Locomotor Activity Differences Between Sympatric Patas Monkeys (*Erythrocebus patas*) and Vervet Monkeys (*Cercopithecus aethiops*): Implications for the Evolution of Long Hindlimb Length in *Homo*

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ABSTRACT   *Homo erectus* is notable for its taller stature and longer lower limbs relative to earlier hominids, but the selective pressures favoring such long limbs are unclear. Among anthropoid primates, patas monkeys (*Erythrocebus patas*) and extant hominids share several extreme characteristics involved with foraging and movement, including the relatively longest lower limb proportions, longest daily travel distances and largest home ranges for their body or group size, occupancy of some of the driest habitats, and very efficient thermoregulatory systems. We suggest that patas monkeys are an appropriate behavioral model with which to speculate on the selective pressures that might have operated on *H. erectus* to increase lower limb length. Here, in a comparison of the locomotor activities of patas monkeys and sympatric, closely related vervet monkeys (*Cercopithecus aethiops*), we provide evidence for the hypothesis that patas use their long stride more to increase foraging efficiency while walking than to run, either from predators or otherwise. Am J Phys Anthropol 105:199–207, 1998.   © 1998 Wiley-Liss, Inc.

Patas monkeys (*Erythrocebus patas*) and extant hominids share several extreme characteristics involved with foraging and movement (Foley, 1987) (Table 1), including relatively longest hindlimb proportions (Napier and Napier, 1967; Hurov, 1987; Meldrum, 1991; Strasser, 1992; Gebo and Sargis, 1994), longest daily travel distances and largest home ranges for their body or group size (Hall, 1965; Clutton-Brock and Harvey, 1977; Foley, 1987; Chism and Rowell, 1988), occupancy of some of the driest habitats (Hall, 1965; Kingdon, 1974), and similar thermoregulatory systems (Gisolfi et al., 1982; Kolka and Elizondo, 1983). We suggest here that patas are also useful as a behavioral model

for studies of the adaptive value of relatively long hindlimb length in *Homo*.

Modern humans have longer hindlimbs relative to trunk height than do pongids (Schultz, 1930) and longer hindlimbs than australopithecines and early *Homo* (Jungers, 1982; Jungers and Stern, 1983; Jungers,

TABLE 1. *Extreme values of several traits associated with locomotor activity in extant primates, excluding prosimians*

Trait	All primates	Non-human primates
Relatively longest lower limbs	*Homo sapiens*	*Erythrocebus patas*
Longest daily travel distances relative to group size	*Homo sapiens**	*Erythrocebus patas**
Largest home ranges relative to group size	*Homo sapiens**	*Erythrocebus patas**
Driest habitats	*Homo sapiens**	*Erythrocebus patas** and *Papio hamadryas**
Most terrestrial	*Homo sapiens*	*Erythrocebus patas, Papio hamadryas,* and *Theropithecus gelada*

* Not all populations are extreme.

1988). This pattern is likely to have had its origin with *H. erectus,* whose height was substantially greater than that of earlier hominids (McHenry, 1991, 1992; Ruff, 1991, 1994; Ruff and Walker, 1993). The appearance of *H. erectus* coincided with expansion of drier, hotter, and more open environments in East Africa (Cerling, 1992; Feibel and Brown, 1993; deMenocal, 1995), and it has been suggested that the long hindlimbs of *H. erectus* were part of a suite of adaptations to such habitats (Ruff and Walker, 1993; Ruff et al., 1993).

Patas differ morphologically from their closest allies (*Cercopithecus* spp.) in their limbs and feet (Gebo and Sargis, 1994), a divergence considered sufficient to warrant their placement into a separate genus (Napier and Napier, 1967; Groves, 1991). Among their specialized adaptations are longer hindlegs and forelegs (Hurov, 1987; Strasser, 1992), longer tarsal bones (Strasser, 1992), and hindfoot digitigrady (Meldrum, 1991), all of which increase stride length (Hurov, 1987; Hildebrand, 1988). Because these are characteristics of cursorial animals in general (Hildebrand, 1988), patas monkeys are viewed as cursorial (Hurov, 1987; Strasser, 1992; Gebo and Sargis, 1994). This is supported in the field by observations that unhabituated patas monkeys typically run fast and far away from observers.

But are patas specifically adapted for running? Given that elongation of legs increases stride length and therefore speed even in the absence of changes in gait (see Jungers, 1982), hindlimb elongation could have been favored by natural selection acting on either of two very different activities occurring at very different actual speeds. High speed running may be used to avoid predators (or otherwise to get from one place to another); greater walking speeds may increase foraging efficiency by increasing the amount of food encountered and obtained per unit time (Chism and Rowell, 1988; Isbell et al., in press).

Both possibilities recognize that patas occur in drier, less productive habitats than most other primates. Patas typically occur in dry woodlands and scrublands between the Saharan desert and dry tropical forests across western and central Africa to eastern Africa (Hall, 1965; Kingdon, 1974). In East Africa (where *H. erectus* is likely to have emerged), patas are found in habitats with about 400–700 mm annual rainfall (Chism and Rowell, 1988; Isbell, in press). Unlike sympatric vervets (*Cercopithecus aethiops*) and baboons (*Papio anubis*), patas do not frequent riverine areas and often have limited access to tall trees or cliffs for sleeping, escaping from predators, or obtaining food.

The possible selective pressures that favored the morphology of speed in patas can best be understood through direct observations and comparison of the behavior of free-ranging patas and vervets. Despite their sympatry and close phylogenetic background (Disotell 1996), vervets do not share the specialized limb morphology with patas. Here we examine the reactions of sympatric patas and vervets to their potential predators, and quantify the time that patas and vervets devote to different activities related to travel and food procurement. We expected that patas would spend more time running than vervets. We hypothesized that if the specialized limb morphology of patas is an adaptation for avoiding predators, patas would run more often from terrestrial predators than would vervets when both are on the ground, either because they encounter predators more often or because they are more likely to run from a given predator than are vervets. We hypothesized alternatively that if their limb specializations are

an adaptation to increase foraging efficiency, patas would spend more time foraging or walking than vervets (walking, but not running or climbing, is compatible with foraging). Support for one but not the other hypothesis would suggest which selective pressure might have operated on patas (but not vervets) to increase limb length, and hence, stride length.

METHODS

Study site and animals

This study was part of an ongoing comparative project at Segera Ranch (36° 50′ E, 0° 15′ N; elevation 1,800 m) on the Laikipia Plateau in north-central Kenya. Segera Ranch is a cattle ranch and conservation area that includes a wide diversity of wild animals, including four species of primates (*E. patas, C. aethiops, P. anubis,* and *Galago senegalensis*) at least four likely mammalian predators of patas and vervets [lion (*Panthera leo*), leopard (*P. pardus*), black-backed jackal (*Canis mesomelas*), and cheetah (*Acinonyx jubatus*)], and ungulates typically found in semi-arid or open habitats, e.g., beisa oryx (*Oryx beisa*), steinbuck (*Raphicerus campestris*), two species of zebras (*Equus grevyi and E. burchelli*), giraffe (*Giraffa camelopardalis*), and elephant (*Loxodonta africana*). The ecosystem is semi-arid, with extremely variable annual rainfall (mean annual rainfall is approximately 700 mm). Two tree species predominate at the study site: *Acacia drepanolobium* (whistling thorn acacia), which occurs away from rivers and streams on vertisolic soils of impeded drainage ("black cotton soil") (Ahn and Geiger, 1987), and *A. xanthophloea* (fever tree), which occurs along rivers and streams. *Acacia xanthophloea* can grow to 25 m or more (Coe and Beentje, 1991) and can form groves with numerous individuals providing a continuous canopy. In contrast, *A. drepanolobium* seldom reaches heights beyond 7 m (Young et al., 1997; Isbell, in press), and although it occurs in the study site at mean densities of 1,000–2,000 individuals per ha (Young et al., 1997), trees are scattered and canopy cover is well under 50%.

Two groups of vervets and one group of patas have been studied intensively since 1992. All individuals were habituated to

TABLE 2. Activities recorded during focal samples of patas and vervets and their operational definitions

Activities without movement
  Feed without moving: chew or ingest food item while being still
  Forage without moving: search, scan, or manipulate food item at close range while being still
  Not moving: resting, sleeping, or being still; excludes other activities
Activities with movement
  Feed while walking: chew or ingest food while walking
  Forage while walking: scan vegetation while walking
  Walk: identified as slowest gait; when feet visible, only one foot off the ground at any given time
  Lope: identified as faster than walking, with a rocking motion; when feet visible, front and hind feet alternating suspension off ground
  Run: identified as fastest gait; when feet visible, all feet suspended simultaneously off ground at some point in the stride
  Climb: quadrupedal movement within trees or bushes
  Leap: substantial vertical movement with all four feet off the substrate at height of vertical movement
Other activities
  Other: auto- and allo-grooming

observers prior to the collection of data reported here. All vervets and all adult patas in these groups were individually identified by natural markings and characteristics. The vervet groups live along the Mutara River and forage in both *A. xanthophloea* and *A. drepanolobium* habitats. The patas group, however, is restricted to *A. drepanolobium* habitat.

Data collection

Predator sightings and alarm calls were noted whenever they occurred from June 1993 through February 1997. For each occurrence, observers were to record the type of predator, type of alarm call, individuals giving alarm calls, the duration of the alarm calls, responses of individuals after the alarm call, and any unusual circumstances that occurred at the time of the event.

From July 1993 until December 1994, excluding July 1994, data on locomotor activities (Table 2) were collected on all 11 adult females in two groups of vervets and 14 of 15 adult females in one group of patas. During each focal sample, the onset and end of the activities defined in Table 2 were recorded onto a data logger (Psion Organiser) using The Observer software program (Noldus Information Technology). Sample

periods for each adult female began as closely as possible to 30 min after each hour, and were initially 30 min in duration but were adjusted to 15 min shortly into the study to facilitate locating the next focal female. With vervets, the order of sampling was predetermined to allow each female to be sampled once in the morning or once in the afternoon. This order was different each sampling day within each month so that all females were sampled equally in each of two time blocks (0800–1200 and 1200–1600) during the observation day each month. A similar sampling order was abandoned for patas because individuals were difficult to locate to sample on time. Adult female patas were therefore sampled opportunistically once per hour on the half-hour and were sampled without replacement in the morning or afternoon. Each group was systematically observed for 4 days each month.

Statistical analyses

The data were imported from The Observer to Excel (Microsoft). The number of seconds and percent of time that each female engaged in each activity were quantified for each focal sample. Percent of time spent in each activity was calculated for each focal sample and then averaged across samples for each female, excluding the time that the focal animal was out of sight. Excluded from analysis were data from three adult female patas because they had three or fewer samples and the adult two females from the smaller (nine individuals, including the two adult females) of the two vervet groups because activities, especially locomotor activities, are known to be affected by group size in vervets (Isbell and Young, 1993; Isbell et al., in press). The large vervet group (29 individuals, with eight to nine adult females) was similar in size to the patas group (about 33 individuals, including 12–15 adult females) and therefore less likely to exhibit differences in activities as a result of a difference in group size alone. Sample size for included females ranged from six to 31 (with numerous samples lost due to mechanical failure of the data logger under field conditions), totalling 6,044 focal minutes (Table 3). Parametric tests (Type I ANOVA) using JMP software program (SAS

TABLE 3. Total observation time (focal minutes) per adult female vervet and patas monkey

Vervets		Patas	
Individual	Minutes	Individual	Minutes
BUR	437.2	CEZ	143.4
CHL	567.2	DAL	168.1
CRV	621.6	GEO	128.9
FRJ	473.6	GYA	154.9
MND	286.0	MNT	158.6
MOO	153.4	PEN	238.0
QSO	353.8	PIC	193.9
SAL	699.7	REM	156.7
TOR	528.0	TAZ	125.8
		VNC	327.2
		WAR	128.0
Total	4,120.5		1,923.4

Institute) were conducted on individual means from data that were arcsine-transformed.

RESULTS
Responses to predators

Patas monkeys gave 77 alarm calls to non-conspecifics during more than 1,322 hr (rate = 5.8 alarm calls/100 hr) of observation, 54 (70%) of which were to identified stimuli. Patas gave alarm calls to birds seven times, alarm calls to reptiles seven times, and alarm calls to mammals 40 times. Of the 40 alarm calls given to mammals, 27 (67%) were given to felids and canids (Table 4). We now focus on responses to these mammalian predators, which were only observed on the ground, since we are primarily interested in responses of the monkeys while also on the ground.

After giving alarm calls to mammalian predators, patas responded somewhat less often by running (n = 9) than by climbing trees (n = 12; Table 4). Their known responses to jackals and domestic dogs (with and without humans), the most frequently observed mammalian predators, involved climbing into trees somewhat more (n = 10) than running away (n = 7). Excluding domestic dogs (and their attendant humans), patas responded to mammalian predators almost equally by climbing trees (n = 7) and running (n = 6). On three occasions, patas ran toward the predator or toward its roar (once each to a leopard, cheetah, and lion). One predation attempt was observed when a juvenile patas was attacked by a jackal

TABLE 4. *Alarm calls and responses of patas monkeys and vervets to carnivores (felids and canids) on Segera Ranch, Laikipia, Kenya from June 1993 to February 1997*

	Alarm calls by						Response[a]		
	Dog	Jackal	Cheetah	Leopard	Lion	Total	Run	Climb trees	Other/unspecified[b]
Patas	14	7	1	3	2	27	9(42.9%)	12(57.1%)	10
Vervets	4	6	1	0	0	11	4(57.1%)	3(42.9%)	6

[a] In four cases of responses by patas and two by vervets, more than one response was recorded. Sample sizes under Response columns therefore do not equal those under Alarm-calls-by columns.
[b] Other responses of patas included running toward the predator (n = 3) and no detectable response (n = 1). All responses of vervets were unspecified.

while it was involved in an aggressive interaction with another juvenile.

Vervets gave 104 alarm calls to nonconspecifics during more than 1,868 observation hours (rate = 5.5 alarm calls/100 hr), 42 (40%) of which were to identified stimuli. Vervets gave alarm calls to birds 17 times, to reptiles eight times, and to mammals 17 times. Of the 17 alarm calls given to mammals, 11 (65%) were given to felids and canids (Table 4).

As with patas, dogs (with and without humans) and jackals were the most frequently observed potential mammalian predators, and vervets (on the ground only) responded after giving alarm calls to them by climbing trees (n = 3) and running (n = 4; Table 4). Excluding humans and domestic dogs, vervets on the ground responded to potential mammalian predators by both running (n = 3) and climbing trees (n = 1). No predation attempts on vervets were witnessed.

Locomotor activities

Patas spent a large percentage (39.5%) of their time not moving (Fig. 1). When they were moving, they were engaged most often in walking. Walking while feeding and foraging occupied 14.4% of their time, while walking unaccompanied by foraging and feeding occupied an additional 7% of their time (total time spent walking with and without food-getting: 21.4%). Loping, which can only be done on the ground, and climbing, which can only be done in trees or bushes, were secondary gaits, and accounted for, respectively, 1.5% and 1.2% of their time. Leaping was less common (0.3%) than loping and climbing but more common than running. Running occupied the least time of all the locomotor activities (0.08%).

Vervets were roughly similar to patas in the rank ordering of the percentages of time spent in most of their activities (Fig. 1). They were inactive (i.e., not moving) for nearly half their time (48.6%). When they were moving, they most often walked (10.1%). Vervets spent slightly more time walking without food-getting (6.0%) than walking while feeding and foraging (4.1%). Reflecting their rather frequent use of taller trees, vervets spent 4.6% of their time climbing. Loping and leaping were relatively infrequent (0.7% and 0.3%, respectively). Running occupied only 0.07% of their time.

Patas and vervets differed most notably in the time they devoted to foraging. Patas foraged while walking nearly four times more than vervets and they foraged while not walking more than twice as often (Fig. 1). As befits their different lifestyles, the more terrestrial patas monkeys spent more than twice as much time loping as vervets, whereas the more arboreal vervets spent nearly four times as much time climbing as patas.

DISCUSSION

The alarm calls and responses of vervets to their predators are well-documented (Struhsaker, 1967a; Seyfarth et al., 1980). Many of the alarm calls of patas are similar acoustically to those of vervets, and, like the alarm calls of vervets, differ acoustically for avian, reptilian, and mammalian predators (LAI, unpub. data). Vervets and patas are sympatric at this study site and share the same guild of predators. Patas gave alarm calls more often to identified mammalian predators than did vervets (72% vs. 40%) but this may be an artefact of differential visibility by observers. The habitat of patas is flatter, with fewer woody plants that
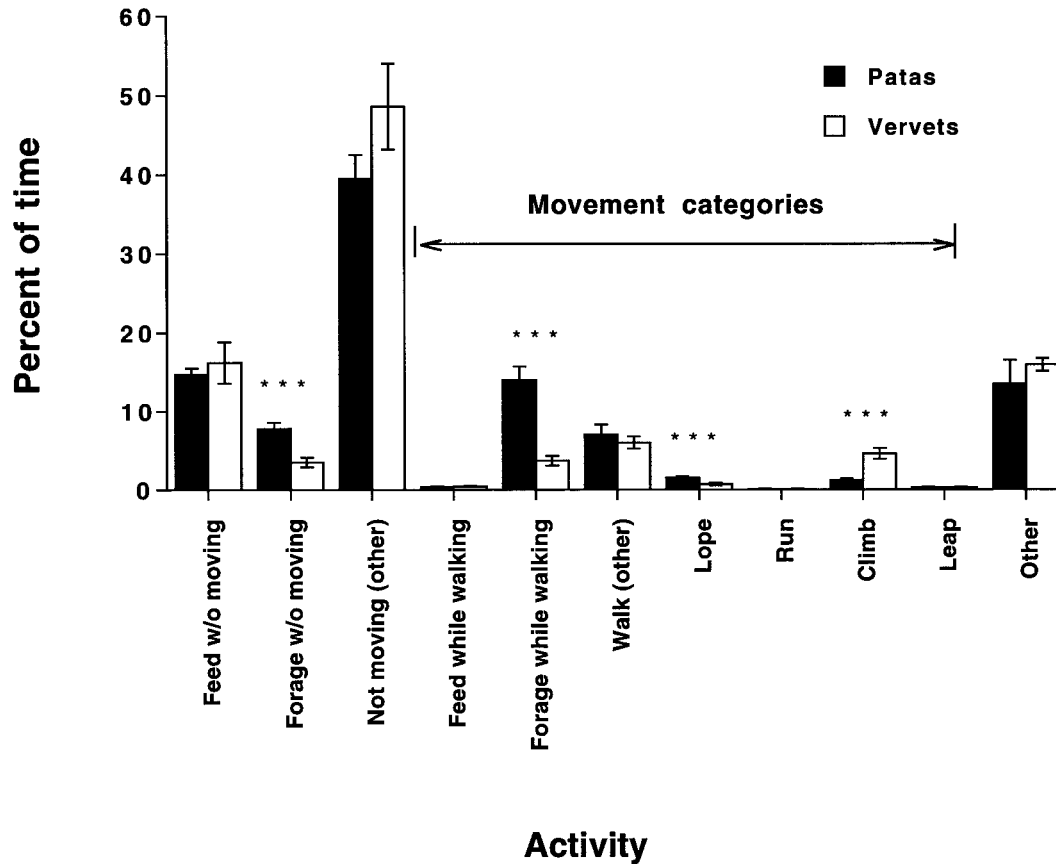
Fig. 1. Percent of time spent in different activities by adult female patas and vervet monkeys at Segera, Laikipia, Kenya. Sample size for patas = 11 individuals; sample size for vervets = nine individuals. Error bars are one standard error. ***$P < 0.005$. The values for "run" were too small to appear (patas, 0.08% ± 0.03; vervets, 0.07% ± 0.04).

obscure predators. As a consequence, observers were able to identify the stimulus for more than two-thirds of the alarm calls of patas but for fewer than half of those of vervets. Of the 62 alarm calls given by vervets in which the stimulus was not determined, 49 were alarm calls typically given in the presence of leopards and other mammalian predators. If these alarm calls are assumed to reflect true presence of such predators, then the percentage of alarm calls to mammalian predators becomes more similar (63%) to the percentage of alarm calls to identified mammalian predators in the more open habitat of patas.

Patas and vervets responded similarly to their mammalian predators while on the ground, with both species climbing trees as

often as they ran (see also Chism et al., 1983; Chism and Rowell, 1988). Both patas and vervets spent similar small absolute times running, and did not differ significantly from each another in the time they spent in that locomotor gait. These results suggest that patas and vervets do not differ substantially in their use of cursoriality to avoid predators or to otherwise run from one place to another.

In contrast, patas foraged while walking nearly four times as much as vervets. Vervets in East Africa feed primarily on gum and other parts of *A. xanthophloea* (Struhsaker, 1967b; Wrangham and Waterman, 1981; Isbell et al., in press). Patas feed primarily on gum of *A. drepanolobium,* but they also feed heavily on arthropods (Chism and Wood,

1994; Isbell, in press),which can be cryptic. Many of the arthropod prey of patas are ants (*Crematogaster* spp.) which aggressively defend domatia (swollen thorns) on *A. drepanolobium* (Hocking, 1970; Young et al., 1997; Isbell, in press). Patas typically only eat one or two swollen thorns per tree (Isbell, in press), presumably because of the actions of the biting ants (see Madden and Young, 1992; Pruetz, 1996). Once these ants have been disturbed, they remain agitated for at least 4 minutes (Madden and Young, 1992). Patas often appear to search trees visually, perhaps in part to determine whether the ants have recently been disturbed, which ant species is present, or which swollen thorn to open, and they often do this as they walk. They also search the ground and vegetation near the ground for invertebrates.

Previous research has shown that patas travel three times farther than vervets per unit time, travel twice the distance of vervets between food sites, and spend about one-third as much time as vervets at each food site (Isbell et al., in press), all of which indicate that the foods of patas are smaller and more widely distributed than the foods of vervets. The results here provide support for the hypothesis that the longer limbs of patas evolved to increase foraging efficiency (food intake per unit time) within a niche of exploiting small and widely distributed food resources. Stride length may increase speed, but for patas monkeys, stride length appears to be used less for high speed running and more for reducing the time moving between food sites.

Productivity is positively associated with rainfall (McNaughton, 1985). Home ranges often reflect productivity, with larger home ranges in more depauperate habitats (McNab, 1963; Struhsaker, 1967b; Milton and May, 1976). Patas monkeys typically inhabit dry habitats and have the largest home ranges for their group biomass of any primate (Clutton-Brock and Harvey, 1977), implying, again, that their foods are effectively less abundant than those of most primates. The environments to which patas are adapted are apparently similar to the environments to which *Homo erectus* was adapted.

The genus *Homo* first appeared in East Africa between 2.4–1.8 mya during an expansion of drier, less productive habitats (Vrba, 1985; deMenocal, 1995; Reed, 1997). The first members of this genus had robust lower limbs relative to modern humans, suggesting heavy reliance on locomotor activity (Trinkaus, 1987; Ruff et al., 1993). With the appearance of *H. erectus* in East Africa by at least 1.8 mya, hindlimbs as long as those of modern *H. sapiens* occur (McHenry, 1991, 1992; Ruff and Walker, 1993; Ruff et al., 1993). Faunal evidence, paleoecological reconstructions, and craniofacial and postcranial evidence suggest that *H. erectus* inhabited arid habitats in East Africa (Trinkaus, 1987; Franciscus and Trinkaus, 1988; Cerling, 1992; Feibel and Brown, 1993; Harris and Leakey, 1993; Ruff and Walker, 1993; Ruff et al., 1993; Reed, 1997), and engaged in locomotor activities that required prolonged muscular exertion (Ruff et al., 1993). This could have been through running or extensive walking.

Relatively long limbs can be adaptations for more effective heat loss in hotter environments (Allen's Rule), and it has been suggested that the long limbs of *H. erectus* were adaptations to such environments (Ruff, 1991, 1994; Ruff and Walker, 1993). While this may be true, it is likely that long stride also conferred a locomotor advantage because modern humans, including those living in cooler climates, have retained longer hindlimbs (Schultz, 1930; Jungers, 1982; Jungers and Stern, 1983; Jungers, 1988). We suggest here that the need to walk long distances to get food in warm, arid habitats with low productivity could have, in fact, driven the evolution of long hindlimbs and other adaptations for more efficient thermoregulation in *H. erectus.* Patas monkeys, which travel farther per day than other primates of similar body size, have a thermoregulatory system comparable in efficiency to that of humans (Gisolfi et al., 1982; Kolka and Elizondo, 1983). It has also been suggested that *H. erectus* was adapted for endurance running (Carrier, 1984), implying that the locomotor advantage was in running, not walking. Indeed, the same has been offered for patas (Hurov, 1987; Strasser, 1992; Gebo and Sargis, 1994), but the cur-

rent study suggests otherwise. The longer hindlimb length of *H. erectus* would have continued directional selection, begun by bipedalism, for adaptations that increased foraging efficiency in environments with ever-diminishing productivity (Yamazaki et al., 1979; Rodman and McHenry, 1980; Isbell and Young, 1996).

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