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ORIGINAL ARTICLE

Using multiple travel paths to estimate daily travel distance in arboreal, group-living primates

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Abstract Primate field studies often estimate daily travel distance (DTD) in order to estimate energy expenditure and/or test foraging hypotheses. In group-living species, the center of mass (CM) method is traditionally used to measure DTD; a point is marked at the group's perceived center of mass at a set time interval or upon each move, and the distance between consecutive points is measured and summed. However, for groups using multiple travel paths, the CM method potentially creates a central path that is shorter than the individual paths and/or traverses unused areas. These problems may compromise tests of foraging hypotheses, since distance and energy expenditure could be underestimated. To better understand the magnitude of these potential biases, I designed and tested the multiple travel paths (MTP) method, in which DTD was calculated by recording all travel paths taken by the group's members, weighting each path's distance based on its proportional use by the group, and summing the weighted distances. To compare the MTP and CM methods, DTD was calculated using both methods in three groups of Udzungwa red colobus monkeys (*Procolobus gordonorum*; group size 30–43) for a random sample of 30 days between May 2009 and March 2010. Compared to the CM method, the MTP method provided significantly longer estimates of DTD that were more representative of the actual distance traveled and the areas used by a group. The MTP method is more time-intensive and requires multiple observers compared to the CM method. However, it provides greater accuracy for testing ecological and foraging models.

Keywords Multiple travel paths method · Center of mass method · Daily travel distance · Daily path length · Udzungwa red colobus monkey · Arboreal primates

Abbreviations

CM	Center of mass
DTD	Daily travel distance
MTP	Multiple travel paths

Introduction

Measurements or estimates of daily travel distance (DTD) are fundamental to understanding a species' behavioral ecology from both theoretical (e.g., testing foraging models, measuring energy expenditure, and understanding habitat use) and applied (e.g., designing corridors) perspectives. The method used to estimate DTD can influence (1) the accuracy of behavioral and ecological assessments for a species, (2) conservation recommendations for a species, and (3) comparative studies within and between species. This study compares two methods for estimating DTD.

For group-living primates, DTD has traditionally been estimated using the center of mass (CM) method. In fact, over the last two decades, every article published in *Primates* that presented estimates of group DTD used the CM method (January 1995–January 2014). Group home range area and habitat use were also commonly assessed from

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CM data (75 % of studies published in *Primates* from January 2010 to January 2014).

The CM method estimates DTD by (1) marking a point at the group's perceived center of mass at regular time intervals or whenever the group moves, (2) measuring the distance between consecutive points, and (3) summing the distances measured throughout the day. The primary problem arises when this method is used for social groups that travel using multiple pathways, e.g., red colobus (group movement behavior described by Clutton-Brock 1975). In this situation, the CM method measures a straight, middle path, which is the shortest of all of the travel paths and may underestimate group travel distance. Furthermore, these estimated central paths may traverse areas that are, in fact, never used (e.g., pond or vine patch), confounding any attempt at fine-scale assessments of habitat use.

Many problems of the CM method can be overcome by installing GPS collars on individuals, which record more complete travel paths and vertical travel within trees. However, GPS data also have minor drawbacks: installing collars on a group is expensive and invasive, requiring either darting or trapping animals; substantial work is often necessary to remove cumulative distance error from the collar's DTD estimate (Ganskopp and Johnson 2007); GPS collar data are rarely complete with reported acquisition rates on wild primates at 74 and 82 % (Pebsworth et al. 2012 and Ren et al. 2008, respectively); and finally, collars have battery and storage limitations. Furthermore, unless all individuals are collared, this method does not record the movement of the entire group and constitutes a focal individual sample.

Observational studies of individuals (focal individual sampling) using the pace-counting method have also been used to estimate DTD (e.g., Altmann and Samuels 1992; Doran 1997, via pedometer). However, this method is most appropriate for terrestrial species living in habitats providing good visibility. Using the pace-counting method to estimate the DTD of an entire group requires one observer per study subject and also makes difficult the collection of any additional data, explaining why it has never been attempted. Furthermore, for arboreal species, like red colobus, full-day focal individual follows are impractical due to poor visibility. For more details on distance error and individual versus group DTD techniques, see Steel (2012).

To address these problems with the CM and focal methods, I designed and field-tested the multiple travel paths (MTP) method for estimating a group's DTD in wild Udzungwa red colobus monkeys (*Procolobus gordonorum*). The MTP method estimates DTD by recording and weighting all travel paths taken by group members. This paper compares estimates of daily travel distance using the center of mass and multiple travel paths methods.

Methods

Study site and groups

Data were collected from May 2009 to March 2010 from three habituated groups of arboreal Udzungwa red colobus monkeys ranging in size from 30 to 43 individuals. Groups were located in two forests of south-central Tanzania. The Hondo Hondo group (mean 42.5, range 42–43 individuals) lived in the Mwanihana Forest (Udzungwa Mountains National Park, centered at 7°49.8′S, 36°53.2′E and at a median elevation of 345 m), while Groups 1 (mean 32, range 30–33 individuals) and 2 (mean 40.5, range 39–42 individuals) were in the Magombera Forest (Kilombero Valley, centered at 7°48.9′S, 36°57.3′E at a median elevation of 282 m). Each study group's home range shared at least one border with the forest edge and was located within disturbed forests that were exploited for firewood collection. While Mwanihana had protective status, tree poles and animals were commonly harvested. Magombera had no protective status and was subject to hunting, animal trapping, timber extraction, tree pole extraction, and intentional fires.

Methods for estimating and comparing DTD

A focal group was observed ≥11.5 h per day from near sunrise to sunset by myself and one assistant. Each tree greater than 20 cm DBH that was entered by any member of the focal group was uniquely numbered with an aluminum tag and a GPS waypoint (Garmin GPSMAP 60Cx unit). Waypoints were taken at the base of each tree entered and used to create a daily travel map.

The CM method defines DTD as the sum of distances between consecutive center of mass points. There are two common variations of the CM method. Originally, researchers marked the group's perceived center of mass when at least one group member left a tree. More commonly now, researchers use a modified method, marking the group's perceived center of mass at a set time interval (typically every 15 or 30 min). In my study, I used the original method. The trees entered by the monkeys were marked with GPS waypoints, noting the number of monkeys per tree, and then center of mass was determined any time at least one group member moved to another tree. The distances between consecutive center of mass points were summed to estimate DTD.

The MTP method calculated DTD by recording all travel paths taken by the group's members, weighting the distance of each path based on its proportional use by the group, and then summing those weighted distances to determine DTD. The group members' travel paths were recorded in the form of a flow chart (e.g., 12 monkeys:

Table 1 Comparison of center of mass (CM) and multiple travel paths (MTP) methods and daily travel distance (DTD) means across groups of Udzungwa red colobus monkeys (*Procolobus gordonorum*)

Group name	Mean group size	CM and MTP: % difference	CM mean (m)	±SD	CV	CM DTD range (m)	MTP mean (m)	±SD	CV	MTP DTD range (m)	*N*
Group 1	32	14.6	796.0	203.0	0.26	411–1,077	932.3	277.9	0.30	446–1,441	9
Group 2	40.5	14.2	918.6	326.5	0.36	439–1,473	1,070.1	369.9	0.35	563–1,718	15
Hondo Hondo	42.5	6.4	1,168.3	259.6	0.22	801–1,481	1248.1	265.5	0.21	818–1,568	6

Column 3 shows the percentage by which the CM method underestimated DTD compared to the MTP method.

N = sample days per group, 30 random days in total, *CM* center of mass method, *MTP* multiple travel paths method, *DTD* daily travel distance, *SD* standard deviation, *CV* coefficient of variation

Tree 1 → Tree 2 → Tree 4; 28 monkeys: Tree 1 → Tree 3 → Tree 4). Using Mapsource software (Garmin 2010), distances were measured between consecutive GPS points in each travel path. To calculate the weighted travel path distance, each path's distance was multiplied by the proportion of the group that used the path. For example, if 70 % of the group travelled 100 m and 30 % of the group travelled 60 m, the total DTD would be calculated as (0.7 × 100) + (0.3 × 60) = 88 m.

DTD was calculated using both methods for a random sample of 30 full-day focal follows. Due to differences in time required for habituation, the groups were not sampled for an equal number of days.

The Shapiro–Wilk test was conducted using JMP (SAS Institute 2010) to determine if DTD data fit the normal distribution. A two-tailed repeated-measures analysis of variance (ANOVA) with an alpha level of 0.05 was conducted using Statistica (StatSoft 2001) to test for differences in DTD based on method of measurement. Two-tailed Wilcoxon signed-rank tests with alpha levels of 0.05 were conducted using R (R Core Team 2012) to test for within-group differences in DTD based on method of measurement. Figures were created in KaleidaGraph (Synergy Software 2003).

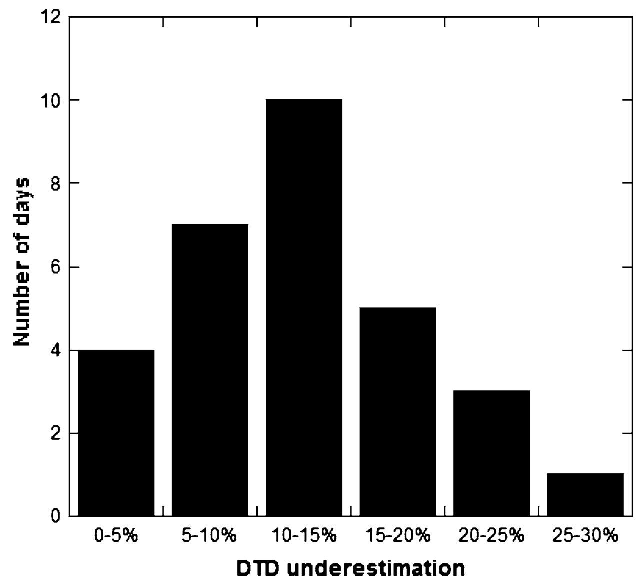

Fig. 1 Frequency distribution showing the percentage by which the center of mass method underestimated daily travel distance (DTD) of groups of Udzungwa red colobus monkeys (*Procolobus gordonorum*) compared to the multiple travel paths method ($N = 30$)

Results

The mean daily travel distance (DTD) among red colobus groups using the multiple travel paths (MTP) method was 1,064 ± SD 335 m (median 1,086 m, range 446–1,718 m) and using the center of mass (CM) method was 932 ± SD 303 m (median 948 m, range 411–1,481 m) (Table 1). DTD data fit a normal distribution (MTP DTD data: Shapiro–Wilk test, $N = 30$, $W = 0.97$, $P = 0.40$; CM DTD data: $N = 30$, $W = 0.96$, $P = 0.35$). The CM method significantly underestimated DTD compared with the MTP method by a mean of 12.5 % or 132 m (repeated measures ANOVA, $df = 29$, $F = 59.3$, $P < 0.00001$).

Every CM method's distance was shorter than its corresponding MTP method's distance. On the majority of sample days, the CM method underestimated DTD by 10–30 % (Fig. 1) or 76–375 m (Fig. 2) compared with the MTP method. On the groups' most cohesive day, the two methods' estimates differed by 0.7 %, and on the least cohesive day, the two methods differed by 28.2 %. Analyses of each group consistently found that the CM method underestimated DTD: by a mean of 14.6 % in Group 1 (Wilcoxon signed-rank test: $N = 9$, $V = 45$, $P = 0.0039$), 14.2 % in Group 2 ($N = 15$, $V = 120$, $P < 0.0001$), and 6.4 % in the Hondo Hondo group ($N = 6$, $V = 21$, $P = 0.031$, Table 1).

Discussion

Udzungwa red colobus group sizes are within the range of sizes across red colobus taxa, yet they have the longest mean DTD (Struhsaker 2010, table 6.12).

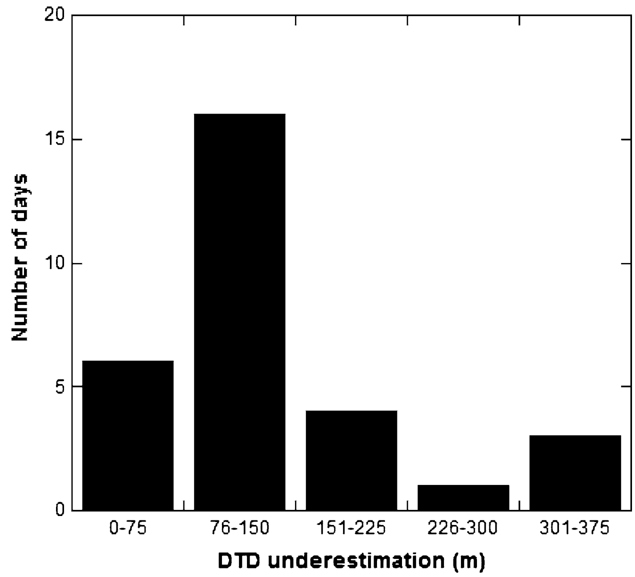

Fig. 2 Frequency distribution showing the center of mass method's metric underestimation of daily travel distance (DTD) of groups of Udzungwa red colobus monkeys compared with the multiple travel paths method ($N = 30$)

Factors relating to inter- and intrataxon variation in DTD are discussed in Steel (2012).

Methodological comparisons

The primary advantages of the CM method are that distance can be calculated by a single observer and relatively easily. The primary advantages of the MTP method are that it is more accurate and precise, and the measurements can be confirmed post hoc. Waypoints are not taken at a group's perceived central location; waypoints are taken at the base of tagged trees and can be recalculated at any time.

The main drawback of the traditional CM method (where individual monkey locations and CM estimates were plotted at each move) is underestimating DTD. Additional problems apply to the more common, modified CM methods (where locations of the group's individuals are not plotted and/or waypoints are taken at time intervals). Habitat use assessments are less informative using the CM modified method because researchers lose information on group spread and areas of use within the home range. Modified CM methods will further underestimate DTD, compared with results presented in this study, by recording points only at predetermined time intervals along a path rather than at each deviation from a straight line. In fact, Isbell et al. (1999) compared the actual distance traveled by an individual to its group's modified center of mass distance. They found that CM at 30-min intervals underestimated the distance traveled by a mean of 34 % for patas monkeys and 31 % for vervet monkeys.

The MTP method has two main drawbacks. First, the data collection and calculations are time-intensive, which distract from collecting data on other topics. Second, to accurately record all travel paths, multiple observers must be present to pursue the various paths; in this study, red colobus sometimes utilized paths greater than 50 m apart.

There are some measurement inaccuracies that neither method can address. First, neither method takes into consideration distance traveled within a tree while foraging. Second, both methods record only two-dimensional movement and do not adjust for topography (but see Sprague 2000 who found, using the CM method, that DTD was 9.5 % longer after correcting for topography in a steep habitat). Third, both methods rely on maintaining visual contact with all study subjects, an ability sometimes impaired by a thick understory, dense canopy, and/or relatively short, closed canopy. In this study, Group 1's and Group 2's home ranges covered flat terrain whereas the Hondo Hondo group's terrain was hilly. Also, the Hondo Hondo group's dominant tree species (*Sorindeia madagascariensis*) was much shorter than the two dominant species in both Group 1's and Group 2's home ranges (*Erythrophleum suaveolens* and *Isoberlinia scheffleri*). These features made observations of the Hondo Hondo group difficult beyond 15 m, sometimes requiring that a straight distance be measured from the last known tree to the next location. As a result of this sampling bias, the CM method underestimated DTD by 14.6 % in Group 1, 14.2 % in Group 2, but by only 6.4 % in the Hondo Hondo group. A GPS collar installed on one group member could be helpful for mitigating these issues, particularly for cohesive groups.

Implementing the MTP method may be problematic for certain taxa such as arboreal primates that move quickly while spread out in a broad front or living in fusion–fission societies. It might be impossible to account for every travel path. In addition, terrestrial primates negotiate a substrate that does not limit an individual to specific path options in the same manner that tree location does for arboreal primates. For arboreal primates, waypoints are taken at the tree's base; what would the waypoints represent for terrestrial primates, and how different must terrestrial paths be to signify a separate path?

Considering these drawbacks, the CM method may be more advantageous than the MTP method in some situations. For instance, a difference averaging 10–15 % may be biologically insignificant depending on the research question. Furthermore, the CM and MTP methods will likely provide similar DTD estimates for (1) very cohesive groups, (2) groups living in habitats with limited potential travel paths, and (3) groups living in habitats with poor visibility.

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