

Research Article

**A comparison of two methods to create tracks of moving objects:
linear weighted distance and constrained random walk**

ELIZABETH A. WENTZ

Department of Geography, Arizona State University, Tempe,
AZ 85287-0104, USA
e-mail: wentz@asu.edu

AIMEE F. CAMPBELL and ROBERT HOUSTON

Environmental Systems Research Institute, 380 New York Street Redlands,
CA 92373-8100, USA

(Received 26 April 2001; accepted 3 March 2003)

Abstract. As an object moves through space, it creates a track (or path) representing the object's past and present position and associated attributes. If data capture fails, then positions along the tracks are unknown. The particular problem we address in this paper is to create tracks of moving objects with missing data. We implement and test two techniques that create continuous tracks of two primate species (*Ateles geoffroyi*, the red spider monkey, and *Cebus capucinus*, the white-faced capuchin). Continuous tracks were needed to calculate home range and to analyze daily ranging patterns for each species. Establishing continuous tracks of primates through field data alone, however, was impossible due to challenging field conditions. The results of the analysis using tracks with interpolated positions helped establish that *Ateles* tend to move directly to their destination while *Cebus* tended to follow a more wandering track.

1. Introduction

As an object moves through space, a track (or path) can be recorded that represents its past and present positions and its attributes. If data capture fails, then positions along the tracks are unknown. The problem we address in this paper is to create complete tracks of moving objects when some of the positions are unknown. Examples of moving objects are fleet management operations (Pfoser and Jensen 1998); hurricane and tornado tracks (Georges *et al.* 1993, Brotak and Le Comte 1994); movement of animals (Crist *et al.* 1992, Wilson 1994); avalanche movement (Walsh *et al.* 1990); airplane movement (Brunk and Davis 2002); and events along storm drains (Carapella 1997). Attributes of the object can be recorded at positions along the track. For example, node values may record the 'behaviour of the animal' or 'intensity of the storm'. We have begun to see geographical information systems (GIS) designed to display tracks. Nevertheless, tools to manipulate and analyze tracking data are not well developed conceptually or are not yet implemented. For example, the Environmental Systems Research Institute (ESRI) offers Tracking

Analyst as an extension to ArcView[®], which has several display functions but few data manipulation or analytical options. The data manipulation techniques presented in this paper extend the options available to scientists studying spatial processes along tracks.

In this study, we develop and test two methods to interpolate missing data along tracks to create a representation of a moving object in both space and time. The first approach we develop and test is based on linear weighted distances, which we simply call a straight line method; and the second is based on a constrained random walk. The straight line approach simply involves creating a new track by drawing a straight line between two known points and distributing the new points evenly along the track. The second approach, the constrained random walk, incorporates direction change and altering the speed of travel into the algorithm.

A major application area of tracking moving objects is animal movement. We therefore test our interpolation methods on the movement of two primate species in Costa Rica (*Ateles geoffroyi*, the red spider monkey, and *Cebus capucinus*, the white-faced capuchin). The estimated locations are combined with known observed positions to answer two basic research questions: (1) what is the home range for each species?, and (2) what are the daily ranging patterns for each species? Scientists interested in animal behavior have long recognized that individuals and groups occupy a 'home range', discrete geographical areas used over the course of their lives. To identify the home range for an individual or a group, a spatially and temporally continuous representation of animal positions is required. However, it may not always be logistically possible to do this. For example, at La Selva Biological Station in northeastern Costa Rica, establishing continuous tracks of primates was impossible because the animals' range over large distances, and dense vegetation, hilly terrain, and heavy rainfall impeded continuous monitoring of their positions. A need therefore arose to develop a method for estimating their positions when their actual positions were unknown.

2. Background

There is a related GIScience literature on how to represent moving objects and to assess uncertainty of their positional accuracy. Moreira *et al.* (1999) develop a method to represent and query moving points derived from sensors (e.g. Global Positioning System). Moving objects are represented as tuples defined with a unique identifier, valid time interval, and an initial state (the location). The data model we use has similar characteristics, although we structure ours based on a specific time stamp rather than an interval. Pfoser and Jensen (1998) examine the positional uncertainty of moving objects. They quantify measurement uncertainty (in their case due to potential inaccuracy of GPS) by creating ellipses that represent regions of possible positional error.

Moving objects create tracks or paths through space. Positions along the track need to be estimated when data capture methods fail (e.g. GPS signal unavailable). The largest body of literature on interpolating the position of moving objects is based on tracking animal movement. Scientists track animal movement to determine microhabitat, to better understand resource use, to establish behavior response to habitat structure, and to find the nesting sites of secretive animals (Wilson 1994, South 1999). Most research has been based on tracking animal locations and attempting to monitor their behavior continuously. Methods of tracking animals include direct observation, use of a spool-line, sensors put directly on animals,

photographs of animals taken at regular intervals, and satellites (Priede and French 1991, Waturu and Yuzuriha 1993, Wilson 1994). With some techniques (e.g., spool-line and sensors put directly on the animals), the continuous locations of the animals are monitored. Their activities (e.g., sleeping, grooming, and eating), however, are not recorded. For microscopic organisms, photographs are taken at regular intervals, recording both their location and the activity. Waturu and Yuzuriha (1993) placed sensors on marine animals to collect data on water temperature, depth, and light intensity. Although they did not collect location information in this study, sensors could be added to collect this type of information.

A more technical approach for recording the movement of animals and allowing for the simultaneous recording of location and behaviour data is through radio-tracking (Rothstein *et al.* 1984, USGS 1997). The problems, however, are that visibility, animal fears, and other physical constraints prevent data from being collected continuously. Consequently, simulation of animal movement and triangulation are techniques used to estimate the locations of the animals when they are not being tracked. Animal movement has been simulated through fractals, negative binomial distributions, correlated random walks, and Monte Carlo simulations (Schmutz and White 1990, Crist *et al.* 1992, Gautestad and Mysterud 1993, Turchin 1996, Schippers *et al.* 1996, Tischendorf 1997, Tischendorf *et al.* 1998). These approaches utilize a broad spectrum of methods to approximate animal movement, but none can be applied generically to interpolating positions of moving objects. Some have been developed with a particular application context and data set in mind. For example, Schippers *et al.* (1996) use a random walk model to simulate animal dispersal in a heterogeneous environment.

There is recent interest in utilizing GIS for studying marine animal movement, as demonstrated by Hooge and Eichenlaub (1997), Bian (2000), and Hooge *et al.* (2001). Bian (2000) evaluates the merits of an object-oriented environment for modelling mobile objects, using the movement of animals in a marine environment as a case study. Although Bian (2000) deals with the problem of objects moving to new locations, the data type is based on the objects rather than the tracks. Hooge *et al.* (2001) wrote extensions to the ArcView[®] environment to analyze the spatial patterns and movement patterns of marine animals. Their extensions, however, are generic enough that they can be applied to terrestrial animal movement as well. The analytical methods described by Hooge *et al.* (2001) are extensive and include random walks and other techniques for animal movement simulations.

3. Methods

3.1. Study Location

Empirical data for our study were collected from La Selva Biological Station, a rainforest research station in north-eastern Costa Rica, 10° 25' N, 84° 01' W, (figure 1). La Selva is in the tropical wet forest life zone with precipitation averaging approximately 4000 mm (Sanford *et al.* 1994). Bisecting the dense vegetation and hilly terrain are approximately 45 km of fixed trails. Three primate species are present, *Alouatta palliata* (the mantled howling monkey), *Ateles geoffroyi* (the red spider monkey), and *Cebus capucinus* (the white-faced capuchin). The combination of dense vegetation, heavy precipitation, and hilly topography, make for extreme field conditions for studying fast-moving primates. The study reported here was the first long-term study of primate ecology at La Selva despite its many years of operation, due expressly to difficult observation conditions.

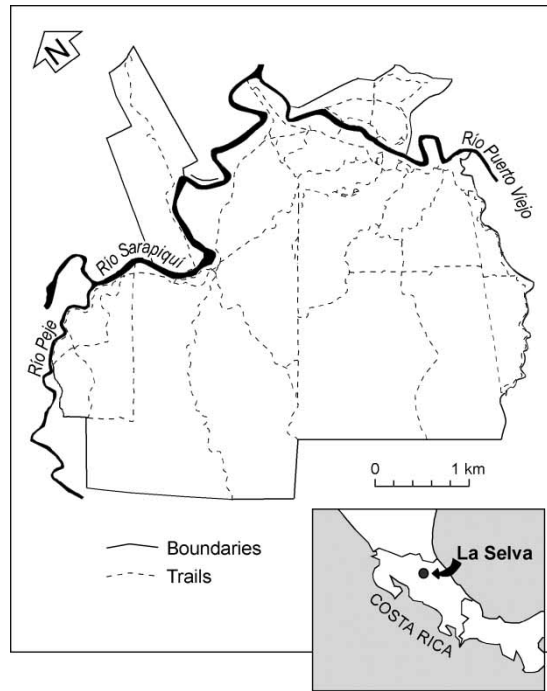


Figure 1. Location of La Selva Biological Station in Costa Rica.

3.2. Data

For the study reported here, positions of one group of *Ateles geoffroyi*, the red spider monkey, and one group of *Cebus capucinus*, the white-faced capuchin, were collected at a five-minute sample rate by direct observation for a 10-month period from March to December 1991. During the study period, each group was observed for eight consecutive hours, two days per week. Radios were used to help locate the animals while we were walking through the forest with handheld receivers (Campbell and Sussman 1994). The density of the rainforest prohibited us from pinpointing the exact locations using radios alone. Their positions were determined by following the animals and marking trees in which they were observed. The trees were later recorded by mapping their position relative to other known locations in the forest.

The final data set consists of two types of records. *Mapped points*, defined by $a = (x_a, y_a)$ or $b = (x_b, y_b)$, are records for which the location was known (*Ateles*, $n = 1446$; *Cebus* $n = 1294$). Records for which the location was unknown are referred to as *intermediate points*, $i = (x_i, y_i)$ (*Ateles*, $n = 2183$; *Cebus*, $n = 2471$). Intermediate points occurred either when contact was maintained with the primates, but due to characteristics of the dense rainforest habitat, their precise location was unknown, or when contact with the primates was not maintained at all. If the intermediate point i is encountered at time t_i on the track between points a and b , then $t_a < t_i < t_b$ and the position (x_i, y_i) needs to be interpolated.

A connected temporal sequence of mapped and intermediate points represents the possible track the group of primates might have taken. Sequences of mapped points when connected are referred to as *known segments*. Sequences of intermediate points are referred to as *unknown segments*. Thus, the objective here is to generate

x, y coordinates for the intermediate points to create estimated tracks of the unknown segments. The known segments and the unknown segments are then connected to create *complete tracks* of primate movement.

The overall method for creating the complete tracks involves implementing and comparing two interpolation methods, a linear weighted distance interpolation and a random walk interpolation (figure 2). In Step One, the known segments, their endpoints, and the time interval (t_i) of the unknown segments are identified. The assessment of two interpolation methods takes place by applying both interpolation techniques to the begin and end points of the known segments (Step Two) to create predicted positions of the known segments. These predicted known segments were then compared to the observed known segments (Step Three). Step Four involves selecting the best interpolation method for each primate species based on several error measures. Finally, complete tracks are created by interpolating all values of

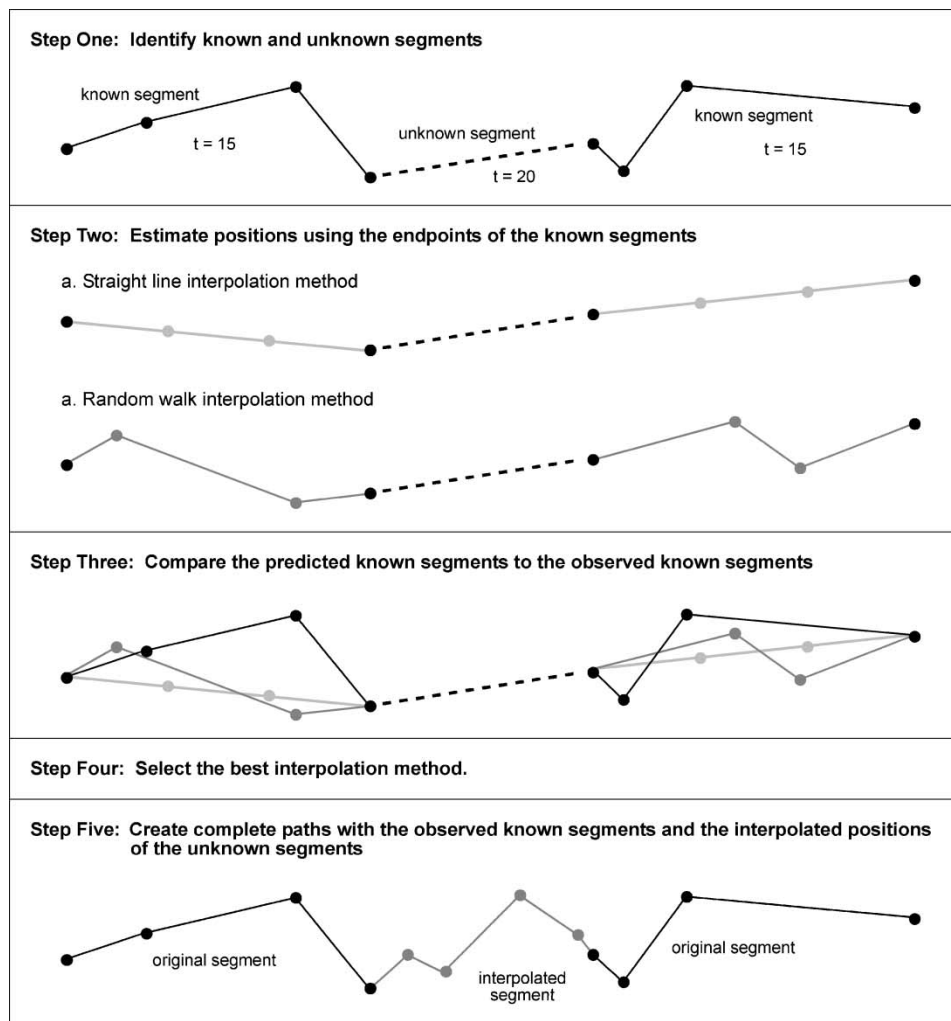


Figure 2. Steps illustrating the implementation and assessment of the two interpolation techniques.

(x_i, y_i) for the unknown segments and combining these interpolated segments with the observed known segments (Step Five). The remainder of this section describes details on each step.

3.3. Interpolation algorithms

The two interpolation techniques implemented in this study were: (1) a linear weighted distance and (2) a constrained random walk. The first method creates new points by generating a straight line from the last known point to the start of the next known segment and distributing intermediate points evenly along the interval. This approach was selected for its simplicity, but it may over-simplify the shape of the track. The second method utilizes a constrained random walk to estimate the shape of the track. The constrained random walk was selected to avoid the assumption that anything other than a random process controls the movement in space. Although other techniques (e.g. fractals) could be used to simulate processes, we chose to start with these two. The algorithms were implemented with a suite of Java programs with output in ASCII text format, suitable for display and subsequent analysis in most GIS software.

3.3.1. Linear weighted distance

The first approach implemented was based on linear weighted distances, which we also call the ‘straight line method’. We assumed that the locations of the intermediate points were distance-weighted averages of data points occurring immediately before and after the mapped point. The following equations were used to interpolate the location (x_i, y_i) of intermediate point i at time t_i :

$$x_i = x_a + (x_b - x_a) \frac{t_i - t_a}{t_b - t_a} \quad (1)$$

$$y_i = y_a + (y_b - y_a) \frac{t_i - t_a}{t_b - t_a} \quad (2)$$

3.3.2. Constrained random walk

The constrained random walk method used a combination of Monte Carlo methods and space-time prism concepts (figure 3). Details of the algorithm are described with pseudocode in the Appendix. Monte Carlo methods are mathematical experiments that use random numbers to simulate processes; they are used in a wide range of disciplines from nuclear physics to biology (Hammersley and Handscomb 1964). The constrained random walk interpolation algorithm also utilized space-time prism concepts, initially developed to model movement of people (Hägerstrand 1970). A three-dimensional prism is constructed that forms the possible space within which an individual can move in a given time. Theory and methods for describing and using space-time prisms continue to evolve (Hariharan and Hornsby 2000) and are often used to describe accessibility, particularly in the field of transportation geography (Burns 1979, Miller 1991). The constraints associated with space-time prism concepts applied here were (1) individuals have a maximum speed at which they can travel; and (2) their movements require the use of time, that is, they do not end up at their destination instantaneously (Burns 1979).

A two-dimensional random walk (a Monte Carlo simulation) represents a sequence of movements in which each step is independent of the previous step. In the case of tracking data, the assumption of independence was maintained but

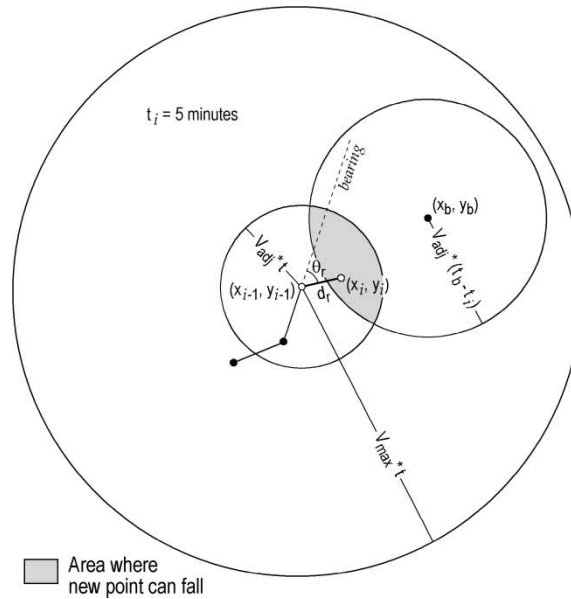


Figure 3. Example of how the next point in a constrained random walk is calculated.

dependent on a probability of turning for each step. To increase the chance of turning in a particular direction, a constraint was created using a frequency table, which is built from the number of turns made in each direction in the observational data. In our study (described below), a five-direction frequency table (right, left, ahead, back, and stay) was utilized. In this example, a random number was generated between 1 and the highest number in the frequency table to assign the turn direction. If any direction other than 'stay' was selected, a second random number was then generated between the minimum and maximum angles for the assigned direction. For example, if the first random number indicates an 'ahead' direction, a second random number between -45° and 45° was generated. This second random number represented the bearing taken during the next step, which required that a current bearing exists. When no current bearing existed (i.e. when the previous turn was 'stay'), the bearing was measured from the known start point (x_a, y_a) to the end point (x_b, y_b) .

The distance of each step in the interpolation was constrained by utilizing concepts of the space-time prism model. Based on the space-time prism, given a specified elapsed time, there is a maximum distance an observer can travel. This distance, d , was calculated by multiplying an adjusted maximum speed, v_{adj} , by the time interval for each step. Assuming a homogeneous surface and no spatial barriers, the distance d was used as the radius of a circle around the originating point. This circle identified the spatial extent within which the object can travel in a single step from the given point (x_{i-1}, y_{i-1}) . The adjusted maximum speed, v_{adj} , was used instead of the known maximum speed (v_{max}) because we found that the radius of a circle calculated with the known maximum speed was too large, which meant in many cases the destination could be reached in very few steps. v_{adj} was determined by starting with the known average speed (v_{ave}) and incrementing at $0.5 * v_{ave}$ until a usable speed was found or until the known maximum speed was reached. For each step (i), a distance (d_i) was established by generating a random number between 0

and the radius of the circle such that $0 < d_r \leq d$. Values for the new coordinates (x_i, y_i) were calculated from the random angle θ_r , the random distance (d_r) , and the coordinates of the previous point (x_{i-1}, y_{i-1}) based on the following equations:

$$x_i = x_{i-1} + d_r \cos(\theta_r) \quad (3)$$

$$y_i = y_{i-1} + d_r \sin(\theta_r) \quad (4)$$

The random walk for interpolating tracks was further constrained because the travel time remaining $(t_b - t_i)$ and the final destination (x_b, y_b) were known. Turchin (1998) refers to this type of random walk as a biased random walk. To account for this constraint, space-time prism concepts were again utilized. A circle was generated with the destination point (x_b, y_b) at the centroid with a radius (d_i) . The radius (d_i) was calculated by multiplying an adjusted maximum speed v_{adj} , by $(t_b - t_i)$, the time left between the current point (x_i, y_i) and destination (x_b, y_b) . Again, the adjusted maximum speed, v_{adj} , was used because if the known maximum speed was used to calculate the radius, a large circle was produced. A large circle allowed the random walk track to ‘wander around’ at the beginning of the interpolation and then be forced to make a ‘beeline’ to the destination at the end. The adjusted maximum speed was a speed that allowed the destination to be reached based on the distance and time between known points. The resulting radius (d_i) was proportional to the average speed of travel and the time needed to get to the destination for that step i . If x_i and y_i , calculated from equations (3) and (4), did not fall within this circle, the destination could not be achieved in the time remaining. These x, y coordinates were then thrown out and a new pair was generated until the resulting point fell within the circle. After a suitable point was found, the destination circle was reset based on the new travel distance (d_{i+1}) and remaining travel time $(t_b - t_{i+1})$. The process was repeated for the number of steps, n , needed to reach the destination.

The random walk model was deliberately calibrated to over-predict because the ultimate goal was to use the model to estimate tracks along unknown segments. The straight line distances of all the unknown segments were longer than the known segments, therefore the primates need to travel faster and farther to reach the destination. Faster travel along the unknown segments makes sense because this was one reason why the field biologists lost contact with the animals.

3.4. Interpolation assessment

Before complete tracks could be generated, the interpolation methods were tested. Using the begin and end points of the known segments, predicted segments were generated with both interpolation algorithms (figure 2, Step Two). For each observed known segment and predicted segment, distance, speed and sinuosity were calculated. Given the variable nature of the random walk method, the simulation was run 50 times and distance, speed and sinuosity were averaged. Distance and average speed are directly correlated, but speed is standardized by the elapsed time. Only those points that were within one standard deviation from the mean were used in the final analysis. Sinuosity is a ratio between the straight-line distance between end points and the distance measured along the track (equation (5)). The resulting value is a real number between 0 and 1 ($0.0 < \text{sinuosity} \leq 1.0$), where 1.0 represents a straight track.

$$\text{sinuosity} = \frac{\text{straight line distance}}{\text{track distance}} \quad (5)$$

All cases in which the observed data reported no movement (track distance = 0) were dropped from the sinuosity analysis to avoid dividing by zero.

Distance, speed, and sinuosity of observed known segments were then compared with the predicted values using several error statistics described by Willmott (1984) (figure 2, Step Three). Summary univariate measures were calculated: mean of the observed (\bar{O}), mean of the predicted (\bar{P}), and the standard deviations (s_o, s_p). Five difference measures were also calculated. The mean absolute error (MAE) and the root mean square error (RMSE) are average difference measures. RMSE is the error measure mostly commonly computed in geographical applications, but MAE is sometimes preferred because it is less sensitive to extreme values. Also calculated were the systematic and unsystematic root mean square errors ($RMSE_s, RMSE_u$). Systematic RMSE assesses whether the model errors are predictable in some fashion. Unsystematic RMSE identifies those errors that are not predictable mathematically. The final error measure, d , was used to estimate the overall relative degree to which O is approached.

In testing the random walk method, we could have used a type of jackknifing but we chose not to because it would have little effect on the final outcome. As a reminder, the random walk model is created with a frequency table of turns ($n = 726$ for *Ateles* and $n = 543$ for *Cebus*) determined from the known segments ($n = 155$ for *Ateles*, $n = 158$ for *Cebus*). Any one of the known segments contains at least two and at most eight turns. Those segments represent only a range of 0.3% to 1.5% of the total number of turns, implying that any one of the known segments contributes only a small amount to the overall model.

3.5. Home range calculation and daily track analysis

After the best interpolation method for each species was selected, complete tracks were created by combining the observed known segments with the interpolated unknown segments (figure 2, Steps Four and Five). Complete tracks were then used to answer two basic research questions: (1) What is the home range of each species?, and (2) What are the daily foraging habits of each species?

We define home range as the area used by the group in its normal daily activities over time (National Research Council 1981). There are numerous methods to estimate home range size, both non-statistical methods (e.g. minimum convex polygon and grid cell) and statistical methods (e.g. kernel density, harmonic mean, Fourier) (Worton 1987, 1995, Loehle 1990, Seaman and Powell 1996, Herbinger *et al.* 2001). Although other methods may be used more commonly in other areas of wildlife biology, the grid cell method was selected to be consistent with other primatology research (Altmann and Altmann 1970, Rasmussen 1982, Chapman 1988, Castro 1991, Ostro *et al.* 1999, Fashing 2001, Kaplin 2001, Singleton and Schaik 2001). In this study, a grid composed of 1-ha (100 m \times 100 m) cells (National Research Council 1981) was superimposed over a map of the site. Home range was calculated by summing the number of grid cells entered by each species during the 10-month study period. Overlap area was calculated by identifying those areas shared by both primate species during the study period.

Seaman *et al.* (1999) report that more than 50 samples are needed for home range size to reach asymptotic levels when using kernel density methods. They also report that other studies have found 100–300 samples are needed for the home range size to stabilize using the minimum convex polygon (MCP) method. No studies were found that describe sample size tests using grid methods. To test whether the home

range size was an artifact of sample size, we calculated home range estimates on random samples of 300, 600, 900, 1200, 1800, and 2100 observations from the set of mapped points. These were then compared to home range estimates on random samples of 300, 600, 900, 1200, 1800, 2100, 2400, 2700, 3000, and 3300 observations from the complete tracks. The complete tracks contained both the mapped points and interpolated positions of the intermediate points.

To gain better insight into the foraging behaviour of both species, a daily track analysis was performed. For each day, track length and total observation time (track duration) were calculated from the complete tracks. Summary statistics of track length and track duration were calculated and completed tracks were analysed through a simple linear regression.

4. Results

4.1. Interpolation assessment

To build the random walk interpolation, frequency tables for direction change were generated from the known segments (table 1). Calculating direction change required that at least three consecutive mapped points existed. For both species, ‘stay’ was the most frequently chosen option. The known segments were also used to generate maximum speed and average moving speed, two parameters used in the random walk algorithm (tables 2 and 3).

Scatterplots of observed track distance versus model-predicted distance are displayed in figure 4 (a. *Ateles*, $n = 155$; b. *Cebus*, $n = 158$). Scatterplots of observed track speed versus the model-predicted speeds for the known segments are displayed in figure 5 (a. *Ateles*, $n = 154$; b. *Cebus*, $n = 157$). The scatterplot graphs demonstrate that there is a systematic and fairly linear relationship between both models and the observed data for the distance and speed variables. Scatterplots were not generated for sinuosity values; predicted sinuosity values for the straight line model were always equal to 1.0 (given the definition of sinuosity, equation (5)). In the case of the random walk model, a simple linear regression showed little relationship between observed versus predicted sinuosity values (*Ateles* $r^2 = 0.40$, $n = 65$ and *Cebus* $r^2 = 0.34$, $n = 105$). This occurs because when a three-point segment contains one ‘stay’ and one ‘move’, a straight line results with a sinuosity value of 1.0. The predicted sinuosity values, however, deviated from the straight line movement.

For distance, the straight line method under-predicted the distance values and the constrained random walk over-predicted, for both *Ateles* and *Cebus*. Likewise, speed and sinuosity were under-predicted for the straight line and over-predicted for the random walk method for both species. For *Cebus*, the random walk method results in smaller differences than the straight line for both distance and speed. These simple measures suggest that the random walk method is slightly better than the straight line for *Cebus*.

The five difference measures (tables 2 and 3) were also used to assess performance of the models. For distance and speed, *MAE*, *RMSE*, and *d* indicated the straight

Table 1. Frequency table on turn direction for *Ateles* and *Cebus*.

Species	Ahead	Left	Right	Back	Stay
<i>Ateles</i>	36	18	14	32	626
<i>Cebus</i>	73	29	32	54	355

Table 2. Quantitative measures of model performance of straight line (SL) and random walk (RW) models for *Ateles*.

	Summary univariate measures					Simple linear OLS coefficients		Difference measures				
	\bar{O}	\bar{P}	s_o	s_p	N	a	b	MAE	$RMSE$	$RMSE_s$	$RMSE_u$	d
Distance												
SL	38.2	32.6	93.1	85.9	155	-2.1	0.9	5.7	19.1	35.3	16.0	0.95
RW	38.2	42.3	93.1	100.9	155	1.3	1.1	10.1	22.8	7.8	21.4	0.94
Speed												
SL	1.6	1.4	3.1	2.8	154	-0.02	0.88	0.20	0.67	0.42	0.54	0.99
RW	1.6	1.8	3.1	3.4	154	0.04	1.1	0.38	0.79	0.30	0.74	0.98
Sinuosity												
SL	0.85	1.00	0.29	0.00	65	1.0	1.00	0.15	0.32	0.32	0.00	0.71
RW	0.85	0.67	0.29	0.26	65	0.18	0.58	0.22	0.29	0.21	0.20	0.79

Table 3. Quantitative measures of model performance of straight line (SL) and random walk (RW) models for *Cebus*.

	Summary univariate measures					Simple linear OLS coefficients		Difference measures				
	\bar{O}	\bar{P}	s_o	s_p	N	a	b	MAE	$RMSE$	$RMSE_s$	$RMSE_u$	d
Distance												
SL	50.7	38.5	74.5	60.4	158	0.96	0.74	12.1	33.5	24.6	22.9	0.71
RW	50.7	52.4	74.5	72.1	158	6.06	0.92	13.9	24.3	23.4	6.5	0.85
Speed												
SL	2.1	1.7	2.3	2.2	157	-0.12	0.86	0.43	1.03	0.89	0.54	0.70
RW	2.1	2.2	2.3	2.5	157	0.14	0.97	0.59	0.97	0.97	0.10	0.74
Sinuosity												
SL	0.81	1.00	0.29	0.00	105	1.00	0.00	0.19	0.35	0.35	0.00	0.71
RW	0.81	0.67	0.29	0.25	105	0.24	0.53	0.21	0.27	0.19	0.19	0.91

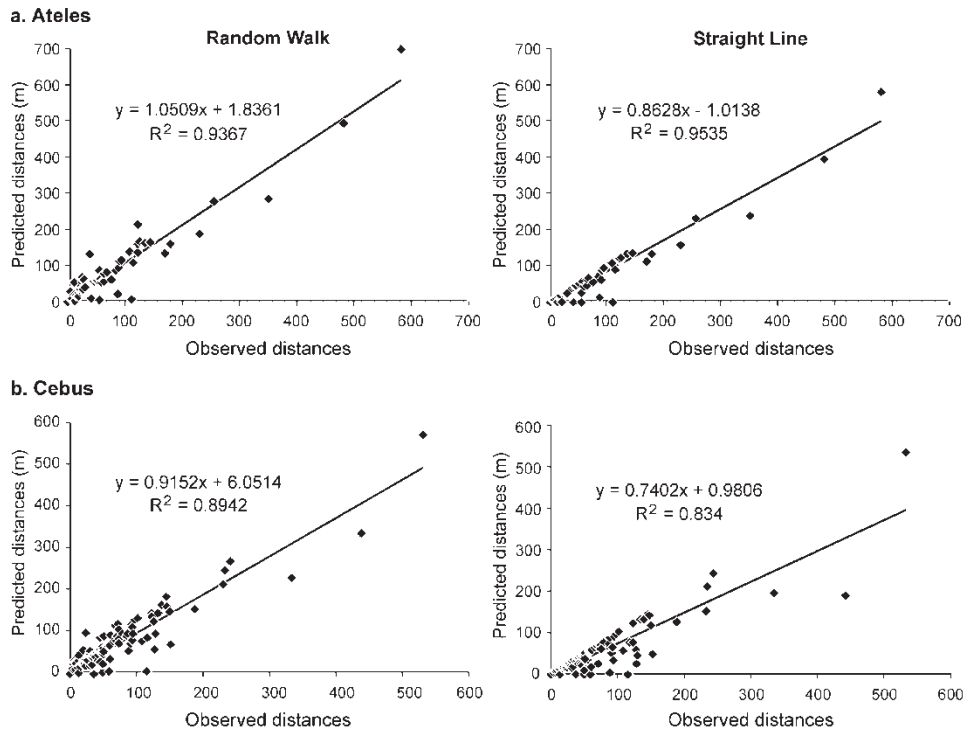


Figure 4. Observed versus predicted distances for (a) *Ateles* and (b) *Cebus*.

line models performed better for *Ateles*. For *Cebus*, this relationship was not as clear. *MAE* suggested the straight line model was better but *RMSE* and *d* suggested the random walk model was better. For sinuosity the *MAE* indicated the straight line was better for both *Ateles* and *Cebus*, but *RMSE* and *d* suggested the random walk method performed better. The difference measures $RMSE_s$ and $RMSE_u$ evaluated whether or not the errors in the model were systematic. As expected, the straight line models had higher amounts of systematic errors and the random walk model had higher levels of unsystematic errors for both distance and speed. $RMSE_s$ and $RMSE_u$ were not calculated for sinuosity because they depend on the OLS, which could not be calculated.

The interpolation method best suited to each species was applied to the unknown segments. The straight line model performed slightly better than the constrained random walk when comparing observed and predicted segments for *Ateles*. For *Cebus*, the random walk model performed better. Overall, however, both the straight line and the constrained random walk generally performed better for *Ateles* than they did for *Cebus*, suggesting that the movements of *Ateles* can be modelled more easily. The predicted unknown segments were then combined with the known segments creating complete tracks, which constitute one complete day at five-minute intervals. Figure 6 illustrates final tracks for both species for one day using both interpolation methods.

4.2. Home range

Home range calculations for the entire 10-month study period are reported in table 4, by month in table 5, and illustrated in figure 7 ((a) mapped points alone;

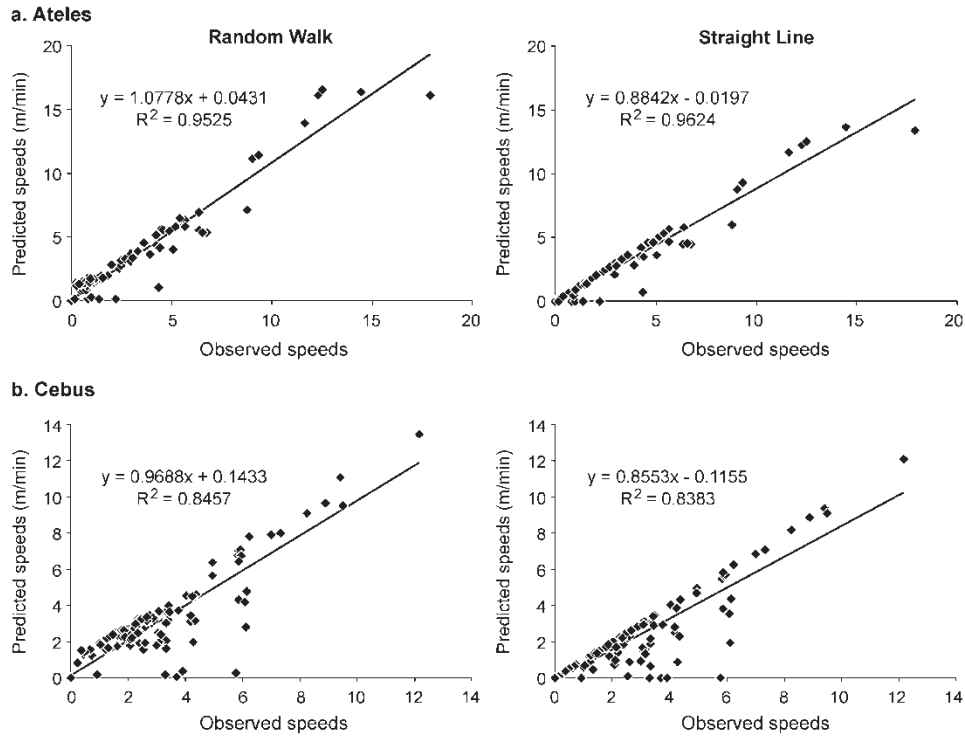


Figure 5. Observed versus predicted speeds for (a) *Ateles* and (b) *Cebus*.

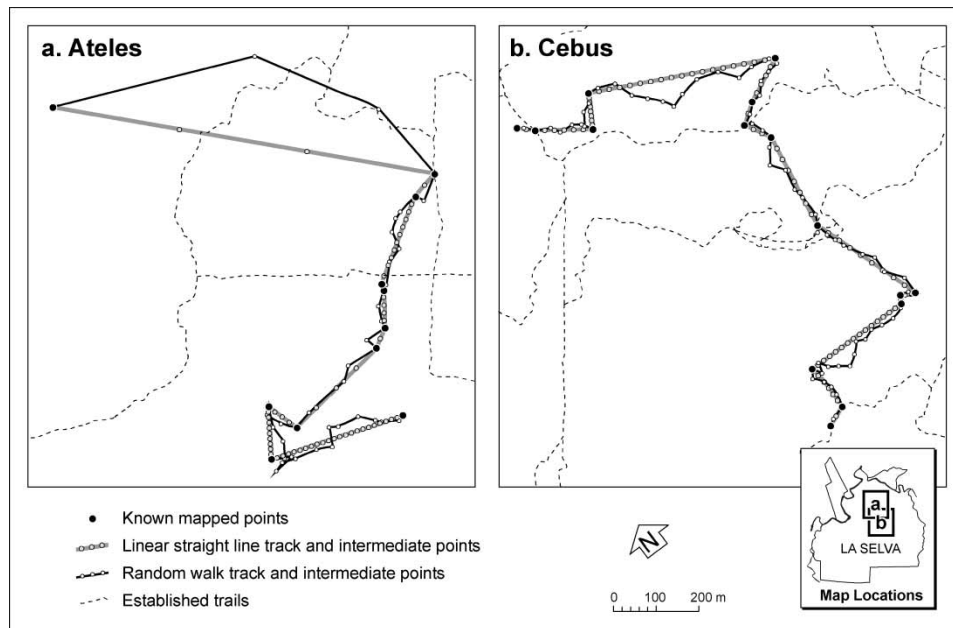


Figure 6. Sample complete tracks showing both the straight line and the random walk techniques for (a) *Ateles* and (b) *Cebus*.

Table 4. *Ateles* and *Cebus* home ranges, and their combined and overlapping home ranges as calculated with interpolated points and with mapped points only.

	Home Range (ha) calculated with mapped and interpolated intermediate points	Home Range (ha) calculated with mapped points only
<i>Ateles</i>	207	157
<i>Cebus</i>	217	185
Combined	306	256
Overlapping area	118	86

Table 5. Home ranges of *Ateles* and *Cebus* by month with mapped points alone and with mapped and interpolated intermediate points.

	Home Range (ha) calculated with mapped and interpolated intermediate points		Home Range (ha) calculated with mapped points only	
	<i>Ateles</i>	<i>Cebus</i>	<i>Ateles</i>	<i>Cebus</i>
March	13	31	9	21
April	96	60	55	42
May	49	60	24	47
June	33	35	25	31
July	58	55	28	35
August	72	42	45	31
September	76	99	53	83
October	50	60	33	49
November	18	51	12	38
December	26	42	22	34

(b) mapped and interpolated intermediate points). *Cebus* consistently had a larger home range than *Ateles* when calculated with and without the interpolated points. *Ateles* home range, however, experienced a greater percentage increase when comparing the interpolated to the home range size without using interpolated points (32% increase versus 17% increase in *Cebus*). They shared 118 ha, or 38.5% of the combined range using interpolated points and 33.6% without.

The size, location, and degree of overlap of home ranges for both species varied over time (table 5). Similar to the overall home range, *Cebus* consistently had a larger home range when calculated with and without the interpolated points. For *Ateles*, home range varied from a minimum of 13 ha in March to 96 ha in April when using the interpolated points. Mean monthly home range size over all months was 49 ha ($n=3465$ over 10 months, standard deviation=27.1). For *Cebus*, the minimum home range was 31 ha in March to a maximum of 99 ha in September, with a 56 ha mean home range size ($n=3494$ over 10 months, standard deviation=19.2). Generally, monthly home ranges were larger for *Cebus* than for *Ateles*, even though the number of observations was similar.

Despite a home range overlap of 118 ha overall, in any particular month the shared home range was relatively small, ranging from 0 ha in May to 24 ha in September. This possibly suggests that despite a moderate amount of overall common usage of forest, interaction between species may be minimal. Although evident with

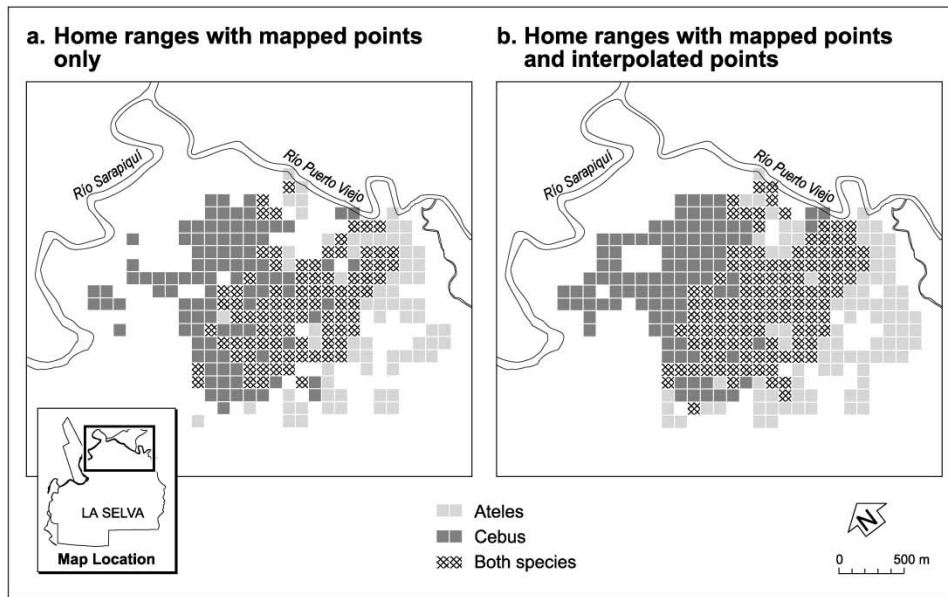


Figure 7. Home range for *Ateles* and *Cebus* with (a) mapped points alone and (b) mapped points and interpolated intermediate points.

the mapped points alone, the pattern is stronger when the interpolated data are included in the home range calculation.

Figure 8 displays the results of our assessment on whether the increase in home range size was an artefact of sample size. For both *Cebus* and *Ateles*, smaller sample sizes resulted in smaller home range estimates for the mapped points alone and the combination of mapped and intermediate points. For *Cebus* (figure 8(a)), for any given sample size, the home range size remained larger with the mapped points and smaller using points from the straight line mapped and intermediate points. The trend for each method is similar and home range size does not appear to stabilize at any sample size. In contrast, for *Ateles* (figure 8(b)), when the sample size was 900, 1200, and 1500, the mapped points alone estimated a larger home range size than the same sample size from the mapped and intermediate points. For both interpolation methods (random walk and straight line), it appears that the home range size stabilized when the number of samples reached 3000. For the mapped points alone, it is possible that the home range size stabilized when the sample number reached 1200, but the trend is not long enough to confirm this.

4.3. Daily track analysis

All daily tracks are summarized in table 6. Overall mean length for *Cebus* was longer than *Ateles* even though mean duration was similar, suggesting that *Cebus* tend to have more continuous travel. The high standard deviation for mean length and duration for both species, however, suggests extreme variation in their travel patterns.

Many of the tracks containing only the mapped points are short in duration (less than 25 minutes). This was due to factors such as losing the animals or animal entry into areas where access by researchers was prohibited. The relationship between

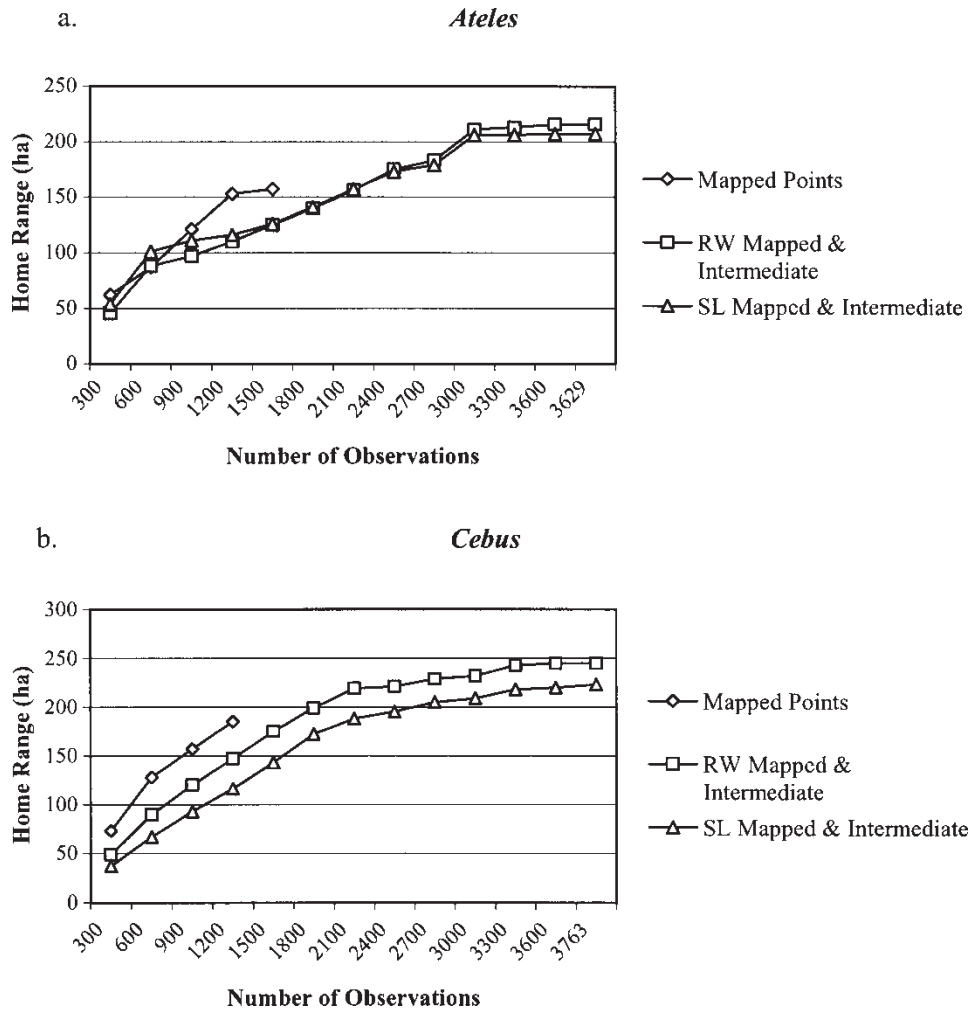


Figure 8. Sample size assessment for (a) *Ateles* and (b) *Cebus*.

track length and duration using just the mapped points is not simple or linear ($r^2 = 0.00$ *Ateles* and $r^2 = 0.11$ *Cebus*). This is particularly apparent for *Ateles*, where track lengths vary from 0 m to 668 m for a 10-minute duration. Even when analysing only those tracks with a 25-minute duration, this relationship improves for *Cebus* ($r^2 = 0.33$), but does not change for *Ateles* ($r^2 = 0.00$).

A clearer pattern emerges when the track analysis is performed using interpolated points. The resulting tracks are longer in duration because known segments are combined with unknown (interpolated) segments and represent travel for a single day rather than pieces of a single day. For *Ateles*, the relationship is stronger ($r^2 = 0.33$) although for *Cebus*, it is still stronger ($r^2 = 0.77$).

5. Discussion

It could be argued that the interpolated points and the resulting complete tracks may not represent true positions and therefore results and conclusions drawn from them are potentially spurious. Further investigation, however, reveals that the results

Table 6. Comparison of travel distance and duration for *Ateles* and *Cebus*, with mapped points alone, mapped points with duration greater than 25 minutes, and with mapped points and interpolated intermediate points.

	<i>n</i>	Mean length (m)	SD	Mean duration (min)	SD	<i>r</i> ²
Tracks with mapped points						
<i>Ateles</i>	157	34.1	86.8	28.1	22.9	0.00
<i>Cebus</i>	158	38.5	60.4	22.2	16.9	0.11
Tracks with mapped points with duration > 25 min						
<i>Ateles</i>	71	41.6	97.2	45.3	24.5	0.00
<i>Cebus</i>	48	54.5	56.6	41.3	19.4	0.33
Tracks with mapped points and interpolated intermediate points						
<i>Ateles</i>	52	118.7	944.5	343.7	171.0	0.33
<i>Cebus</i>	51	2323.4	1239.5	363.8	166.2	0.77

not only represent reasonable approximations of primate positions, but they actually reflect field observations of the movement patterns of both species. The development of these two algorithms supported observational hypotheses on primate behaviour that was only speculative before.

In the assessment of the two interpolation models for each species, the straight line model performed better for *Ateles* and the random walk model performed better for *Cebus*. This result agrees with observational experience, which indicates that *Ateles* tend to stay in one place for fairly long periods of time then move in a systematic and straight path toward their destination. Their feeding habit is to move directly from one feeding tree to another (Chapman 1988). In this situation, the straight line model is likely to be a better representation of their movement. Field observation of *Cebus* suggested that movement patterns are not straight and systematic due to their omnivorous feeding habits. Their habits involve stopping to forage for insects while moving between feeding trees (Chapman 1988). For these reasons, the constrained random walk did a better job of simulating their movement patterns.

The comparative assessment of foraging habits of the two species is further evaluated with an examination of their home ranges. Two distinct patterns are apparent: (1) in six of the ten months studied, the home range of *Ateles* and *Cebus* differ notably, with *Cebus* greater in all but one month; (2) in four of the ten months studied, the home ranges of both species were strikingly similar. The larger home ranges of *Cebus* suggest that although these primates do not travel as fast as *Ateles*, they travel more continuously using more overall forest space. Examination of monthly home range sizes further confirms this. This interpretation could have been drawn using the mapped points alone, but a larger home range was reported when using the interpolated points. A larger home range provides conservation agencies with data to justify making recommendations to policy makers to protect larger areas of land.

Although conservationists prefer to report a need for larger home ranges, the results of assessing sample size to calculate home range size are not conclusive. The estimation of home range size using mapped points alone did not stabilize for either species, so it is difficult to assess whether the increase in home range size using interpolated points is misleading. The home range size does stabilize for *Ateles*,

however, when the combination of mapped points and interpolated points is used. This suggests that for this species, the home range size reaches equilibrium when 3000 samples or more are used to estimate home range size.

We do not believe the results of the sample size assessment impact our reasoning for creating the interpolated segments and using them to estimate home range size. This rationale is based on the fact that both species must have traveled along some path over the unknown segment. We know that we lost the animals at the end of a known segment (point *(a)*, for example) and found them again at the start of the next known segment (point *(b)*, for example). The unknown segment from the end of *(a)* to the start of point *(b)* is part of their home range and part of their daily path and some estimation of these locations should be included in the analyses.

Unlike home range results that could have been made without the interpolated points, the results from daily track analysis without the interpolated points would have been more difficult to interpret. For *Ateles*, no relationship between travel distance and time emerged using only the mapped points or using the complete tracks. This is because these primates spend long periods of time in one location and then move quickly and directly to the next destination. In many cases, it was during this travel period that visibility with the animals was lost. We know, however, that they started at one location and eventually ended up at an observed destination, so clearly there must be a track between the two points. Field observations of *Cebus*, on the other hand, suggest they tend to move more slowly and more frequently, implying a more linear relationship between travel distance and time. Using only the mapped points, this relationship is weak ($r^2 = 0.11$) because, like *Ateles*, they were occasionally not visible or entered a restricted area of the forest limiting the monitoring of them. Using the constrained random walk interpolation, a data set was created containing approximations of their positions and a stronger relationship between travel distance and time ($r^2 = 0.77$) emerged.

6. Conclusion

With continued pressure of tropical deforestation and the protection of species, research to understand movement patterns of primates is critical. This research introduced two approaches to interpolating tracking data to explore and to analyse the tracks of two primate species in Costa Rica. This study helped to identify that *Ateles* tend to move directly to their destination, thus the straight line method performed reasonably well. *Cebus*, on the other hand, tended to follow a more wandering track, so the random walk model performed better. The final interpolated tracks assisted in calculating the home range and in describing the daily ranging habits for each species. Future research will involve describing the patterns of concentration in their home range, identifying the core area, and attempting to understand why these patterns emerge. Seasonal changes to home range size and distribution will also be compared with variations in plant phenology and seasonal climate variations.

Future research could also involve modifications to the interpolation methods. We could modify the random walk method to generate missing track segments through a local interpolator rather than a global interpolator. The current approach involves creating a large scale model of their movement patterns and then creating turns to generate tracks at a smaller scale, similar to global interpolators regression analysis and trend surface analysis. Creating a local interpolator for creating missing track segments may reflect possible patterns currently lost at the local scale.

Other modifications can be made to both interpolation models. One possibility is to create weighted distances with a non-homogenous surface representing impedances to travel or to include barriers to travel (e.g. a large body of water that the primates are unable to cross). Another modification could be to use the model to extrapolate points either prior to the beginning of the known data or past the last known point. These modifications are not included in this implementation but may be required depending on the application.

Although the present research represents only one empirical study, two algorithms for interpolating tracking data have been presented and evaluated. The development of these tools represents new methods to assist researchers as they examine the complex spatio-temporal relationships of tracking data. Although we present data on animal tracking, results of our research can be expanded to other types of tracking data. We would anticipate that the algorithms could be expanded to objects in a constrained trajectory (Moreira *et al.* 1999). In this context, researchers could, for example, interpolate and potentially assess bus, truck, and automobile movement in an urban street network. We hope that this research is simply the first step in building more extensive tools for analysing tracking data.

Appendix

Set the following variables:

Set numRight = number of times movement is between 135 and 45 degrees
 Set numLeft = number of times movement is between -135 and -45 degrees
 Set numAhead = number of times movement is between 45 and -45 degrees
 Set numBack = number of times movement is between 135 and -135 degrees
 Set numStays = number of times no movement occurred
 Set numMoves = numRight + numLeft + numAhead + numBack

For a known starting point (x_{Prev} , y_{Prev}) and a known destination (x_{Next} , y_{Next}) and at least one point ($i > 1$) in between that needs to be interpolated, do the following:

Set the following variables:

Set goRatio = $\frac{1}{2} * ((\text{numMoves} / (\text{numMoves} + \text{numStays})) + 1)$ /* a ratio used to decrease the possible distance travelled from the origin so that the random walk does not wander around the origin and then need to make a beeline to the destination in order to arrive in time. the represents a compromise between the true goRatio, which would be numMoves/(numMoves + numStays, and a 'going all the time ratio' (i.e. 1).

Set maxSpeed = a speed that will work based on the distance and time between known points, using the known average speed as a starting point and incrementing at $0.5 * \text{known average speed}$ until a usable speed is found or until the known maximum speed is reached. The algorithm rejects speeds if the destination cannot be met in the time given.

Set deltaTimePC = time from previous known point to the current point to be interpolated. This is usually a fixed time interval for the entire interpolation, but the data may have fluctuations in it

Set maxDistPC = maxSpeed * deltaTimePC /* maximum distance that can be traveled from previous known to the point that needs to be interpolated.

For all the points i between two known points, do the following:

Get the coordinates for the previous known point, $xPrev, yPrev$

Set deltaTimeCN = time from current point to be interpolated to the next known point—the destination ($xNext, yNext$)

Set $\text{maxDistCN} = \text{maxSpeed} * \text{deltaTimeCN}$ /* the maximum distance that can be travelled from the destination point in the time remaining. This decreases as the number of points left to interpolate goes to zero

If $\text{maxDistCN} = 0$, multiply numStays by 10 /* This gives a higher chance for a stay

Do the following loop:

Set ranDistPC as a random distance between $0 \leq \text{maxDistPC}$

Set ranAngle as an angle based on a frequency table:

Select a random number between 1 and $\text{numMoves} + \text{numStays}$:

Set Case RIGHT: If the random number is > 1 and $< \text{numRight}$ then Set ranAngle = a new random number between 135 and 45 degrees

Set Case LEFT: If the random number is $> \text{numRight}$ and $< \text{numRight} + \text{numLeft}$ then Set ranAngle = a new random number between -135 and -45 degrees

Set Case AHEAD: If the random number is $> \text{numRight} + \text{numLeft}$ and $< \text{numRight} + \text{numLeft} + \text{numAhead}$ then Set ranAngle = a new random number between 45 and -45 degrees

Set Case BACK: If the random number is $> \text{numRight} + \text{numLeft} + \text{numAhead}$ and $< \text{numMoves}$ then Set ranAngle = a new random number between 135 and -135 degrees

Set Case STAY: If the random number is $> \text{numMoves}$ and $< \text{numMoves} + \text{numStays}$

If Case = STAY then

/* don't move, just set the new points equal to the old points

Set $xTry = xPrev$

Set $yTry = yPrev$

Else

/* set the new points based on the random distance selected and the random angle selected

Set $xTry = xPrev + \text{ranDistPC} * \cos(\text{ranAngle})$

Set $yTry = yPrev + \text{ranDistPC} * \sin(\text{ranAngle})$

Calculate trialDist = distance between $xTry, yTry$ and the destination, $xNext, yNext$

While $\text{trialDist} > \text{maxDistCN} * \text{goRatio}$, do the above loop body until $xTry$ and $yTry$ are acceptable

/* the new coordinates are set as the previous known point and continue through the For loop until the destination is reached

Set $xPrev = xTry$

Set $yPrev = yTry$

References

ALTMANN, S.A., and ALTMANN, J., 1970, *Baboon Ecology: African Field Research* (Basel: S. Karger).

- BIAN, L., 2000, Object-oriented representation for modelling mobile objects in an aquatic environment, *International Journal of Geographical Information Science*, **14**, 603–624.
- BROTAK, E., and LE COMTE, D., 1994, Software Review of Hurrtrak, *Weatherwise*, August/September, 54–55.
- BRUNK, B., and DAVIS, B., 2002, SDAT enterprise: Application of geospatial network services for collaborative airspace analysis. In *CADD/GIS Symposium Proceedings*, San Antonio.
- BURNS, L. D., 1979, *Transportation, Temporal and Spatial Components of Accessibility* (Lexington, Massachusetts: Lexington Books).
- CAMPBELL, A. F., and SUSSMAN, R. W., 1994, The value of radio tracking in the study of neotropical rain forest monkeys, *American Journal of Primatology*, **32**, 291–301.
- CASTRO, N. R., 1991, Behavioral Ecology of Two Coexisting Tamarin Species (*Saguinus fuscicollis nigrifrons* and *Saguinus mystax mystax*, Callitrichidae, Primates) in Amazonian Peru. PhD. Dissertation. Washington University, St. Louis, Missouri.
- CARAPPELLA, R., 1997, Tracking storm water with GIS. *Earth Observation Magazine*, **6**, 34–36.
- CHAPMAN, C. A., 1988, Patterns of foraging and range use by three species of neotropical primates, *Primates*, **29**, 177–194.
- CRIST, T.O., GUERTIN, D. S., WIENS, J. A., and MILNE, B. T., 1992, Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie, *Functional Ecology*, **6**, 536–544.
- FASHING, P. J., 2001, Activity and ranging patterns of Guerezas in the Kakamega Forest: Intergroup variation and implications for intragroup feeding competition, *International Journal of Primatology*, **22**, 549–577.
- GAUTESTAD, A. O., and MYSTERUD, I., 1993, Physical and biological mechanisms in animal movement processes. *Journal of Applied Ecology*, **30**, 523–535.
- GEORGES, T. M., HARLAN, J. A., MEYER, L. R., and PEER, R. G., 1993, Tracking hurricane Claudette with US Air Force One over the horizon radar. *Journal of Atmospheric and Oceanic Technology*, **10**, 441–451.
- HÄGERSTRAND, T., 1970, What about people in regional science. *Papers of the Regional Science Association*, **24**, 7–21.
- HAMMERSLEY, J. M., and HANDSCOMB, D. C., 1964, *Monte Carlo Methods* (London: Methuen).
- HARIHARAN, R., and HORNSBY, K., 2000, Modeling intersections of geospatial lifelines. In *GIScience 2000*, edited by A. R. Caschetta, (Savannah, Georgia: NOAA), pp. 208–210.
- HERBINGER, I., BOESCH, C., and ROTHE, H., 2001, Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology*, **22**, 143–167.
- HOOGHE, P. N., and EICHENLAUB, B., 1997, Animal movement extension to arcview ver. 1.1. Alaska Science Center—Biological Science Office, US Geological Survey, Anchorage, AK USA.
- HOOGHE, P. N., EICHENLAUB, W. M., and SOLOMON, E. K., 2001, Using GIS to analyze animal movements in the marine environment. http://www.absc.usgs.gov/glba/gistools/animal_mvmt.htm
- KAPLIN, B. A., 2001, Ranging behavior of two species of Guenons (*Cercopithecus lhoesti* and *C. mitis doggetti*) in the Nyungwe Forest Reserve, Rwanda, *International Journal of Primatology*, **22**, 521–548.
- LOEHLE, C., 1990, Home range: A fractal approach. *Landscape Ecology*, **5**, 39–52.
- MOREIRA, J., RIBEIRO, C., and SAGLIO, J.-M., 1999, Representation and manipulation of moving points: an extended data model for location estimation. *Cartography and Geographic Information Science*, **26**, 109–123.
- MILLER, H. J., 1991, Modelling accessibility using space-time prism concepts within geographical information systems. *International Journal of Geographical Information Systems*, **5**, 287–301.
- NATIONAL RESEARCH COUNCIL, 1981, *Techniques for the Study of Primate Population Ecology* (Washington, D.C.: National Academy Press).
- OSTRO, L. E. T., YOUNG, T. P., SILVER, S. C., and KOONTZ, F. W., 1999, A geographic information system method for estimating home range size. *Journal of Wildlife Management*, **63**, 748–755.

- PFOSER, D. and JENSEN, C., 1998, Capturing the uncertainty of moving-object representation. *Advances in Spatial Databases*, edited by R. H. Güting, D. Papadias, and F. Lochovsky, Lecture Notes in Computer Science 1651 (Berlin: Springer), pp. 111–131.
- PRIEDE, I. G., and FRENCH, J., 1991, Tracking of marine animals by satellite. *International Journal of Remote Sensing*, **12**, 667–680.
- RASMUSSEN, D. R., 1982, Clumping and consistency in primates' patterns of range use: definitions, sampling, assessment, and applications. *Folia primatologica*, **34**, 111–139.
- ROTHSTEIN, S. I., VERNER, J., and STEVENS, E., 1984, Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird, *Ecology*, **65**, 77–88.
- SANFORD, R. L. JR., PAABY, P., LUVALL, J. C., and PHILLIPS, E., 1994, Climate, Geomorphology, and Aquatic Systems. In *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (Chicago: University of Chicago Press).
- SCHIPPERS, P., VERBOOM, J., KNAAPEN, J. P., and VAN APLEDOORN, R. C., 1996, Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography*, **19**, 97–106.
- SCHMUTZ, J. A., and WHITE, G. C., 1990, Error in telemetry studies: effects of animal movement on triangulation. *Journal of Wildlife Management*, **54**, 506–510.
- SEAMAN, D. E., MILLSPAUGH, J. J., KERNOHAN, B. U., BRUNDIGE, G. C., RAEDEKE, K. J., and GITZEN, R. A., 1999, Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, **63**, 739–747.
- SEAMAN, D. E., and POWELL, R. A., 1996, An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- SINGLETON, I., and VAN SCHAİK, C. P., 2001, Orangutan home range size and its determinants in a Sumatran swamp forest. *International Journal of Primatology*, **22**, 877–911.
- SOUTH, A., 1999, Extrapolating from individual movement behaviour to population spacing in a ranging mammal. *Ecological Modelling*, **117**, 343–360.
- TISCHENDORF, L., 1997, Modelling individual movements in heterogeneous landscapes: potentials of a new approach. *Ecological Modelling*, **103**, 33–42.
- TISCHENDORF, L., IRMLER, U., and HINGST, R., 1998, A simulation experiment on the potential of hedgerows as movement corridors for forest carabids. *Ecological Modelling*, **106**, 107–118.
- TURCHIN, P., 1998, *Quantitative Analysis of Movement* (Sunderland, Massachusetts: Sinauer Associates, Inc.).
- USGS, 1997, Forum on Wildlife Telemetry: Innovations, Evaluations, and Research Needs. In *Forum on Wildlife Telemetry: Innovations, Evaluations, and Research Needs*. US Geological Survey and The Wildlife Society. Jamestown, ND: Northern Prairie Wildlife Research Center, Snowmass Village, Colorado.
- WALSH, S. J., BUTLER, D. R., BROWN, D. G., and BIAN, L., 1990, Cartographic modeling of snow avalanche path location within Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing*, **56**, 615–621.
- WATURU, S., and YUZURIHA, H., 1993, Tracking free-swimming marine animals. *Sea Technology*, **34**, 25.
- WILLMOTT, C. J., 1984, On the evaluation of model performance in physical geography. In *Spatial Statistics and Models*, edited by G. L. Gaile and C. J. Willmott (Dordrecht, Holland: Reidel Publishing Co.), pp. 443–460.
- WILSON, D. W., 1994, Tracking small animals with thread bobbins. *Herpetological Review*, **25**, 13–14.
- WORTON, B. J., 1987, A review of models of home range for animal movement. *Ecological Modelling*, **38**, 277–298.
- WORTON, B. J., 1995, Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, **59**, 794–800.