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The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability

One hypothesis for the evolution of hominid bipedalism is that bipedalism was more efficient than quadrupedalism for long-distance terrestrial locomotion, and was favored when resources became scarcer and more widely separated during the drying of African forests in the Miocene. Here we extend this scenario for the evolution of bipedalism based on principles of behavioral ecology of extant primates. Daily travel distance is not only an increasing function of resource scarcity, but also of group size (because of intragroup scramble competition). When faced with Miocene drying, hominoids were forced to evolve either energetically more efficient locomotory abilities or smaller group sizes. The cost of the latter strategy is that smaller groups are less successful than larger groups in intergroup contest competition (smaller groups are supplanted from limiting resources). Among the earliest hominids, bipedalism may have been favored over small group size as an alternative energetic response to decreased resource availability. The alternative was to maintain quadrupedal locomotion but evolve fission–fusion grouping to reduce daily travel distance for individuals and hence, their energetic costs of travel. We suggest that this strategy represents the evolutionary pathway taken by chimpanzees. This divergence of strategies may have been a result of inherent differences in feeding ecology, but could also have been enhanced by the pre-empting of niche space by the two closely related and presumably competing hominoid ancestors of humans and chimpanzees. If so, it could have been a potential factor in the speciation process that led to modern humans and chimpanzees. © 1996 Academic Press Limited

Introduction

Bipedalism provides the earliest evidence of a morphological and behavioral difference between hominids and pongids, and numerous scenarios have been proposed for its evolution (reviewed in McHenry, 1982; Rose, 1991; Senut, 1992). Examples of selective pressures for bipedalism include (1) beginning to carry objects (Brace, 1979), dependent offspring (Zihlman & Tanner, 1978), or food (Zihlman & Tanner, 1978), (2) provisioning group members (Lovejoy, 1981), (3) changing feeding postures (Wrangham, 1980a; Rose, 1991; Hunt, 1994), (4) decreased thermal loading (Newman, 1970; Wheeler, 1984), and (5) increased locomotory efficiency (Rodman & McHenry, 1980; Susman *et al.*, 1985; Foley, 1992).

Most of these scenarios invoke environmental change as the underlying cause of the evolution of bipedalism, usually the disappearance of forest and expansion of open grassland or savannah. Growing evidence suggests that during (and perhaps even before) the period in which bipedalism evolved, the East African environment was a temporal and spatial mosaic of habitat types varying from forest and woodland to wooded grassland and grassland (Hill, 1987; Andrews, 1989; Kappelman, 1991; Cerling, 1992; Kingston *et al.*, 1994; WoldeGabriel *et al.*, 1994). Recent evidence suggests that the drying of East Africa in the Miocene was not

accompanied by a shift to grassland dominance (Kingston *et al.*, 1994). This calls into question those scenarios that rely on the importance of open grasslands or savannahs as the ultimate pressure favoring the evolution of bipedalism (Hill, 1987; Kingston *et al.*, 1994). Indeed, *Ardipithecus ramidus*, the earliest hominid yet found, appears to have lived in wooded habitats (White *et al.*, 1994, 1995; WoldeGabriel *et al.*, 1994). However, it is not our goal here to resolve current debate among contrasting theories for the evolution of bipedalism. Instead, we offer an extension of one of these models in the hope that it will advance discussion of the evolution of bipedalism and hominid social systems.

Rodman & McHenry (1980) argued that the need to maintain food intake as resources were becoming more widely separated in drying forests could have favored the evolution of bipedalism as a more energetically efficient form of terrestrial locomotion for hominoids. Evidence that only distantly related quadrupedal primates are as efficient in locomotion as bipedal humans (Steudel, 1994) is not evolutionarily relevant; bipedal humans are apparently more efficient than closely related brachiating apes, which are not committed quadrupeds (Rodman & McHenry, 1980; Steudel, 1994). The earliest bipedal hominids need not have been as efficient as modern humans; even marginal advantages of short bipedal trips could have driven the eventual evolution of full bipedalism (Rodman & McHenry, 1980; Susman *et al.*, 1985). A reduction in resource availability could have been associated with any of the following: (1) a reduction in food density within closed forest, (2) increasing distance between forest patches, or (3) widespread increase in savannah habitat. Because it does not require a full shift in habitat use to savannah ecosystems to explain the evolution of bipedalism, their argument may be more robust than others against variation in the precise physiognomy of the drying habitat.

However, Rodman & McHenry did not suggest a reason for continued quadrupedal locomotion in the pongid ancestor of extant chimpanzees (*Pan* spp.), which are argued by many to be our closest relatives (Sibley & Ahlquist, 1984; Miyamoto *et al.*, 1987; Caccone & Powell, 1989; Hasegawa, 1992; but see Marks, 1992), and which today often live in dry forest habitat (Kortlandt, 1983). No model of human bipedalism is complete without an explanation of why (dry habitat) pongids did not also evolve this adaptation (Tooby & DeVore, 1987).

Paleontological and paleoecological evidence indicates that East Africa was wetter and more dominated by forested habitats 14 mya Between that time and 4 mya, the environment became progressively drier and warmer, resulting in reduction of forested habitats (Hill & Ward, 1988; Retallack *et al.*, 1990; Cerling *et al.*, 1991). Regardless of the degree of physiognomic change, a drying trend would almost certainly be accompanied by decreasing ecosystem productivity (Coe *et al.*, 1976; McNaughton, 1985). Molecular evidence suggests that present-day humans and chimpanzees last shared a common ancestor between 8–5 mya (Sibley & Ahlquist, 1984; Miyamoto *et al.*, 1987; Caccone & Powell, 1989). Paleontological evidence suggests that hominids were already habitually bipedal by 3·9 million years (Leakey *et al.*, 1995). Therefore, it appears that three phenomena occurred in East Africa at around the same time: drying of forest with subsequent reduction in resource availability, the divergence of hominids from hominoids, and the evolution of hominid bipedalism.

We propose here a process for the evolution of bipedalism in hominids that is compatible with Rodman & McHenry's argument, and we use the behavioral ecology of extant primates to extend their argument to include effects of contest and scramble competition. We make two specific points. The first is that although bipedalism may have been a response to the energetic demands on hominoids, as a result of decreased resource availability in the Miocene, smaller group size would have also solved this problem, because it would have resulted in shorter daily travel distances. A scenario for the evolution of bipedalism invoking its increased efficiency is

incomplete without a consideration of the costs and benefits of its alternative, reduced group size. Second, we suggest that the fission–fusion social organization of chimpanzees may have evolved as this alternative response to decrease resource availability at about the same time as hominid bipedalism and the divergence of hominids and pongids. The validity of the first point does not rely on the validity of the second.

Contest and scramble competition

Primates, regardless of whether they live in savannah, woodland, or forest, compete for food using both contest and scramble competition (Janson & van Schaik, 1988; Isbell, 1991). In contest competition, animals gain access to food through overt aggression or the threat of aggression. In scramble competition, access to food resources depends on the numbers of others nearby that eat the same food and therefore deplete its availability. As numbers of conspecifics living in a shared area increase, the amount of food available for each individual decreases.

In group living primates, contest competition can occur both between and within groups. Intergroup contest competition is expressed as aggression between groups, whereas intragroup contest competition is expressed as strong dominance hierarchies (Isbell, 1991). Because success in aggressive encounters between groups is positively related to group size in many species (reviewed in Cheney, 1987), intergroup contest competition can act as a selective force for increased group size (Wrangham, 1980b).

Scramble competition can also occur both between and within groups. Intergroup scramble competition is reflected in changes in home range size with changes in group size. In almost all primates (and other mammals) larger groups have larger home ranges (Milton & May, 1976; Clutton-Brock & Harvey, 1977; Isbell, 1991). This suggests that the abundance or density of foods ultimately determines home range size (Isbell, 1991). When groups increase in size and expand into the home ranges of other groups, the number of animals using the resources in areas of overlap increases, and the food that is available for other groups decreases. One way to reduce encroachment is to act aggressively toward neighboring groups. Indeed, all primates species in which larger groups are known to have larger home ranges also show aggression between groups (Isbell, 1991).

Intragroup scramble competition is reflected in changes in daily travel distance with changes in group size. In many, but not all, primate species living in multi-female groups, daily travel distance increases as group size increases (reviewed in Isbell, 1991 and Wrangham *et al.*, 1993). This association is hypothesized to be determined by food distribution. Among species that spend most of their day feeding and foraging on clumped foods such as fruits, larger groups travel longer daily distances than smaller groups (Isbell, 1991). Larger groups are expected to deplete patches more quickly and eat less food per individual than smaller groups at each patch. Therefore, individuals in larger groups may be required to visit more patches per day to obtain the same amount of food per individual as individuals in smaller groups (Waser, 1977; Isbell, 1991). Resource abundance also affects daily travel distance; groups in richer habitats travel less far each day than groups in habitats with lower resource availability (Dunbar, 1988: p. 49).

These patterns of contest and scramble competition are apparently more sensitive to the abundance and distribution of foods than to broad habitat type. Primates adjust their ranging behavior to group size independently of whether they live in forest, woodland, or savannah.

Ecology and social organization of ancestral hominoids

We suggest that these patterns shown by extant primates can be applied to the ancestors of chimpanzees and humans, based on patterns of diet and social organization of extant chimpanzees and *Australopithecus afarensis*. We use *A. afarensis* in the absence of inferences about the probable diet and social organization of *Australopithecus anamensis* (Leakey *et al.*, 1995). Extant chimpanzees are largely frugivorous (Goodall, 1986). They live in fission–fusion societies in which individuals forage in variable-sized parties (Goodall, 1986; White & Wrangham, 1988). Daily travel distance of extant chimpanzees varies with party size: lone individuals or individuals in smaller foraging parties travel shorter distances than individuals in larger parties (Wrangham, 1977; White & Wrangham, 1988). Evidence from fossil teeth suggests that *A. afarensis* was also largely frugivorous (Andrews & Martin, 1992).

Moreover, evidence from several directions suggests that *A. afarensis* lived in groups of multiple females. First, the fossils of at least 13 individuals found at AL-333 (Johanson *et al.*, 1982) included at least two adult females and three adult males (McHenry, 1991). Second, the degree of sexual dimorphism in *A. afarensis* was between that of extant chimpanzees and gorillas (*Gorilla gorilla*) (McHenry, 1991; White *et al.*, 1993), suggesting that they lived in groups of multiple females (and that multiple males lived with them) (McHenry, 1991), not in male–female pairs (but see Lovejoy, 1981). All extant primate species that live in multi-female social groups and that are hypothesized to feed primarily on clumped resources (i.e., fruits, but not insects or leaves) show a clear positive relationship between group size and daily travel distance (see Figure 1 in Isbell, 1991). Because chimpanzees and *A. afarensis* appear to share these characteristics, the hominoid ancestor of humans and chimpanzees was also likely to have been frugivorous and to have lived in multi-female groups. It is reasonable to assume, therefore, that the ancestor of chimpanzees and hominids adjusted daily travel distance (and home range size) to group size.

Alternative solutions to increasing competition: trade-offs between intergroup contest and intragroup scramble competition

Group size in ancestral hominoids (like many other primate species) was likely to have been a compromise between selection for larger group size (because of intergroup contest competition and/or predation) and selection for smaller group size (because of intragroup scramble competition). Group size appears to be constrained by energetic costs of daily travel as group size increases (Wrangham *et al.*, 1993; Chapman *et al.*, 1995; Janson & Goldsmith, 1995). Thus, at a certain point, the increased benefits of living in larger groups (improved intergroup contest competition) should be balanced by the increased costs of living in larger groups (increased intragroup scramble competition). This balance was almost certainly upset by the drying of the African Miocene forest habitats.

As they became drier, Miocene forests may have been thinned from within as the more susceptible species died off, or reduced at their peripheries, or both. Regardless of the actual process of forest reduction, resource availability would have invariably decreased with regional drying (Coe *et al.*, 1976; McNaughton, 1985). Reduced resource availability would require groups of a given size to travel farther (all else being equal) to harvest the same amount of food (solid lines in Figure 1). For frugivorous hominoids living in groups, there were at least two alternative strategies available to cope with this increasing food limitation (dashed lines in Figure 1).
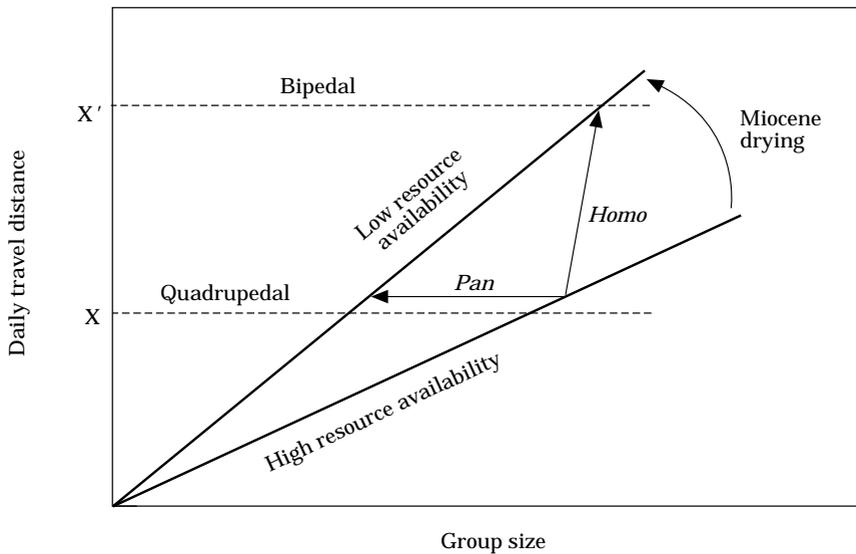
Figure 1. Alternative evolutionary responses to decreasing resource availability. The solid lines represent the relationship between daily travel distance and group size under conditions of high and low resource availability. Miocene drying is suggested to have resulted in a shift from the lower line to the upper line. X and X′ represent maximum daily travel distances supportable by terrestrial quadrupedal locomotion and more energetically efficient terrestrial bipedal locomotion, respectively. The labelled lines represent the alternative evolutionary trajectories of the ancestors of humans and chimpanzees.

One strategy would have been to maintain or even increase group size, maintaining the advantage larger groups have over smaller groups in intergroup contest competition for food. For example, in a population of vervet monkeys (*Cercopithecus aethiops*) facing increased competition for food as a result of a natural die-off of trees, larger groups gained access to more food by supplanting smaller groups from their home ranges (Cheney & Seyfarth, 1987; Isbell *et al.*, 1990). Some of the smaller vervet groups eventually became so small that their groups disintegrated while the larger groups continued to exist (Isbell *et al.*, 1991). Larger hominoid groups may have also been less susceptible to predation (Alexander, 1974; reviewed in Isbell, 1994).

However, larger hominoid groups would have suffered greater intragroup scramble competition because they would have been required to travel farther each day than smaller groups to maintain the same per capita food intake. This would have been an especially restrictive cost during an era of decreased resource availability that would have resulted in increased day range length even without a change in group size. Under such conditions, selection would have favored those individuals that minimized the energetic costs of daily travel while living in larger groups. One solution to this pressure is habitual bipedalism, a form of locomotion that is efficient in conserving energy while walking terrestrially over long distances (Rodman & McHenry, 1980; Figure 1). Not only would the increased efficiency of bipedal locomotion enable greater daily travel distances relative to group sizes, it may also have enabled the evolution of larger body sizes (Foley, 1992). Animals using this strategy are here called pre-hominids.

The alternative strategy would have been to reduce group size, thus decreasing daily travel distance and the costs of intragroup scramble competition (Figure 1). Although reducing group size might have placed individuals in small groups at a disadvantage in intergroup

competition, the cost could have been outweighed by the energy saved in lowering their travel requirements.

Animals living in smaller groups could thrive on smaller patches that were less available to larger groups. Eventually, animals using this strategy might travel alone or, when the distribution of foods allowed, in small foraging parties. They could minimize the potential costs of solitary living, e.g., increased vulnerability to predation (Alexander, 1974; but see Boesch, 1991) and intraspecific attacks (Manson & Wrangham, 1991), by traveling in groups during periods when resources allowed or when intergroup encounters were likely (or even sought after), in a fission–fusion social system. Animals using this strategy are here called pre-chimpanzees.

Each of these two evolutionary responses entailed costs as well as benefits. The evolution of bipedalism required major anatomical adjustments that millions of years later still leave humans with weak knees and lower backs (Williams & Nesse, 1991). In addition, the new posture may have made terrestrial foraging at higher vegetation levels more efficient (Wrangham, 1980*a*; Hunt, 1994), but probably made terrestrial foraging at ground level less efficient. Conversely, the evolution of small group size is likely to have left individuals more vulnerable to intraspecific and interspecific enemies. For example, in competition between communities of modern chimpanzees, individuals traveling alone are at risk of fatal attacks from individuals from the adjacent community traveling in groups (Manson & Wrangham, 1991).

The divergence of hominids and pongids

Given that there may have been two very different hominoid solutions to the problem of decreased resource availability during the Miocene, how might pre-hominids and pre-chimpanzees have solved the problem the ways they did? We envision four possible answers.

First, because even small differences in initial location on an adaptive landscape can result in divergent trajectories (Ridley, 1992), similar but distinct niches may have predisposed each species to solve their problems differently. For example, if pre-chimpanzees fed on resources that could be more readily acquired by small groups, or were less likely than pre-hominids to suffer a predation cost of living alone or in small groups, they may have been more likely to respond to the Miocene drying by reducing group size than by evolving bipedalism.

Second, the existence of closely related and competing species may have limited the evolutionary options of these two primates. If there was simultaneous evolution of a ''bipedal, large groups'' solution and a ''quadrupedal, small groups'' solution to decreasing resource availability, the presence of a species specializing on one solution would have left the other species fewer opportunities to exploit that same solution.

A third possibility is sympatric (or parapatric) speciation (Bush, 1994), if there was positive assortative mating in which the more terrestrially energy-efficient males and females preferentially reproduced with one another and vice versa. Such assortative mating could potentially be driven also by differential transfer or individuals to and from groups of different sizes.

Finally, the common ancestor of humans and chimpanzees could well have existed as a series of isolated populations, especially at this time of forest breakup. The origination of the Rift Valley could have provided an additional isolating mechanism separating pre-chimpanzees and pre-hominids (Kortlandt, 1983). As the forests thinned, one or more

populations could have solved their energetic problem by evolving bipedalism; others could have evolved small group sizes and a fission–fusion social organization. Founder effects (genetic drift) would determine the particular outcome. In the absence of paleontological and paleoecological evidence, we cannot rule out any of these processes in the establishment of behavioral and morphological differences between hominids and pongids.

Gorillas

Gorillas are closely related to both humans and chimpanzees (Marks, 1992). In the context of our model, gorillas may represent hominoids that either remained more centrally in the shrinking forests of the Miocene and Pliocene, with greater resource availability, or were able to shift their diets to more ubiquitous and dispersed foods. In either case, they could therefore afford to retain both quadrupedal locomotion and a cohesive multi-female group structure. The latter possibility is supported by the responses of extant sympatric gorillas and chimpanzees to fruit scarcity. Both gorillas and chimpanzees in Gabon feed heavily on fruits (Tutin *et al.*, 1992). When fruit is scarce, gorillas switch to feeding primarily on leaves, an abundant and dispersed resource. In contrast, chimpanzees continue to feed on fruits. During these times of fruit scarcity, gorillas remain in cohesive groups, whereas chimpanzees adjust their group size, either foraging alone or in small subgroups (Wrangham, 1977; Tutin *et al.*, 1992).

Implications for reconstructing hominid social evolution

The model presented here suggests that near the time of divergence, the earliest hominids maintained the ancestral social organization of cohesive, multi-female groups (and became bipedal) while the earliest chimpanzees diverged from the ancestral form by changing to a fission–fusion social organization. According to this model, the fission–fusion social organization of chimpanzees is derived from the ancestral form. This calls into question the value of chimpanzees as models for the evolution of hominid social systems (e.g., Ghiglieri, 1987; Susman, 1987; Wrangham, 1987). If not chimpanzees, what then? As others have pointed out (e.g., Tooby & DeVore, 1987; Foley & Lee, 1989; Foley, 1992), and as we have done here, the best approach may be to draw broadly from general principles of primate behavioral ecology, invoking examples from comparison of many populations from many species. The contributions of behavioral ecology in reconstructing hominid social behavior should increase as support from traditional biological anthropology recognizes its value in addressing such problems.

Acknowledgements

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