods and taking advantage of the vertical structure of the microclimate in the tropical forest (i.e., higher temperatures in higher positions). Am J Phys Anthropol 124:81–92, 2004. © 2004 Wiley-Liss, Inc.

The proportion of time allocated to arboreal behavior in African great apes varies across species and study site. Sex differences in the degree of arboreality are also recognized within each site (Doran, 1996). Generally, larger animals are assumed to be more terrestrial. Doran (1996) listed habitat type, diet, and predator pressure as factors affecting the degree of arboreality. In Gombe, East Africa, however, chimpanzees spent much more time in trees in the wet season compared to the dry season (Wrangham, 1977). This seasonal change in the distribution of time budgets for terrestrial or arboreal behavior may not be influenced by body size or habitat type, but rather by seasonal changes in some ecological factors.

Wrangham (1977) stated that the seasonal differences in arboreality of chimpanzees resulted from a shift in the vertical distribution of food. The lower proportion of arboreal behavior during the dry season in his study probably reflected ground-level production (e.g., fruiting shrubs) and the preference of chimpanzees for eating some fruits after they have fallen (e.g., *Parinari curaetellifolia*). Doran (1993) also reported a monthly variation in time spent on the ground for both sexes in Taï chimpanzees (Ivory Coast), and reasoned that the consumption of *Parinari excelsa* nuts was the motivating factor.

At the same time, Wrangham (1977) gave an additional factor other than the vertical distribution of food. He suggested that because chimpanzees dislike sitting on wet ground, they spend more time resting or grooming in trees in the wet season than in the dry season. Soil water storage is related to rainfall, flux of solar radiation, temperature, and humidity in a given period, since water balance is determined by precipitation and evapotranspiration (transpiration by plants and evaporation from the soil), except for surface runoff and deep percolation. For these reasons, soil water content is regarded as representative of the microclimate in the forest. Mean daytime temperatures in tropical forests are usually lower in the rainy season than in the dry season. Maximum, mean, and diurnal range of temperature are also significantly lower beneath the rain-forest canopy than within it. This vertical difference in tempera-

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ture shows the same trends in the dry season and in the rainy season, or in primary and secondary forests (Richards, 1996).

If the seasonal change in terrestriality is influenced by the vertical distribution of food, the rate of utilization in trees should increase in relation to an increase in tree-fruit availability, whereas that on the ground should decrease. Furthermore, if fruit-bearing trees form clumped spatial patterns, it might lengthen travel distance or moving time between food patches. As a result, time spent on the ground is likely to increase. Given that seasonal change in terrestriality is influenced by microclimate in the forest, the rate of utilization on the ground may change according to the fluctuation of temperature, humidity, and rainfall. The utilization height of chimpanzees also possibly varies in each season for selecting the comfortable place in the forest.

In order to clarify the factors affecting seasonal change in the terrestriality of chimpanzees, this paper investigates seasonal change in the rates of terrestrial- and arboreal-based activities of chimpanzees by comparing two factors. These two factors were 1) the seasonal change of vertical and horizontal distribution of tree fruits, and 2) the microclimatic variables of the Bossou forest.

METHODS

Data collection

A basic description of the study site and observation methods were given in Takemoto (2002). The study was conducted in Bossou, Guinea, West Africa (for details of the research history and study area at Bossou, see Sugiyama and Koman, 1992; Yamakoshi, 1998). Data were collected from June–November 1996 and November 1997–June 1998. Activity patterns of three individuals (one subadult male (VI) and two adult females (Jr, Vl)) were recorded by focal animal sampling (Altman, 1974), following one focal chimpanzee for an entire day or as long as possible to avoid introducing observation biases associated with grouping patterns or visibility. The data from each day in which observations lasted more than 1 hr were used in this analysis. Total observation time of data presented here was 379 hr over 121 days. The body weight of the subadult male (9 years old in 1996) was estimated to be similar to that of an adult female. In this respect, there is expected to be little effect of body weight on degree of terrestriality reported among these focal animals.

Since whole-day samples were scarce and the observation hours were scattered throughout the day, I examined whether there were any biases in the time of day of observations using three-way ANOVA. A day was divided into three periods: morning (6:00–10:00 hr), midday (10:00–14:00 hr), and evening (14:00–18:00 hr); daytime period, month, and focal animal were used as factors in the analysis.

Differences among focal animals (df = 2, 255; f = 0.30; ns), months (df = 11, 255; f = 1.14; ns), and interactions among these three factors were not found. there was a significant difference in day time-period (df = 2, 255; f = 3.82; $p < 0.05$). the evening period had fewer observations. mean observation time (hour)/individual/day was 1.2 in the morning, 1.1 in the midday, and 0.8 in the evening period. since chimpanzees was usually active until 18:30 hr, actual mean observation time in the evening period was greater than 0.8.

Behavioral categories

In order to estimate the proportion of activities on the ground, behaviors were classified as being either feeding, moving, or resting (including all activities except feeding and moving), and further classified into occurring either on the ground or in trees. Consequently, activity budgets were composed of six categories: arboreal feeding (AF); arboreal resting (AR); arboreal moving (AM); terrestrial feeding (TF); terrestrial resting (TR); and terrestrial moving (TM). The criterion for terrestrial behavior was whether or not the animal placed at least one of its feet on the ground. When a focal animal was sitting on a fallen tree, it was regarded as terrestrial behavior only in cases where all of the fallen tree's trunk touched the ground. Terrestrial behavior also included behavior on rocks or resting in a ground day-bed. Terrestrial feeding included even those activities when the focal animal was standing and eating fruits of liana or shrubs, unless its feet left the ground. Likewise, arboreal feeding included cases when the focal animal was eating foods which are basically terrestrial (e.g., Manioc, fruit of terrestrial herbaceous vegetation) after carrying them into a tree, or in the case of a chimpanzee holding onto lianas or shrubs while dipping a wand to the ground for catching ants. Since undergrowth at Bossou is dense, overall time spent for terrestrial behavior may be underestimated. The present paper focused on the seasonal change in the degree of terrestriality in the Bossou forest, and does not concern the comparison of overall terrestriality among study sites of the great apes.

Seasonal change in percentage of time spent in trees or on the ground, i.e., arboreality or terrestriality, was investigated, and the correlation between each behavior was calculated. Correlations between terrestrial behavior in total observation time and terrestrial behavior when feeding, when resting, and when moving were also calculated. Terrestriality is defined as TF + TR + TM. The terrestriality in each behavior is calculated as follows: when feeding, TF/(AF + TF); when resting, TR/(AR + TR); and when moving, TM/(AM + TM).

Relation between distribution of fruit products and terrestrial behavior

The study transect extended 1,600 m in total for the first half of the study period and 2,200 m in the later half, with a width of 5 m. All trees (greater than 5 cm DBH) were identified and marked, and basal area was measured. Since the forest of Bossou is divided and surrounded by bush or cultivated areas, transects were established in three main forest areas. Woody plants identified in the transects numbered 1,065 trees of 120 species. Trees in transects were divided into two categories: 5–10 cm, and >10 cm in DBH, in order to examine seasonal change in fruit availability (FAI) for each DBH category (Takemoto, 2002). Chimpanzees rarely eat fruit from trees more than 5 cm in DBH without leaving the ground. However, the FAI of trees >10 cm DBH was used to represent the vertical distribution of fruit products.

Fruit production was estimated with binoculars, targeting all trees in the transects twice per month. Fruit abundance for each tree was ranked on a relative scale from 0–3 (modified from Chapman and Wrangham, 1994). The fruit availability index (FAI) was calculated by

$$\mathrm{FAI} = [\Sigma(\mathrm{Pi} \times \mathrm{Fi})/\Sigma(\mathrm{Pi} \times 3)] \times 100$$

where FAI is the fruit availability index (%), Pi is the basal area of tree i (cm^2), and Fi is the fruiting score of tree i (0–3). FAI was calculated for each food-tree species used by chimpanzees. The seasonal change of FAI of chimpanzee fruit food-tree species (n = 26, 206 trees) was strongly correlated with the change of FAI of all tree species in the transects ($rs = 0.89$, $P < 0.01$, $n = 10$). The dispersion of fruit bearing trees (>10 cm DBH) was calculated using the standardized Morisita index (SMI; Smith-Gill, 1975, as per Krebs, 1999) as a unit 50 m in length. SMI ranged from −1.0 to +1.0, with 95% confidence limits at +0.5 and −0.5. Random patterns give an SMI of zero, clumped patterns occur above zero, and uniform patterns below zero. When the SMI is above 0.5, the sample data can form a clumped distribution with 95% confidence.

The 12 months were classified into two phenological seasons: high/low fruit production based on average FAI during the study period, or clumped ($\mathrm{SMI} > 0.5$)/nonclumped ($\mathrm{SMI} < 0.5$) fruit-bearing trees. The differences in time spent for terrestrial behavior between the two seasons were tested using two-tailed Mann-Whitney U tests. Daily correlation between three basically terrestrial main foods and the degree of terrestriality were also examined.

Relation between microclimatic variables and terrestrial behavior

Daily rainfall was measured by a pluviometer at the field station. Air temperature and air humidity in the forest were measured by a digital thermo-hygro meter (CTH-180, Custom Corp.) with a determination range (± precision) of −10–60°C (±1°C) and 10–98% RH (±6%). This thermo-hygro meter was placed in a mature forest inside the home range of the chimpanzees at an altitude of 650 m. The meter was attached to a tree trunk at a height of 1.5 m above the ground, and placed under a small roof to avoid exposing it directly to wind and rain. Maximum and minimum temperature, and maximum and minimum humidity, were recorded manually at 17:30 hr each day. Between June–July 2002 (wet season), two automatic thermo-hygro recorders (HN-CHN, Chino Corp.: −10–60 ± 0.5°C, 0–100 ± 2%) were attached to the same tree as above at 1.5 m and 11 m height to measure vertical differences in microclimate. Data were automatically recorded every 10 min.

The climate at Bossou, in general, may be divided into the dry season (November–February) and the wet season (March–October) (Yamakoshi et al., 1999). However, the 12 months were classified into two sets of categories for warm/cool months and dry/wet months, based on monthly average temperature or average rainfall and humidity. The difference in terrestriality between these climate seasons was tested using the two-tailed Mann-Whitney U-test. The data for June and July 1996, however, were omitted from the monthly analysis because there were too few observation days for the meteorological data in these months. The correlation between daily proportion of time spent on the ground and meteorological indices of that day was tested using Spearman's rank correlation test. Monthly number of tree day-beds made and average day-bed height were used for estimating the resting height of chimpanzees. The data were analyzed only when day-bed-making were observed.

Factors determining terrestriality

Each microclimatic variable and the phenology of trees presumably correlate with each other. For this reason, on the basis of monthly and daily data, I estimated the factors affecting terrestriality, according to generalized linear models (GLZ, Statistica) using all variables. The GLZ is a generalization of the general linear model. Normal distribution and identity link functions were used for the analysis of the general custom designs in GLZ.

RESULTS

Seasonal change in terrestriality

Overall activity budgets calculated from monthly averages based on the daily activity budget of each animal were 23.4% for terrestrial behavior (TF, 4.2%; TR, 16.9%; TM, 2.2%) and 76.6% for arboreal behavior (AF, 21.3%; AR, 52.3%, AM, 3.1%). The proportion of terrestrial behavior varied remarkably throughout the year, from 2.9% in August (18.4% on the average of wet season) to 42.1% in November (32.2% on the average of dry season) (Fig. 1, Friedman test, $k = 12$, $m = 3$, $\chi^2 = 20.54$, $P < 0.05$). The mean percent of terrestrial behavior for focal animals was 30.1 ± 3.8% (± SE, n = 38) for VI, 20.4 ± 3.5% (n = 38) for Jr, and 19.7 ± 3.7% (n = 45) for Vl. The subadult male tended to spend more time on the

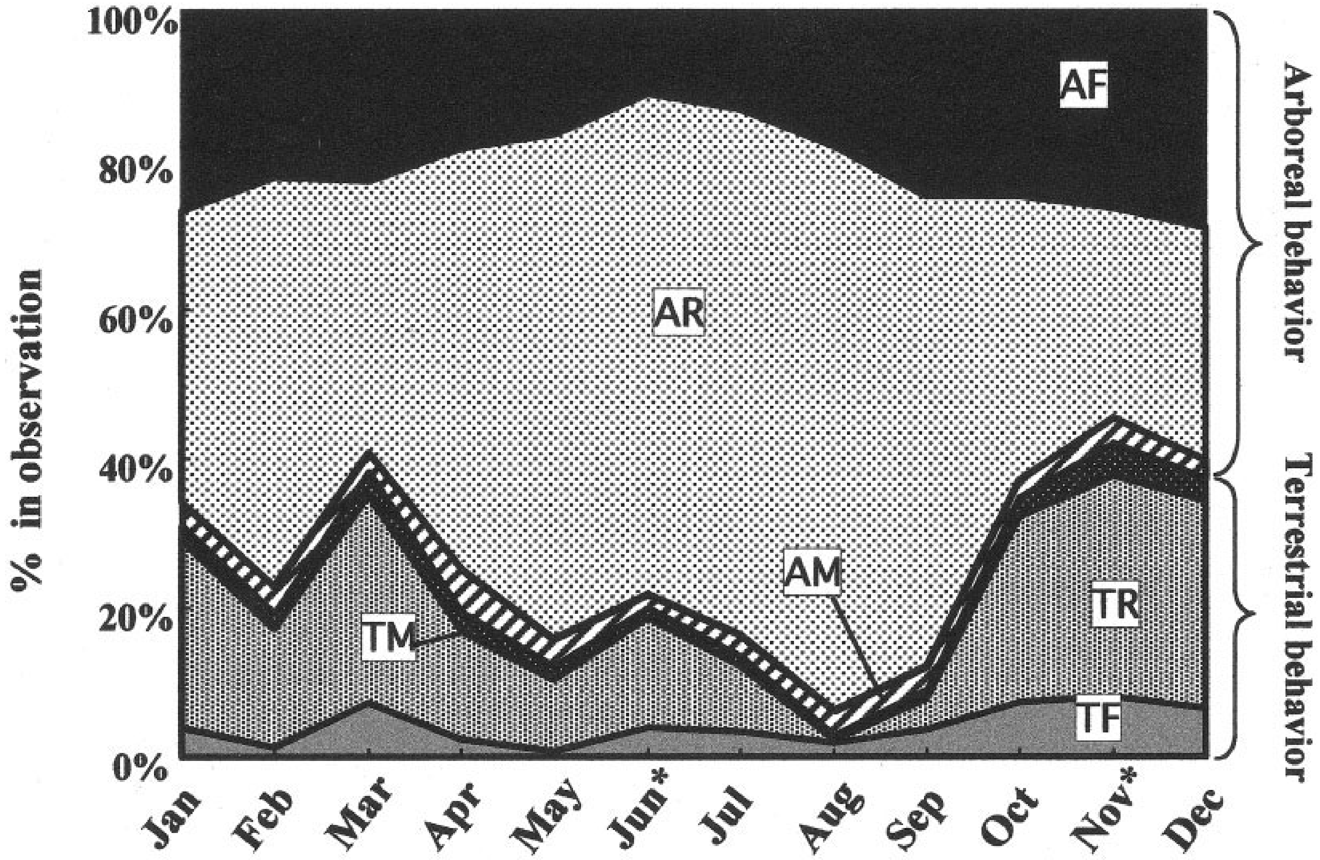

Fig. 1. Seasonal change in activity budgets. AF, arboreal feeding; AR, arboreal resting; AM, arboreal moving; TF, terrestrial feeding; TR, terrestrial resting; TM, terrestrial moving. *June and November represent averages of two different years.

TABLE 1. Correlations between activities[1]

Activities	Monthly correlation (n = 12)	Daily correlation: All animals (n = 121)	Jr (n = 45)	Vl (n = 38)	VI (n = 38)
AF vs. TF	**0.59***	−0.01, ns	−0.14, ns	−0.22, ns	0.15, ns
AR vs. TR	**−0.93****	**−0.81*****	**−0.78*****	**−0.81*****	**−0.75*****
AM vs. TM	0.11, ns	−0.04, ns	−0.15, ns	0.00, ns	−0.28, ns
AF vs. AR	**−0.79***	**−0.51*****	**−0.39***	**−0.46*****	**−0.59*****
AF vs. AM	−0.05, ns	**0.24****	**0.33***	**0.45****	0.12, ns
TF vs. TR	**0.75***	**0.45*****	**0.77*****	0.17, ns	0.14, ns
TF vs. TM	0.55, ns	**0.51*****	**0.61*****	**0.40***	**0.53****
Terrestriality vs. terrestriality in feeding	**0.69***	**0.62*****	**0.83*****	0.31, ns	**0.39***
Terrestriality vs. terrestriality in resting	**0.96****	**0.93*****	**0.97*****	**0.94*****	**0.88*****
Terrestriality vs. terrestriality in moving	**0.91****	**0.78*****	**0.81*****	**0.77****	**0.76*****

[1] Boldface represent significant correlation coefficients (Tables 1–3). ns, not significant (Tables 1–4).
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

ground than females, but the difference was not significant (Friedman test, k = 3, m = 12, $\chi^2 = 4.67$, ns).

Table 1 shows the relationship among activity categories. Strong negative correlations were found between terrestrial resting (TR) and arboreal resting (AR) in both daily and monthly analyses. Whether a focal animal rested in a tree or on the ground changed seasonally. This relationship was not found in feeding and moving behavior. An increase in arboreal feeding (AF) did not increase arboreal resting (AR). Terrestrial resting (TR) tended to increase as terrestrial feeding (TF) increased; nevertheless, these correlations varied among focal animals. The proportion of terrestriality in all observation times positively correlated with the proportion of terrestriality in feeding, resting, and moving, respectively, although terrestrial resting had the strongest correlation among the three correlations.

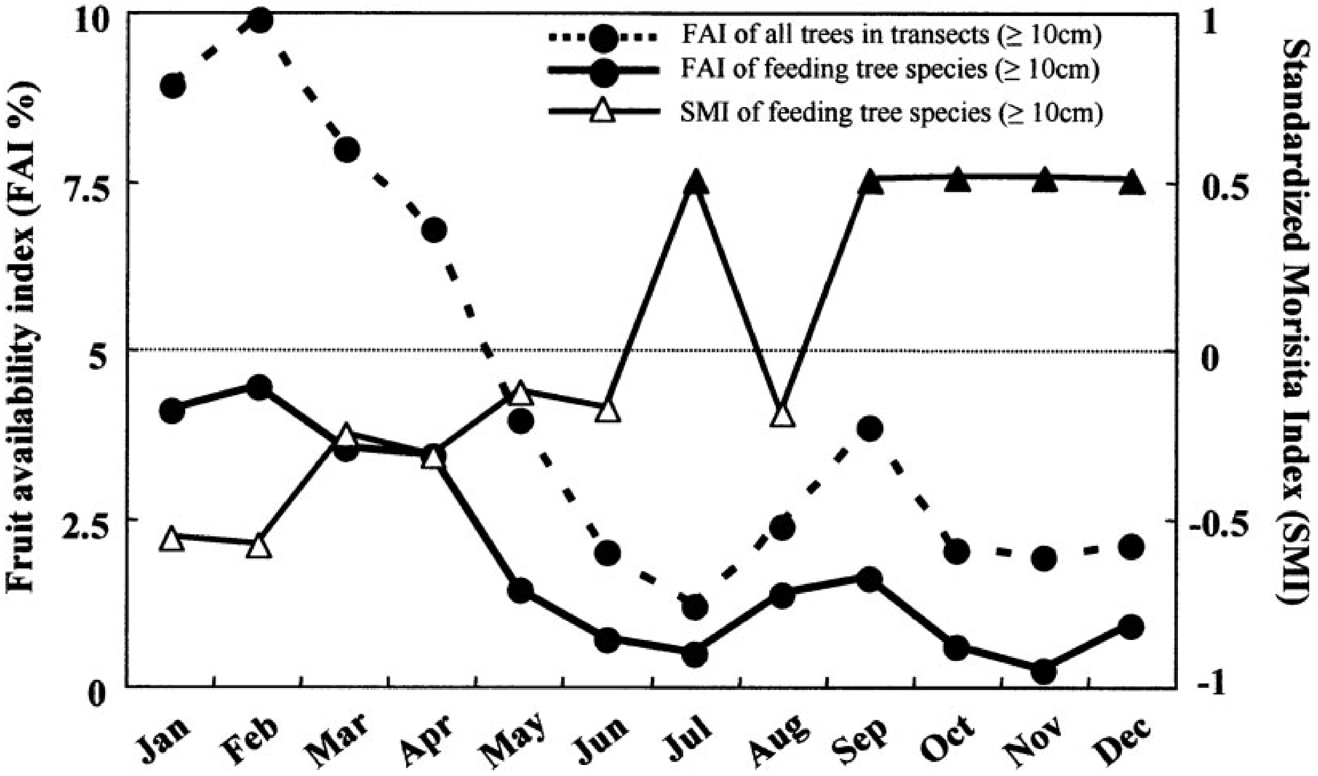

Fig. 2. Seasonal change in vertical and horizontal distribution of fruit production represented by fruit availability index (FAI) and standardized Morisita index (SMI). Solid triangles show months with clumped distribution of fruit-bearing trees (i.e., SMI > 0.5).

Distribution of fruit products and terrestriality

Monthly variations in FAI and SMI are given in Figure 2. Trees >10 cm in DBH bore fruits abundantly from January–April, although a small peak was found in September. High FAI months (January–April) and low FAI months (May–December) were observed. There were also clumped months (July and September–December) and nonclumped months (January–June and August) in fruit-bearing tree dispersion.

The extent of terrestriality differed between phenological seasons. The proportion of terrestrial behavior, however, was higher in high FAI months (28.8 ± 3.7%, average ± SE, n = 40) than in low FAI months (20.4 ± 2.6%, n = 67). Terrestriality increased when fruit up in the trees was abundant (U test; z = −2.27, $P < 0.05$). In clumped months, time spent on the ground accounted for 25.7 ± 4.2% (n = 38), and that in nonclumped months accounted for 21.6 ± 2.7% (n = 69), but there was no significant difference between these 2 months (U test; z = −1.35, ns).

TABLE 2. Daily correlations between terrestriality and percentages of three food categories in total feeding[1]

Activity	THV	Oil palm nut	Ants
AF	−0.05 ns	−0.03, ns	0.05, ns
AR	**−0.21***	−0.17, ns	0.02, ns
AM	**−0.21***	−0.09, ns	−0.01, ns
TF	**0.59*****	**0.39*****	0.16, ns
TR	**0.30****	0.14, ns	−0.01, ns
TM	**0.34*****	**0.22***	0.05, ns
Terrestriality	**0.37*****	**0.25****	0.02, ns

[1] N = 121.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

In terrestrial feeding, chimpanzees primarily consumed THV piths, which accounted for 43.4% of the total terrestrial feeding time. In the diet, the fallen nuts of *Elaeis guineensis* accounted for 8.3%, and ants accounted for 4.4% of terrestrial feeding time. These chimpanzees also often ate arboreal foods such as figs or cultivated fruits such as oranges while staying or traveling on the ground, after taking the foods from trees and descending. Table 2 shows the daily analysis for three specific items, which were consumed mainly terrestrially. Feeding time for THV and oil palm nuts were correlated with terrestriality; nevertheless, the consumption of oil palm nuts was not related to terrestrial resting. Chimpanzees ate THV pith in great proportion in the dry season, and consumed ants mainly in the wet season (Fig. 3). Feeding time for oil palm nuts had two peaks at June in the wet season and at December in the dry season, yet total feeding time was small.

Chimpanzees, in general, rarely ate fallen fruits in large amounts except for the *Parinari excelsa* fruit. At least two *Parinari excelsa* trees exist in the chimpanzees' home range. Chimpanzees were ob-

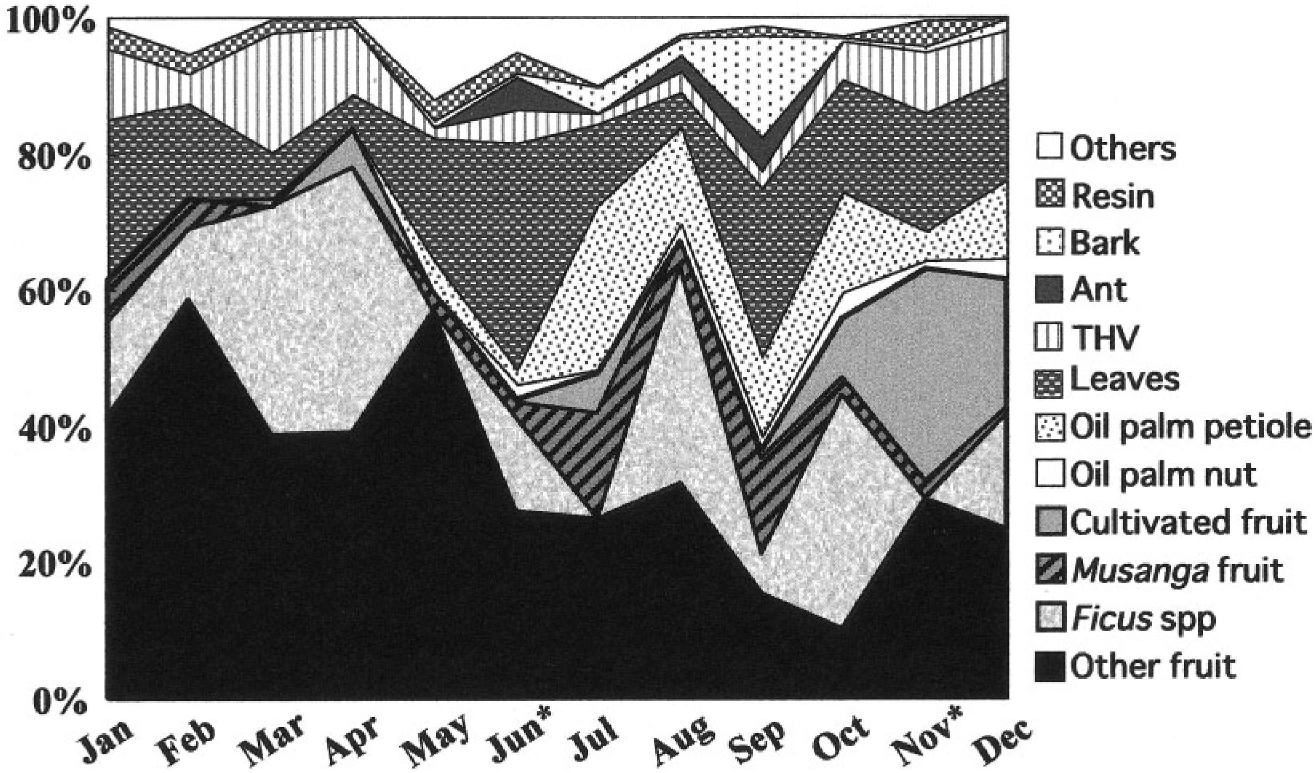

Fig. 3. Seasonal change in dietary composition of three focal chimpanzees. Each food category is shown in proportion to total feeding time in each month. *June and November represent averages of two different years.

served feeding on these fruits in large amounts, including fallen fruits, from November–December 1995. *Parinari excelsa*, however, did not bear fruit annually, and fruiting was not observed during the survey period.

Microclimate in the forest and terrestriality

Microclimate at a height of 1.5 m above the ground in the Bossou forest was characterized by an average maximum temperature of 26.1°C (range, 21.2–31.2°C, n = 106), a minimum temperature of 21.0°C (range, 18.4–23.6°C, n = 106), a maximum RH of 93% (32–98%, n = 107), and a minimum RH of 74% (17–98%, n = 107). Study months were divided into warm months (January–May and November) and cool months (June–October and December), or dry months (January–March and November–December) and wet months (April–October), on the basis of averages of monthly rainfall, monthly maximum temperature, and monthly minimum humidity during the study period (Fig. 4). Height differences in climatic variables were observed in the wet season of 2002. The space higher up in the forest at 11 m showed a higher maximum temperature (25.5°C on average, n = 20) and lower minimum humidity (77.5% on average, n = 20) than the lower space at 1.5 m (23.9°C and 92.5% on average, n = 20).

Time spent in terrestrial behavior varied with climate-season. Chimpanzees spent significantly more time on the ground in warm months (27.8 ±

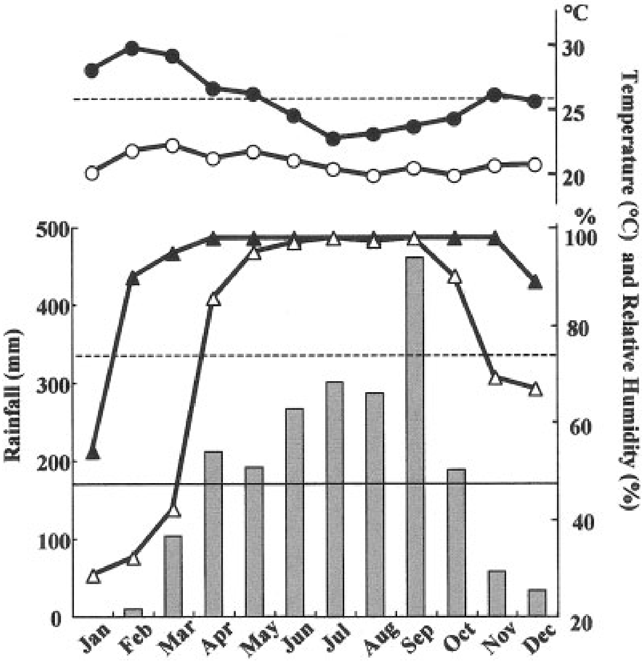

Fig. 4. Monthly rainfall at field station and microclimatic variables in forest at a height of 1.5 m above ground during study at Bossou. Shaded bar, monthly rainfall; solid line with solid circles, maximum temperature; solid line with open circles, minimum temperature; solid line with solid triangles, maximum humidity; solid line with open triangles, minimum humidity; straight line, average monthly rainfall (175 mm); dashed lines, average of monthly maximum temperature (26.1°C) and average of monthly minimum humidity (74%).

TABLE 3. Correlation between daily activity budgets and daily climate

Activity (N)	Maximum temperature (106)	Minimum temperature (106)	Maximum humidity (107)	Minimum humidity (107)	Rain (121)
AF	−0.03, ns	−0.09, ns	**−0.23***	−0.07, ns	−0.09, ns
AR	**−0.21***	−0.04, ns	**0.27****	**0.33*****	**0.21***
AM	0.16, ns	0.03, ns	−0.12, ns	−0.11, ns	−0.10, ns
TF	−0.05, ns	−0.09, ns	0.00, ns	−0.03, ns	0.00, ns
TR	**0.35*****	0.14, ns	**−0.30****	**−0.40*****	**−0.20***
TM	**0.29****	**0.25****	−0.14, ns	**−0.33*****	**−0.30****
Terrestrial behavior	**0.28****	0.10, ns	**−0.25***	**−0.34*****	**−0.20***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

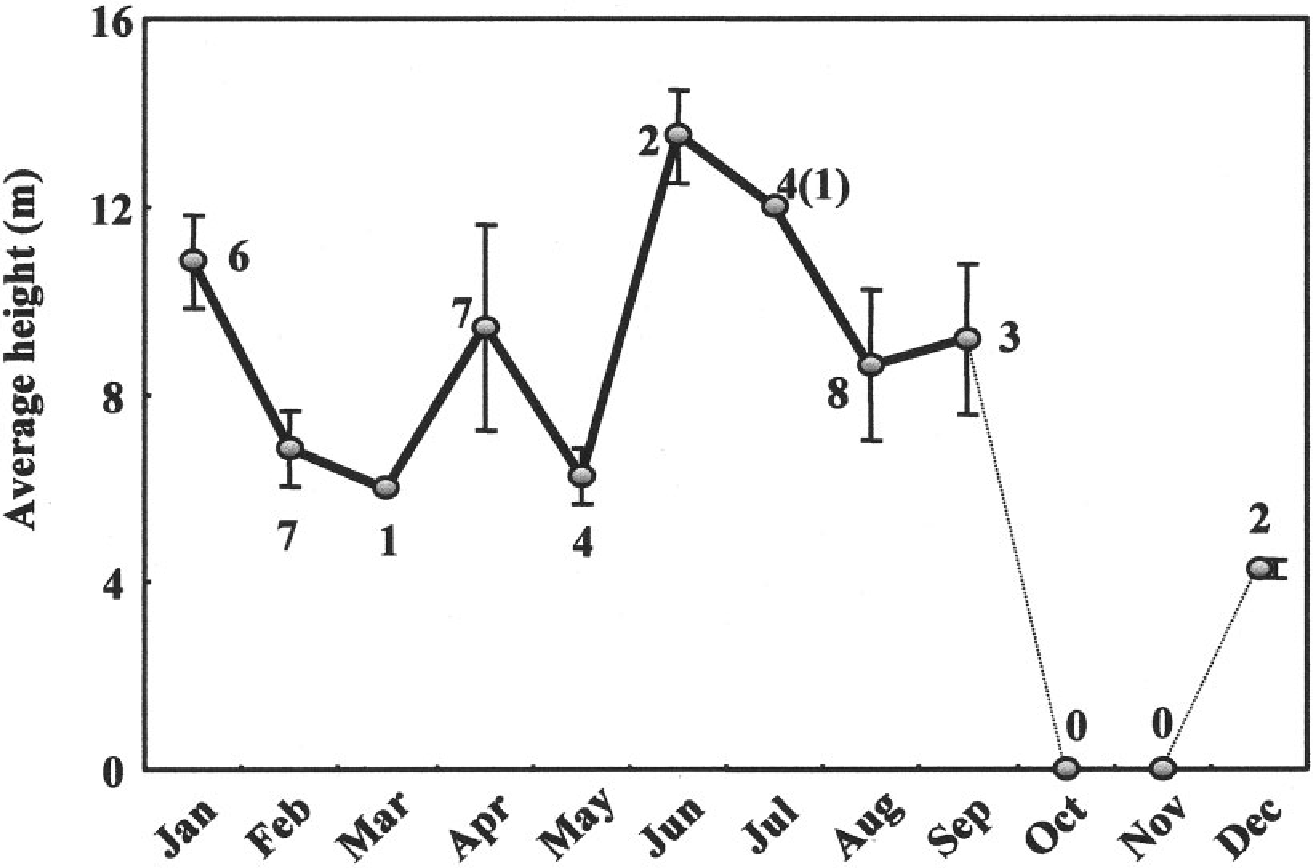

Fig. 5. Height variations of tree day-bed sites in each month. Numbers are actual numbers of times chimpanzees were observed making beds during daytime. Error bars represent standard error (± SE). In July, bed-making was observed four times, but estimation of height was made only once. There were no significant differences between warm months (8.3 ± 0.7 m, n = 23) and cool months (9.0 ± 1.0 m, n = 16), and dry months (8.0 ± 0.8 m, n = 16) and wet months (9.0 ± 0.8 m, n = 23) (U test; z = −0.37, ns; z = −0.66, ns, respectively).

3.3%, n = 57) than in cool months (19.5 ± 3.1%, n = 50) (U-test; z = −2.18, $P < 0.05$), and used the ground significantly more in dry months (32.5 ± 3.9%, n = 44) than in wet months (18.0 ± 2.6%, n = 63) (U-test; z = −3.13, $P < 0.01$). Table 3 shows the correlations between daily activity budgets and daily measurements of microclimate variables. Time budgets on the ground showed positive correlations with temperature, and negative correlations with rainfall and humidity. Resting behavior (AR, TR), especially, showed relatively strong correlation coefficients with microclimatic variables.

Day-bed-making in tree was observed 44 times in 121 days (Fig. 5). The average height of a day bed was 8.6 ± 0.6 m (± SE, n = 39), and heights ranged from 4–16 m. Day-bed-making was observed throughout the study period except for October and November. Bed-making height had no significant difference between climate-seasons, because chimpanzees built comparatively higher numbers of day

TABLE 4. Results of influences on terrestriality by GLZ

	Monthly analysis[1]		Daily analysis[2]	
Effects	Wald statistic	P	χ^2	P
Intercept	0.59	ns		
Maximum temperature	9.07	**	6.61	*
Minimum temperature	6.64	*	0.19	ns
Maximum humidity	1.06	ns	0.85	ns
Minimum humidity	0.73	ns	1.41	ns
FAI	6.30	*	5.82	*
SMI	24.82	***	4.08	ns
Rainfall	0.12	ns	0.03	ns
Focal animal			5.22	ns

[1] Test of all effects.
[2] Likelihood type 1 test.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

beds in the dry season (January–February). Chimpanzees often built day beds in trees several times in a day. In cases where focal animals were lost and relocated, they were often observed to be already resting in day beds, and thus the number of day beds made may be much greater. Day beds built higher than 16 m were sometimes observed in such cases.

Influences on terrestriality

Table 4 summarizes the results of calculations made by the generalized linear models (GLZ) from monthly means and daily data. Monthly averages of maximum and minimum temperature, FAI, and SMI could be regarded as the factors most affecting degree of terrestriality. In the daily analyses, the maximum temperature of the observation day and FAI (monthly value) significantly influenced the terrestriality of chimpanzees studied.

DISCUSSION

Why is there seasonality in terrestrial and arboreal behavior?

The relationship between climatic variables and degree of terrestriality showed clear trends. Terrestrial activities of chimpanzees increased when ambient temperature was higher or humidity was lower. In contrast, the influences of vertical and horizontal distribution of foods were unclear. Fruit availability had a great influence on the time budget for terrestrial behavior according to GLZ (Table 4). However, terrestrial behavior increased when fruit was abundant, contrary to previous expectations. When fruit-bearing trees were found in a clumped distribution, terrestrial behavior tended to increase, but did not achieve statistical significance. This factor had great effect on terrestrial activity in monthly value, but little effect on daily analysis according to GLZ (Table 4). Arboreal feeding did not lead to arboreal resting, and terrestriality correlated with terrestrial resting more strongly (Table 1). Feeding on THV was associated with an increase in degree of terrestriality (Table 2); even so, THV are available year-round at Bossou and, at least, its density does not increase in the dry season at Lopé, Gabon (White et al., 1995). There seems to be no reason for chimpanzees to search for THV more in the dry season than in the wet season. Feeding on oil palm nuts may have partly been responsible for increasing terrestriality, but this did not correlate with terrestrial resting (Table 2). It was certain for resting behavior but not for feeding or moving behavior that seasonality exists in proportion to terrestriality or arborеality (Fig.1, Table 1). The facts that have been clarified so far indicate that while seasonal change in the rate of ground usage is affected to some extent by the vertical or horizontal distribution of food, the main effect seems to be from microclimate fluctuations in the forest.

If this is so, how does the microclimate inside a forest affect the time spent in terrestrial behavior? The vertical structure of the microclimate of a tropical forest has been reported at many sites (see Richards, 1996). Because the forest canopy, rather than the ground, is the main heating and radiation surface, the diurnal range of temperature is greater within the canopy than on the surface of the ground. Consequently, the higher one goes up in the canopy, the more the air temperature rises and the more the relative humidity decreases compared to the ground surface during daytime in a tropical forest. At Banco, Ivory Coast, the air temperature around the canopy is 6.4°C higher in the dry season and 3.3°C higher in the wet season than at ground level (Cachan and Duval, 1963; cited by Richards, 1996). Aoki et al. (1975) in Southeast Asia and Takehara (2001) in South America reported similar results, and this trend is consistent in the secondary forest (Ross, 1954) and at night (Shuttleworth et al., 1985). Schallar (1976) reported that the air-temperature differences between the ground surface and 5 feet (about 1.5 m) above the ground at night range from 1–5°C in Albert National Park, Uganda. The Bossou forest showed the same trends of vertical structure in microclimate. The differences between 11 m and 1.5 m in height were 1.6°C and 15% RH in the wet season. The difference will be greater in the dry season and between forest canopy and ground level height.

Seasonal differences in effective temperature appear to be narrow as animals move to higher places above the ground during the wet season and move nearer to ground level during the dry season, thus reducing the metabolic costs of thermoregulation. In general, most tropical mammals, including humans, have lower critical temperatures between +20–30°C; below these temperatures, their metabolic rates increase rapidly (Scholander et al., 1950). For example, "a monkey with a body temperature of 38°C and a lower critical temperature of 28°C must double its metabolic rate by a further 10°C drop in temperature to 18°C" (Schmidt-Nielsen, 1997). The neutral zones for heat balance (i.e., the ranges between lower and upper critical temperatures) in pri-

TABLE 5. Thermoneutral zone in primates

Suborder	Species	Thermoneutral zone (°C)	Literature cited
Prosimii	*Microcebus murinus*	25–28	Aujard et al., 1998
	Galago spp.	22.5–27.5, 30–32.5, 30	Müller, 1995
	Nycticebus coucang	31.4–36.6	Whittow et al., 1977
	Tarsius syrichta	32–35	McNab and Wright, 1987
Anthropoides	*Cebuella pygmaea*	27–34	Genoud et al., 1997
	Leontopithecus rosalia	28.1	Thompson et al., 1994
	Cercopithecus mitis	24–25	Müller et al., 1983
	Homo sapiens	28–32	Davson, 1970; Erikson et al., 1956

mate species are mostly less than 5°C (Table 5). Below these ambient temperatures, heat production increases. Above this, heat production also increases because of the use of energy-demanding processes to dissipate heat, i.e., panting or sweating. According to Ward and Archibald (1970), young chimpanzees (2–5 years old), 12–25 kg in body weight, exhibited marked dehydration after a 20-hr duration test at more than 29.4°C and constant 50% RH conditions. Theoretical values (ΔTlc) for the difference between body temperature (Tb) and lower critical temperature (Tlc) can be calculated from the allometric equation for primates: $\Delta \mathrm{Tlc} = 3.4 \times \mathrm{W}^{0.25}$ (W in kilograms; McNab, 1974). Given an average body weight of 33.7 kg for adult female chimpanzees (Kay and Ross, 1999), and body temperature at daytime of around 36°C (Fowler et al., 1999), ΔTlc is calculated to be 8.2°C, yielding a Tlc of 27.8°C.

Lower relative humidity would result in higher water and energy requirements due to an increase in total evaporative water loss (TEWL) (Müller, 1995). In *Galago garnetti*, the TEWL value doubled and heat production was about 15% higher when RH was reduced from 75% to 30% (Müller, 1986; cited by Müller, 1995). Resting on the ground in the dry season would effectively maintain optimal body temperature and prevent water loss, because the air in the undergrowth contains a relatively high amount of water vapor, even during the daytime in the dry season, which generally shows a low RH (Evans, 1939).

Seasonal changes of microclimate in the Bossou forest are thought to have a significant impact on the metabolism of chimpanzees, and effective temperature can vary largely with wind or rain. The thermoneutral zone can shift to a lower or higher temperature, or be extended in range according to changing ambient temperatures by acclimatization and acclimation (Bligh, 1973). In tropical forests such as Bossou, the minimum temperature is stable throughout the year (Fig. 4), but the diurnal temperature range becomes great in the dry season. Chimpanzees possibly shift their thermoneutral zone to a high temperature or extend its range. However, reducing the seasonal variation in ambient temperature by using the vertical structure of temperature in the forest will cause a reduction in the range of physiological acclimatization, which would help chimpanzees deal with ambient temperature change more readily.

Forest utilization height

Many day beds were found in trees not only in cool months but also in the warm months of January and February (dry season). Bed site heights were far above the ground during these months (Fig. 5). This might result from seasonal *Harmattan* winds (a dry dusty wind that blows along the northwest coast of Africa) and the associated decrease in effective temperature during this season at Bossou. Wind velocity is slower in areas of thick leaf growth than on the ground surface (Pianka, 1978; Robbins, 1993). It is probably convenient to rest in a day bed in trees to avoid such winds. Fruiting of tall trees (i.e., >30 cm in DBH), which bear fruits in these months, might also have had an effect on day-bed height and the frequency of day-bed making. The time budgets or frequency of height utilization, however, could not be analyzed in this study. In the case of the Bossou forest, canopy height rarely exceeded 30 m and was usually less than 20 m. Materials for beds are less abundant within 5 m of the ground. Chimpanzees are thus unable to use a very wide range of heights for bed making.

Both chimpanzees and bonobos are reported to build their beds higher up during the wet season than the dry season (Fruth and Hohmann, 1994; Baldwin et al., 1981). This fact is consistent with the present study, given that those cases are also affected by the vertical structure of the forest microclimate. The fact that beds of chimpanzees are built with no covers in the wet season in equatorial Guinea and Senegal (Baldwin et al., 1981) is difficult to explain. This is probably because day and night beds serve different functions (Brownlow et al., 2001), and the analysis of Baldwin et al. (1981) lumped both together. Day beds can be made several times daily in the rainy season, and chimpanzees may prefer to expose themselves to sunshine after the rain.

Gorillas also build their ground nests in the dry season more frequently than in the rainy season (Tutin et al., 1995; Remis, 1993). Tutin et al. (1995) showed that the wetness of the ground was not the only factor affecting seasonal differences in the proportion of tree nests, because the proportion of tree nests was not different between rainy nights and nonrainy nights in the wet season. As Schaller (1976) reported, the place just above 1.5 m height from the ground has a considerably higher temperature compared to the ground surface in some cases, and the nests above the ground at least seem to be more comfortable than nests on the ground surface in cooler wet months.

Comparison and implications of ground use

Few data comparable to those presented here have pointed out behavioral differences related to vertical structure of the microclimate inside the forest at other research sites. Chimpanzees in Gombé, Tanzania, spend more time in the trees in the wet season than in the dry season (Wrangham, 1977). Total activity time in trees was 66.8% in the wet season. In contrast, that was 35.5–44.0% in the dry season. When chimpanzees engage in feeding, activity time spent in the trees was 87.9% in the wet season, and that was 56.6–68.7% in dry season. When resting or grooming, total activity time in trees was 62.9% in the wet season, while it was 7.5–13.5% in the dry season ($P < 0.05$). A drastic change is found in resting behavior but not in feeding behavior, as in this study. *Lemur catta* in Madagascar is also reported to spend more time in the lower parts of the forest in the dry season when temperatures are higher (Budnitz and Dainis, 1975).

Wrangham (1977) surmised that this trend is due to a dislike of wet ground. Admittedly, chimpanzees often rested on a windthrow or in a ground bed in the wet season, and I too think they dislike wet ground because of its slipperiness and coldness. This explanation, however, is insufficient to interpret the seasonal change of time spent on the ground observed in this study, because activity on a fallen tree or in a ground day bed was included in terrestrial behavior in the present analysis. The logic of reducing thermoregulation costs seems to stand up independent of a "dislike of wet ground." Furthermore, behavior related to ambient temperature for thermoregulation was reported in several primate species: *Lepilemur leucopus* (Nash, 1998), *Cercopithecus sabaeus* (Harrison, 1985), *Colobus polykomos* (Dasilva, 1993), *Macaca fuscata* (Watanuki and Nakayama, 1993; Schino and Troisi, 1998), and *Alouatta caraya* (Bicca-Marques and Calegaro-Marques, 1998); thus it appears to be a widespread pattern among primates.

The possibility also exists that an increased risk of infection by some intestinal parasite species influences the seasonal arboreality of chimpanzees, since the infective stage larvae of species of the genera *Strongyloides* and *Oesophagostomum* is concentrated on the ground and in low-level vegetation (Marquardt et al., 2000). Parasite infection levels of *Oesophagostomum*, whose infective stage is ingested with forage, increase in the rainy season in Mahale chimpanzees (Tanzania) (Huffman et al., 1997). If parasite prevalence increases in the wet season at Bossou, it is difficult to explain why chimpanzees make many arboreal day beds in the dry season of January–February. Reducing terrestrial feeding might cause a reduction in infection rate by oral infection, but will not cause an increase in arboreal behavior directly. Where chimpanzees eat and where they rest were almost independent, and time spent for resting behavior necessarily decided whether chimpanzees engaged in arboreal or terrestrial behavior (Table 1, Fig. 1).

Increasing terrestrial behavior may lead to an increase in the threat of predation. It is possible for chimpanzees to respond to the threat of predators by forming larger parties. Chimpanzees tend to form large parties when they travel or stay on the ground, although no predators exist at Bossou. Monthly change in party size from October–March, as shown by Sakura (1994), correlated significantly with time spent for terrestrial resting (TR) in this study (with TR, $rs = 0.89, P < 0.05, n = 6$; with TF, $rs = 0.37$, ns, $n = 6$; with terrestriality, $rs = 0.77$, ns, $n = 6$; with FAI (≥ 10 cm), $rs = -0.43$, ns, $n = 6$). When they are crossing roads, which are found in their home-range area, the party size is larger than that within the forest (Sakura, 1994). This is probably an adaptive response when facing dangerous situations or locations, and this is also probably effective when facing predators.

The question of why humans acquired a terrestrial life habit has been discussed largely in relation to the origin of bipedalism. Various theories on the adaptive significance of hominid bipedalism have been proposed (see Fleagle, 1999). Most of these scenarios invoke environmental change as an underlying cause of the evolution of bipedalism, usually the disappearance of forest and the expansion of open grassland or savannah (Isbell and Young, 1996). Chimpanzees, however, walk bipedally at a higher frequency in trees than on the ground (Hunt, 1992). Bipedalism and terrestrial living are not necessarily linked to one another, nor need they be caused by the same events (Richmond et al., 2001). Stronger seasonality resulting from a cooler and drier climate throughout the Miocene period could have promoted semiterrestrial life. It can be assumed that climatic change itself was the direct factor moving hominids toward terrestrial life, although food distribution may have effected the acquisition of terrestrial life for hominids. The conclusions of this study suggest the possibility that the acquisition of terrestrially may not have occurred outside the forest in order to explore for foods in or across the savannah, but rather inside the forest to reduce the energetic loss effected by climatic change. Assuming that early hominids were species with a lighter body mass than extant chimpanzees, they were probably much more sensitive to changing climate than are chimpanzees.

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