

News and Views

The endurance running hypothesis and hunting and scavenging in savanna-woodlands

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Introduction

Recently, Bramble and Lieberman (2004: 345) provided a review of morphological evidence suggesting to them “that endurance running is a derived capability of the genus *Homo*, originating about 2 million years [Myr] ago, and may have been instrumental in the evolution of the human body form.” The authors went on to hypothesize that long-distance endurance running (ER) may have been critical to encephalized early *Homo* in gaining access to high-quality food resources, including especially meat, marrow, and brains. They discussed the potential of hunting and scavenging as behaviors that may have selected for ER, concluding that testing this idea “will be challenging given the limitations of the archaeological and ethnographic records” (Bramble and Lieberman, 2004: 351). We, as researchers (1) who have generated primary data on meat and marrow consumption by Plio-Pleistocene hominids (e.g., Bunn, 1981, 1982, 1997; Bunn and Kroll, 1986, 1988; Pickering et al., 2004, 2005, in press; Domínguez-Rodrigo et al., 2005) and (2) who are convinced that meat eating was critical to the evolutionary success of our lineage (e.g., Stanford and Bunn, 2001; Bunn, 2006), are very sympathetic to any hypothesis that bolsters the potential meat-acquisition capabilities of our earliest African ancestors.

However, as with any provocative idea, there are several aspects of the ER hypothesis pertaining to carcass acquisition that warrant deeper examination. We believe that even within the “limitations of the archaeological and ethnographic records” there are data available to test the hypothesis that hunting and scavenging selected for ER in early *Homo*. Here, we focus on paleohabitat and paleoecology as factors that, when considered in combination with the realities of pursuit-foraging, diminish the plausibility of early *Homo* using ER in hunting and scavenging.

The ca. 2.3–1.5-Myr-old African environments of *H. habilis*, *H. rudolfensis*, and earliest *H. ergasterlerecetus* are reconstructed as savanna-woodlands (e.g., Hay, 1976, 1990; Cerling, 1992; Cerling et al., 1988; Sikes, 1994; Reed, 1997). What constitutes a savanna ecosystem is often broadly defined, but most experts agree that the fundamental requirement is that the groundcover is dominated by C₄ grasses (e.g., Huntley and Walker, 1982; Bourlière, 1983; Mistry, 2000). More specifically, savanna-woodlands possess a mix of open and closed components. However, in terms of overall vegetation physiognomy, they are intermediate between forest and open savannas, and they can be anything from “miombo” woodland, with its regularly spaced trees, to true mosaic systems, with swaths of open grassland adjacent to riparian forests and wooded thickets (e.g., Moore, 1992). Thus, depending on the type of savanna-woodland, ground- and eye-level visibility is variable but generally lower than that of open savannas and deserts. Soils of African savanna-woodlands are diverse, but what is important relative to this discussion is that they tend to be more compacted than the

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loose sands found in deserts and are certainly more obscured by groundcover than are desert sands (Mistry, 2000).

Hunting with ER

Bones of ungulates of various sizes predominate in archaeofaunal assemblages associated with early *Homo* in eastern and southern Africa (e.g., Leakey, 1971; Brain, 1981; Bunn, 1982, 1997; Watson, 1993). The majority of fossils bearing traces of hominid butchery (stone-tool cutmarks and hammerstone percussion damage) are also ungulate (e.g., Bunn, 1982, 1997; Bunn and Kroll, 1986; Brain, 1993; Pickering et al., 2004) to the near exclusion of other taxa. Ungulates can sprint faster than can humans (e.g., Garland, 1983) and would have initially outrun an early hominid hunter who (1) penetrated it with a projectile weapon or (2) began a chase in the anticipation of running the animal to exhaustion (i.e., “persistence hunting” [Liebenberg, 1990]). Necessarily then, hunting with ER would have required that hominid predators possessed the ability to track prey (tracking is defined here as the process of following a prey animal in the absence of visual contact with that animal). This assessment is corroborated by Liebenberg (2006) in his recent study of modern persistence hunting and its paleoanthropological implications.

The first scenario would have likely involved following a fresh blood trail, a decidedly easier undertaking than detecting and interpreting other types of spoor (e.g., footprints, saliva, dung, urine, hair) during a tracking episode. However, there is no evidence that early *Homo* possessed a penetrating projectile technology. While early *Homo* individuals may have thrown sticks or rocks at prey, sharpened wooden spears do not appear in the archaeological record until ca. 400,000 years ago (Thieme, 1997), and stone projectile points are known securely only after ca. 40,000 years ago (Shea, 2006).¹

Tracking is a highly sophisticated skill employed effectively by modern humans in a variety of habitats (Fig. 1). In one of the most exhaustive studies of human tracking, Liebenberg (1990: 29–30) argued that “tracking, as practised by recent hunter-gatherers in savanna-woodland conditions, requires above average scientific intellectual abilities, [implying] that it is unlikely that tracking could have originated in savanna-woodland habitat. It is likely that tracking evolved in conditions where tracking is easiest ... namely arid environments where ground is sparsely covered with vegetation [i.e., deserts], and cold environments where simple tracking is possible in snow.” As reviewed above, neither of the latter-



Fig. 1. Hadza men tracking a large animal recently shot by a poisoned arrow. The Hadza are a group of Tanzanian foragers who employ sophisticated projectile technology in hunting and possess the modern human ability to successfully track animals in a cognitively challenging savanna-woodland environment. There is no evidence to suggest that early *Homo* was similarly equipped materially or mentally.

mentioned habitats characterized those reconstructed for early *Homo*, while savanna-woodlands do typify the environments in which early *Homo* is inferred to have lived. Not only is tracking more difficult in savanna-woodland, with its relatively compact soil and vegetation-obscured ground, but persistence hunting is also particularly challenging in this habitat compared to more arid environments.

As Bramble and Lieberman (2004) acknowledged, ER hunting is not common among modern foragers. In fact, persistence hunting is actually quite rare ethnographically and restricted to very open and very hot habitats, such as the central Kalahari, portions of the American Southwest, and the interior of Australia (e.g., Lowie, 1924; Sollas, 1924; Schapera, 1930; McCarthy, 1957; Lee, 1979; Silberbauer, 1981; Steyn, 1984). Driving a prey animal across loose and especially wet sand tires it more effectively than does pursuit across the more consolidated soils of a savanna-woodland. An ER hunting strategy is rare to nonexistent among the Hadza of the Lake Eyasi basin, a savanna-woodland habitat in the East African Rift Valley, and among the Kua San of the east-central Kalahari, an arid, desert habitat. From direct observation over a twenty-year period of well over 100 successful hunts by Hadza using bows and arrows, and of an even greater number of unsuccessful hunting and scavenging opportunities, we have never observed persistence hunting by the Hadza, nor have informant interviews revealed this as a strategy they practice. Independent research on the Hadza by others has, likewise, produced no reference to persistence hunting. In fact, the Hadza often decide to abandon the blood trail of a wounded animal headed into heavy vegetation, choosing to satisfy immediate hunger by collecting some honey and figuring that the odds of encountering another prey animal are likely enough to obviate the need for further, difficult tracking (Bunn et al., 1988).

Liebenberg's (2006) recent observations of persistence hunting by central Kalahari foragers using ER are interesting, but his attempt to extrapolate the relevance of those

¹ It is important to note that Domínguez-Rodrigo et al. (2001) have inferred the possibility of spear production in the early Pleistocene based on *Acacia* wood-working residues on large stone bifaces from Peninj, Tanzania. Micro-wear evidence of the sawing or scraping of wood with stone flakes has also been reported from Koobi Fora (Keeley and Toth, 1981). No actual spears have been recovered from this remote time period, but if they were produced by the Peninj or Koobi Fora hominids there is no reason to conjecture that they had to have been throwing spears. Another way in which sharpened sticks could have been employed to dispatch animals was as pikes braced in the bottom of pit traps. Sharpened sticks, of course, could also have been used to dig up deeply buried tubers.

observations to a critical stage in human evolution falls short. First, nothing in Liebenberg's data contradicts the statement above that persistence hunting with ER is extremely uncommon, even among people employing sophisticated tracking skills in the most ideal ecological environment for the behavior. Over the course of 20 years, only two of the ER hunts observed by Liebenberg were spontaneous. Eight others were prompted by Liebenberg so that they could be filmed for television documentaries. Second, based on Liebenberg's observations, the success of the technique is equivocal. While the two spontaneous ER hunts were successful, it must be noted that they were undertaken by the same four individual hunters; perhaps these four men were uncommonly good at this particular rare technique or were lucky twice. Further, only three of the eight prompted ER hunts were successful, even though those hunts were commenced from a vehicle and hunters refilled their water bottles during hunting.

In contrast, HTB's observations among the Kua San suggest that hot dry-season hunting by walking, not ER, is another viable but physically demanding activity (Bartram et al., 1991; see Steyn [1984] for an informant's report of a similar strategy by southern Kalahrai San). However, the very ecological conditions that facilitate persistence hunting in the Kalahari do not characterize the savanna-woodland mosaics of the present or of the Plio-Pleistocene in which early *Homo* evolved. The most common prey targeted by the Kua San with walking hunts is the bush duiker (*Sylvicapra grimmia*; live weight ~20 kg), followed by steenbok (*Raphicerus campestris*; live weight ~10 kg), but walking also yields large bovids, including greater kudu (*Tragelaphus strepsiceros*; live weight ~200 kg.). On a successful hunt in which HTB and a graduate assistant participated, the main hunter, armed only with a digging stick, identified the fresh hoof prints of a duiker and followed its trail at a steady, relentless walk for approximately three hours. The duiker was thereby pushed from one uncommon shade tree to the next in the hot sun. The bare ground beneath each shade tree was pock-marked with duiker tracks from many different animals, which slowed the hunter, who circled the perimeter of the shaded areas and was able to pick out the tracks of the targeted duiker as it left the location. Toward the end of the hunt, when the tiring duiker was sighted for the first time approximately 250 m ahead, it was running at a right angle to the direction the hunter was walking along its recent trail. Rather than changing direction and walking or running directly toward the fleeing animal or making any effort to maintain visual contact with it, the hunter continued along the hoof-print trail. At the end, the duiker was standing, incapacitated, beneath a small cluster of trees, with its head lowered and tongue hanging out. The hunter walked up to it, clubbed it with the digging stick, and then carried it back to camp. In sum, successful persistence hunting by walking requires truly phenomenal tracking skills, with the added risk of dehydration and heat exhaustion even for the physically fit. On days following a walking hunt, Kua hunters typically spent a recuperative day of inactivity in camp. Liebenberg's (2006) observations of persistence hunting with ER suggest that this very rare undertaking requires even greater tracking

skills than walking hunts and an elevated risk of dehydration and heat exhaustion for the hunter.

Scavenging with ER

When invoking scavenging, the ER hypothesis assumes that it was likely a highly competitive and probably confrontational activity: "Wild dogs and hyenas often rely upon remote olfactory or visual cues such as circling vultures to identify scavenging opportunities, and then run long distances to secure them.... Early *Homo* may thus have needed to run long distances to compete with other scavengers, including other hominids" (Bramble and Lieberman, 2004: 351). However, numerous general ethological studies (e.g., Kruuk, 1972; Schaller, 1972; Sinclair, 1979) and more specific paleoanthropological ones of hominid scavenging opportunities in modern savanna-woodlands (e.g., Blumenshine, 1986, 1989; Domínguez-Rodrigo, 1996, 2001) have identified riparian microhabitats as areas of low competition for scavengeable carcasses. It is precisely because they are less visible to mammalian carnivores and vultures in riparian woodland that carcasses tend to persist much longer there than in more open components of ecosystems like the Serengeti and Maasai Mara. In addition, a majority of extant African carnivores, as well as extinct Plio-Pleistocene ones, are (or were) adapted morphologically and socially for hunting and scavenging in open country (e.g., Kruuk, 1972; Schaller, 1972; Van Valkenburgh, 1987; Marean, 1989; Lewis, 1997). Thus, they less often frequent closed portions of their habitats.

We have argued repeatedly that a strong pattern of stone-tool butchery marks on the midshaft sections of meat-bearing humeri, radioulnae, femora, and tibiae from East and South African Plio-Pleistocene sites suggests early access to carcasses by hominids, before choice parts could be consumed by other carnivorous competitors (e.g., Bunn, 1982, 1997, 2001; Bunn and Kroll, 1986, 1988; Domínguez-Rodrigo and Pickering, 2003; Pickering et al., 2004, 2005, in press). There are several potential ways in which hominids could have gained early access to carcasses, including hunting and confrontational (power) scavenging.² Opportunistic power scavenging by the Hadza yields approximately 20% of the carcasses acquired, and it is accomplished without dedicated ER (Bunn et al., 1988; O'Connell et al., 1988; Bunn, 2001). Although they occasionally run toward perceived scavenging opportunities, the Hadza run more commonly to avoid approaching rain showers, stinging bees, and marauding elephants than to benefit any meat foraging by persistence hunting or scavenging. Exploiting previously undiscovered carcasses of animals that died naturally in riparian woodlands

² Some researchers have suggested that hominids could have gained early access to carcasses through the theft of abandoned kills cached in trees by leopards (Cavallo and Blumenshine, 1989) or in the wake of catastrophic events, such as mass drownings of wildebeest herds (Capaldo and Peters, 1995). However, zooarchaeological data from relevant sites do not meet predictions—in terms of the combined evidence of butchery, animal body size, and age patterns—that emanate from such hypotheses (see Domínguez-Rodrigo and Pickering, 2003; Pickering et al., 2004).

is another possible way in which early *Homo* gained early access to carcasses. With its superior intellect, good climbing capabilities and visual acuity, early *Homo* may have possessed a distinct advantage over its competitors in systematically investigating dense riparian woodland for carcasses, with minimal risk to itself in terms of direct confrontation.

Regardless of the exact method(s) of carcass acquisition by early *Homo*, new analyses of Plio-Pleistocene archaeofaunas are beginning to suggest that their hominid-derived components formed largely independently or with very minimal input from carnivores (e.g., Egeland et al., 2004; Pickering et al., in press; Domínguez-Rodrigo and Barba, 2006; contra Blumenschine et al., 1994; Blumenschine, 1995). Such a pattern suggests to us that hominids were exploiting conditions of low competition when carcass foraging, which contradicts the assumption of the ER hypothesis that scavenging was a highly competitive undertaking for early *Homo*. Furthermore, the catastrophic (or living structure) mortality profile reported for the well-known FLK *Zinjanthropus* (Olduvai Gorge, Tanzania) archaeofauna (Bunn and Kroll, 1986), which is generally dominated by the butchered bones of prime adult ungulates, contradicts expectations (i.e., selection for young, old, and diseased prey) for carcass acquisition by scavenging from cursorial predators (hyenas, cheetahs, wild dogs) or by hunting as a cursorial ER predator.

Conclusions

We agree with the opinion of Bramble and Lieberman (2004) that early *Homo* required a high-quality diet, which included a substantial meat component, and that it was thus a capable carcass forager. However, our understanding of the paleoenvironment, paleoecology, and archaeology of early *Homo* sites, reviewed here, makes us dubious about their further suggestion that ER might have been employed regularly and successfully in service of that foraging pursuit. We are reluctant to assign to early *Homo* the impressive tracking skills of the Kalahari San, when the cognitive and meat-foraging abilities of Plio-Pleistocene *Homo* are active research issues. The behavioral pattern that selected for ER in the genus *Homo* remains unclear, but it seems likely that hunting and scavenging contributed minimally, if at all.

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