“Savanna” Chimpanzees

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INTRODUCTION: WHY STUDY SAVANNA CHIMPANZEES?

For obvious reasons, most primatologists seek out “optimal,” or at least “normal,” habitats and large, habituated troops when they choose study sites. Research on savanna-dwelling chimpanzees has been of a fundamentally different sort; sites have been chosen for their marginality in the belief that: (1) chimpanzee adaptation to arid conditions can yield insights into the adaptation of early hominids to similar habitats (Suzuki, 1969), and (2) comparison of chimpanzees in widely differing habitats can shed light on the sources and functions of variability in chimpanzee behavior and social structure (McGrew, 1983; McGrew *et al.*, 1981). Far from seeking comfortable sites with high densities of chimpanzee subjects, there has been a virtual competition to find the most marginal habitat in which chimpanzees are able to eke out a living (cf. Kortlandt, 1983).

In this paper I briefly review savanna chimpanzee research and then discuss several specific attributes of early hominids that are consistent with origins in a habitat similar to that of modern “savanna” chimpanzees. Where I use quotation marks around the term savanna, it is to emphasize that the botanical term covers a great range of vegetation physiognomies. This range, and its consequences for models of hominid origins and evolution, are discussed below.

HISTORY OF RESEARCH ON SAVANNA CHIMPANZEES

Research on savanna-dwelling chimpanzees began with the arrival of the Kyoto University Africa Primatological Expedition (KUAPE) at Kabogo Point, Tanzania, in 1961 (Fig. 1). The twin aims of the expedition were to study “chimpanzees living in dry open forest country, the knowledge of which is expected to throw some light on the ecology of Early Man, when *Hominidae* evolved from its anthropoid ancestors...[and] the social life of chimpanzees" (Azuma and Toyoshima, 1961–2:61). The chimpanzees of Kabogo Point proved difficult to observe, so the primary camp was moved inland to the Kasakati Basin in 1963; persistent difficulty in habituating chimpanzees led to the establishment of additional camps at Filabanga and the more forested site of Mahale (also known as Kasoge or Kasoje). Habituation was successful only at Mahale, and when KUAPE was forced to cut back on expenses in 1967, only Mahale was maintained (Nishida, 1990).

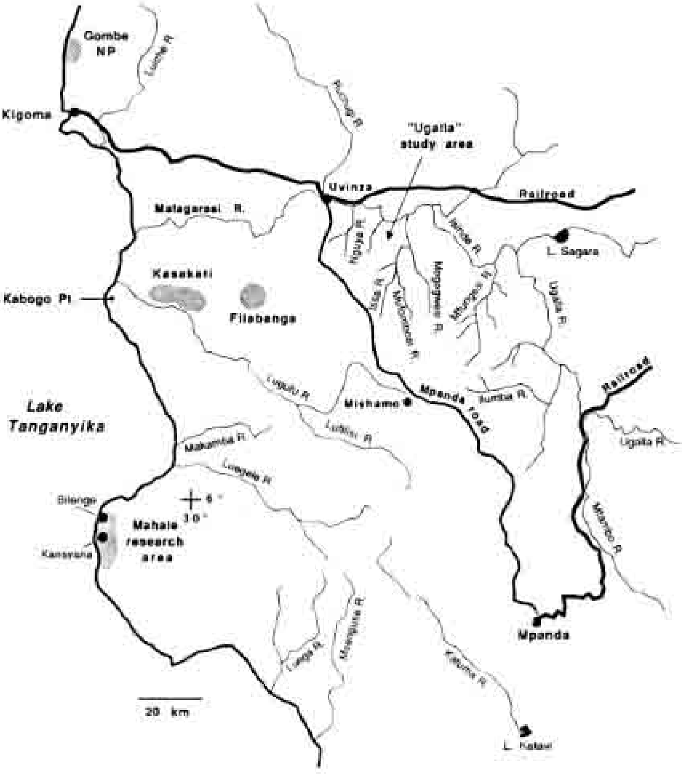

Fig. 1. Chimpanzee study sites in Tanzania. Shaded areas indicate chimpanzee study sites. The chimpanzee population of the "Ugalla" area (Tongwe Forest Reserve) is probably contiguous with Filabanga and Kasakati. Chimpanzees have been observed as far south as the Ilumba River in the Ugalla area (Nishida, 1989). See also distribution map in Kano (1972).

Despite the difficulty of observing chimpanzees at the savanna woodland sites of Kasakati and Filabanga, researchers were able to document important aspects of diet and ranging using mostly indirect means, such as fecal contents, vocalizations, and so on (Izawa, 1970; Izawa and Itani, 1966; Kano, 1971; Kawabe, 1966; Suzuki, 1966, 1969). In addition, a survey in 1966 by Kano and Itani (Kano, 1972; Itani, 1979) noted the presence of chimpanzees in the even drier Tongwe Forest Reserve, just west of the Ugalla River. Since 1966, several researchers have made short (less than two weeks) surveys of Ugalla (Moore, 1986; Nishida, 1989), and I recently spent several months there (Moore, in prep.).

In early 1976, the Stirling African Primate Project began a study of savanna chimpanzees at Mt. Assirik in Senegal, with a focus on quantitative comparisons of chimpanzee ecology and social structure across habitats; again, the underlying goal was to understand hominoid adaptation to habitats resembling those of early hominids. Here too, chimpanzees were hard to find, habituation proceeded slowly, and behavioral observations were scant; when the project ended after forty-seven months, only 367 contacts with chimpanzees had been made —such are the problems inherent in studying savanna chimpanzees (Tutin *et al.*, 1983). Project members continue to publish a number of comparatively oriented papers (Baldwin *et al.*, 1981; Baldwin *et al.*, 1982; McBeath and McGrew, 1982; McGrew, 1983; McGrew *et al.*, 1981; McGrew *et al.*, 1988; McGrew *et al.*, 1989; Tutin *et al.*, 1983).

SAVANNA VS. FOREST—WHAT IS A "SAVANNA" CHIMPANZEE?

"In recent years the term 'savanna' has become synonymous with African plainslands—grasslands studded with flat-crowned acacias and carrying a profusion of wild ungulates" (Huntley, 1982). Although commonly held, this view is misleading; the definition hinges on the domination of the groundcover by C_4 grasses, and such ecosystems include everything from the nearly treeless plains of the Serengeti to closed woodlands (Huntley, 1982).

Physiognomies of the East and West African "savanna" chimpanzee sites differ dramatically (in Gabon, *P. t. troglodytes* have also been reported in savanna-forest mosaic but have not been studied formally in such habitats; Garner, 1918). Mt. Assirik is drier and is a true mosaic with 55% of the study area open grassland (the popular image of "savanna") and the rest mostly woodland, with small amounts of

Table 1. Rainfall at Chimpanzee Study Sites

Site	Rainfall (mm) (Mean±SE)	No. of dry months	Mean±SE of *Q*s	*Q* of mean	Period (*N*)
Mt. Okoro	2112	3	NA	43	? (13)
Biko	3528.5	3	33.3	NA	1967 (1)
Budongo	1489.3±196.6	2.6±0.9	36.3±16.4	13	1934–42 (9)
	1861.7±245.6	2.0±0.9	25.3±11.8	11	
Kibale	1536	1	NA	14	1941–70 (30)
	1664	2	28.6	NA	1977 (1)
Gombe	1819.8±580.7	4.3±0.9	71.8±33.4	50	1968–87 (20)
	2542.7±169.6	3.7±0.8	48.6±11.3	50	1976–82 (7)
	1430.6±225.1	4.6±0.9	84.3±33.4	67	remainder (13)
M: Kansyana	1817.8±184.4	4.4±0.8	66±14.9	57	1974–88 (14)
M: Myako	1704.7±189.2	4.7±0.7	70.4±17.8	57	1976–84 (9)
M: Bilenge	1327.9±150.6	5±0	91.5±9.8	83	1978–80;1982 (4)
Ugalla	1012.3±139.1	5.2±0.8	108.8±38.7	83	1973–88 (16)
Kasakati	962	6	NA	100	1941–70 (30)
Mt. Assirik	954.5±182	6.8±1	160±27.1	140	1976–79 (4)

Q : [(dry months/ wet months) × 100], where a *dry* month has ≤ 60 mm rainfall and a *wet* one has > 100 mm (Whitmore, 1975). No. of dry months: Mean ± SE where presentation of raw data made calculations possible. NA = Not applicable (N=1 or only averages presented in data source). Mt. Okoro Biko: Top line from means for unspecified 13-year period at Niefang (Griffiths, 1972); lower from Jones and Sabater Pi (1971). Budongo: Data from Eggeling (1947); lower line corrected (×1.25) for estimated greater rainfall in the forest. Kibale: Data from Ft. Portal (≈16 km NW of forest); top: Anon. (1983); lower: Ghiglieri (1984). Gombe: Primarily from Anon. (1988) (see text). M: Mahale Mountains camps (Anon., 1988; Takasaki *et al.*, 1990). Ugalla: Data from Uvinza (≈10 km NW of nearest observations of chimpanzees) (Anon., 1988). Kasakati: Data from Kigoma (Anon., 1983), ≈70 km NW (see text). Mt.Assirik: Data from McGrew *et al.* (1981: Table 3).

riverine forest and bamboo thicket (McGrew *et al.*, 1981). In contrast, the Tanzanian sites (Kasakati, Filabanga, and Ugalla) are 60–90% *Brachystegia/Julbernardia* ("miombo") woodland (Suzuki, 1969; Kano, 1972). Miombo woodland consists of regularly spaced trees extending to the horizon in all directions. While important chimpanzee resources are patchily distributed, the habitat cannot easily be characterized as "mosaic." [See below and McGrew *et al.* (1981) for discussions of the significance of habitat mosaics in hominid evolution.] In this paper I will refer to Mt. Assirik, Kasakati (including Filabanga), and Ugalla as "savanna" sites. However, since the label "savanna" masks important habitat variation, it is necessary to compare study sites quantitatively. Several approaches are possible, probably the easiest being a measure of rainfall.

Table 1 compares annual rainfall totals and Q for chimpanzee study sites. Because variable onset of rains tends to spread out rainy seasons when data are pooled over a number of years, Q is sensitive to averaged rainfall data. Table 1 presents both the average of Q calculated separately for each full year and Q calculated for average monthly rainfall figures.

As discussed by McGrew *et al.* (1981), different researchers have reached different conclusions about rainfall at Kasakati relative to lakeside recording stations. Kortlandt (1983) argues for lower rainfall at Kasakati, correctly noting that the difference between shoreline (Myako) and inland (Kansyana) rain gauges at Mahale should not be generalized to other sites, since the higher rain at Kansyana is at least partially due to local orographic effects. However, about 40% of the Kasakati site itself is mountainous and consists in part of tableland at an elevation of ca. 600–1,000 m above the level of Lake Tanganyika (Suzuki, 1969). Under the circumstances, one can only conclude that Kasakati probably receives about 950–1,050mm per year, with five to six dry months.

A number of sources were consulted regarding rainfall at Gombe (Anon., 1988; Clutton-Brock, 1972; Wrangham, 1975; unpublished Gombe records); unfortunately, they do not all agree, and the best estimate, based primarily on Anon. (1988) and D. A. Collins (personal communication), shows a sudden and unexplained shift toward higher rainfall during the years 1976–1982 (Table 1). The Gombe average exclusive of these years falls between Kansyana and Bilenge but is closer to Bilenge, as would be expected on the basis of vegetation (cf. Collins and McGrew, 1988). I feel that the evidence suggests a methodological rather than meteorological origin for the high-rainfall years, and provisionally consider the 1968–75/1983–87 data subset more reliable.

Mt. Okoro Biko (Rio Muni), Budongo, and Kibale (both in Uganda) are more or less considered to be moist evergreen forest sites. Kansyana and Myako camps at Mahale fall within a mixture of semievergreen "Kasoje forest" and semideciduous woodland; Bilenge, about 7 km north of Myako, is primarily semideciduous woodland. Gombe has been called woodland, Kasakati and Ugalla savanna woodland, and Mt. Assirik, savanna; see McGrew *et al.* (1981) and Collins and McGrew (1988).

The measure that best distinguishes the "savanna" sites of Mt. Assirik, Kasakati, and Ugalla is the simplest—the three sites form a cluster with mean annual rainfall of ca. 1,000 mm (Fig. 2). Within that cluster, *Q* clearly distinguishes the Tanzanian sites from Mt. Assirik; as noted above, these are physiognomically very different.

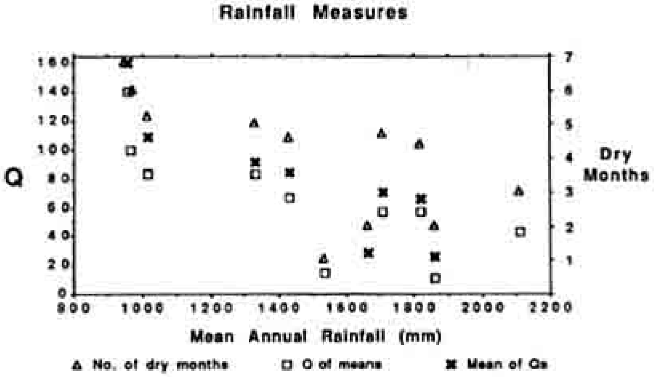

Fig. 2. Rainfall measures. Three different means of characterizing rainfall regime are illustrated for sites listed in Table 1: average annual rainfall (horizontal axis), *Q* (see Table 1; left vertical axis), and average number of dry months per year (right vertical axis). The three "savanna" sites of Mt. Assirik, Kasakati, and Ugalla form a distinct cluster.

Rainfall itself cannot be the whole story, however; local topography (cf. discussion of Kasakati, above) and regional weather [e.g., the Saharan harmattan winds at Mt. Assirik (Kortlandt, 1983)] are also important. For this reason, direct, quantitative descriptions of habitat are necessary if we are to understand social and behavioral variability among chimpanzees, and these should be in terms of vegetation types/physiognomies (rather than species lists) if we are to successfully extrapolate findings to paleontological contexts (Sept, 1990:98). Collins and McGrew (1987, 1988) have taken an important step in this direction, providing such data for three Tanzanian sites, and data from a preliminary survey in Ugalla are forthcoming (Moore, in progress).

PRIMARY CONCLUSIONS

a) Population Density and Home Range Size

Given that they are "marginal" sites, it is not surprising that population density estimates for Mt. Assirik and Ugalla are ca. 0.08–0.12 chimps/km^2 (Baldwin *et al.*, 1982; Kano, 1972; Moore, unpub. data). Kasakati is only slightly richer: 0.3–0.75/km^2 (Baldwin *et al.*, 1982). Comparison with more forested sites is slightly problematic since similarly derived density estimates are not available for Mahale or Gombe. My own estimates of ecological density using methods outlined in NRC (1981:74–78) and based on data and figures in Nishida *et al.*, (1990:70–71) and Goodall (1986:82, 228) suggest population densities of 3–5/km^2 for Gombe and 5–7/km^2 for the M and K group ranges at Mahale.

"Savanna" chimpanzees thus live at densities perhaps 1/50th that of some forest-dwelling chimps. It is worth noting that the only detailed survey of nonstudied chimpanzees in evergreen forest habitat also yields density estimates of < 1/km^2 (Tutin and Fernandez, 1984).

Despite this range in population density, there is no obvious association between population density and community size (Tutin *et al.*, 1983). Consequently, home ranges at the low-density sites are extraordinarily large. Baldwin *et al.* (1982) show that the Mt. Assirik community probably ranges over more than 275 km^2, and crude estimates for Ugalla reach 560 km^2 (Kano, 1972; but see Baldwin *et al.*, 1982).

b) Party Size and Composition

Data from nest counts (Baldwin *et al.*, 1981) and direct observations (Tutin *et al.*, 1983) indicate that the size of temporary parties tends to be larger at Mt. Assirik than at other sites (Fig. 3), and that within the site they are slightly larger in more open habitats. Furthermore, solitary chimpanzees and mother-offspring units tend to avoid open woodland significantly more than do mixed parties (i.e., adults of both sexes present), and circumstantial evidence suggests that parties are more stable (Tutin *et al.*, 1983). These authors note that the observed differences may be aspects of antipredator tactics. Support for this conclusion comes from the observation that in nearby Mali (which has a similar habitat but from which nearly all predators have been exterminated), nest group size appears to be considerably smaller (Moore, 1985). (While differences in observed party sizes may also reflect observational bias toward larger parties in poorly habituated communities, similar differences in nest group size are unlikely to be due to such bias.) Comparable data on party size are not available for Kasakati, but large, stable mixed parties seem to be relatively common there as well (Izawa, 1970; Kano, 1971).

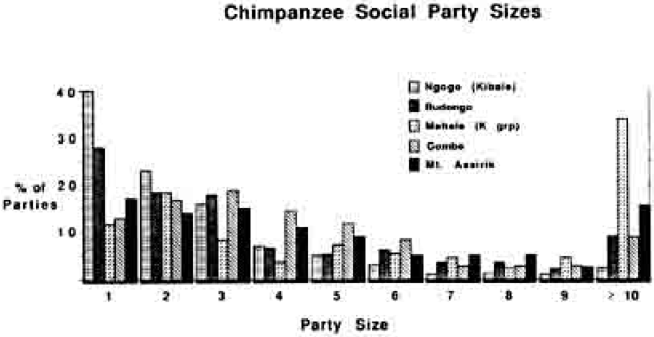

Fig. 3. Chimpanzee social party sizes. Data sources: Ngogo—calculated from Ghiglieri (1984), Fig. 15; $N \approx 483$ parties. See Wrangham *et al.* (this volume) for discussion of methodological issues concerning Ngogo party sizes. Budongo—pooled data for Tables 2 and 3 in Sugiyama (1968); $N = 514$. Mahale—K-group data from provisioning site, calculated from Nishida (1968), Fig. 6; $N = 218$. The high incidence of parties ≥ 10 almost certainly reflects provisioning. Gombe—calculated from Goodall (1965); $N = 498$. Mt. Assirik—calculated from Tutin *et al.* (1983), Fig. 1; $N = 267$.

At Mt. Assirik, travelling parties were much larger than groups engaged in other activities (median size 19, vs. 8 overall) (Tutin *et al.*, 1983). In contrast, at Budongo feeding parties tended to be larger than travelling parties on average (Reynolds and Reynolds, 1965; Sugiyama, 1968), and Goodall (1968:211) indicates that at Gombe smaller travelling groups would join to feed, "forming large groups of 15 or more [when] it was seldom possible to make accurate counts." Note, though, that at both Gombe and Budongo the largest groups counted were travelling (Goodall, 1968; Sugiyama, 1968), suggesting a bimodal distribution of travelling group sizes at these sites.

At both Kasakati and Mt. Assirik, cohesive range shifts by the entire community have been inferred from marked changes in the frequency of hearing/sighting chimpanzees in "core areas" (Baldwin *et al.*, 1982; Izawa, 1970; Kano, 1971; Tutin *et al.*, 1983). Taken together, these findings give an impression of a "savanna chimpanzee adaptation" of larger, more stable, mixed-sex groups that nomadically exploit resources distributed patchily within a large home range—an image of obvious relevance to hominid origins models.

However, large parties also seem to be common at two forested sites, Taï Forest (Boesch and Boesch, 1989:566) and Mahale, where subgroups of more than 50 are "frequently" seen during some seasons (Nishida, 1990:26). The tendency for Mahale's chimpanzees to travel more cohesively than Gombe's has been the basis for argument about the nature of chimpanzee social organization (Kawanaka, 1984), an argument that neglects the role of ecological influences on intraspecific variability in primate social systems (Suzuki, 1979; Yoshiba, 1968). Until party size figures comparable to those evaluated by Tutin *et al.* (1983) are reported for these sites, the significance of the apparent savanna/forest difference in party size and stability remains uncertain.

c) **Diet**

The diets of Kasakati and Mt. Assirik chimpanzees are described in Suzuki (1969) and McGrew *et al.* (1988). There are indications that savanna chimpanzees utilize fewer plant taxa than do forest chimpanzees (McGrew *et al.* 1988), and McGrew *et al.* also note for Mt. Assirik an apparently greater reliance on foods that are "tedious to obtain (e.g., underground storage organs) or to process (e.g., seeds and pods)" relative to other chimpanzee populations (p. 225). Implications of reliance on such foods for hominid origin models are discussed in Suzuki (1969) and below.

One important finding is that, contrary to what a "chimpanzee as early hominid" model might predict, savanna chimpanzees seem to eat less meat than those of forest sites (McGrew, 1983; McGrew *et al.*, 1988; see also Boesch and Boesch, 1989). At least two factors may contribute to this difference: first, the favorite prey of chimpanzees in forest sites is red colobus monkeys, which are not found in savanna woodland habitats; second, increased diversity and numbers of predators at savanna sites may (a) weed out vulnerable prey; (b) make prey taxa more alert; and (c) make terrestrial hunting more dangerous (McGrew, 1983).

McGrew (1979) and Uehara (1986) note inverse relationships between rates of consumption of insects and mammals, suggesting that chimpanzees who eat less vertebrate prey are able to compensate nutritionally by increasing their intake of insects. While it is tempting to think that high rates of insectivory at Mt. Assirik (McGrew, 1983) reflect such compensation, Suzuki (1966) found extremely low incidence of both insect and vertebrate remains in feces at Kasakati (6.7% and

0.5% respectively, vs. ca. 40–60% and 1–6% for Gombe, Mahale, and Mt. Assirik). Much remains to be done on quantifying rates of consumption of animals across sites; see McGrew (1983), Collins and McGrew (1987), McGrew *et al.* (1988), Boesch and Boesch (1989), and Wrangham and van Z. B. Riss (1990).

d) Behavior

There have been too few direct observations of chimpanzees at savanna sites to say anything useful about their behavior *vis à vis* "forest chimps." However, what is known of their ranging and social organization suggests that they should exhibit significant differences, for the simple reason that a loose fission/fusion system would have difficulty operating in a home range of several hundred square kilometers. Once a party wanders off, simply locating other chimpanzees would be difficult; the community would be undefinable to an observer (Tutin *et al.*, 1983). Three primary solutions to this problem can be envisioned.

First, the chimpanzees could maintain a dispersed fission/fusion community, but with lower frequencies of reunions between community members. Given the political complexity of chimpanzee life and the significance of social relationships in maintaining coalitions among males (Nishida, 1983), one might expect this to place significant cognitive demands on chimpanzees.

Second, the community might become undefinable to the chimpanzees themselves, forming an open network of relatively peacefully interacting parties, with operational clusterings of associations but no solid social boundaries.

Finally, the community might travel more cohesively, members either monitoring each other vocally or travelling on predictable routes such that temporarily separated parties are unlikely to get lost. The community's total range might be large (cf. Mt. Assirik's ≥ 275 km^2, above) but actual social dispersion remain comparable to that seen at other sites. This appears to be the closest to what has been reported (Baldwin *et al.*, 1982; Izawa, 1970; Kano, 1971; Tutin *et al.*, 1983), with the descriptions of Izawa and Kano in particular emphasizing the cohesiveness of bands.

Again, there is a complication. The large cohesive bands reported by Kano vanished from his study area after about three months and were not seen there again for the remaining seven months of the study; instead, he occasionally encountered small parties of one to four (Kano, 1971:241). Izawa also notes the presence of solitaries and of small groups (one a male-female-juvenile trio which may have been stable for 30 months) (Izawa, 1970:12–13). While Kano argues that the small parties at Filabanga were too few to account for the entire bands (which therefore must have migrated away), Wrangham suggests that if small parties rarely call, their numbers may be underestimated, and hence evidence for migrations and very large home ranges is "equivocal" (Wrangham, 1975:5.25). On the other hand, exhaustive searches by Tutin *et al.* (1983) documented the absence of *any* chimpanzees in a 42 km^2 core area during presumed migrations.

These observations suggest that savanna chimpanzees employ a mix of behavioral tactics for dealing with low population density, with the relative roles of interindividual and intersite variation still obscure. The nature of social relationships between cohesive communities, among isolated peripheral parties within a community, and between such parties and the "core" of their own community must be complex, even more so than is the case for "forest" chimpanzees. Such complexity is all the more significant given the nature of intercommunity interactions and consequent threats to small, "interstitial" parties reported at both Gombe and Mahale (Goodall, 1986). Alexander (1989:473–5) and Ghiglieri (1989) emphasize the potential significance of these sorts of relationships among chimpanzees for our understanding of human evolution.

THE MIOMBO MODEL

In this section I briefly discuss several hypotheses for the origin of traits known to be important in hominid evolution and suggest aspects of modern and/or prehistoric woodland that would play a part in these hypotheses. The discussion is necessarily brief and is intended only to emphasize the potential contributions that research on savanna woodland chimpanzees may make to an understanding of our own origins.

A number of analyses of early hominoid and hominid sites conclude that these creatures were woodland dwellers (Nesbit Evans *et al.*, 1981; Retallack *et al.*, 1990), though such reconstructions are open to debate (Shipman, 1986a). Such debate is not surprising, given the combinations of species that characterize modern woodland habitats (Itani, 1979; Nishida, 1989). Though I believe the discussion below applies to other savanna-woodland types, I focus here on miombo woodland, which characterizes the Tanzanian savanna chimpanzee sites. This has "an open or lightly closed canopy of semievergreen trees 15–21 meters high, characterised by species of *Brachystegia*, *Isoberlinia*, [&] *Julbernardia*" (Fanshawe, 1971:38).

a) Bipedalism

Rodman and McHenry (1980) argue that because chimpanzee knuckle-walking is energetically inefficient, an early knuckle-walking hominoid whose habitat changed such that it needed to travel more on the ground would be under strong selective pressure to become either fully quadrupedal or bipedal. In the context of late-Miocene habitat changes, this suggests an image of not-quite-bipedal apes rapidly traveling from one forest patch to another, across unhospitable grasslands populated by predators and devoid of initially recognizable resources; see Figure 4 (a). Such movements have been observed among the Mt. Assirik chimpanzees (Baldwin *et al.*, 1982; Tutin *et al.*, 1983).

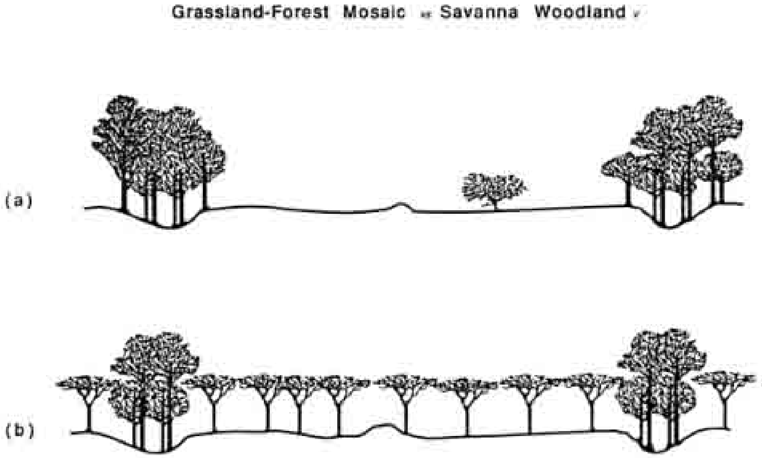
Grassland-Forest Mosaic – Savanna Woodland

Fig. 4. To travel between major resource patches, a medium-sized hominoid would have to travel long distances on the ground in either grassland-forest mosaic (the traditional image of "savanna") **(a)** or savanna woodland **(b)**. There would be less risk of predation for a hominoid or early hominid in the savanna woodland. See text for further discussion.

The same pressure for long-distance terrestrial locomotion is found in savanna woodland [Figure 4 (b)], where patches of evergreen forest are widely separated by open woodland. Relative to a forest/short grass mosaic, several features of woodland make it more hospitable. Foremost is the obvious advantage of numerous trees, representing sleeping sites, seasonal food sources, and above all, refuges from terrestrial predators. In the absence of lianas or low secondary branches, their trunks must be climbed vertically. Prost (1980) discusses the role such climbing may have played in the evolution of bipedalism. Savanna woodland could thus be seen as a comparatively safe evolutionary intermediate between forest and short grass savanna; more important (since there are no "intermediate" adaptations), it would have been a rich habitat in its own right (see below).

b) Postcanine Megadonty

A number of hypotheses have been forwarded to explain australopithecine megadonty and thickened enamel: three major ones are reliance on grass seed, hard seeds and nuts, or underground roots and tubers. All three resource types appear to be abundant in miombo woodland.

Suzuki (1969) found remains of *Julbernardia* and *Brachystegia* seeds in more than 50% of chimpanzee feces during the summer dry season at Kasakati. As he points out, such a highly nutritious staple could have played an important seasonal role for early hominids as well. This model is significantly elaborated upon by Peters (1987), who notes that because of the seasonal nature of seed eating, early microwear analyses indicating a frugivorous diet for australopithecines might be misleading; recently described variable microwear patterns among individual *A. afarensis* suggest such a seasonal reliance on "hard gritty foods such as seeds, roots, and rhizomes from the savanna" (Ryan and Johanson, 1989).

Ryan and Johanson also conclude that *afarensis* "pulled plants containing fine particles of grit across their incisors" (p. 265); Suzuki notes that grain of the grass *Brachiaria brizontha* is frequently eaten during the early dry season, and that "chimpanzees grasp the stalk of this grass, put its ear in the mouth, and strip it off with the teeth" (1969:120).

Savanna chimpanzees have been observed eating plant underground storage organs (USOs) (McGrew *et al.*, 1988). USOs generally represent adaptations to seasonal droughts and/or fire, as plants sequester resources in safety from environmental extremes (Hatley and Kappelman, 1980), and miombo woodland is both seasonal and fire-adapted. Indirect evidence for the abundance of USOs in miombo woodland comes from Kingdon's observation that mole rats (*Heliophobius*), which eat tubers and bulbs, are "strikingly numerous in *Brachystegia* woodland" (Kingdon, 1974:33).

Much needs to be done to quantify the resources actually available to a hominoid in miombo (or similar) woodland before we can really evaluate the potential role of such habitat in hominid evolution (cf. Sept, 1990). However, it seems likely that a miombo habitat would have allowed and probably required seasonal reliance on one or more of the above food classes for any hominoids inhabiting it.

c) Meat Eating

It is widely accepted that an important aspect of the divergence between chimpanzees and hominids is the increased reliance on meat and/or marrow in the diet of hominids. It is less clear how these items were obtained (Potts, 1984); recent attention has focused on the possible role of scavenging rather than hunting (Shipman, 1986b). Studies of modern African habitats (Blumenschine, 1989), gatherer-hunter peoples (O'Connell *et al.*, 1988), and chimpanzees (Hasegawa *et al.*, 1983) all support the proposition that scavenging from the kills of predators—chiefly cats—could have been a potentially significant source of meat for early hominids.

Thanks to saber-toothed tigers there likely would have been even more carrion available to a Pliocene scavenger (Marean, 1989). This conclusion stems primarily from the observation that the elongate canines of sabertooths (*Homotherium*, *Megantereon*, and *Dinofelis*) seem designed for killing large prey by penetrating thick skin while avoiding bone; for example, attacking the abdomens of proboscideans. To avoid damage to the canines, sabertooths probably concentrated feeding on viscera and exposed muscle; see Marean (1989) for discussion.

Marean summarizes evidence regarding sabertooth habitats and their contemporary carnivore/scavenger guilds in East Africa, and concludes that (1) all three cats inhabited dense forest (*Megantereon*, *Dinofelis*) or woodland (*Homotherium*), and (2) the closed-habitat scavenger niche made available by the sabertooths does not seem to have been occupied by any known carnivore. He goes on to make a strong case for the possibility that *Homo habilis* could have filled the vacant woodland/forest scavenging niche.

Such an expanded scavenging niche would have been available throughout the Pliocene, and I suggest that earlier woodland hominoids/hominids also would have had increased scavenging opportunities. The high ground-level visibility combined with abundant trees would make it relatively safer than either open savanna (no refuge) or evergreen forest (danger of ambush from hiding). I do not suggest that such scavenging was "the key adaptation" for hominids, only that a Mio-Pliocene woodland habitat probably would have been richer in safer scavenging opportunities than any other contemporary habitat, and as such would be ideal for promoting an increasing incorporation of meat/marrow into the diet of these hominids.

CONCLUSION

Savanna-dwelling chimpanzees differ from those of more forested sites in aspects of diet and ranging, and hence in the pattern, rate, and consequently perhaps form of social interactions. Several of the known differences appear to be in the direction we believe our ancestors took shortly after their divergence from the chimp-human last common ancestor (LCA), suggesting that studies of savanna chimpanzees may be uniquely useful to those interested in trying to reconstruct early hominid behavioral ecology. The potential significance of such studies has been recognized for almost 30 years now, but the difficulties inherent in studying chimpanzees at low population densities, without provisioning, have prevented any study from lasting more than a few years and there is still much to be learned from these populations that is relevant to understanding the adaptive nature of social systems among apes and to understanding our own origins.

Compared with rainforests, tropical deciduous woodlands seem relatively insignificant from a conservation standpoint. Species diversities are not tremendously high, and for most taxa population numbers are relatively low. From the standpoint of conserving chimpanzees *qua* chimpanzees, regions such as Mt. Assirik, Kasakati, and Ugalla must receive low priorities. However, such regions, and the chimpanzees which inhabit them, may hold important keys to our own past and richly deserve protection on that account at least.

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