

RESEARCH ARTICLES

Comparing Measures of Travel Distances in Primates: Methodological Considerations and Socioecological Implications

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Travel costs can influence numerous aspects of the lives of primates, including net energy balance (and therefore reproductive success of females) and maximum group size. Despite their potential impact, there has been no systematic comparison of different measures of travel distance. We compared three measures of travel distance in 30 min (actual distance of individuals, straight-line distance of individuals, and straight-line distance of groups) and their ratios in a small group and a large group of vervet monkeys (*Cercopithecus aethiops*) and between the large group of vervets and a group of patas monkeys (*Erythrocebus patas*) of roughly similar size. The large group of vervets traveled farther than the small group regardless of the measure used, but the ratios of the different measures were not significantly different between those groups. Patas monkeys traveled significantly farther than the large group of vervets regardless of the measure used. In both vervets and patas, straight-line distances of individuals (ISLD) and groups (GSLD) underestimated actual distances traveled by individuals (IAD), but the degree to which they did so differed between species. IAD is more accurate than the other two measures and is preferred for studies of energetics and individual reproductive success, although ISLD or GSLD may be substituted when the ratios of IAD/ISLD or IAD/GSLD do not differ between groups or species. The ratio of IAD/ISLD was larger in vervets than in patas, suggesting that individual vervets meander more over short periods of time than patas. The ratio of ISLD/GSLD was larger in patas than in vervets, suggesting that patas move at angles or across the group's center-of-mass whereas vervets move more consistently along with others in their group. This has implications for the formation of spatial subgroups and alliances within groups. *Am. J. Primatol.* 48:87–98, 1999. © 1999 Wiley-Liss, Inc.

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INTRODUCTION

It is becoming increasingly evident that the cost of travel is an important selective pressure impinging on lifetime reproductive success of primates through its influence on net energy balance and limits to group size. For example, baboons (*Papio cynocephalus*) that fed primarily on artificially high densities of foods (garbage dumps) were heavier than free-ranging baboons that fed on naturally occurring foods [Altmann et al., 1993]. Examination of their activity budgets and diets indicated that the heavier baboons gained their greater weight by reducing travel distance rather than by increasing food intake [Altmann & Muruthi, 1988; Muruthi et al., 1991]. Free-ranging female vervets (*Cercopithecus aethiops*) that are better fed are often younger when they have their first offspring and have shorter interbirth intervals than females that are less well-fed [Whitten, 1983; Cheney et al., 1988]. If reproductive success of females is indeed limited by access to foods, a more positive net energy balance should lead to greater lifetime reproductive success, up to a point. For species in which females typically remain in their natal groups and for which travel costs increase with group size, e.g., baboons, macaques (*Macaca* spp.), and vervets [Isbell, 1991; Wrangham et al., 1993; Janson & Goldsmith, 1995; Isbell et al., 1998], successful reproduction may lead eventually to poorer reproductive success as maturing offspring increase group size, thus increasing travel costs for individuals within groups. Limits to group size in such species appear to occur at a point at which energy output (travel costs) exceeds tolerable levels relative to energy intake for all group members [Wrangham et al., 1993; Chapman et al., 1995; Janson and Goldsmith, 1995].

Travel costs have usually been inferred from the distances individuals or groups move. Distances of individuals per unit time (often a 12 h day) have been measured by pacing the route of individual animals [e.g., Watts, 1991; Yamagiwa & Mwanza, 1994] or by estimating their distances with meter tape, by animal pace number and length, or by eye [e.g., Stacey, 1986; Altmann & Muruthi, 1988; Isbell et al., 1998]. Measuring or estimating the route of individuals has been done for some of the more terrestrial animals such as gorillas (*Gorilla gorilla*) or baboons. Distances of groups per unit time have typically been measured by plotting onto maps the center-of-mass of a group at timed intervals as the group moves through its environment and then calculating the distance as the summation of the most direct path between successive chronological points [e.g., Altmann & Altmann, 1970; Struhsaker 1975; Isbell, 1983; Bennett, 1986; Cords, 1987; Butynski, 1990; Olupot et al., 1994; Ostro et al., 1998]. This is commonly referred to as the straight-line distance (SLD) of the group. Group estimates of travel distances have been employed more often than individual estimates for arboreal animals (although there is no a priori reason why estimates of individual distances of arboreal animals cannot be obtained).

Although Altmann [1987] suggested that SLD estimates may underestimate actual distances by individuals by up to a factor of three or more, a comparison of the results of the different methods has not previously been published. In this paper, we first compare SLD of individuals and their groups with actual distances moved by those individuals (IAD) within a large and a small group of vervets, a species in which group size is known to affect travel distances of individuals [Isbell et al., 1998], to determine if differences in IAD are reflected by similar differences in SLD. We then compare the same between vervets and patas monkeys (*Erythrocebus patas*), two phylogenetically closely related species that are known to have different ways of moving through their environments

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[Hall, 1965], to examine whether species differences in IAD are also apparent in SLD. Finally, we compare the ratios of the three measures to examine the extent to which straight-line distances of individuals (ISLD) and groups (GSLD) underestimate (IAD) and explore the descriptive value of the ratios in furthering our understanding of movements of individuals relative to their groups. We use IAD as the baseline measure for comparison with the other two measures because, unlike SLD, IAD includes circuitous movements over short periods of time and therefore reflects more accurately travel costs to the individual [Altmann, 1987], the unit upon which natural selection acts.

METHODS

Study Site and Species

The study was conducted on Segera Ranch (36°50'E, 0°15'N) on the Laikipia Plateau of north-central Kenya. The Laikipia Plateau is a semi-arid ecosystem, with mean annual rainfall at the study area of approximately 600–700 mm but with considerable yearly variation. Segera Ranch is a working cattle ranch and conservation area with most of its natural mammalian biodiversity still intact. Two habitat types occur in the study area. *Acacia xanthophloea*-dominated woodlands along rivers and streams also support a dense woody shrub layer (*Carissa edulis*, *Euclea divinorum*). *Acacia drepanolobium*-dominated woodlands away from rivers and streams on vertisolic (black cotton) soils of impeded drainage [Ahn & Geiger, 1987] support a dense understory of grasses, primarily by *Pennisetum mezianum*, *P. stramineum*, and *Themeda triandra* [Young et al., 1997, 1998].

Comparative data on total distances of individuals, straight-line distances of individuals, and straight-line distances of groups were collected from May to December 1994, excluding July 1994, on one small and one large group of vervets living in adjacent home ranges ($n = 7-9$ and $26-28$) and one group of patas living about 4 km from the vervets ($n = 45$). All individuals were habituated to the presence of observers. All vervets were identified individually by natural markings and characteristics. All adult female patas were identified initially with Nyanzol-D dye (Belmar, Inc., North Andover, MA) sprayed on their pelage with a SuperSoaker 300 water gun (Larami Corp.) and then later identified by natural markings and characteristics. The two vervet groups live in adjacent home ranges along the Mutara River and sleep and forage in *A. xanthophloea* habitat, but also forage in adjacent *A. drepanolobium* habitat. The patas group is restricted to *A. drepanolobium* habitat.

Data Collection

Data were collected by B.M.N. on the movements of groups. Data were collected by J.D.P. on the movements of all ten adult females in the two groups of vervets ($n = 2$ and 8) and all 14 adult females in one group of patas (8–13 adult females in any 1 month; monthly sample sizes varied mainly because of difficulty in locating particular individuals). Each group was systematically observed 4 days each month. During each of the 4 days, an adult female was sampled for 30 min beginning at the top of the hr. With vervets, the order of sampling was predetermined to allow each female to be sampled once in the morning or once in the afternoon. This order was different each sampling day within each month so that each female was sampled evenly between morning (0800–1200 hr) and afternoon blocks (1200–1600 hr) during each month. With patas, a similar predetermined order of sampling had to be abandoned because individuals were difficult

to locate in time to sample on the hr. Adult females were instead sampled opportunistically on the hour and were sampled for 30 min without replacement in the morning or in the afternoon.

The Measures

Actual distance of individuals (IAD). During each focal sample, the observer estimated by eye the distance of the focal individual when it moved, where a move was defined as any locomotion involving the hindlimbs. When individuals moved out of sight, their time out of sight was recorded, and their minimum travel distance was estimated based on where they disappeared and where they reappeared.

Straight-line distances of individuals (ISLD). Straight-line distances of individuals were determined by estimating by eye the distance between a flag placed where the focal animal was located at the beginning of the focal sample and her location at the end of the sample.

Straight-line distances of groups (GSLD). The group's straight-line distance was determined by measuring the distance between a flag placed at the group's center-of-mass at the beginning and at the end of the 30 min sample. The group's center-of-mass was estimated by eye after locating all group members that could be seen within a reasonable amount of time. The shortest distance between the flags was measured initially by meter tape and, later in the study, by paces of known average distance (one pace = 1 m).

The accuracy of the observers in estimating variable distances was examined each month at the research camp by estimating distances between flags set up by another person (monthly $n = 40\text{--}80$). Estimates of distances were found to be within 5% of true distances in each month.

Statistical Analyses

All data were entered into Microsoft Excel and imported into JMP (SAS Institute, Cary, SC) for statistical analyses. Regression analyses were conducted on data lumped by group. All other analyses were conducted on means taken from individual adult females within each group. The following means were calculated for each female: 1) her actual distance traveled in 30 min, including minimum distances moved while out of sight (IAD); 2) her straight-line distance over the same time period (ISLD); 3) the group's straight-line distance over the same time period covered by the focal sample (GSLD); 4) actual individual distance relative to the straight-line distance of that individual (IAD/ISLD); 5) actual individual distance relative to the straight-line distance of the group (IAD/GSLD); and 6) straight-line distance of the individual relative to the straight-line distance of its group (ISLD/GSLD). The latter three measures are not directly inferable from the first three because the ratio of two means is not the same as the mean of the ratios [Templeton & Lawlor, 1981]. Data were log-transformed to normalize distributions when necessary. The distributions of the three measures had no obvious outliers and were normally distributed, as were means across females. When values were made into ratios, however, nine (4 from patas monkeys and 5 from vervets, involving 7 out of 21 females) were 10–30 standard deviations above the means. These extreme outliers were considered, therefore, to be likely errors in estimating or recording one of the three distances and were excluded from analyses. Also excluded from analyses were individuals (three patas) with five or fewer data points [see Isbell & Young, 1993]. Resultant sample sizes

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ranged from 13–23 for individual vervets (small group's overall $n = 44$; large group's overall $n = 144$) and 7–19 for individual patas (group's overall $n = 133$). Type I ANOVAs compared the large and small vervet groups, and the patas group and large vervet group. Tests were two-tailed. The smaller vervet group was excluded from interspecific analyses because group size is known to affect travel distance in vervets [Isbell et al., 1998].

RESULTS

Travel Distances Relative to Group Size and Species

Mean IAD was 67.6 m (± 0.5 m SE) per 30 min among adult females in the small group of vervets, 107.6 m (± 8.2) per 30 min among adult females in the large group of vervets, and 218.8 m (± 8.0) per 30 min among adult females in the group of patas monkeys (Fig. 1; Table I). For the same sample period per female, mean ISLD was 34.1 m (± 2.7) in the small group of vervets, 65.8 m (± 6.2) in the large group of vervets, and 168.0 m (± 5.4) in the patas group (Fig. 1; Table I). Mean GSLD was 46.6 m (± 4.1) in the small vervet group, 74.2 m (± 5.4) in the large vervet group, and 144.9 m (± 11.7) in the patas group (Fig. 1; Table I).

Actual distances of individuals in the large vervet group were expected to be greater than actual distances of individuals in the small vervet group despite the apparently higher-quality habitat of the large group [see Isbell et al., 1998], and indeed, they were ($F = 5.3$, $df = 8$, $P = 0.05$; Table I). Straight-line distances, both of individuals and of the group, mirrored this difference (ISLD: $F = 5.9$, $P = 0.04$; GSLD: $F = 5.9$, $P = 0.04$; Fig. 1; Table I). Actual distances of individual patas monkeys were also expected to be greater than actual distances of individual

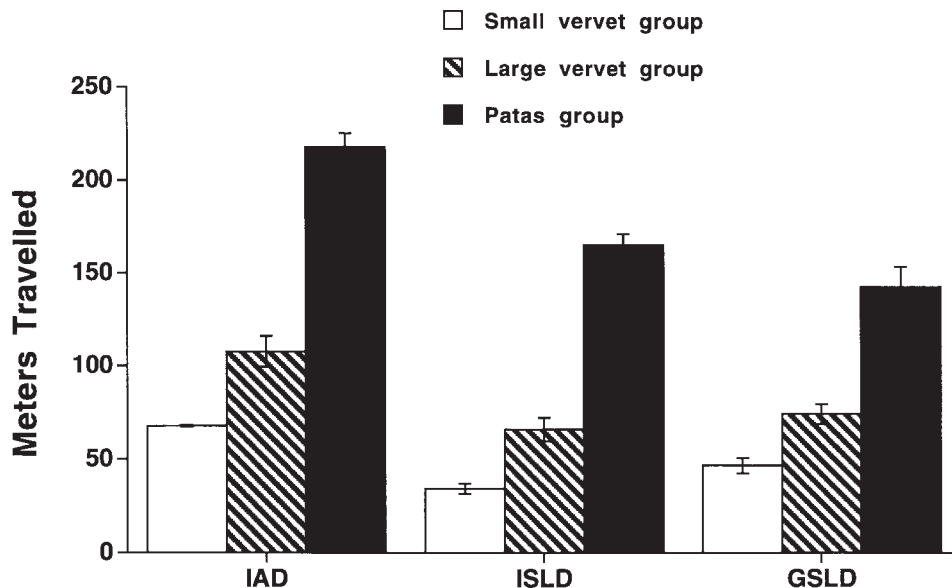


Fig. 1. Differences between small and large vervet groups and between vervets and patas in estimates of travel distance. IAD, actual distance travelled by individuals within groups; ISLD, straight-line distances of individuals within groups; GSLD, straight-line distances of the groups. Individuals in the large vervet group travelled significantly farther than individuals in the small vervet group in all three measures (all: $P \leq 0.05$), and individuals in the patas group travelled significantly farther than individuals in the large vervet group (all: $P \leq 0.0002$).

TABLE I. Summary of Distances Measured Over 30 min Periods and Their Ratios in Vervets and Patas Monkeys

	Vervets		Patas monkeys
	Small group	Large group	
Actual distance of individuals (IAD)	67.6 m \pm 0.5*	107.6 m \pm 8.2	218.8 m \pm 8.0**
Straight-line distance of individuals (ISLD)	34.1 m \pm 2.7*	65.8 m \pm 6.2	168.0 m \pm 5.4**
Straight-line distance of groups (GSLD)	46.6 m \pm 4.1*	74.2 m \pm 5.4	144.9 m \pm 11.7**
IAD/ISLD	2.94 \pm 0.28	2.35 \pm 0.24	1.51 \pm 0.07**
IAD/GSLD	2.79 \pm 0.32	2.14 \pm 0.26	2.50 \pm 0.63
ISLD/GSLD	0.92 \pm 0.05	1.09 \pm 0.13	1.66 \pm 0.38**

*Comparison between small and large group of vervets, $P \leq 0.05$.

**Comparison between large group of vervets and group of patas monkeys, $P < 0.01$.

vervets [see Isbell et al., 1998]; IAD of patas monkeys was more than twice as great as that of vervets ($F = 94.4$, $df = 18$, $P < 0.0001$; Table I). The greater travel distance of patas monkeys is reflected also in both measures of SLD (ISLD: $F = 127.1$, $P < 0.0001$; GSLD: $F = 22.6$, $P < 0.0002$; Table I).

ISLD and GSLD as Estimators of IAD

In both vervet groups, ISLD and GSLD underestimated IAD by more than a factor of two (\bar{x} of IAD/ISLD: large group, 2.35 ± 0.24 ; small group, 2.94 ± 0.28 ; \bar{x} of IAD/GSLD: large group, 2.14 ± 0.26 ; small group, 2.79 ± 0.32 ; Fig. 2; Table I). On the other hand, ISLD was nearly similar to GSLD (\bar{x} : large group, 1.09 ± 0.13 ; small group, 0.92 ± 0.05 ; Fig. 2; Table I). Regression analyses indicated that both ISLD and GSLD were positively correlated with IAD, although ISLD was a stronger correlate of IAD than was GSLD for both groups (large group, ISLD: $r^2 = 0.64$, $n = 142$, P

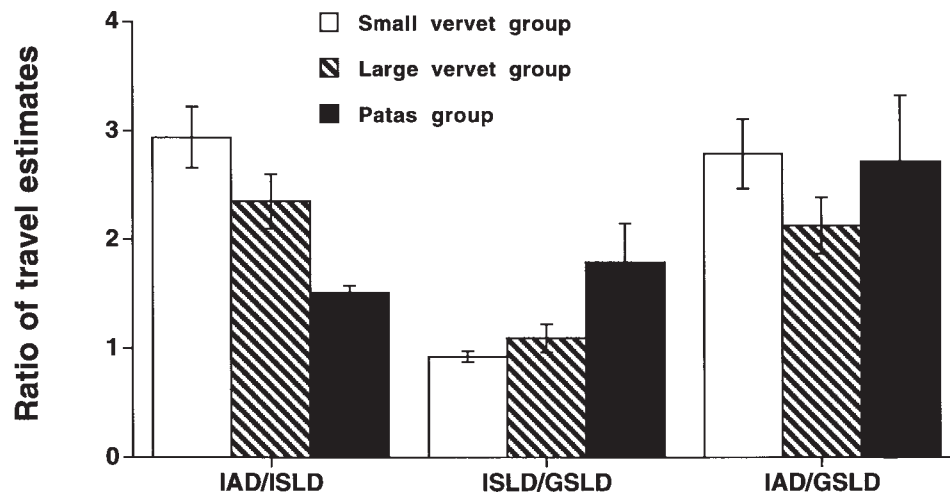


Fig. 2. Differences between small and large vervet groups and between vervets and patas in ratios of individual actual distance to individual straight-line distance (IAD/ISLD), and individual straight-line distance to group straight-line distance (ISLD/GSLD), and individual actual distance to group straight-line distance (IAD/GSLD). None of the ratios was significantly different between vervet groups (all: $P > 0.20$); IAD/ISLD was significantly greater in the large vervet group compared to the patas group ($P = 0.0009$), whereas ISLD/GSLD was significantly greater in the patas group compared to the large vervet group ($P = 0.008$).

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< 0.0001; GSLD: $r^2 = 0.23$, $n = 139$, $P < 0.0001$; small group, ISLD: $r^2 = 0.46$, $n = 44$, $P < 0.0001$; GSLD: $r^2 = 0.22$, $n = 40$, $P = 0.002$).

Among patas monkeys, GSLD also underestimated IAD by more than a factor of two (\bar{x} : 2.50 ± 0.63). In contrast, ISLD underestimated IAD, and GSLD underestimated ISLD, by only approximately 50% (\bar{x} of IAD/ISLD: 1.51 ± 0.07 ; \bar{x} of ISLD/GSLD: 1.66 ± 0.38 ; Fig. 2). As for vervets, although both ISLD and GSLD were positively correlated with IAD, ISLD was the stronger correlate of IAD (ISLD: $r^2 = 0.65$, $n = 142$, $P < 0.0001$; GSLD: $r^2 = 0.22$, $n = 117$, $P < 0.0001$).

The fact that ISLD and GSLD are positively correlated with IAD and have very small P values does not mean, however, that either can simply be substituted for IAD by using fitted regression lines. The confidence limits on estimating a given IAD from a given ISLD or GSLD are surprisingly broad for even relatively high r^2 values. The 95% confidence limits on the IAD for a given ISLD or GSLD in our data set were often greater than half of the mean value of the predicted IAD itself. However, across multiple individual estimates, the confidence intervals on the regression coefficients are much smaller. Thus, the significant differences between groups and species in mean ISLD and GSLD also differ in the harder-to-measure IAD, and by a similar magnitude (but see Discussion).

Ratios as Indicators of Individual Movements Relative to the Group

None of the three ratios was significantly different between vervet groups (all F values < 1.4, all P values > 0.20; Fig. 2; Table I), suggesting that vervets in the two groups moved similarly relative to others in their groups despite the difference in group size and despite differences in average distance traveled.

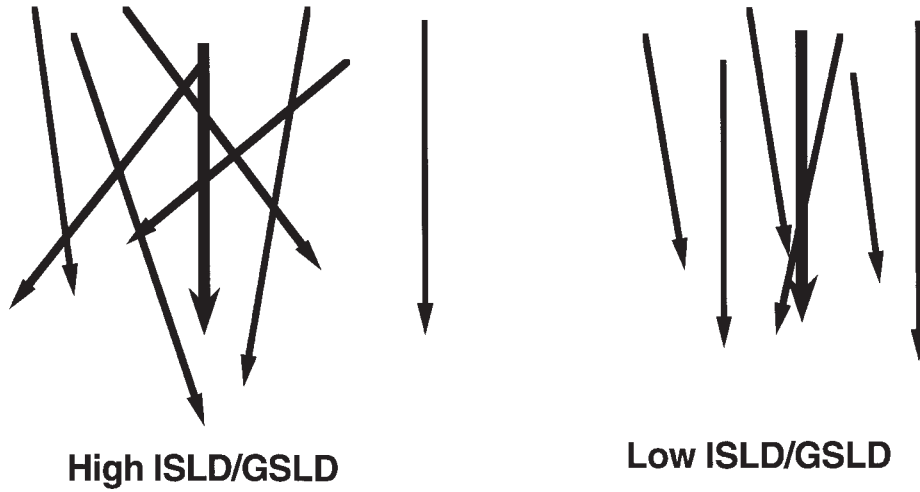
Between vervets and patas monkeys, IAD/GSLD was not significantly different (log-transformed: $F = 1.8$, $P = 0.20$) whereas ISLD underestimated IAD significantly less; ($F = 15.7$, $P = 0.0009$), and GSLD underestimated ISLD significantly more, in patas than in vervets (log-transformed: $F = 8.8$, $P = 0.008$; Fig. 2). The lower IAD/ISLD of patas monkeys suggests that they move in a more directed manner than vervets, at least over short time periods (Fig. 3a). The higher ISLD/GSLD of patas monkeys suggests that individual patas monkeys move laterally or at angles across the center-of-mass of the group (Fig. 3b). Vervets, on the other hand, had a ISLD/GSLD close to parity, suggesting that they move more in association with each other rather than laterally or at angles to the group's center-of-mass (Fig. 3b). Individual patas monkeys did not differ significantly in either IAD or ISLD (both: $F < 1.2$, $P > 0.30$) but did differ significantly in all three ratios (IAD/GSLD, log-transformed: $F = 3.82$, $P = 0.0002$; ISLD/GSLD, log-transformed: $F = 2.75$, $P = 0.005$; ISLD/GSLD: $F = 6.25$, $P < 0.0001$), whereas there were no statistically significant differences between individuals in the large vervet group in either IAD or ISLD or the three ratios (all F values ≤ 1.8 , all P values ≥ 0.09). This provides further evidence that individual patas monkeys move relatively independently of other members of their group whereas vervets move less independently of other group members.

DISCUSSION

Straight-Line Distances as Substitutes for Actual Distances of Individuals

Mean actual distance of individuals was longer than their own mean straight-line distance and that of their groups in all three groups of primates, underscoring the greater accuracy of IAD in measuring travel costs. For studies of energetics

a



b

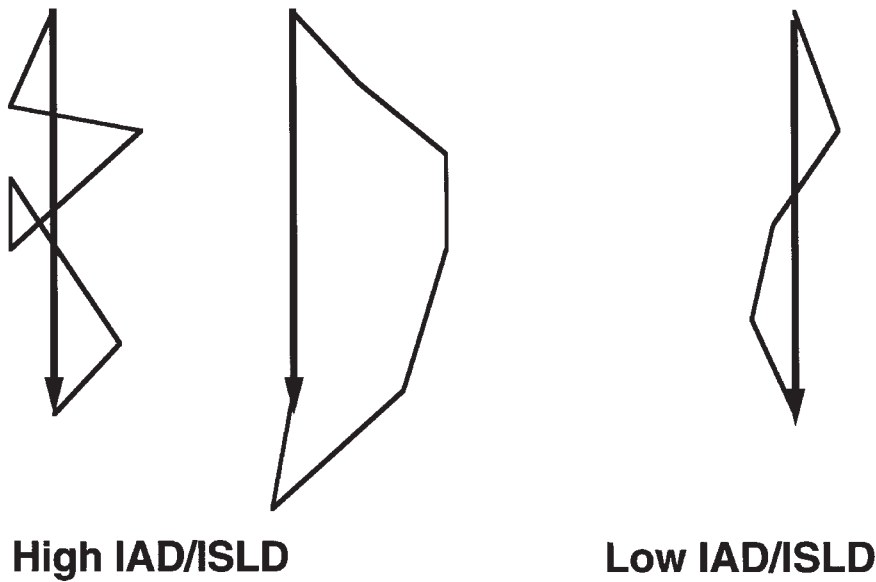


Fig. 3. Schematic of movement patterns that could affect values of (a) IAD/ISLD and (b) ISLD/GSLD. Thickest lines represent group straight-line distances, intermediate lines represent individual straight-line distances, and thinnest lines represent individual actual distances.

and individual reproductive success, the best measure is IAD because it most accurately reflects the energetic output of the individual. IAD is more time-intensive to measure than SLD, however, because estimating actual distances of individuals requires continuous sampling, whereas estimating SLD requires only point sampling. When making broad-scale comparisons, the use of the less time-intensive distance measures (ISLD and GSLD) can be appropriate for energetic

comparisons when the ratios of these measures to IAD are independent of variation in the trait being considered. In our data set, this means that differences in mean ISLD and GSLD between groups are likely to represent similar differences in mean IAD because the ratios of IAD/ISLD and IAD/GSLD were independent of group size. Similarly, mean GSLD is likely to represent a similar difference in mean IAD between species because IAD/GSLD was independent of species. However, because variation in IAD/ISLD was significantly different between species, ISLD would not be a valid proxy for IAD in interspecific comparisons.

The Ratios as Tools for Describing Movements of Individuals Relative to Their Groups

A promising descriptive tool for studies of movements of individuals in relation to their groups is the use of the ratios of the different measures, in which case data on all three distance estimates are required. These ratios have the value of being directly comparable both within and between species. The ratio of actual distances of individuals to straight-line distances of individuals (IAD/ISLD) can be interpreted as a measure of the directedness of individuals as they move during the sampling period. This directed movement is akin to the “self-avoiding walks” and “non-reversing walks” modeled by Hayes [1998]. As ratios deviate farther from 1.0, individuals meander more. Similarly, the ratio of straight-line distances of individuals to straight-line distances of groups (ISLD/GSLD) can be interpreted as a measure of the consistency by which individuals move relative to other group members. As ratios deviate farther from 1.0, individuals become more independent in their movements relative to particular neighbors.

Among vervets, although group size was positively related to overall distances of individuals and groups, the ratios of the different measures did not differ significantly between large and small groups. This is intriguing because it implies that although individuals respond to differences in habitat and to group dynamics by quantitatively adjusting their travel distances, their movements are qualitatively similar regardless of habitat quality or group size. This consistency may contribute to our perception of a gestalt for the behavior of a given species across habitats and group sizes.

The differences between vervets and patas monkeys in these ratios suggest that individual patas monkeys move in a more directed manner than vervets over short periods of time. This contrasts with the subjective impression by numerous fieldworkers that patas travel more circuitously than vervets [see Hall, 1965], and less predictably. It may be, however, that patas travel more circuitously than vervets over longer time periods (e.g., several hours). This subjective impression may also be reconciled by the fact that individual patas monkeys move more independently of their group than do vervets, which can give the appearance of more circuitous travel. Patas monkey groups typically have wide group spreads [often 300–500 m wide; Chism & Rowell, 1988], allowing individuals to have a longer SLD than the group while still remaining with the group. Vervets, on the other hand, have smaller group spreads (typically 50–100 m; LAI, unpub. data), and it would be difficult for individual vervets to travel at angles to the center-of-mass of the group and still remain with the group.

The difference between patas monkeys and vervets in the degree of independence of individual monkeys in their movements relative to their groups has implications for the expression of social relationships. The movements of individual vervets should facilitate the formation of spatial subgroups (e.g., relatives who could provide coalitionary support if necessary) or reflect their existence

within groups to a greater extent than the movements of patas. If ISLD/GSLD is a measure of the consistency by which individuals move relative to other group members, assuming that consistent spatial proximity is required for the formation of alliances, one might expect the ratio to deviate less from 1.0 for populations in which females frequently form alliances relative to species that seldom form alliances. The proportion of agonistic interactions that involved coalitions was indeed greater in this population of vervets (5.8% of 138 agonistic interactions) than in patas (1.0%; $n = 209$) [J. Pruettz, unpublished data; see also Struhsaker, 1967; Cheney, 1983], and as predicted, vervets deviated less from unity in ISLD/GSLD than patas (1.09 vs. 1.66). The possibility of an association between coalitionary support and movements of individuals relative to their groups is worthy of further study to determine causality, i.e., whether the movements of individuals determine the potential for alliance formation or whether the need for alliances constrains movements of individuals within their group.

CONCLUSIONS

1. A comparison of three measures of travel distance (individual total distance, straight-line distance of individuals, and straight-line distance of groups) and their ratios in vervets revealed that individuals in the large group traveled farther than those in the small group regardless of the measure. The ratios of these measures were not, however, statistically different between the two groups.

2. A comparison of the same measures in the large group of vervets and a group of patas monkeys showed that patas traveled farther than vervets regardless of the measure. These species also differed in their ratios of distance measures. Vervets had a greater ratio of individual actual distance to individual straight-line distance than patas, suggesting that vervets meander more over short time periods. In contrast, patas had a greater ratio of individual straight-line distance to group straight-line distance than vervets. Patas monkeys can move twice as far as the group as a whole and still remain with the group because group spread is large and relative position within the group is fluid.

3. All three measures have their advantages, and the appropriate one to use depends most on the research question. Ratios of the three measures can be useful in describing movements of individuals relative to their groups.

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REFERENCES

- Ahn PM, Geiger LC. 1987. Kenya soil survey: soils of Laikipia District. Kabete, Kenya, Ministry of Agriculture, National Agricultural Laboratories.
- Altmann SA. 1987. The impact of locomotor energetics on mammalian foraging. *J Zool Lond* 211:215–225.
- Altmann SA, Altmann J. 1970. Baboon ecology: African field research. Chicago: University of Chicago Press.
- Altmann J, Schoeller D, Altmann SA, Muruthi P, Sapolsky RM. 1993. Body size and fatness in free-living baboons reflect food availability and activity levels. *Am J Primatol* 30:149–161.
- Altmann J, Muruthi P. 1988. Differences in daily life between semi-provisioned and wild-feeding baboons. *Am J Primatol* 15: 213–221.
- Bennett EL. 1986. Environmental correlates of ranging behaviour in the banded langur, *Presbytis melalophos*. *Folia Primatol* 47:26–38.
- Butynski TM. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol Monog* 60:1–26.
- Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: an analysis of spider monkeys and chimpanzee subgroups. *Behav Ecol Sociobiol* 36:59–70.
- Cheney DL. 1983. Extrafamilial alliances among vervet monkeys. In: Hinde RA, editor. *Primate social relationships: an integrated approach*. Oxford: Blackwell. p 278–286.
- Cheney DL, Seyfarth RM, Andelman SJ, Lee PC. 1988. Reproductive success in vervet monkeys. In: Clutton-Brock TH, editor. *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press. p 384–402.
- Chism J, Rowell TE. 1988. The natural history of patas monkeys. In: Gautier-Hion A, Bourliere F, Gautier J-P, Kingdon J, editors. *A primate radiation: evolutionary biology of the African guenons*. New York: Cambridge University Press. p 412–438.
- Cords M. 1987. Mixed-species association of *Cercopithecus* monkeys in the Kakamega Forest, Kenya. Berkeley: University of California Press.
- Hall KRL. 1965. Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. *J Zool Lond* 148:15–87.
- Hayes B. 1998. How to avoid yourself. *Sci Am* 86:314–319.
- Isbell LA. 1983. Daily ranging behavior of red colobus monkeys (*Colobus badius tephrosceles*) in Kibale Forest, Uganda. *Folia Primatol* 41:34–48.
- Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol* 2:143–155.
- Isbell LA, Pruett JD, Young TP. 1998. Movements of vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) as estimators of food resource size, density, and distribution. *Behav Ecol Sociobiol* 42:123–133.
- Isbell LA, Young TP. 1993. Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav Ecol Sociobiol* 32:377–385.
- Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326–336.
- Muruthi P, Altmann J, Altmann S. 1991. Resource base, parity, and reproductive condition affect females' feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* 87:467–472.
- Olupot W, Chapman CA, Brown CH, Waser PM. 1994. Mangabey (*Cercocebus albigena*) population density, group size, and ranging: a twenty-year comparison. *Am J Primatol* 32:197–205.
- Ostro LET, Silver SC, Koontz FW, Young TP, Horwich R. 1999. Ranging behavior of translocated and established groups of black howler monkeys (*Alouatta pigra*) in Belize, Central America. *Biol Conserv* 87:81–90.
- Stacey PB. 1986. Group size and foraging efficiency in yellow baboons. *Behav Ecol Sociobiol* 18:175–187.
- Struhsaker TT. 1967. Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behav* 29:83–121.
- Struhsaker TT. 1975. The red colobus monkey. Chicago: University of Chicago Press.
- Templeton AR, Lawlor LR. 1981. The fallacy of the averages in ecological optimization theory. *Am Natur* 117:390–391.
- Waser P. 1977. Feeding, ranging and group size in the mangabey *Cercocebus albigena*. In: Clutton-Brock TH, editor. *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes*. New York: Academic Press. p 183–222.
- Watts DP. 1991. Strategies of habitat use by mountain gorillas. *Folia Primatol* 56:1–16.
- Whitten PL. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159.
- Wrangham RW, Gittleman JL, Chapman

- CA. 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav Ecol Sociobiol* 32:199–209.
- Yamagiwa J, Mwanza N. 1994. Day-journey length and daily diet of solitary male gorillas in lowland and highland habitats. *Int J Primatol* 15:207–224.
- Young TP, Stubblefield C, Isbell LA. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. *Oecologia* 109:98–107.
- Young TP, Kinyua D, Okello BN, Palmer TM. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *Afr J Range Forage Sci* 14:94–102.