Persistence Hunting by Modern Hunter-Gatherers

Louis Liebenberg

Cyber Tracker Conservation, P.O. Box 1211, Noordhoek, Cape Town 7985, South Africa (louis@cybertracker.co.za). 11 VII 06

Endurance running may be a derived capability of the genus *Homo* and may have been instrumental in the evolution of the human body form. Two hypotheses have been presented to explain why early *Homo* would have needed to run long distances: scavenging and persistence hunting. Persistence hunting takes place during the hottest time of the day and involves chasing an animal until it is run to exhaustion. A critical factor is the fact that humans can keep their bodies cool by sweating while running. Another critical factor is the ability to track down an animal. Endurance running may have had adaptive value not only in scavenging but also in persistence hunting. Before the domestication of dogs, persistence hunting may have been one of the most efficient forms of hunting and may therefore have been crucial in the evolution of humans.

Bramble and Lieberman (2004) assess evidence that endurance running is a derived capability of the genus *Homo* and may have been instrumental in the evolution of the human body form. Two possible hypotheses are given for why early *Homo* would have needed to run long distances. One hypothesis is scavenging. Competition to reach carcasses before other scavengers would have increased the fitness benefits of features that improve endurance running capabilities. Another hypothesis, presented by Carrier (1984), is that early hominin hunters used endurance running to run some mammals to exhaustion. Bramble and Lieberman suggest that such behavior might have been too energetically expensive and low-yield for the benefits to have outweighed the costs (for details see appendix A). Data from observations of !Xo and /Gwi hunters of the central Kalahari in Botswana presented here suggest that persistence hunting was a very efficient method under certain conditions. Compared with other forms of hunting, it may have been one of the most efficient.

Historical Records of Persistence Hunting

Various forms of persistence hunting have been recorded in the Kalahari. Small animals were knocked down with a throwing club and finished off at close quarters or, if the animal took off, run down. The young of small mammals were frequently run down on foot and caught by hand (Lee 1979). Slow-moving animals such as aardvark and porcupines were easily run down when encountered in open country (Silberbauer 1981). Animals such as eland, kudu, gemsbok, hartebeest, duiker, steenbok, cheetah, caracal, and African wild cat were run down in the hotter part of the day and killed when exhausted (Steyn 1984). Duiker, steenbok, and gemsbok were run down in the rainy season and wildebeest and zebra during the hot dry season (Schapera 1930). It was believed that when a ruminant was prevented from chewing its cud during the chase it developed indigestion which eventually slowed it down, allowing the hunter to come close enough to kill it with spears (Heinz and Lee 1978).

Native American tribes also had various traditions of chasing down animals on foot (Nobokov 1981; Heinrich 2001). Tarahumara chased deer through the mountains of northern Mexico until the animals collapsed from exhaustion and then throttled them by hand (Bennett and Zingg 1935; Pennington 1963). Paiutes and Navajo in the American Southwest are reported to have used this technique to hunt pronghorn antelope (Lowie 1924; Foster 1830, cited by Lopez 1981, 111). Aborigines of northwestern Australia are known to have hunted kangaroo in this way (Sollas 1924; McCarthy 1957).

Observations of the Persistence Hunt

In the past 20 years, the only hunters known to practice the persistence hunt have lived in the central Kalahari, in the areas of Lone Tree, Bere, and ≠Xade. I first recorded the persistence hunt in July 1985 when I accompanied four hunters, !Nam!kabe, !Nate, Kayate, and Boro//xao, from Lone Tree. We were separated during the hunt, however, and they told me only after the hunt how they had run down the kudu. I first witnessed this hunt on foot in August 1990 when I accompanied the same four hunters. Finally, on two expeditions with film crews, I followed the hunters in a vehicle. A total of eight attempts resulted in three kudus killed. In November 1998 I worked with Craig and Damon Foster in filming *The Great Dance* (I asked them to remove my name from the credits) and in October 2001 I worked with the BBC to film Karoha, !Nate, and /Uase (also from Lone Tree) persistence hunting for the last episode of David Attenborough's *Life of Mammals* (for more information, see appendix B).

The hunt takes place during the hottest time of the day, with maximum temperatures of about 39–42°C. Before starting, the hunters drink as much water as they can. Then they run up to the animal, which quickly flees, and track its footprints at a running pace. Meanwhile, the animal will have stopped to rest in the shade. The hunters must find the animal and chase it before it has rested long enough. This process is repeated until the animal is run to exhaustion.

The hunts I observed involved three or four hunters starting the hunt, even when some of them were too old or not fit enough to complete it. A team of hunters can track much faster than one individual on his own. In the beginning the fittest runner may adopt an easy pace while the other hunters do most of the work tracking and running. While tracking as fast as possible, hunters are often slowed down when they lose the trail and struggle to find it again. When the others drop out, the fittest runner must pace himself to run down the animal on his own.

The shortest hunt I witnessed lasted less than two hours (the exact time is not known, since I had to catch up with the hunter) (table 1). In this hunt !Nate ran the entire way, although he sometimes slowed down when he lost the spoor. However, after the hunt !Nam!kabe said that they did not have to run that fast and that it was possible to run down a kudu if the hunter walked some of the time. On one successful hunt in 1998 the distance covered by Karoha was measured with the vehicle odometer. The hunt took 3 hours 35 minutes to cover about 35 km, for an average speed of about 10 km/hr. On two successful hunts in 2001 a global positioning system was used to record the route followed by Karoha. One hunt took 3 hours 50 minutes to cover 25.1 km, for an average speed of 6.3 km/hr. The other took 4 hours 57 minutes to cover 33 km, for an average speed of about 6.6 km/hr.

An average speed of 6.3 km/hr may not seem very fast, but the challenge to the hunter is not so much the speed as the difficult conditions that need to be overcome, including extreme heat, soft sand, and sometimes thick bush. The hunter may be slowed down when he loses the trail. The most difficult task for the tiring hunter is keeping on the right track when the animal joins the rest of the herd again, since its tracks must be distinguished from those of the other animals. When the animal is still running strongly, this can be very difficult, but when it starts to show signs of tiring it becomes easier to distinguish its tracks. Another difficulty is that the animal may circle back onto its own tracks and the hunter must decide which set of tracks to follow. The hunter does not always run on the tracks but often leaves the trail in order to pick it up ahead, and a number of times the hunter lost time following the wrong trail and then going back to find the right one. The trail may also be lost when herds of other antelope species cross the tracks. Losing the tracks was the main reason the hunters gave up in unsuccessful attempts (see table 2). Figure 1 plots the route of Karoha running down a kudu bull in October 2001, showing the kudu crossing back over its own tracks a number of times and joining other groups of kudu bulls.

Local Knowledge and Practice

!Xo and /Gwi hunters at Lone Tree maintain that they concentrate on different species at different times of the year. They say that steenbok, duiker, and gemsbok can be run down in the rainy season because the wet sand forces open their hoofs and stiffens the joints. This is consistent with what Schapera (1930) reported. Kudu, eland, and red hartebeest can be run down in the dry season because they tire more easily in loose sand. Kudu bulls tire faster than cows because of their heavy horns. Kudu cows are run down only if they are pregnant or wounded. Animals weakened by injury, illness, or hunger and thirst are also run down. When there is a full moon, animals are active all night, and by daybreak they are tired and easier to run to exhaustion. The best time for the persistence hunt is at the end of the dry season (October/November), when animals are poorly nourished. During August/September, insects (*!oam/neli*) bite the kudu, making them sick. After the first rains (November/December), the dry leaves make "hard balls" in the stomach of the kudu that give it diarrhea. After it has rained, it is easier to follow the fresh tracks in the wet sand. In February/March, the mixture

Table 1. Data on Persistence Hunts

Research Objective	Date	Hunter	Age	Species	Lowest and Highest Temperature (°C)	Distance (km)	Time	Average Speed (km/hr)	Result
Hunting on foot	July 26, 1985	!Nam!kabe	Not known	Kudu	Not recorded	Not recorded	Not recorded	Not recorded	Successful
Hunting on foot	August 29, 1990	!Nate	34	Kudu	Not recorded	Not recorded	< 2 hr	Not recorded	Successful
Filming persistence hunt	November 12, 1998	Karoha	35	Gemsbok	36–42	31	5hr05m	6	Failed
	November 18, 1998	Karoha	35	Kudu	32–39	35	3hr35m	10	Successful
Filming persistence hunt	October 5, 2001	Karoha	38	Kudu	Not recorded	25.5	4hr06m	6.2	Failed
	October 6, 2001	Karoha	38	Kudu	Not recorded	33	4hr57m	6.6	Successful
	October 9, 2001	Karoha	38	Kudu	35–41	17.3	3hr40m	4.8	Failed
	October 10, 2001	Karoha	38	Kudu	35–42	20.5	4hr52m	4.2	Failed
	October 12, 2001	Karoha	38	Kudu	39–42	35.2	6hr38m	5.3	Failed
	October 13, 2001	Karoha	38	Kudu	Not recorded	25.1	3hr50m	6.3	Successful

Table 2. Field Notes on Failed Persistence Hunts

October 9, 2001		October 10, 2001		October 12, 2001	
Time	Notes	Time	Notes	Time	Notes
12:02:43 P.M.	Start hunt	10:31:29 A.M.	Start hunt	11:35:54 A.M.	Start hunt
12:08:04 P.M.	Hunting magic	10:42:20 A.M.	Run	11:39:48 A.M.	Kudu hunting magic
12:20:36 P.M.	35 degrees	11:03:18 A.M.	Spoor joins another 2	11:43:40 A.M.	39 degrees
01:00:16 P.M.	Run	11:10:49 A.M.	See 4 to 5 young bulls	11:48:35 A.M.	Run
01:18:52 P.M.	Walk	11:36:04 A.M.	1 missing go back to look for spoor	11:53:12 A.M.	41 degrees
01:19:49 P.M.	Run	11:40:48 A.M.	35 degrees	12:36:55 P.M.	Walk
01:24:24 P.M.	Walk	12:01:38 P.M.	Find missing spoor which turned away	12:43:21 P.M.	3 kudu split into 2 and 1
01:29:05 P.M.	Run	12:08:15 P.M.	Spoor shows it is getting tired, start run	12:59:56 P.M.	Run
01:47:45 P.M.	Run	12:56:54 P.M.	Walk thick bush	01:02:02 P.M.	Kudu separated
02:04:56 P.M.	Walk	12:59:19 P.M.	Run	01:23:10 P.M.	42 degrees
02:14:08 P.M.	39 degrees	01:00:40 P.M.	Walk	01:34:21 P.M.	Kudu mix with females
02:21:10 P.M.	Run	01:03:12 P.M.	Run	01:46:02 P.M.	!Nate finished
02:31:21 P.M.	Walk	01:07:42 P.M.	Run	01:48:36 P.M.	Kudu tired
02:32:43 P.M.	Run	01:23:03 P.M.	41 degrees	01:56:40 P.M.	/Uase finished
02:39:36 P.M.	41 degrees	01:47:31 P.M.	Walk	03:12:54 P.M.	Mix with females
02:48:18 P.M.	Female	01:53:55 P.M.	Kudu walking slowly	03:36:28 P.M.	40 degrees
02:52:07 P.M.	Lost spoor	01:57:22 P.M.	Refill water run	03:48:00 P.M.	Herd of hartebeest mix
02:54:07 P.M.	Run	02:04:48 P.M.	38 degrees	03:58:14 P.M.	1 male 1 female
03:04:35 P.M.	Walk	02:14:02 P.M.	40 degrees	04:58:40 P.M.	Hartebeest follow kudu spoor
03:32:30 P.M.	Lost spoor	02:17:55 P.M.	Wash faces	06:13:01 P.M.	Leave spoor for tomorrow
03:42:51 P.M.	Abandon chase	02:40:01 P.M.	39 degrees		
		02:50:21 P.M.	41 degrees		
		02:50:45 P.M.	!Nate finished		
		02:59:38 P.M.	42 degrees		
		03:23:40 P.M.	Lost spoor in herd of eland with babies		

of green vegetation with dry vegetation can cause diarrhea, making it easier to run animals down, but cloudy, cool days make it more difficult. In the winter months (June/July) the shorter days make hunting difficult. However, hunters maintain that it is possible to run down animals at any time of the year (I recorded one persistence hunt in July).

When running down a herd of kudu, trackers say that they look to either side of the trail to see if one of the animals has broken away from the rest of the herd and then follow that animal. The weakest animal usually breaks away from the herd to hide in the bush when it starts to tire, while the others continue to flee. Since a predator will probably follow the scent of the herd, the stronger animals have a better chance of outrunning it, while the weaker animal has a chance to escape unnoticed (for more information, see appendix C).

Endurance Running by Humans

A critical factor in the success of persistence hunting is the fact that humans can keep their bodies cool by sweating while running. If an antelope is forced to run in the midday heat on an extremely hot day it overheats and eventually drops from exhaustion or simply stops running, allowing the hunter to kill it with a spear. The normal core body temperature of eutherian mammals is 36–38°C (Morrison and Ryser 1952), and the lethal core temperature of these mammals is 42–44°C (Adolph 1947). Most medium-sized-to-large mammals rely on evaporative cooling to maintain body temperature while running (Richards 1970; Taylor 1974, 1977). In humans the critical thermal maximum, beyond which life-threatening damage develops, has been estimated at 41.6–42°C (Kosaka et al. 2004), but humans can tolerate heat stresses well above this limit (Kenney, DeGroot, and Holowatz 2004).

Carrier (1984) presents a convincing theory that explains how humans are able to run down antelope. Some of the most important points may be summarized as follows: In mammals generally, evaporative cooling is accomplished by two separate mechanisms: (1) respiratory evaporation occurring at the nasal mucosa, buccal, and tongue surfaces (panting) and (2) evaporation of sweat from the general body surface. The flexibility and possibly the total effectiveness of panting as a means of evaporative cooling may be limited in a running mammal. The amount of heat that can be lost through evaporation from the respiratory surfaces severely

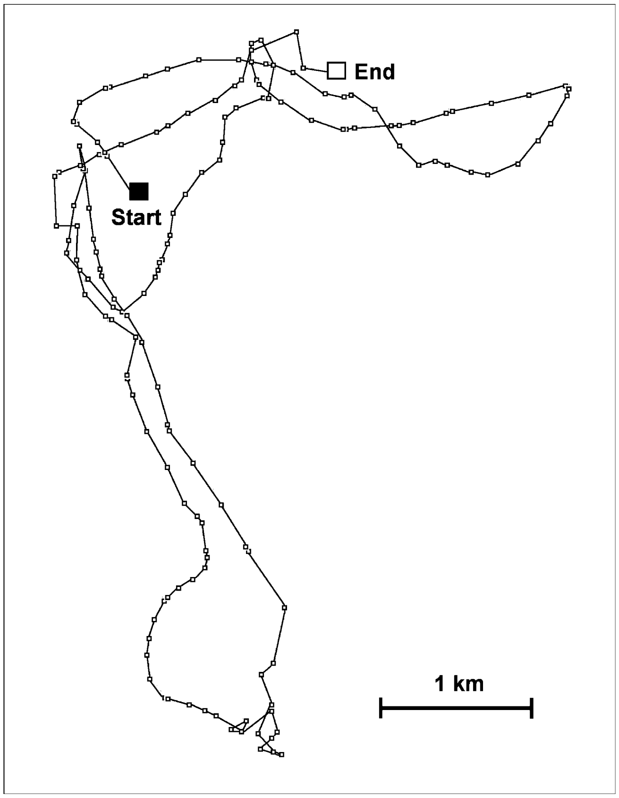

Figure 1. The route of Karoha running down a kudu bull on October 13, 2001, plotted with a global positioning device.

limits the maximum rate of heat dissipation during running in animals that rely solely on panting (Carrier 1984; Taylor and Rowntree 1974). The sweat glands of humans are distinctive for the high secretory level at which they operate. No other species is known to sweat as much per unit surface area as humans (Eichna et al. 1950; Schmidt-Nielsen 1964; Newman 1970). The great increase in eccrine (as opposed to apocrine) sweat glands and their copious secretions have permitted modern humans to undertake vigorous exercise in hot environments. The rate at which heat is lost in running humans is greatly increased by their relative lack of hair and by convection during running. The combination of well-developed sweat glands and the relative absence of body hair makes it probable that running humans display very high thermal conductance, with maximal values well above those of most cursorial mammals (Carrier 1984).

Distinct advantages would also have been conferred by bipedalism, allowing hominins to forage at higher temperatures and over greater distances while consuming less food and water than quadrupeds (Wheeler 1991*b*). In addition to bipedalism (Wheeler 1984, 1991*a*, 1991*b*), the loss of functional body hair (Wheeler 1985, 1992*a*), and increase in body size (Wheeler 1992*b*), a more linear physique would have reduced thermal and water stress in such conditions, reinforcing the argument that thermoregulatory selection pressure was an extremely important influence on human evolution (Wheeler 1993). The increase in body size observed in the hominin fossil record would have been associated with significant advantages. Larger hominins dehydrate more slowly and are able to cover a greater distance each day before encountering thermoregulatory constraints (Wheeler 1992*b*). Although the major benefit conferred by bipedalism is a dramatic reduction in direct solar radiation exposure, additional advantages also result from the higher distribution of the body surfaces. Wind speeds are higher and air temperatures lower away from the ground, increasing the rate at which a biped dissipates heat by convection. The greater air flow and low relative humidity above any surface vegetation will also increase the rate at which sweat can be evaporated from the skin (Wheeler 1991*a*).

In contrast to most quadrupeds, humans increase speed during endurance running mostly by increasing stride length. Long stride lengths in humans are made possible by a combination of effective leg springs and relatively long legs (Bramble and Lieberman 2004). Lower–limb length has a demonstrable effect on the energetic cost of locomotion, resulting in lower costs at all speeds. The gradually increasing lower–limb lengths seen in the hominin fossil record would have resulted in increasing locomotor efficiency through time (Steudel-Numbers and Tilkens 2004).

Humans walking at optimal speed consume only half the energy required to cover the same distance while running (Cavagna and Kaneko 1977; Rodman and McHenry 1980). Data on the metabolic benefits of changing gaits for ponies suggests that quadrupedal mammals have specific speeds at which energy expenditure is minimized for each of their various gaits (Hoyt and Taylor 1981). In contrast, the energy required for a running human does not depend on speed (Boje 1944; Margaria et al. 1963; Cavagna and Kaneko 1977). A constant cost of transport could provide humans with the option of running at a wide variety of speeds, while quadrupeds appear to be specialized for a narrow range of speeds within each gait (Carrier 1984).

When chased, the animal outruns the hunter and then stops to rest in the shade. It is forced into an intermittent running pattern by the contrasting needs to avoid the hunter and to avoid fatigue and heat stress. Although intermittent running provides brief rest periods, it may be less economical than continuous running (Carrier 1984). Compared with continuous exercise, intermittent exercise has (for humans) also been shown to elevate core body temperature and decrease evaporative heat loss as a result of reduced sweating (Ekblom at al. 1971). Whether the prey ran at a pace set by the hunter or chose to run intermittently, the end result would have been inefficiency. A hunter whose cost of transport did not vary with running speed would likely have had a substantial advantage over a prey animal with restricted, energetically optimal speeds in each gait (Carrier 1984). During the persistence hunt, the hunter needs to run at a fast pace when tracking is easy but slow down when tracking is difficult—sometimes losing the trail, sometimes walking to regain strength. His speed is determined not only by his physical speed and endurance but also by how fast he can track the animal. Flexibility in running speed allows a human hunter to pursue an animal persistently at various speeds, depending on his fitness, the heat, and varying tracking conditions.

Relative Success Rates of Hunting Methods

In July 1985 I worked with Bahbah, Jehjeh, and Hewha at Ngwatle Pan in Botswana. During one field trip, five days of hunting resulted in one gemsbok and two bat-eared foxes killed by hunting with dogs. Although five days may not be enough to get a reliable estimate of success rate, hunting with dogs is evidently much more efficient than hunting without them. Four field trips adding up to 46 days of hunting focused on hunting with bow and arrow, club, and spear (without dogs). In July 1985, August 1990, February and March 1991, and June 1992 I worked with !Nam!kabe, !Nate, Kayate, /Uase, and Boro//xao from Lone Tree, and in these periods two persistence hunting attempts resulted in the killing of two kudus. There were 41 attempts at bow-and-arrow hunting, which involved following fresh tracks and stalking steenbok, duiker, springbok, hartebeest, wildebeest, kudu, and gemsbok. Of these, 39 attempts failed. One wildebeest and one duiker were killed with bow and arrow. Animals killed with club and spear included aardvark, porcupine, and gemsbok (a calf). These involved following fresh tracks and killing animals dug out of their burrows or surprised where they were sleeping under bushes. Eleven attempts resulted in the killing of two aardvark, two porcupines (killed in one attempt), and one gemsbok calf. Animals killed with a springhare probe included three springhares and one ground squirrel in 29 attempts. No reliable data on the success rate of snaring were obtained.

Table 3 shows the meat yield, estimated, following Lee 1979), to be 50% of the weight of the animals hunted. Meat yields in kilograms per day hunted offer an estimate of the relative efficiency of the different hunting methods. Table 4 presents data obtained for hunting methods on seven field trips with three different research objectives. The number of animals killed per number of days hunted gives an indication of the success rate per day.

Data obtained while filming the persistence hunt give some indication of the success rate per attempt, but the number of days hunting is inapplicable. The success rate while filming may have been lower than normal, since the hunters were under pressure to attempt hunts that they might not have performed under normal conditions. For example, the failed gemsbok hunt of November 12, 1989, was attempted only after a long debate in which Karoha expressed his reservations. (They would normally run down gemsbok in the rainy season, not the dry season.) On October 6, 2001, the camera crew did not film the moment when the kudu collapsed and asked Karoha to repeat the hunt. A hunter would not normally attempt another persistence hunt three days after a successful one. If the data from the research and filming expeditions are combined, omitting the hunts that would not have been attempted if it were not for the sake of filming (those of November 12, and October 9–13, 2001) then the amended data in table 4 would include four successful hunts out of five attempts, giving an 80% success rate. The amended yield (4 kg/day) is 80% of the yield estimate based on the two hunts observed while hunting on foot.

It is possible that the success rate of persistence hunting has deteriorated in the past 20 years as the last few hunters who have been practicing it get older. It may be significant that in 1990 they ran for the entire hunt, killing the kudu in less than two hours, while in 1998 and 2001 the hunter sometimes walked. !Nam!kabe, who performed the hunt in 1985, has died. His son !Nate, who ran down the kudu in 1990, when he was 34, is now unfit to do so. Karoha, who was 35 when he performed the hunt in 1998 and 38 when he did so

Table 3. Meat Yield (kg/day)

Method	Days	Species	Weight (kg)	Edible Yield (kg)	Number	Yield (kg/day)
Dogs	5	Gemsbok	240	120	1	24
	5	Bat-eared fox	4	2	2	0.8
Total						24.8
Persistence hunt	46	Kudu	230	115	2	5
Total						5
Bow and arrow	46	Wildebeest	250	125	1	2.7
	46	Duiker	20	10	1	0.2
Total						2.9
Club and spear	46	Aardvark	52	26	2	1.1
	46	Porcupine	18	9	2	0.4
	46	Gemsbok calf	10	5	1	0.1
Total						1.6
Springhare probe	46	Springhare	3	1.5	3	0.1
	46	Ground squirrel	0.6	0.3	1	0.007
Total						0.1

Note: Figures rounded to the nearest 0.1 kg/day.

Table 4. Success Rates of Different Hunting Methods

Research Objective	Method	Days Hunted	Attempts	Successful	Success Per Attempt (%)	Animals Killed/Day	Yield (kg/day)
Hunting with dogs	Dogs	5	5	3	60	0.6	24.8
Hunting without dogs	Persistence hunt	46	2	2	100	0.043	5
	Bow-and-arrow	46	41	2	5	0.043	2.9
	Club and spear	46	11	5	45	0.109	1.6
	Springhare probe	46	29	4	14	0.087	0.1
Filming persistence hunt	Persistence hunt	N/A	8	3	37	N/A	N/A
Amended data[a]	Persistence hunt	N/A	5	4	80	N/A	4
Extrapolated data[b]	Snaring	N/A	N/A	N/A	N/A	N/A	5

[a]Omits persistence hunts attempted for the sake of filming which would not have been attempted under normal hunting conditions.
[b]Estimate based on data published by Lee (1979).

in 2001, may soon be too old. As far as is known, Karoha may well be the last hunter in the central Kalahari who has been practicing the persistence hunt. However, since only three individuals were observed, the apparent deterioration could simply be individual variation in skill.

Recent hunter-gatherers utilize a range of hunting methods depending on conditions and circumstances. My observations and data from Lee (1979) suggest that the highest success rate and the highest meat yield are achieved by hunting with dogs. A relatively high success rate is also achieved with snaring small antelope (steenbok and duiker) and birds (korhaan, kori bustard). Although I obtained no reliable data on using snares, a rough extrapolation can be made using data from Dobe, Namibia, published by Lee (1979, 267). Over a 28-day period, hunting with dogs produced a meat yield of 151.1 kg while using snares produced 32.1 kg. Assuming that the hunters I worked with had a similar success rate, the equivalent meat yield from snaring per days hunted would be about $(32.1/151.1) \times 24.8 = 5.26$, or roughly 5 kg/day hunted (table 4). This would be about the same as the meat yield for persistence hunting.

Digging out animals sleeping in burrows or killing animals sleeping under bushes with clubs and spears has a relatively high success rate compared with other methods. However, the meat yield is relatively low. Using the springhare probe for small mammals in burrows produces the lowest meat yield. Larger animals (when hunting without dogs) would be either pursued with bow and arrow or run down in the midday heat.

The bow and arrow is the most flexible method, allowing a large number of opportunities from small antelope to the largest, including eland and giraffe. However, for most of the hunts I witnessed, the success rate per attempt was very low. Often, when tracking one animal, the hunters would abandon the trail for a more promising lead or to dig up an animal in a burrow. Hunters would often attempt a stalk and not get close enough (25–30 m) to shoot, or, when they did get close enough, the arrow would miss the target. Even when they did hit the target, it might take hours or even days to track the wounded animal, and sometimes the animal would recover and escape or be finished off during the night by other predators or scavengers. Because of the opportunistic nature of hunting and gathering, hunters are continuously changing their methods depending on changing opportunities. They may start out on a bow-and-arrow hunt and end up digging out an aardvark. It requires many attempts to kill an animal with a poisoned arrow.

In contrast, persistence hunting is limited to fewer species and favorable conditions for it occur less often, but the success rate per opportunity seems to be much higher. When the conditions are right, hunters appear to be more confident of succeeding with the persistence hunt than with the bow and arrow. For example, the persistence hunt I witnessed in August 1990 took place at the end of the dry season, when the thick dry grass made it difficult to stalk silently. After a number of failed attempts with the bow and arrow, the hunters had expressed confidence that they had a better chance of running down the kudu.

The fact that the duration of persistence hunts varies considerably may explain why the success rate per attempt is much higher than for bow-and-arrow hunting. When hunting with bow and arrow, the hunter may spend a considerable period of time tracking and stalking an animal, but in the end he has only one chance. When conditions are right for persistence hunting, the hunter has a much larger margin of error. As long as he is able to pursue the animal at a reasonable pace and not lose the trail, whether it takes two hours or five hours he has a good chance of running it down.

Compared with other hunting methods, persistence hunting is, given the right conditions, an effective method with a relatively good success rate and meat yield. The data presented suggest that it produces a higher meat yield than hunting with bow and arrow, clubs and spears, or springhare probes and about the same as snaring. Only hunting with dogs produces a significantly higher meat yield.

Conclusion

Endurance running may have had adaptive value not only in scavenging but also in hunting. Before the domestication of dogs, persistence hunting may have been one of the most efficient forms of hunting. Endurance running and persistence hunting may therefore have been crucial factors in the evolution of humans.

Acknowledgments

I thank David Carrier, Dan Lieberman, Bernd Heinrich, Jessica Perkins, and four anonymous reviewers for critical reading of the manuscript. I also thank the late !Nam!kabe, !Nate, Karoha, /Uase, Kayate, and the late Boro//xao of Lone Tree and Bahbah, Jehjeh, and Hewha of Ngwatle Pan for their hospitality and friendship and for sharing their knowledge of tracking. Lefi Cooper of Hukuntsi, Jim Morris of D'Kar, and Xamaha of Kagcae assisted me with translation.

Appendix A: Evolutionary Hypothesis

Carrier (1984) has hypothesized that endurance running evolved in early hominins for predator pursuit. However, it is unlikely that early *Homo* would have been able to develop persistence hunting unless it already had well-developed endurance running abilities as well as tracking skills. As Bramble and Lieberman (2004), suggest, it is very likely that endurance running was first practiced in the context of scavenging. Races against nonhuman scavengers and others of their own species could have become the bridge to races with live prey (Heinrich 2001).

If hominins used endurance running to increase the yield from scavenging, then there would have been strong selective pressure to increase the speed of endurance running, and once they had achieved high-speed endurance running they would have had the potential to develop persistence hunting. Persistence hunting would have produced a higher yield than scavenging, since the hunter gets the whole carcass rather than a partially consumed one. Two million years of endurance running for increasingly competitive scavenging may have preadapted *Homo* for persistence hunting. It is unlikely that *Homo* would have been able to make the transition to persistence hunting without first using endurance running for scavenging.

A prerequisite for persistence hunting would have been the invention of water containers. In contrast to horses and camels, humans cannot consume large amounts of water at one time. Human thermoregulation requires considerable water for evaporative cooling, and this would have made it essential to carry water in containers (Scott 1984).

While modern hunter-gatherers have available to them a wide range of hunting methods, it is likely that persistence hunting would have been more important before the invention of the spear-thrower and the bow and arrow or the domestication of dogs. Without a spear thrower or bow and arrow it would have been very difficult for slow-running hominin hunters to get close enough to an animal to catch and kill it.

Tracking skills would have been a prerequisite for the development of persistence hunting as well as hunting with the spear-thrower or the bow and arrow. It is possible that tracking was first developed to find animals sleeping in burrows such as aardvark and porcupine. Hunters have all day to track the animal, and when an occupied burrow is found the animal does not run away. Persistence hunting, however, would have required much more sophisticated tracking. Simple forms of persistence hunting may have first developed in easy tracking terrain such as the arid, sparsely vegetated, sandy southern Kalahari. Systematic tracking involves following footprints where they are reasonably easy to see. When the ground is harder and the vegetation cover thicker it is not easy to see them, and in woodland the animal will soon run out of sight. In these conditions speculative tracking would have been essential. Speculative tracking involves the interpretation of signs—creating a hypothesis to explain what the animal is doing and then using it to predict where the animal is going (Liebenberg 1990). Instead of "following" footprints the speculative tracker predicts where tracks will be found and then looks for them where they are expected. In difficult terrain, where tracks are not easy to see, this makes tracking much faster. The art of tracking as practiced by recent hunter-gatherers requires considerable skill and intelligence, and it has been suggested that the creative hypothetico-deductive reasoning necessary to track effectively in difficult terrain is also important in other complex human behaviors such as scientific research (Liebenberg 1990; Carruthers 2002, n.d.). This level of sophistication may well have been a very recent development.

The evolution of tracking may be indicated in the archaeological record by the species hunted. Systematic tracking may be represented mainly by grassland species in areas where the substrate is soft. Speculative tracking may be represented by grassland species together with woodland species. It may also be indicated by hunting in areas of hard substrate where systematic tracking could have been difficult. Faunal remains from the Klasies River Mouth caves have been considered to indicate that during the Middle Stone Age the exploitation of cover-loving medium-sized animals was part of a scavenging strategy whereas the exploitation of grassland antelope was a component of a hunting strategy. Toward the end of the Middle Stone Age, it is argued, there was a trend toward increased hunting and a more marginal role for scavenging. During the Late Stone Age there was an increase in the hunting and/or trapping of cover-loving animals (Binford 1984). If this interpretation is correct, the Middle Stone Age increase in the hunting of grassland species may represent the development of systematic tracking while the Late Stone Age increase in hunting of cover-loving animals may indicate the development of speculative tracking.

Persistence hunting is known to be practiced only by men. This raises the issue of how complex changes in anatomy can be driven by natural selection acting primarily on one sex. In this case, both natural and sexual selection may have operated to bring about changes in the modern human body form. For example, successful male persistence hunters would have been more attractive as potential mates. As far as tracking is concerned, women are also highly skilled trackers (Biesele and Barclay 2001).

It is possible that early *Homo* practiced a simple form of persistence hunting using systematic tracking in easy tracking terrain. The efficient form of persistence hunting practiced by modern hunters in difficult tracking terrain may have appeared only very recently.

Appendix B: Methods

Field research expeditions were conducted from 1985 to the present in the Kalahari in Botswana and Namibia. Their main objective was the study of the tracking expertise of hunters. Some field trips specifically focused on hunting with bow and arrow, clubs, and spears (without dogs), since these methods involve intensive tracking. One field trip looked at hunting with dogs for comparison with other methods. During these field trips I and two to four hunters camped near a pan from which they hunted on foot. A tape recorder, camera, and notebook were used to record observations in the field. I participated in the tracking. In the evenings a translator helped transcribe the tape recordings, and interviews were conducted at the camp.

The first two persistence hunts were recorded while I accompanied hunters on foot, but many of the data on persistence hunting were obtained on the two field expeditions with the objective of making television documentaries. On these expeditions the main focus was the persistence hunt almost to the exclusion of all other hunting methods. To speed up the process, the initial scanning for fresh tracks was done with a four-wheel-drive vehicle, but as soon as the animals were spotted the hunters left the vehicle and started the persistence hunt on foot. For the purpose of filming the hunters were allowed to refill their two-liter plastic water bottles during the hunt, since it was felt that it was unjustifiable to risk their lives for the sake of a film and the objective was to show not that they could perform the persistence hunt but how they did it. The film crew followed the hunters in the vehicle. While the filming expeditions provided an opportunity to get good data, working with film crews can be exhausting and distracting. On three of the hunts (including two successful hunts) I did not take detailed field notes.

Appendix C: Participatory Observations

Tracking involves intense concentration resulting in a subjective experience of projecting oneself into the animal. The tracks indicate when the animal is starting to get tired; its stride becomes shorter, it kicks up more sand, and the distances between consecutive resting places become shorter. When tracking an animal, one attempts to think like an animal in order to predict where it is going. Looking at its tracks, one visualizes the motion of the animal and feels that motion in one's own body. Karoha explained: "When the kudu becomes tired you become strong. You take its energy. Your legs become free and you can run fast like yesterday; you feel just as strong at the end of the hunt as in the beginning." When the hunter finally runs the animal to exhaustion, it loses its will to flee and either drops to the ground or just stands looking at the approaching hunter with glazed eyes. Karoha explained that when the kudu's eyes glaze over, it is a sign that it feels that there is nothing it can do any more: "What you will see is that you are now controlling its mind. You are getting its mind. The eyes are no longer wild. You have taken the kudu into your own mind." The hunter will then finish off the animal with a spear.

Apart from their tracking skills, hunters' knowledge of heat stroke and how to treat it also demonstrates the level of expertise required to practice this hunting method. Hunters push themselves to their limits and usually know when to stop. When I ran with them, I failed to monitor my own condition until it was almost too late. By the time I caught up with !Nate, I was no longer sweating. The hunters immediately recognized the early symptoms of heat stroke, and after having run down the kudu !Nate ran eight kilometers back to the camp to get his father, !Nam!kabe, to bring water. When !Nam!kabe finally reached me with water, he told me not to drink it because drinking too much too quickly would kill me. I was told to wet my hair and wash my face first to cool down my brain and to sip the water, holding it in my mouth as long as possible. Afterward they explained that when running down an animal the hunter must continuously compare the condition of his own body with that of the animal, and I had become too focused on the animal.

References Cited

Adolph, E. F. 1947. Tolerance to heat and dehydration in several species of mammals. *American Journal of Physiology* 151:564–75.

Bennett, W. C., and R. M. Zingg. 1935. *The Tarahumara: An Indian tribe of northern Mexico.* Chicago: University of Chicago Press.

Biesele, M., and S. Barclay. 2001. Ju/'hoan women's tracking knowledge and its contribution to their husbands' hunting success. *African Study Monographs,* suppl.26:67–84.

Binford, L. R. 1984. *Faunal remains from Klasies River Mouth.* New York and London: Academic Press.

Boje, O. 1944. Energy production, pulmonary ventilation, and length of steps in well-trained runners working on a treadmill. *Acta Physiologica Scandinavica* 7:362–75.

Bramble, D. M., and D. E. Lieberman. 2004. Endurance running and the evolution of *Homo. Nature* 432:345–52.

Carrier, D. R. 1984. The energetic paradox of human running and hominid evolution. *Current Anthropology* 25:483–95.

Carruthers, P. 2002. The roots of scientific reasoning: Infancy, modularity, and the art of tracking. In *The cognitive basis of science*, ed. P. Carruthers, S. Stich, and M. Siegal. Cambridge: Cambridge University Press.

———. n.d. *The architecture of the mind.* Oxford: Oxford University Press.

Cavagna, G. A., and M. Kaneko. 1977. Mechanical work and efficiency in level walking and running. *Journal of Physiology* 268:467–81.

Eichna, L. W., C. R. Park, N. Nelson, S. M. Horvarth, and E. D. Palmes. 1950. Thermal regulation during acclimatization to a hot dry environment. *American Journal of Physiology* 163:585–87.

Ekblom, B., C. J. Greenleaf, J. E. Greenleaf, and L. Hermansen. 1971. Temperature regulation during continuous and intermittent exercise in man. *Acta Physiologica Scandinavica* 81:1–10.

Heinrich, B. 2001. *Why we run.* New York: HarperCollins.

Heinz, H. J., and M. Lee. 1978. *Namkwa: Life among the Bushmen.* London: Jonathan Cape.

Hoyt, D. F., and C. R. Taylor. 1981. Gait and the energetics of locomotion in horses. *Nature* 292:239–40.

Kenney, W. L., D. W. DeGroot, and L. A. Holowatz. 2004. Extremes of human heat tolerance: Life at the precipice of thermoregulatory failure. *Journal of Thermal Biology* 29: 479–85.

Kosaka, M., M. Yamane, R. Ogai, T. Kato, N. Ohnishi, and E. Simon. 2004. Human body temperature regulation in an extremely stressful environment: Epidemiology and pathophysiology of heat stroke. *Journal of Thermal Biology* 29:495–501.

Lee, R. B. 1979. *The !Kung San: Men, women, and work in a foraging society.* Cambridge: Cambridge University Press.

Liebenberg, L. W. 1990. *The art of tracking: The origin of science.* Cape Town: David Philip.

Lopez, B. H. 1981. *Winter count.* New York: Scribner.

Lowie, R. H. 1924. *Notes on Shoshonean ethnography.* Anthropological Papers of the American Museum of Natural History 20, pt. 3.

McCarthy, F. D. 1957. *Australian Aborigines: Their life and culture.* Melbourne: Colorgravure Publications.

Margaria, R., P. Cerretelli, P. Aghemo, and G. Sassi. 1963. Energy cost of running. *Journal of Applied Physiology* 18: 367–70.

Morrison, P. R., and F. A. Ryser. 1952. Weight and body temperature in mammals. *Science* 116:231–32.

Newman, R. W. 1970. Why is man such a sweaty, thirsty, naked animal? A speculative review. *Human Biology* 42: 12–27.

Nobokov, P. 1981. *Indian running: Native American history and tradition.* Santa Fe: Aneburt City Press.

Pennington, C. W. 1963. *The Tarahumara of Mexico.* Salt Lake City: University of Utah Press.

Richards, S. A. 1970. The biology and comparative physiology of thermal panting. *Biological Reviews* 45:223–64.

Rodman, P. S., and H. M. McHenry. 1980. Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology* 52:103–6.

Schapera, I. 1930. *The Khoisan peoples of South Africa: Bushmen and Hottentots.* London: Routledge and Kegan Paul.

Schmidt-Nielsen, K. 1964. *Desert animals: Physiological problems of heat and water.* New York: Oxford University Press.

Scott, E. C. 1984. Comment on: The energetic paradox of human running and hominid evolution, by D. R. Carrier. *Current Anthropology* 25:483–95.

Silberbauer, G. B. 1981. *Hunter and habitat in the Central Kalahari Desert.* Cambridge: Cambridge University Press.

Sollas, W. J. 1924. *Ancient hunters and their modern representatives.* New York: Macmillan.

Steudel-Numbers, K. L., and M. J. Tilkens. 2004. The effect of lower limb length on the energetic cost of locomotion: Implications of fossil hominins. *Journal of Human Evolution* 47:85–94.

Steyn, H. P. 1984. Southern Kalahari San subsistence ecology: A reconstruction. *South African Archaeological Bulletin* 39: 117–24.

Taylor, C. R. 1974. Exercise and thermoregulation. In *Environmental physiology,* ed. D. Robertshaw. London: Butterworths.

———. 1977. Exercise and environmental heat loads: Different mechanisms for solving different problems. In *Environmental physiology 2,* ed. D. Robertshaw, 119–46. Baltimore: University Park Press.

Taylor, C. R., and V. J. Rowntree. 1974. Panting vs. sweating: Optimal strategies for dissipating exercise and environmental heat loads. *Proceedings of the International Union of Physiological Science, XXVI International Congress, New Delhi,* vol. 11, 348.

Wheeler, P. E. 1984. The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution* 13:91–98.

———. 1985. The loss of functional body hair in man: The influence of thermal environment, body form, and bipedality. *Journal of Human Evolution* 14:23–28.

———. 1991*a*. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: The contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution* 20: 107–15.

———. 1991*b*. The influence of bipedalism on the energy and water budgets of early hominids. *Journal of Human Evolution* 20:117–36.

———. 1992*a*. The influence of the loss of functional body hair on the energy and water budgets of early hominids. *Journal of Human Evolution* 23:379–88.

———. 1992*b*. The thermoregulatory advantages of large body size for hominids foraging in savannah environments. *Journal of Human Evolution* 23:351–62.

———. 1993. The influence of stature and body form on hominid energy and water budgets: A comparison of *Australopithecus* and early *Homo* physiques. *Journal of Human Evolution* 24:13–28.