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Comparison of Two Methods for Measuring Daily Path Lengths in Arboreal Primates

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ABSTRACT: Researchers have used a variety of methods to measure patterns of animal movement, including the use of spatial data (mapping the position of a moving animal at specified intervals) and direct estimation of travel path length by pacing under a moving animal or group. I collected movement data from five groups of siamangs (*Symphalangus syndactylus*) using two different methods concurrently to estimate the effects of the method of data collection on estimates of daily path length (DPL). Estimates of DPL produced from spatial data collected at 15-minute intervals were 12% lower than estimates of DPL produced by pacing under the traveling animal. The actual magnitude of the difference was correlated with the travel distance, but there was no correlation between the proportional difference and the travel distance. While the collection of spatial data is generally preferable, as spatial data permit additional analyses of patterns of movements in two or three dimensions, the relatively small difference between the DPL's produced using different methods suggests that pacing is an acceptable substitute where the collection of spatial data is impractical. I also subsampled the spatial data at increasing time intervals to assess the effect of sampling interval on the calculation of daily path lengths. Longer sampling intervals produced significantly shorter estimates of travel paths than shorter sampling intervals. These results suggest that spatial data should be collected at short time intervals wherever possible, and that sampling intervals should not exceed 30 minutes. Researchers should be cautious when comparing data generated using different methods.

Key words: Daily path length, Gibbon, Primate, Siamang

INTRODUCTION

Animal movement patterns are among the most fundamental aspects of animal ecology. The ranging behavior of an individual or group is determined in part by its taxon-specific physiological, ecological, and social requirements (Jetz et al. 2004), and ranging behavior may in turn be an important determinant of population-level phenomena such as population density, mating system, group size and composition, and population growth rate. Understanding a population's space requirements and patterns of movement is critical for conservation planning, and also plays an important role in studies of many aspects of animal behavioral ecology (Isbell et al. 1999). Accordingly, quantification of animal movement patterns is an important component of many ecological studies.

A variety of field methods have been developed to estimate animal travel distances and ranging patterns, including mark-recapture studies (Plissner and Gowaty 1996, Priotto et al. 2002), aerial surveys (Serneels and Lambin 2001), the use of radio or satellite transmitters to assist in tracking animals (Corbin and Schmid 1995, Bonfil et al. 2005), and visually tracking known individuals or groups. The method chosen in a given study may depend on budgetary considerations, but is also likely to be affected by the characteristics of the animals and their environments. Technological solutions such as aerial surveys and the use of satellite transmitters are useful in open environments, but are often ineffective in studies of animals living in forested environments with a relatively closed canopy. Similarly, mark-recapture studies and the use of radio transmitters are only possible for animals that can be safely captured and re-released without affecting their natural behaviors. Therefore, for researchers working with endangered arboreal animals in forested environments, foot tracking of known individuals or groups is often the method of choice. This method has the advantage of providing detailed information about the movements of known individuals or groups, but is labor-intensive, and imposes many logistical challenges. Observers may have difficulty finding or maintaining contact with small, nocturnal, or cryptic animals (Gursky 1998). Animals may also be wary of observers, requiring extensive habituation before they can be monitored regularly (Tutin and Fernandez 1991). When animals travel rapidly, over large areas, or across difficult terrain, human observers may find following them impossible. Finally, even when routine monitoring of the animals is

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feasible, the accurate measurement of travel distances and mapping of locations can impose technical challenges.

In this study, I collected movement data from five groups of wild siamangs (*Symphalangus syndactylus*) using two different methods simultaneously, in order to compare the advantages and disadvantages of each method, and to establish guidelines for future studies of animal movement in this and related species. Siamangs are arboreal primates inhabiting forested areas of Sumatra and peninsular Malaysia. Siamangs and other gibbons (family Hylobatidae) defend relatively small home ranges (~15~90 ha) throughout the year, and have relatively short mean daily path lengths (DPL) of ~700~1,700 m (Chivers 2000, Bartlett 2007). However, within these parameters, gibbons are reported to display substantial inter-specific and intra-specific variation in ranging and movement patterns (Chivers 1987, Bartlett 2007). Researchers are often forced to compare results generated using different methods, making it difficult to assess the importance of fine-scale inter-population variation.

Researchers have used a variety of methods to monitor gibbon movement patterns (Chivers 1974). A method frequently used for collecting spatial data on gibbons is to map the location of the focal group or individual at regular intervals and use these data to plot home ranges, and to estimate DPL by calculating the straight-line distances between mapped points. Sampling intervals in previous gibbon studies using this method ranged from 10 minutes (Chivers 1974, Srikosamatara 1987, Ahsan 2000) to 30 minutes (Bartlett, 1999). However, in many gibbon field studies, researchers did not include routine collection of travel distance or ranging patterns (Palombit 1995), or sampled movement patterns only sporadically and opportunistically (Kappeler 1981, Cheyne 2004). These decisions were in most cases made for pragmatic reasons, as monitoring gibbon locations in space requires complete habituation of the gibbons to human observers, can be labor intensive and can interfere with the collection of other types of behavioral or ecological data.

The collection of spatial data (i.e., data recording the actual or relative location of animals in two-dimensional or three-dimensional space) is desirable for many reasons. Spatial data may be used for many purposes, including mapping home ranges, calculating of DPL, and conducting analyses of range overlap and territory size (in territorial animals), and of daily, seasonal, and annual patterns of range use. Therefore, the collection of spatial data is a routine part of many observational field studies. However, mapping actual locations of highly mobile study animals at regular intervals in a complex environment requires a network of well-demarcated landmarks of known location. Therefore, considerable time must be invested in the development and mapping of a trail system prior to the collection of behavioral data. Furthermore, mapping of the location of mobile animals at fixed time intervals may also require substantial labor for observers, as at any given point in time, the animal may be some distance from a previously mapped place marker, requiring that the new location be mapped between sampling intervals. Therefore, the time and opportunity cost for researchers can be considerable. Furthermore, calculations of DPL based on straight-line distances between mapped locations tend to underestimate actual travel paths, producing bias that varies across taxa (Isbell et al. 1999).

An alternative method of estimating DPL, pacing the travel route of an individual animal to estimate actual travel distance, has been used in several studies of wild primates (Watts 1991, Yamagiwa and Mwanza 1994, Isbell et al. 1999). This method has the advantages of not requiring the production of detailed maps and the placement of markers of known location throughout the home range of the target animal, not requiring the use of any additional equipment, and being compatible with the concurrent collection of behavioral data by a single observer, but the disadvantage of producing data that cannot be used in analyses of patterns of movement in two or three dimensions. This method is promising for gibbon studies for which mapping is impractical, as it involves little in the way of time or opportunity costs for the observer. However, it is not yet clear whether pacing data (which estimate actual path length) are directly comparable to data produced through the use of spatial data (which calculate the shortest travel distance between points mapped at regular intervals).

Three field assistants and I collected movement data from five groups of wild siamangs using two different methods simultaneously: pacing under the focal animal and mapping the focal animal's location at 15-minute intervals. The resulting estimates of daily path length were compared in order to determine the reliability of each method, and the comparability of different methods of daily path length estimation. The mapping data were also subsampled and compared at different sampling intervals to assess the effects of sampling interval on daily path length estimates in gibbons.

METHODS

Study Area

The Way Canguk Research Station is located in the southern part of the Bukit Barisan Selatan National Park on the island of Sumatra, Indonesia, at an elevation of 50 meters above sea level (Fig. 1). The research area, which is run collaboratively by the Wildlife Conservation Society-Indonesia Program (WCS-IP) and the Indonesian Ministry of Forestry's Department for the Protection and Conservation of Nature (PHKA), encompasses 900 hectares of forest. The study area consists of a mosaic of primary forest and forest damaged by drought, wind, earthquakes, and fire, contiguous with a large area of undisturbed lowland forest, as well as with areas disturbed by illegal logging and agricultural activity (Kinnaird and O'Brien 1998, O'Brien et al. 2003). The research area is bisected by the Canguk River, and crossed by a grid of trails at 200-meter intervals.

Study Animals

Siamangs are large-bodied (10～11 kg) arboreal primates that live in small groups (2～6 individuals) and defend a substantial proportion of their home range as an area of exclusive use. The most common group composition is a single adult male, a single adult female, and 1～3 immatures, although multi-male grouping has also been reported (Lappan, 2007a). Siamangs, like all gibbons, use brachiation, or arm-swinging, as their primary mode of locomotion, and are strictly arboreal, very rarely descending to the ground.

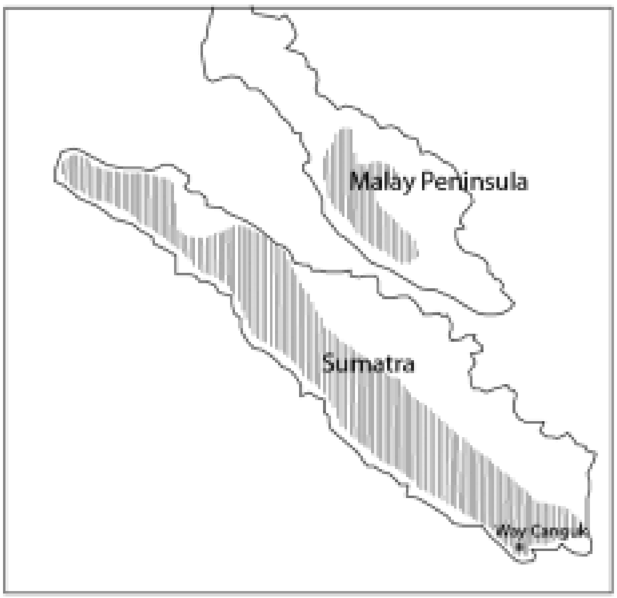

Fig. 1. Map of Sumatra and the Malay peninsula indicating the location of the study site. The shaded area represents the distribution range for siamangs (*Symphalangus syndactylus*).

Five siamang groups were selected as the primary study groups, and supplementary data from a sixth group were also included in some analyses. Group compositions in March 2001 are described in Table 1. All groups were well habituated to human observers prior to the beginning of data collection.

Behavioral Data Collection

Three field assistants and I collected movement data from groups A, B, C, F and G from January to August 2002, and from group S from April to June 2002. All field assistants had been trained in the collection of behavioral data for at least one year prior to the beginning of this study. Inter-observer reliability of distance estimates was repeatedly verified prior to the collection of behavioral data. Behavioral data were collected by pairs of observers.

Data were collected during sleeping-tree-to-sleeping-tree follows of the study groups. Groups were followed on a rotating basis. On each day a single adult was selected as the focal individual (Martin and Bateson 1993). Adults within a group served as focal individuals on a rotating basis until each adult had served as the focal animal twice before the observers moved to the next group. Both spatial data and estimated actual distance data were collected from groups A, B, C, F, and G, whereas only spatial data were collected from group S.

Spatial Data

The location of the sleeping tree was recorded using a coordinate system at 1 m intervals oriented around the trail system. Then the location of the tree in which the focal individual was located was recorded at 15-min intervals by one observer throughout the day until the focal individual entered the next sleeping site at the end

Table 1. Composition of main study groups A, B, C, F and G, and secondary study group S in January 2002. Each individual is designated by a three-letter code

Group	Adult		Subadult female	Juvenile		Infant (sex)	Total
	Female	Male		Large	Small		
A	AMA	AMI				ARJ (m)	3
B	BAM	BMO, BAR		BRA (m)	BIM (m)	BMG (m)	6
C	CON	CGO, CKR		CBR (m)		CHE (f)	5
F	FRI	FRE, FRA	FUL	FIF (f)		FRN (f)	6
G	GAR	GAT				GAN (m)	3
S	SON	SYA				SUY (?)	3

of the activity period. When the focal individual was in a tree that had not been previously mapped, the observer mapped the location of the tree using a compass and rangefinder and existing location markers.

Estimated Actual Distance Data

The second observer paced under the focal individual, and recorded the estimated distance traveled at 5-min intervals. When it was impossible to pace directly under the animal, the animal's actual travel distance was estimated by eye.

Data Analysis

Daily path lengths (DPL) were calculated in one of two ways. The spatial data were converted into DPL by calculating the straight-line distance between subsequent mapped data points. These distances were then summed throughout the day to generate an estimate of DPL, indicated as DPL_{15}. The data were then subsampled at 30 min intervals (on the hour and the half-hour) and at 1 h intervals (at 45 min after the hour), and the procedure was repeated, to generate estimates based on 30-min samples of spatial data (DPL_{30}) and 1-h samples of spatial data (DPL_{60}) respectively. For the estimated actual distance data, the travel distances recorded at 5-min intervals were summed throughout the day to generate an estimate of the actual DPL, indicated as DPL_A.

Preliminary analyses suggested that the estimates of DPL_{15}, DPL_{30}, DPL_{60}, and DPL_A were not normally distributed. Therefore, all statistical analyses were conducted using non-parametric statistical tests. All tests were two-tailed unless otherwise indicated.

RESULTS

Estimated Siamang Mean DPL_A

DPL_A did not differ significantly among individuals within a group for any group (Kruskal-Wallis Test; group A: χ^2=1.195, N=44, df=2, p=0.550, group B: χ^2=0.084, N=58, df=2, p=0.959, group C: χ^2=4.388, N=58, df=2, p=0.111, group F: χ^2=2.173, N=32, df=2, p=0.337, group G: χ^2=0.013, N=39, df=1, p=0.911). This is not surprising, as group members were quite cohesive during travel, spending most of their time <20 m apart (Lappan 2007b), and almost invariably shared the same sleeping tree. Therefore, all data from each group were combined for further analyses. DPL_A ranged from 396 m to 2,933 m, and the mean DPL_A for the study groups ranged from 1,068 m to 1,289 m (Table 2). Mean DPL_A differed significantly among groups (Kruskal-Wallis Test, χ^2=11.104, N=226, df=4, p=0.025).

Table 2. Minimum, maximum and mean daily path lengths (DPL_A) for groups A, B, C, F and G

Group (N)	Minimum DPL (m)	Maximum DPL (m)	Mean DPL ± SE (m)
A (44)	396	2,933	1,289 ± 78
B (53)	402	1,927	1,068 ± 51
C (58)	482	2,114	1,227 ± 44
F (32)	457	1,800	1,088 ± 64
G (39)	441	1,915	1,067 ± 65
Mean of group means			1,148 ± 46

Comparison of DPL_A and DPL_{15}

For all five groups, mean DPL_A was significantly longer than mean DPL_{15} (one-tailed Wilcoxon signed ranks test; group A: Z=−3.059, N=12, p<0.001, group B: Z=−1.728, N=17, p=0.044, group C: Z=−3.006, N=17, p=0.001, group F: Z=−2.227, N=20, p=0.011, group G: Z=−3.179, N=19, p<0.001) (Fig. 2). Mean DPL_{15} underestimated mean DPL_A by 12%, or 151 ± 20 m.

Comparison of Daily Path Lengths Produced Using Spatial Data with Different Sampling Intervals

For DPL's calculated from spatial data, there was a clear relationship between the sampling interval and the resulting estimate of DPL. DPL_{15} were consistently longer than daily path lengths produced by recording the focal animal's position at 30 min or 1 h intervals (DPL_{30} or DPL_{60}, respectively) (Fig. 3). Mean DPL_{15} were significantly longer than mean DPL_{30} for every group (one-tailed Wilcoxon signed ranks test, group A: Z=−3.180, N=13, p<0.001;

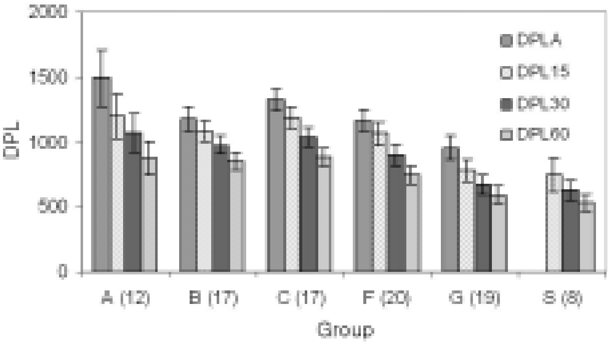

Fig. 2. Estimated mean daily path length (DPL) ± SE for groups A, B, C, F, G, and S by estimation of actual travel distances (DPL_A) of a focal animal, and by mapping the location of the traveling animal at 15 minute (DPL_{15}), 30 minute (DPL_{30}), and 1 hour (DPL_{60}) intervals, and calculating the straight-line distance between mapped points. Numbers in parentheses indicate the sample size (days).

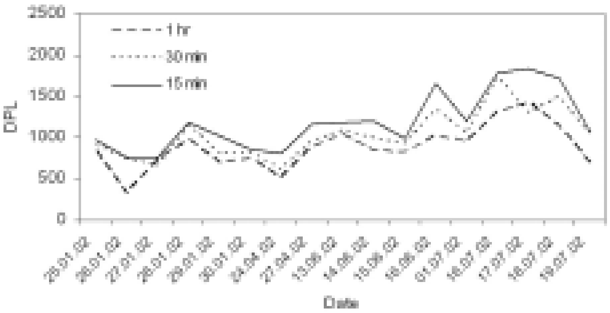

Fig. 3. Plots of DPL estimated from spatial data collected at 15 min, 30 min and 1 h intervals for group C.

group B: $Z=-3.621$, $N=17$, $p<0.001$; group C: $Z=-3.621$, $N=17$, $p<0.001$; group F: $Z=-4.200$, $N=24$, $p<0.001$; group G: $Z=-3.829$, $N=24$, $p<0.001$; group S: $Z=-2.100$, $N=8$, $p=0.020$). On average, DPL_{30} underestimated DPL_{15} by 13%, or 137 ± 14 m, and underestimated DPL_A by 23%, or 283 ± 20 m.

DPL_{60} were generally shorter than DPL_{30}. Discrepancies from this pattern did occur, as the 30 min samples were collected on the hour and half hour, whereas the 1 h samples were collected at 45 min after the hour, so deviations from the main direction of travel occurring between the half-hour and the hour were detected by the 1 h samples, but not the 30 min samples. Nonetheless, mean DPL_{60} was significantly shorter than mean DPL_{30} in all six groups (one-tailed Wilcoxon signed ranks test, group A: $Z=-3.180$, $N=13$, $p<0.001$; group B: $Z=-3.053$, $N=17$, $p=0.001$; group C: $Z=-2.911$, $N=17$, $p=0.001$; group F: $Z=-3.314$, $N=24$, $p<0.001$; group G: $Z=-3.971$, $N=24$, $p<0.001$; group S: $Z=-1.820$, $N=8$, $p=0.039$). On average, DPL_{60} underestimated DPL_{15} by 25%, or 272 ± 20 m, and underestimated DPL_A by 34%, or 419 ± 27 m.

Does the Measurement Error Associated with the Use of Spatial Data Vary with DPL?

Analysis by Spearman rank correlation detected a significant correlation between DPL_A and the difference between the DPL_A and DPL_{15} ($\rho=0.297$, $N=85$, $p=0.006$), which indicates that the magnitude of the difference is not random with respect to travel distance, but rather increases with increasing DPL_A. This suggests that estimation of DPL using instantaneous spatial data, as opposed to estimation of actual travel path, will tend to underestimate DPL to a greater extent on animals with longer daily path lengths. However, there is not a significant correlation between the ratio of the difference between DPL_A and DPL_{15} to DPL_A ($(DPL_A - DPL_{15})/DPL_A$) and DPL_A ($\rho=-0.021$, $N=85$, $p=0.847$), which suggests that the difference is proportional to DPL_A.

Similarly, there is a significant relationship between DPL_A and the difference between DPL_{15} and DPL_{60} ($\rho=0.644$, $N=85$, $p<0.001$)

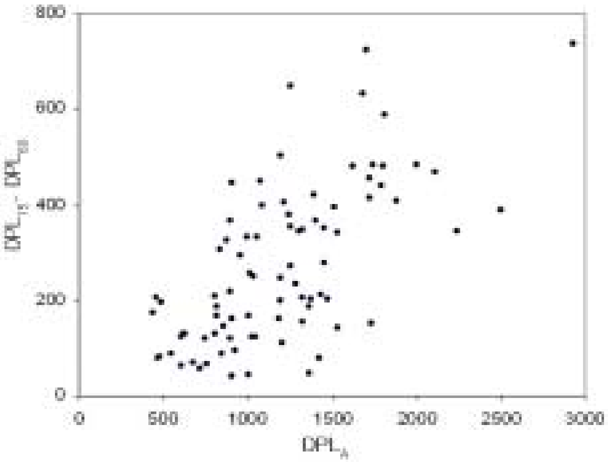

Fig. 4. Scatterplot of the difference between the DPL calculated from spatial data at 15 minute intervals and 1 hr intervals ($DPL_{15} - DPL_{60}$) plotted against the estimated actual DPL.

(Fig. 4). Therefore, the sampling interval will also affect the magnitude of the discrepancy between methods, with longer sampling intervals underestimating DPL_A to a greater extent in animals with longer DPL. Again, the absence of a significant relationship between $(DPL_{15} - DPL_{60})/DPL_A$ and DPL_A ($\rho=0.083$, $N=85$, $p=0.448$) suggests that the error is proportional to DPL_A.

DISCUSSION

A previous study of primate movement patterns conducted on semi-terrestrial African cercopithecine monkeys found that the use of straight-line distances to estimate travel paths tends to produce underestimates of DPL (Isbell et al. 1999). This study confirms that result in arboreal Asian apes with relatively short daily path lengths. However, the fact that the difference between DPL_A and DPL_{15} in this study was relatively small suggests that large differences in daily path lengths between groups, study sites, or species are unlikely to be artifacts produced by different methods if the sampling interval is short, and that both methods will produce reasonable estimates of daily path lengths in gibbons.

The pronounced effects of sampling interval on estimates of DPL caution against the direct comparison of data collected with dramatically different sampling intervals. Researchers using spatial data to calculate DPL should use the shortest sampling interval that is feasible under field conditions, and the use of sampling intervals greater than 30 minutes is strongly discouraged. In addition, as the magnitude of the difference between DPL's calculated using different sampling methods depends on the actual DPL, appropriate data transformations should be employed in quantitative comparative analyses using data generated by different methods.

Both DPL_A and DPL_{15} can be affected by measurement error. The procedure used to derive DPL_A assumes that trained observers are able to accurately estimate actual travel paths. However, occasional lapses of attention or areas of difficult terrain may produce random errors in measurement, and a systematic tendency of observers to overestimate or underestimate travel distances can produce biased results. Careful checking of inter-observer reliability and regular calibration of observer estimates are recommended to reduce the probability of systematic bias.

The procedure used to estimate DPL_{15} will also involve both random and systematic measurement error. Random error will occur because the distance between trees occupied by a focal animal in subsequent intervals may not correspond exactly to the straight-line distance traveled by the animal. Animal movements of as little as one meter may result in the animal entering a different tree, the trunk of which may be located 20 m from the original tree occupied by the animal. Conversely, in trees with large canopies, the focal individual may move 20 m or more without entering a different tree. Systematic error will be produced when the animal's actual travel path deviates from a straight line, which is likely to be a frequent occurrence in the complex three-dimensional environment of a tropical rain forest.

The results of this study suggest that DPL's calculated from instantaneous samples of spatial data (i.e. the mapping of actual locations at set intervals and the calculation of straight-line distances between sample points) underestimate DPL_A, and that this bias will be increasingly pronounced with longer sampling intervals and longer travel distances. This suggests that researchers should give careful consideration to both practical considerations and to the goals of their study when choosing a research method.

While methods based on the collection of instantaneous spatial data offer several practical advantages, including a shorter training time for observers and the generation of data that can be used for multiple different types of analyses of animal ranging and movement, they are also more labor-intensive, and tend to produce biased results for analyses of daily path lengths. To some extent, there will be a trade-off between these two problems. Sampling at shorter intervals will minimize bias, but requires greater effort on the part of observers. At the Way Canguk study site, a single observer working alone might have difficulty consistently recording the location of a moving focal animal at short time minute intervals, as observers are often required to use a range-finder and compass to determine the location of a target tree relative to trees or markers of known location, which may result in the loss of contact with the focal animal if the instantaneous sample falls during a period of rapid travel. Sampling at longer intervals should allow a lone observer ample time to relocate a lost focal animal to collect the subsequent instantaneous sample, but involves a greater loss of measurement accuracy.

Ideally, researchers interested in animal movement should collect spatial data at short intervals, as this solution represents the best way to simultaneously maximize data quality and the general applicability of data to numerous problems involving one-dimensional and two-dimensional patterns of movement. However, as critical field data are rare or absent for most rain forest animals, it is imperative that researchers collect as many basic natural history data as possible whenever they are in the field. Pacing under the traveling animal is the simplest way to calculate DPL, as it does not require the use of special equipment, and does not increase the risk of the observer losing contact with the focal individual, and the results of this study suggest that the difference between DPL generated by pacing and DPL generated through the use of spatial data at short sampling intervals is relatively small. Therefore, when the goals of the study do not permit the collection of spatial information, this method may be substituted. In this study, a single observer was able to collect DPL_A by pacing under the focal individual while concurrently collecting instantaneous samples of other behavioral data (e.g. activity, food type and plant food species, inter-individual distance data) at 5-minute intervals, and opportunistically recording sexual interactions and incidents of aggression for a concurrent study on siamang social behavior (Lappan 2005). This suggests that pacing under a focal individual does not substantially affect the ability of researchers to pursue other research goals.

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