Tracking and the interpretation of spoor:
a scientifically sound method in ecology

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(With 3 figures in the text)

Methods of studying wildlife are often restricted by habitat. Tracking, the reconstruction of activity from the spoor of animals, is an age-old technique that is still frequently used by modern-day hunter/gatherer communities. Although previously used in behavioural studies, tracking has not been tested for its scientific merit. In this paper, we provide data towards such a description by first testing the reliability of tracking, and second attempting to measure the techniques of tracking. In a test for accuracy, the Ju/'Hoan San team was correct in most (98% of 569) spoor reconstructions. Most significant of these were the correct identification of individually known animals and the reconstruction of complex behaviour from spoor. Measurements of the spoor of different species and age/sex groups in some species showed significant differences. Variation in different soil conditions, however, affected spoor measurements so that subtle differences between individually known animals could not be measured. Measurements of the spacing distances and placement of feet during different gaits gave statistical and schematic values to indicate some of the techniques used by trackers during the reconstruction of behaviour. Indigenous peoples, such as the Ju/'Hoan, have an in-depth knowledge of nature. Collaboration between western science and traditional knowledge could greatly benefit studies in behaviour and wildlife.

Introduction

Studying the behaviour of wild animals in their natural habitat poses many practical problems. These are especially pronounced among the nocturnal species such as carnivores. Long-term habituation of individual animals (e.g. Mills, 1990) and the use of radio-telemetry (Amlaner & Macdonald, 1980) often enable workers to study behaviour. However, observation techniques are subject to suitable habitat, resulting in studies of behaviour, such as the African lion (*Panthera leo*) being restricted to open plains (Schaller, 1972; Packer, Scheel & Pusey, 1990; Scheel & Packer, 1991; Stander, 1992; Stander & Albon, 1993). Such a limitation may affect, for example, the discussions around the evolution of sociality in lions (see Caro, 1994; Legge, 1996). In this paper, we discuss the use of tracking as an indirect method of studying the behaviour of nocturnal large African carnivores in a wooded habitat.

Tracking (defined as the identification, following and interpretation of signs, such as spoor, of animals), an integral part of hunting, is a skill fundamental to the evolution of *Homo sapiens* (Laughlin, 1968; Washburn & Lancaster, 1968; Pfeiffer, 1978; Liebenberg, 1990). Modern-day

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trackers (such as the Ju/'Hoan San) are remarkably skilled in interpreting animal behaviour from spoor. The hunting skills and potential knowledge of behavioural ecology, of several subsistence hunting peoples have been emphasized before (Baerends, 1958; Laughlin, 1961; Bicchieri, 1972; Blurton Jones & Konner, 1976; Liebenberg, 1990). San trackers have been used in the study of large carnivore behaviour (Smith, 1977; Eloff, 1984; Bothma & Le Riche, 1984, 1990; Mills, 1990). Although recognized as a resourceful technique (Teer, 1982) and a useful tool for studying a range of species in a range of habitats, tracking has not yet been described in terms of its reliability and potential scientific contribution to the biological sciences.

Tracking involves the observation of all types of signs that indicate the presence and activity of an animal. The spoor of an animal may range in clarity from a clear footprint in soft ground to a mere trace on hard soil (Brown, 1978; Brown, Lawrence & Pope, 1992). The feet of most species are distinct, mainly due to morphological adaptations (e.g. digitigrade or unguligrade limbs). The activity of an animal is normally determined from a trail: a sequence of signs such as spoor and scrape marks.

Tracking has been described by Liebenberg (1990) at three basic levels: simple, systematic, and speculative. Simple tracking relates to the identification and following of spoor under ideal conditions. Systematic tracking is the following of a trail where trackers continuously gather information to interpret an activity. Speculative tracking is the formulation of an initial hypothesis of the animal's activities, based on the interpretation of observed signs. The trackers continuously search for clues to accept or refute the hypothesis. Both simple and systematic tracking are based on inductive approaches (Mentis, 1988), whereas speculative tracking is based on hypothetico-deductive reasoning (Lakatos, 1978). All three levels of tracking may, however, be subject to a large degree of bias and speculative tracking may even seem unscientific or unquantifiable.

In this paper, we address only the inductive approach to tracking, i.e. simple and systematic tracking, by descriptive analyses of the quantitative values of the technique. The skills of four experienced Ju/'Hoan hunters and a trained western biologist were combined in an attempt, first, to quantify the reliability and accuracy of tracking and second, to understand what techniques are used by the Ju/'Hoan during tracking. We also discuss its potential application to wildlife ecology and the ways in which the knowledge and skills of local people can similarly be applied.

Materials and methods

The study was conducted in the Kaudom Game Reserve and Bushmanland, in north-eastern Namibia (19°S, 20°E). The vegetation consisted of forest and shrub savanna woodland (Giess, 1971) with 152 ± 82 woody plants (≥ 60 cm) per hectare. The soil, classified as arenosols, formed hard surfaced topsoil with soft interior sands. The region forms part of the northern extension of the Kalahari desert.

One of us (PS) recorded animal activities directly by observing the species, age, sex, group composition, position and behaviour of animals (Tables I & IV). The Ju/'Hoan trackers were then taken 'blind' to the general vicinity and asked to find the spoor of animals which were identified to within the broad taxonomic group of the target animal (e.g. carnivore if a lion was observed). After assessing the area they would then reconstruct the events, which were scored as either correct or incorrect within the categories established during the direct observation phase. They often volunteered additional information but this was ignored. The 4 Ju/'Hoan hunters were treated as one sample unit. Group decisions were made after critical and rational discussion (see Medawar, 1969) among the individuals, a behavioural characteristic of the Ju/'Hoan society (Marshall, 1976; Lee, 1979).

Tracking accuracy was measured by means of the binomial probability of being correct or incorrect. This assumption was made simply for want of a more applicable null-hypothesis (H_0). For example, in identifying the track of a leopard (*Panthera pardus*) the Ju/'Hoan team may have a basis of 3 possibilities (including cheetahs (*Acinonyx jubatus*) and young lions). This would give them a probability element of $P = 0.33$. However, since the
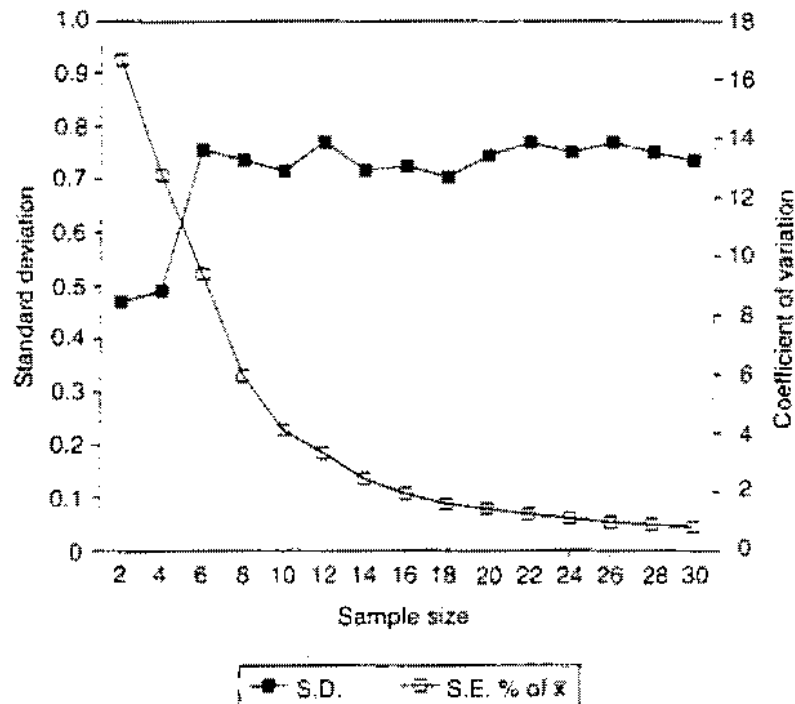
FIG. 1. The number of random measurements between the left back and left front spoor (pace) of an adult male leopard, from a sample of 30 measurements. Sampling intensity for measuring spoor spacing for all locomotive activities was determined by plotting sample size by standard deviation (S.D.) and coefficient of variance (S.E. as the % of the mean). Desired degree of accuracy was < 5% of the mean. In this example, 10 measurements provided a representative sample of the pace distance of a leopard. This measurement would then be 19.5 ± 0.7 cm, with 95% confidence interval, and would fall within the desired level of accuracy.

science of tracking is so poorly understood, and the possible choices available under different conditions are unknown, the establishment of a more realistic H_0 would be pointless. By maintaining a H_0 of $P = 0.5$, the Ju/'Hoan team does not necessarily receive the full credit deserved for the correct interpretation of a spoor or activity. There may be a multitude of possible choices which would make a correct choice more significant.

In some cases, one of us (PS) measured the size of spoor in an attempt to understand the subtle distinctions used by the Ju/'Hoan trackers to identify the spoor of different animals. The width and length of the spoor of the front and back feet (both left and right) were measured to indicate size and possible proportional variations in shape between the feet of different species, between different age and sex classes of the same species and between different individuals. Two soil-related variables were recorded when spoor was measured. First, the depth of the impression, and second, the angle of the walls of the impression. For example, a lion spoor in soft deep sand may measure 50 mm in depth with loose sand sloping down to the centre of the depression at an average angle of approximately 30°. The same lion's spoor on harder soil may be 2 mm deep with a 90° wall angle. Potential errors in comparing measurements of spoor in such diverse soil strata are enormous (Smallwood & Fitzhugh, 1993), so only measurements where the depth was less than 5 mm and the angle of the wall of the impression was greater than 60° were analysed.

The sequence of footprints and the relative distance between them were measured to help distinguish between different gaits. Spacing of the feet was grouped into 3 categories: a) a stride, the distance between 2 impressions made by the same foot; b) a pace, the distance of the step between the leading front foot and trailing back foot on

either left or right sides; and c) a straddle, the step distance between the leading foot on either left or right side and the trailing foot of the opposite side. The lengths of strides, paces and straddles, and foot sequences are known to be correlated with an animal's speed of locomotion and with its gait (Grogan, 1951; Hildebrand, 1959; Dagg, 1973). Sampling intensity for measuring locomotory activity was determined for each gait and species sampled. At first, a large sample of measurements was collected (e.g. pacing distance of an adult male leopard while walking; Fig. 1). Two measurement samples were then randomly selected and the sample increased to 4, 6, 8 … x, with a fresh mean, standard deviation and coefficient of variance (CV) (Grieg-Smith, 1957) calculated each time, and the results plotted (Fig. 1). A sample size was then selected that would account for most of the variance, in which the mean would fall within a 95% confidence interval, with the coefficient of variance less than 5%. This sample size was then used as the sampling intensity within that particular category.

Statistical means are given with standard deviation (S.D.) as a summary statistic of the variation of the data, and standard error (S.E.) as a measure of the precision of the means (Sokal & Rohlf, 1995). Data were tested for normality using a Komogorov-Smirnov 2-sample test. Non-parametric tests were used where behavioural data could not be normalized. Significance was measured at 5% and all P values are 2-tailed.

Results

Spoor identification

The identification of spoor by species proved to hold no difficulties for the Ju/'Hoan team. They correctly identified all 147 cases (Table I). This high level of accuracy (CV = 0.68%) is conceivable since the spoor of different species shows distinct anatomical variations. The measurements (Table II) of the spoor of four species of large carnivores, and four age groups in lions, indicate size variations between species. This size variation is further distinguished by proportional differences between front and back paws. A graphic comparison between the front spoor of different animals indicates both size and shape variations of spoor (Fig. 2). Leopard and brown hyena (*Hyaena brunnea*) spoors are symmetrical, whereas some individuals among spotted hyenas (*Crocuta crocuta*) and lions show slightly elongated spoor.

Correct identification of the age and sex of the more commonly observed carnivore species proved more difficult, although accuracy levels (CV = 1.45%) were still high (Table I). The sex of a lion was always correctly identified, but sub-adults were sometimes identified as adults. Both leopard and cheetah spoors were always correctly identified by age, but sex was incorrectly identified once for both species.

Spoor size varies with both age and sex. Spoor of adult male lions was significantly larger than that of adult females (t-test: $t = 12.77$; $d.f. = 54$; $P < 0.001$). The spoors of sub-adult lionesses were smaller than those of sub-adult males (Mann–Whitney U-test: $U = 10.0$; $P < 0.05$), but similar to adult lionesses ($U = 329$; $P = 0.657$). Sub-adult male spoors were larger than those of adult lionesses ($U = 287.5$; $P < 0.001$) but smaller than those of adult males ($U = 521$; $P < 0.01$).

The Ju/'Hoan team was able to identify the spoor of individual animals, with a 93.8% success rate (Binomial test: $P = 1$; CV = 3.13%; Table I). The possible choice of individual animals available to the team was impossible to measure in the open ecological system of the study area. However, the estimated minimum likely number of known individuals was, on average, 4·3 (range 2–11; Table I). Individual recognition of such spoor by the team was based on both the shape and size of the spoor and on the manner of walking. For example, on one occasion PS observed two adult male lions walking side by side for several hundred metres. Since it was known that the two lions walked at exactly the same speed, the distances between the spoor of the four paws of each individual was measured, to determine possible differences in the gaits. The paw sequence of both males was RB : RF : LB : LF (see

Table 1

The probab… y of correctly identifying the spoor of African wildlife by species, age, sex and known individuals. Cases presented were based on direct observations recorded by one observer (PS) only. The spoor was then identified by the Ju/'Hoan team within 24 hours of the observation. P values depict the probabil… y of a correct interpretation under a binomial distribution where $P = 0.5$, either correct (1) or incorrect (0), and a significance level P < 0.001. Precision of the data is high when sample sizes increase above 20 (CV < 5%).

Categories	Cases presented	Correct identification	% correct	P value
Species:				
Carnivore				
Lion	22	22	100	1
Leopard	19	19	100	1
Cheetah	12	12	100	1
Spotted hyena	14	14	100	1
Wild dog	12	12	100	1
Herbivore				
Steenbok	10	10	100	1
Duiker	10	10	100	1
Kudu	10	10	100	1
Hartebeest	10	10	100	1
Wildebeest	10	10	100	1
Gemsbok	10	10	100	1
Roan	8	8	100	1
Sub-total:	147	147	100	1
Age:				
Lion	39	34	87.18	1
Leopard	17	17	100	1
Cheetah	13	13	100	1
Sub-total	69	64	92.75	1
Sex:				
Lion	39	39	100	1
Leopard	17	16	94.12	1
Cheetah	13	12	92.23	0.9999
Sub-total	69	67	97.1	1
Individuals[2]				
Lion	12	11	91.67	0.9998
Leopard	17	16	94.12	1
Cheetah	3	3	100	1
Sub-total	32	30	93.75	1
Total	317	305	96.37	1

[1] Scientific names of herbivores: steenbok *Raphiceros campestris*; duiker *Sylvicapra grimmia*; kudu *Tragelaphus strepsiceros*; hartebeest *Alcelaphus buselaphus*; wildebeest *Connochaetes taurinus*; gemsbok *Oryx gazella*; roan *Hippotragus equinus*

[2] The possible number of individuals from which a choice could be made was impossible to determine. The study area was within an ecological unit where movements of animals were free and unrestricted. The number of known individuals that were likely to occur in the area of observation was estimated as the minimum number of possible choices for each observation. These were based:

Lion (X = 5.5, N = 12) = 6, 5, 5, 4, 5, 7, 4, 5, 3, 7, 2, 11

Leopard (X = 3.6, N = 17) = 3, 3, 4, 5, 4, 5, 3, 3, 2, 3, 5, 4, 5, 2, 3, 4, 4

Cheetah (X = 3.3, N = 3) = 3, 4, 3

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TABLE II

Measurements (cm) of the spoor of some large carnivore species in north-eastern Namibia. Width measured the widest point of the spoor. Length was the longest line, including claws when they were present. N = the number of different individual animals

Species	Age/sex		Front paw		Back paw	
			width	length	width	length
Lion	A ♀	mean	10.6	11.2	9.36	11.4
		S.D.	1.12	0.53	0.7	0.63
		S.E.	0.22	0.1	0.14	0.12
		N	26	26	26	26
	SA ♀	mean	10.5	11.8	8.73	11.6
		S.D.	0.23	0.37	0.17	0.64
		S.E	0.11	0.18	0.07	0.26
		N	4	4	6	6
	A ♂	mean	12.9	13.8	11.8	13.7
		S.D.	0.78	0.67	0.86	0.56
		S.E.	0.11	0.09	0.14	0.09
		N	49	49	40	40
	SA ♂	mean	11.6	12.9	10.4	12.6
		S.D.	0.36	0.51	0.59	0.56
		S.E.	0.14	0.19	0.26	0.25
		N	7	7	5	5
Spotted hyena		mean	8.8	10.8	7.5	9.7
		S.D	0.88	0.88	0.71	0.87
		S.E.	0.17	0.17	0.15	0.18
		N	28	28	23	23
Brown hyena		mean	8	10.2	5.9	8.4
		S.D.	0.46	0.69	0.36	0.4
		S.E	0.16	0.24	0.13	0.14
		N	8	8	8	8
Leopard		mean	7.2	7.8	6.7	8.3
		S.D.	1.09	1.72	1.17	0.9
		S.E.	0.45	0.7	0.42	0.32
		N	6	6	8	8

Note: A ♀ = adult female; SA ♀ = sub-adult female; A ♂ = adult male; SA ♂ = sub-adult male

Fig. 3.iii for example). The stride of lion A ($\bar{x} = 1.547$ m; S.D. = 0.026) was shorter than that of lion B ($\bar{x} = 1.706$ m; S.D. = 0.028). Lion A made longer paces ($t = 23.05$; $d.f. = 41$; $P < 0.001$) than lion B, although the straddle of lion A was shorter than that of lion B ($t = 14.1$; $d.f. = 41$; $P < 0.001$). However, the extent of individual variation in the measurements of the size and shape of spoor could not be determined statistically owing to variable soil conditions. Where sample sizes of spoor measurements were large ($n > 15$ per individual), the standard deviations (front paw, width: S.D. = 0.7, 0.82 and 0.79) and standard errors (respectively, S.E. = 0.2, 0.16 and 0.21) per individual were the same or larger than that of all the measurements of the species combined (Table II).

Interpretation of activities

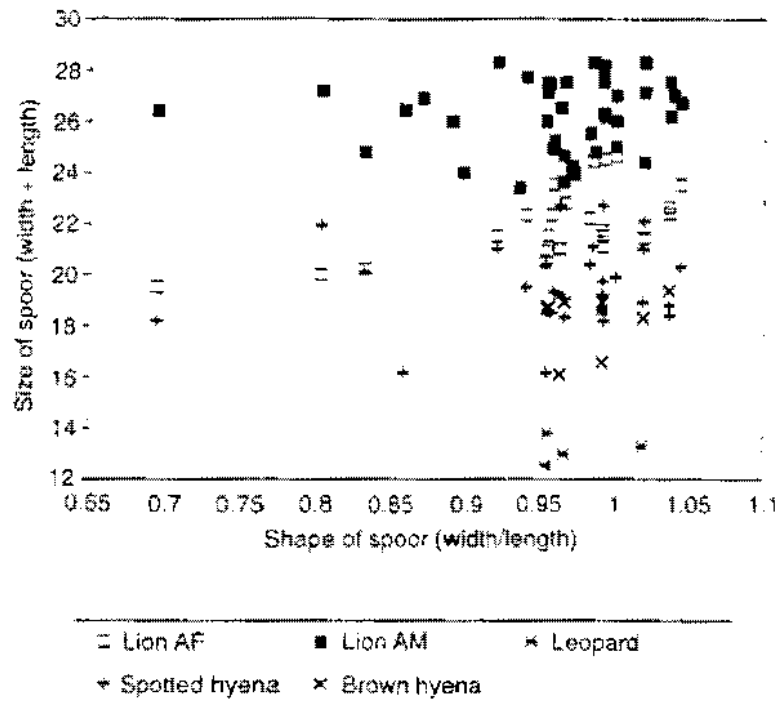Stride measurements were allocated to four categories: walking and stalking for both lions and

Fig. 2. A comparison between spoor measurements of spotted hyena, brown hyena, leopard, and lion; adult male (AM) and adult female (AF). Measurements (cm) are of the front paws of different individuals. The size of the spoor (width + length) is indicated on the x-axis, while the y-axis (width/length) depicts the shape of the spoor. For example, a symmetrical print will have a value of 1, whereas an elongated print will indicate less than 1.

leopards, trotting for leopards and galloping for lions. A schematic illustration of the average measurements of the gaits (Fig. 3) indicates the cues a tracker may use when interpreting the type of behaviour. Walking represents fairly even spacing between the feet. The distance of the left and right straddle for both leopards and lions is slightly shorter than the distance of the respective pace (Table III). During stalking, both animals take longer strides while the back foot is placed in the same position as the preceding front foot, hence perfect registration with the left and right pace mostly measures 0 cm. As a result the straddle distance increases markedly from that of the walk. Trotting leopards increase the pace distance but the straddle decreases dramatically. During this symmetrical gait with obliquely positioned feet, the two alternate limbs are off the ground at the same time (Hildebrand, 1968). The asymmetrical gait of the galloping lion displays the use of a rotary or lateral gallop (Muybridge, 1899). All four feet are off the ground at the same time and the lion leads with the left front leg.

The Ju/'Hoan team was consistent in correctly interpreting behavioural activities relating to large carnivores (Table IV). Through the inductive reasoning of systematic tracking, the team accurately reconstructed all the behavioural categories of both predator and prey during all the cases with which they were presented. These include interpretations such as deducting that carnivores scavenged a carcass rather than killed it, and identifying the number and species of other carnivores visiting carcasses. The trackers also correctly explained the cause of death of four ungulates that died of

TABLE III

The measurements (cm) of spacing distances between feet during different gaits for lions and leopards

Species	Gait		Stride	Straddle	Pace
Leopards	walking	mean	99.5	20.5	29.2
		S.D	3.7	3.3	4.1
		N	15	15	15
	stalking	mean	137.3	68.7	0
		S.D.	5.5	5.5	0
		N	7	7	7
	trotting	mean	158.5	4.7	74.5
		S.D.	3.4	4.2	3.6
		N	2	2	2
Lions	walking	mean	154.5	33.9	43.5
		S.D.	5.8	7.8	2.5
		N	4	4	4
	stalking	mean	116.5	58.2	0.1
		S.D.	8.7	8.6	0.3
		N	2	2	2
	gallop	mean	455.7	52.7/74.7	56.8/272.2
		S.D.	37.1	25.7/20.1	35.4/57.1
		N	1	1	1

Notes: A stride is the distance between two prints made by the same foot; a straddle is the distance between the left and right tracks either front or back, and a pace is the distance between the front and back foot either left or right (See Fig. 3)

In one record of a galloping lion, measurements of the straddle differed between left and right, as did the pace, between front and back. The data are shown, respectively. The left straddle during this asymmetrical gait is also known as a suspended motion (Hildebrand, 1965)

Standard deviation (S.D.) indicates the variation of the measurements and N equals the number of individual animals, where data for each individual were collected following the procedure described in Fig. 1

anthrax (*Bacillus anthracis*) and were consumed by carnivores. With the exception of estimating the time that the event took place, which was considered correct if it fell within four broad day-time categories (early morning; late morning; early afternoon; late afternoon) indicated by the position of the sun, and two night-time categories (first half and last half of the night), the reconstructions were flawless. During direct observations PS noted several points (such as those listed in Tables I and IV) which were crucial facts in summarizing an observed event. The Ju/'Hoan team correctly summarized all 30 spoor reconstructions.

Discussion

In a test for reliability and accuracy, the Ju/'Hoan team showed remarkable skill in correctly interpreting 557 (97.9 %) of the 569 cases they were presented with, an accuracy level with a S.E. of only 0.17 % of the mean. The identification, from spoor, of age and sex, known individual animals, and estimation of the time that an event occurred were sometimes inaccurate. These incorrect interpretations, however, were trivial and did not statistically influence the results.
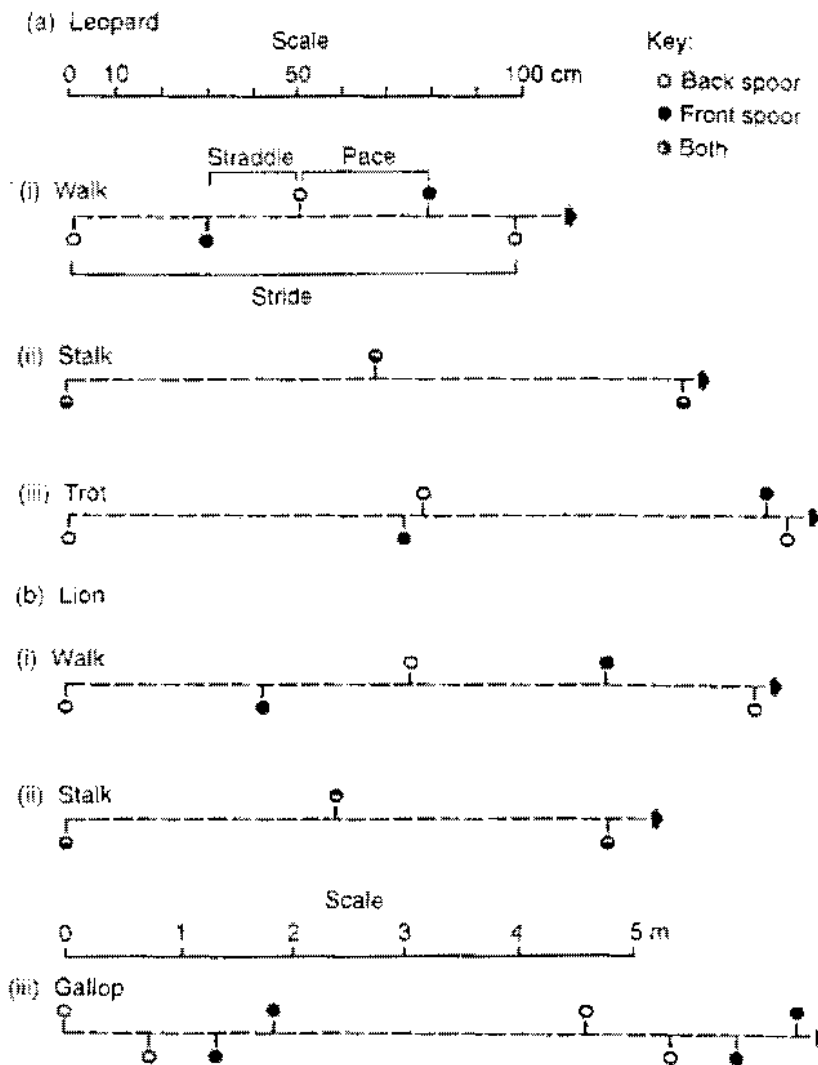
(a) Leopard

Scale

0   10   50   100 cm

Key:
○ Back spoor
● Front spoor
◍ Both

(i) Walk

Straddle   Pace

Stride

(ii) Stalk

(iii) Trot

(b) Lion

(i) Walk

(ii) Stalk

Scale

0   1   2   3   4   5 m

(iii) Gallop

Fig. 3. A schematic illustration of the biomotric patterns of four activities. (a) Walking, stalking and trotting by leopards and (b) walking, stalking and galloping by lions. Back feet are indicated by open circles and front feet by closed circles. When the back foot is super-imposed on the spoor of the front foot, the point is indicated by a half closed circle. Direction of movement is from left to right, as indicated by the arrow, with the left and right feet placed on their respective sides of an imaginary central line. A stride (a) is the distance between two spoor made by the same foot; a pace is the distance between the front and back feet either left or right; and a straddle, the distance between the left and right tracks.

The following anecdotal account may further illustrate our experiments.

An adult zebra (*Equus burchelli*) was observed dying of anthrax, blood samples were taken and the cause of mortality confirmed. Over the following two days a pride of lions fed on the carcass, followed by several spotted hyenas and vultures, leaving only skin and bones. The Ju/'Hoan team was taken to the spot three days after the death and asked to reconstruct the sequence of events related to the

TABLE IV

The probability of correct interpretation of various activities of some large carnivores and their prey during hunts. All observations of large carnivores (consisting of cheetahs, lions and leopards) were combined. See Table I for P value description

Activity	Cases presented	Correct interpretation	% correct	P value
Carnivore:				
Lying	14	14	100	1
Walking	15	15	100	1
Stalking	9	9	100	1
Crouching	9	9	100	1
Running	18	18	100	1
Capture prey	5	5	100	1
Kill prey	9	9	100	1
Drag carcass	16	16	100	1
Feeding	15	15	100	1
Sub-total	110	110	100	1
Prey:				
Species	16	16	100	1
Age & sex	8	8	100	1
Number	4	4	100	1
Position[1]	7	7	100	1
Walking	11	11	100	1
Running	11	11	100	1
Sub-total	57	57	100	1
General:				
Scavenging[2]	12	12	100	1
Other carnivores[3]	16	16	100	1
Disease death[4]	4	4	100	1
Time of event[5]	23	20	86.93	1
Summary of event[6]	30	30	100	1
Sub-total	85	82	96.47	1
Total	252	249	98.81	1

[1]Position: the position of the prey in relation to the predator and terrain
[2]Scavenging: carnivores acquired a carcass through scavenging and did not capture or kill the prey
[3]Other carnivores: the presence of other large and small carnivores at a carcass, either before, during, or after the carnivore observed was feeding
[4]Disease death: an ungulate that died of anthrax and was then consumed by one or several species of carnivore
[5]Time of event: the estimated time that an event took place
[6]Summary of event: the ability of the Ju/'Hoan team to provide a correct summary of a behavioural event

carcass. After approximately two hours of investigation the team started the reconstruction several hundred metres from the spot, pointing at a set of zebra tracks explaining that the spoor was made by the dying animal. They followed the spoor indicating how the animal had walked unsteadily, where it had fallen, got up, and continued walking towards the point where it had expired. The Ju/'Hoan team, not familiar with anthrax, explained that the animal was sick and died. They deduced that lions were present and fed on the zebra but did not kill it. They also commented that spotted hyenas and vultures attended the carcass in that order. The team's estimate of the time of the event was also correct.

An attempt was also made to measure and quantify the different aspects of tracking in order to understand the techniques and skills employed by the Ju/'Hoan. This was done in two phases.

Irregularity in soil types led to considerable variation in the spoor measurement of individual animals, yet the trackers were not only capable of recognizing such variations, but also appeared to allow for them during interpretations of spoor. The team explained that they recognize different individuals by idiosyncratic variation in the size and shape of spoor. The coarseness of spoor measurements does not allow for such subtle distinctions. Smallwood & Fitzhugh (1993) showed statistical differences in spoor shape and size of individual cougars (*Felis concolor*) but cautioned against the effects of substratum variations. Individual variation of spoor size, for example, forms the basis of census techniques of tigers (*Panthera tigris*) in India (Choudhury, 1971; Panwar, 1979; Sagar & Singh, 1990). However, the extent of soil and terrain bias in measuring spoor does not appear to be considered by these authors, and therefore may seriously affect the credibility of their technique.

In the second phase, the measurement of the spacing distances between feet during different gaits gives the reader an appreciation of the distinction between those gaits, as viewed by a tracker. Proportionate stride, straddle, and pace lengths within each gait are functions of speed and individual variation (Hildebrand, 1959, 1961). This complicates statistical comparisons between different individuals when the exact speed of locomotion is not known. Only under controlled conditions can the true extent of individual variation be determined. The Ju/'Hoan team, however, maintains that each individual animal has a particular way of walking, regardless of the speed of locomotion. Among humans an idiosyncratic walking style is a common phenomenon and one may recognize an acquaintance simply from such characteristics. This phenomenon was measured once during the present study when the stride, straddle and pace lengths of two male lions showed significant statistical variation.

Tracking has a major advantage in this regard as spoor can be followed in most habitats, and a day or two after the event, therefore being completely non-intrusive (Bothma & Le Riche, 1993). Given the accuracy of tracking presented here, we have employed this technique by assessing the hunting behaviour of lions and leopards in the woodland habitat of Kaudom Game Reserve and Bushmanland, Namibia (Stander et al., 1997). Such data have not been collected previously.

In Africa, western scientists have been conducting ecological and conservation studies for several decades. Such studies often occur in areas inhabited by people partly or fully involved in subsistence hunting, with either traditional or modern equipment. The skills and knowledge of local peoples, especially in southern Africa, are often ignored in a scientifically sound but culturally chauvinistic approach (Carruthers, 1993). Local people have generally seldom been involved, and when included in such programmes, relegated to restricted roles of general labourer or 'native rangers' (Carruthers, 1993). The need to involve local communities in biological conservation, in order to ensure the long-term conservation of natural resources, has been stressed frequently (Eltringham, 1984; Martin, 1984; Owen-Smith & Jacobsohn, 1989; Stander, 1993).

Local African communities, such as the Ju/'Hoan, have an understanding and knowledge of their natural environment, the extent of which has not yet been identified or documented. Indigenous people with very little or no formal education may have a perception of their natural environment that is not necessarily unscientific. In fact, such perception may well be based on scientifically sound thought processes (as perhaps is the case with the Ju/'Hoan). Collaboration with local communities in wildlife-related studies has become imperative and may uncover the potential contribution which local knowledge can make towards a study. Wildlife ecology and conservation studies may benefit greatly from the collaboration of skills from western science and traditional knowledge. Furthermore, successful wildlife conservation depends largely on involving and incorporating the aspirations of the local inhabitants.

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