

SHORT-DURATION DAYTIME MOVEMENTS OF A COW HERD OF AFRICAN ELEPHANTS

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We examined daytime movements of a herd of African elephants (*Loxodonta africana*) at 10-min, 15-min, and 20-min intervals in Pongola Game Reserve, South Africa. This group tended to proceed in a consistent direction during consecutive movements, especially during long moves. Serial movement lengths and serial movement angles were autocorrelated at 10-min and 15-min intervals but not at 20-min intervals, indicating that 20-min intervals may be a suitable temporal scale to avoid oversampling. Herd movements followed a Lévy-modulated correlated random walk. In addition, looping movements were detected. Spatial scale of the loops averaged about 1 km. Movement strategies that include both Lévy walks and correlated random walks are thought to optimize foraging.

Key words: animal movement, elephant, Lévy walk, looping, *Loxodonta africana*

Individual-based movement models can help in understanding relationships between animals and their habitats. Models of this type require knowledge of small-scale movement patterns of isolated individuals or closely associated groups that are determined by underlying ecological processes and result in differential habitat use. This understanding can be used for both animal management and habitat conservation (Dickson et al. 2005).

Random walk models have been widely used in the analysis of animal movement paths (Turchin 1998). The simplest of these is a pure random walk where angles between successive movements are entirely random. This approach ignores the fact that many animals have a tendency to move in preferred directions, a situation better modeled by a correlated random walk. These models use turning angles and movement lengths from independent distributions but the angles are not distributed uniformly as in a random walk (Austin et al. 2004; Bartumeus et al. 2005). The resulting paths are characterized by a certain degree of directional persistence.

Several studies have shown animal movements that are characterized by a long-tailed power-law distribution of movement lengths, called a Lévy distribution (Ramos-Fernández et al. 2004; Viswanathan et al. 1999). Lévy movement processes can be classified into Lévy flights and Lévy walks (Shlesinger et al. 1993). Lévy flights do not possess finite mean squared

displacements and particles can execute long jumps instantaneously. For most physical systems with Lévy movement length distributions it is more realistic to introduce finite particle speed, a model referred to as a Lévy walk (Metzler and Klafter 2000). Bartumeus et al. (2005) combined the properties of correlated and Lévy walks to introduce a Lévy-modulated correlated random walk where turning angles show directional persistence and step lengths follow a power-law distribution.

There are many examples of organisms that use Lévy movement strategies such as amoeba (Schuster and Levandowsky 1996), microzooplankton (Bartumeus et al. 2003), foraging ants (Shlesinger and Klafter 1986), *Drosophila* (Cole 1995), bees, deer, wandering albatross (Viswanathan et al. 1999), female reindeer (Mårell et al. 2002), jackals (Atkinson et al. 2002), gray seals (Austin et al. 2004), and spider monkeys (Ramos-Fernández et al. 2004). Viswanathan et al. (1999) demonstrated that a Lévy distribution results in efficient foraging. For the power-law distribution of movement lengths an exponent close to 2 is an optimal value for searches to find sparsely and randomly distributed resource targets. Lévy distributions result in optimal searching because greater numbers of food patches are visited with fewer repeat visits (Austin et al. 2004; Bartumeus et al. 2005; Ramos-Fernández et al. 2004; Viswanathan et al. 1999). Bartumeus et al. (2005) have shown theoretically that a Lévy-modulated correlated random walk can result in even greater search success. For nondestructive foraging, optimal searching success increases with an increase in directional persistence.

Looping is another movement pattern detected in insects, birds, and mammals (Bengtsson et al. 2004; Cameron et al. 1988; Cant et al. 2005; Conradt et al. 2000; Weimerskirch et al.

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2000; Wiktorsson et al. 2004) that may be linked to optimal searching. Looping can occur when animals reach the edge of a preferred habitat or feeding patch and turn to remain in it.

To date some researchers have investigated African elephant (*Loxodonta africana*) movement broadly in terms of habitat occupancy or seasonal shifts in home range (De Villiers and Kok 1997; Douglas-Hamilton et al. 2005; Duffy et al. 2002; Verlinden and Gavor 1998; Whitehouse and Schoeman 2003), but analysis of movement paths has not as yet been attempted. Elephant cow herds, known as family units, consist of a matriarch with her daughters and their offspring. The individuals in a family unit are always in close proximity to each other and frequently make physical contact. They consequently move about the landscape in a tightly knit unit. Adult males occur singly, in small associations with 2 or 3 other elephants, or with female herds.

In this study, we describe the short-duration movement characteristics of 1 herd of elephants found in a small South African game reserve. Food for elephants in African Savannas occurs in patches of varying nutritional quality (Scholes and Walker 1993). This elephant herd, in common with all others, exhibits strong selection for particular plant species and particular habitat types (Shannon et al. 2006; Viljoen 1989). Thus, we predicted that, if they are behaving optimally, short-duration movements of the elephant group will have turn angles with directional persistence, Lévy walk properties, and paths that loop.

MATERIALS AND METHODS

Study area.—The 82-km² Pongola Game Reserve is located in South Africa and lies along the western edge of Jozini Dam, in northeastern KwaZulu-Natal, South Africa, bordering southeastern Swaziland (27°25'S, 31°57'E). It comprises several private game farms but is fenced and managed as a whole. There are 7 vegetation types. The terrain is relatively flat and bisected by several small drainage lines. The climate is hot and arid with 400–600 mm of rainfall per year and more than 60% of the rain falling in summer months (mid-October to mid-March). Elephants and other wildlife have been reintroduced for tourism. During the study period the Pongola Game Reserve had 3 distinct elephant groups: a cow herd of 38 elephants, a separate orphan group of four 15-year-old females, and 4 free-ranging adult bulls. The cow herd used only the 34-km² area adjacent to the dam.

Movement data.—Between December 2002 and October 2004, the movements of the cow herd were observed in daytime from a vehicle using the extensive road network on the reserve. Cow herds frequently have a few adult males temporarily with the group, and the data analyzed are for the cow herd with at least 1 adult male present. The orphan group was not considered. The initial location of the herd was found using a very-high-frequency radiocollar on the matriarch that was fitted by a veterinary surgeon in a humane manner, and in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and the laws governing animal anticruelty in South Africa. Once located, the position of the herd was calculated trigonometri-

cally from the global positioning system position of the observer, a compass bearing, and the distance to the center of the group estimated using a laser range finder. Observations were made between 50 and 200 m away and the center of the group was estimated to an accuracy of approximately 10 m. Positions were recorded at 10-min and 15-min intervals for 1–3.5 h. The optimal sampling interval for studies of movement of elephants has not been determined, so we analyzed the data for 3 sampling intervals to determine if the data are over-sampled at 10 min or 15 min. Subsampling the 10-min data set to obtain a 20-min data set halved the number of samples. We therefore collected additional data at 20-min intervals. No individuals of the group were disturbed when followed. For this and other reasons, sampling at exact intervals was sometimes not possible. Only those paths with regular time intervals (10 ± 1 min, 15 ± 1 min, and 20 ± 1 min) and at least 3 movement segments were selected for analysis. In all, 108 paths made up of 710 positions and 602 segments were used. The total duration of tracking was 144.8 h. For further analysis elephant locations were projected into universal transverse mercator 1983 (Zone 36, WGS84 datum) with the Projector Extension from ArcView 3.3 (ESRI 2002).

Movement statistics.—We used Hawth's Analysis Tools for ArcGIS version 3.x (Beyer 2004; <http://www.spatial ecology.com/htools>) to calculate movement length l (segment distance in meters), movement angle β (segment direction with 0° representing true north), and turning angle α (the absolute angle between the previous step and the next step, with 0° representing continuing in the existing direction), of the herd.

Mean direction was computed by treating all angular measurements as points on 1 unit circle, and the mean resultant length ρ was used to measure any concentration of angles. This value falls in the interval [0, 1], with ρ close to 1 when the data are highly concentrated around 1 direction, and close to 0 for widely dispersed data. A Rayleigh test of uniformity was performed to assess whether the angles were concentrated around 0° (Zar 1999). The average sine of the turning angle s (close to 0) was used to determine if the distribution was symmetric.

For each data set (10-min, 15-min, or 20-min intervals), we calculated linear–circular or circular–circular correlation coefficients (Jammalamadaka and Lund 2006; Liddell and Ord 1978; Mardia 1976) to determine if there were any correlations between mean movement length, turning angle, and movement angle. To test for autocorrelation (serial correlation), we computed the linear correlation coefficient between all pairs of movement length l_i and the length of previous move l_{i-1} , circular–circular correlation coefficients between all pairs of turning angle α_i and the previous α_{i-1} , between all pairs of movement angle β_i and the previous β_{i-1} (Turchin 1998). All the above analyses were completed using circular and CircStats packages of the R environment (R Development Core Team 2006).

Path analysis.—We calculated the observed net squared displacement $\overline{R_n^2}$ (averaged $\overline{R_n^2}$ over all the paths). A displacement R_n is the straight-line distance from the starting point to the position after n moves. The observed $\overline{R_n^2}$ was compared with the correlated random walk $\overline{R_n^2}$ given by the equation for when the turning angle distribution is symmetric:

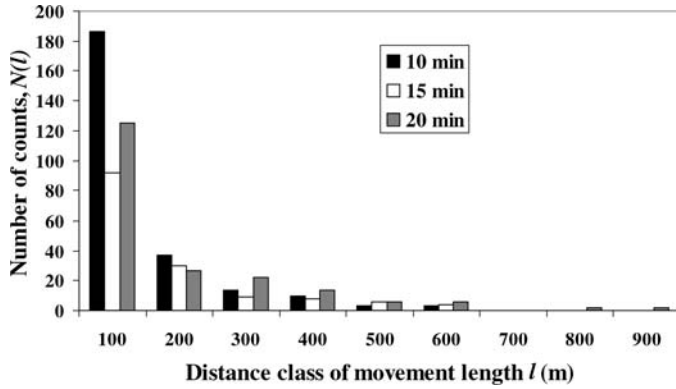


FIG. 1.—Histogram of movement lengths at 10-, 15-, and 20-min intervals.

$$\overline{R_n^2} = nm_2 + 2m_1^2 \frac{\varphi}{1 - \varphi} \left(n - \frac{1 - \varphi^n}{1 - \varphi} \right) \quad (1)$$

where $m_1 = \frac{1}{k} \sum_{i=1}^k l_i$, $m_2 = \frac{1}{k} \sum_{i=1}^k l_i^2$, $\varphi = \frac{1}{k} \sum_{i=1}^k \cos \alpha_i$, and α_i are turning angles (Kareiva and Shigesada 1983). The α_i and l_i were taken directly from the original data.

For a Lévy process, the frequency distribution of movement lengths (l) will vary with the power law $N(l) \sim l^{-\alpha}$ where $1 < \alpha \leq 3$ (Viswanathan et al. 1999). For a Lévy walk the mean squared displacement will vary as $\overline{R^2}(t) \sim t^c$ where $1 < c < 2$ (Ramos-Fernández et al. 2004; Zumofen and Klafter 1995). Waiting or sticking times have been shown to follow the relation $W(t) \sim t^{-b}$ (Ramos-Fernández et al. 2004). Zumofen and Klafter (1995) show that in Lévy walk situations with waiting or sticking the relationship between the exponents (a , b , and c) of the above power laws is such that

$$c^* = \begin{cases} 2 + \min(b, 2) - a & 2 < a \leq 3 \\ 2 + \min(b, a) - a & 1 < a \leq 2 \end{cases} \quad (2)$$

These relationships were used to determine the suitability of the Lévy walk model to describe elephant movements. Data for stopped locations were pooled to obtain a frequency distribution of waiting times. The exponents were determined from linear regressions on log transforms of the data.

RESULTS

Movement lengths (mean \pm SE) averaged 103 ± 12 m over 10-min intervals (0.62 ± 0.07 km/h), 145 ± 18 m over 15-min intervals (0.58 ± 0.07 km/h), and 197 ± 17 m over 20-min intervals (0.59 ± 0.07 km/h). The majority of the individual segments (81.4%) were less than 100 m (Fig. 1).

The herd tended to keep its previous direction when moving. Mean turning angle was $8.3^\circ \pm 3.2^\circ$ for the 10-min interval paths, $-8.5^\circ \pm 4.0^\circ$ for the 15-min interval paths, and $12.9^\circ \pm 3.7^\circ$ for the 20-min interval paths. Rayleigh tests ($\rho = 0.356$, $df. = 203$, $P < 0.01$; $\rho = 0.425$, $df. = 115$, $P < 0.01$; $\rho = 0.385$, $df. = 145$, $P < 0.01$ for 10-, 15-, and 20-min interval paths, respectively) indicate that turning angles are not evenly

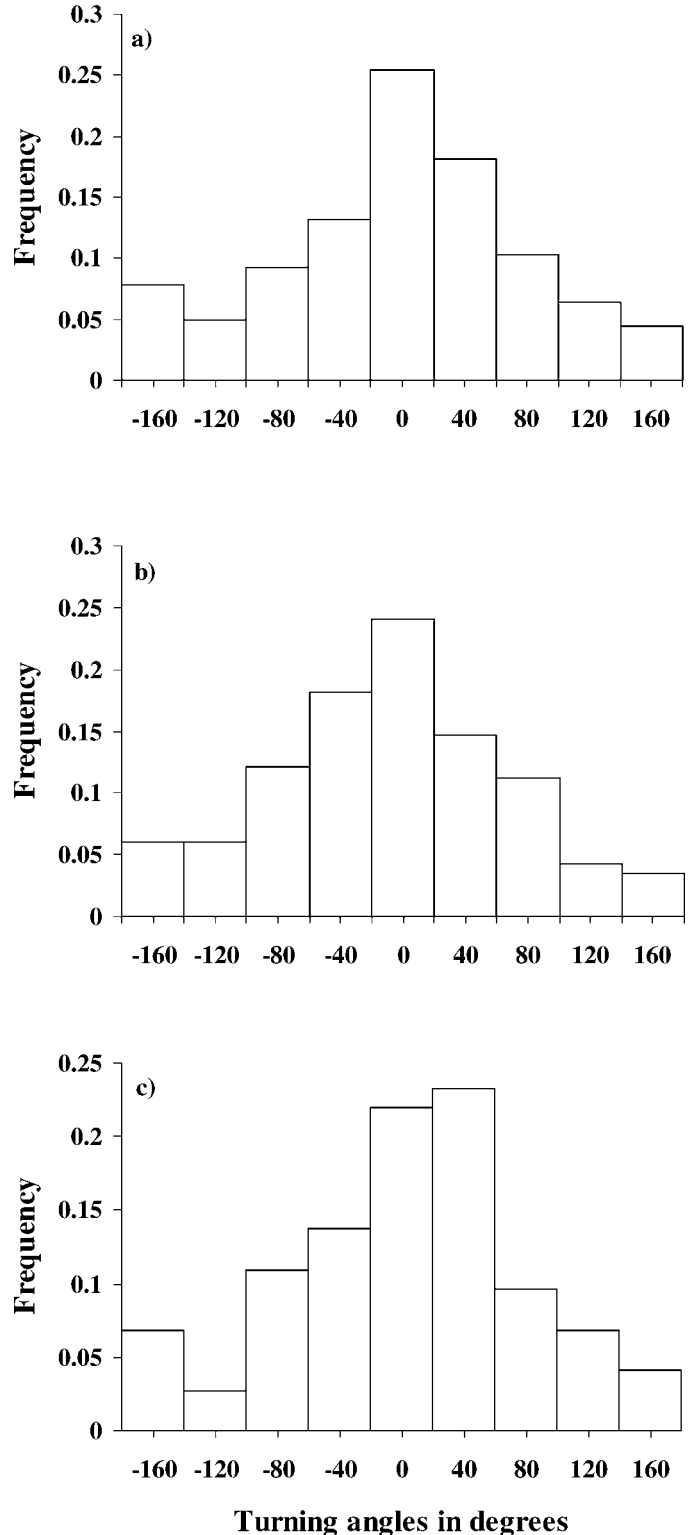


FIG. 2.—Frequency of turning angles for a) 10-min intervals, b) 15-min intervals, and c) 20-min intervals. Turning angles range from -180° to 180° . Data are grouped in bins of 40° for presentation.

distributed in all directions and concentrate around 0° ($\rho > 0$). The distribution of turning angles was nearly symmetrical around 0° ($s = 0.057, -0.076, 0.096$ for 10-, 15-, and 20-min intervals, respectively; Fig. 2).

TABLE 1.—Serial correlation coefficients between all pairs of movement lengths l_i and the previous l_{i-1} , all pairs of turning angles α_i and the previous α_{i-1} , and all pairs of movement angles β_i and the previous β_{i-1} . The $l_i \sim l_{i-1}$ are linear-linear correlations, and $\alpha_i \sim \alpha_{i-1}$ and $\beta_i \sim \beta_{i-1}$ are circular-circular correlations.

Time interval	$l_i \sim l_{i-1}$		$\alpha_i \sim \alpha_{i-1}$		$\beta_i \sim \beta_{i-1}$	
	r	P	r	P	r	P
10 min	0.168	0.01	-0.212	<0.01	0.193	<0.01
15 min	0.471	<0.01	-0.140	0.16	0.340	<0.01
20 min	0.150	0.08	-0.067	0.54	0.093	0.22

No significant bivariate correlations between movement length, turning angle, and movement angle were detected for the 3 time intervals ($P > 0.05$). Bivariate plots for lengths ≥ 100 m and turning angles had angles concentrated closer to 0° .

Significant autocorrelations existed between the consecutive movement lengths and between the consecutive movement angles in both 10-min and 15-min interval movements, but there was no such autocorrelation for the 20-min intervals (Table 1). Consecutive turning angles were autocorrelated for 10-min interval paths, whereas no autocorrelations were found between sequential turning angles for 15- and 20-min time intervals (Table 1).

For the 10-min interval data, a log-log regression between observed $\bar{R}^2(t)$ and time t up to 60 min result in an exponent $c = 1.215$ ($r^2 = 0.86$, $d.f. = 5$, $P < 0.01$). The frequency distribution of movement length $N(l)$ and l followed a power-law function with exponent $a = 2.363$ ($r^2 = 0.98$, $d.f. = 4$, $P < 0.01$). For waiting at successive intervals $W(t)$ the relationship with time t also followed a power law with an exponent $b = 1.567$ ($r^2 = 0.71$, $d.f. = 5$, $P < 0.05$). For the 15-min interval data, $c = 1.488$ (time $t \leq 75$ min; $r^2 = 0.94$, $d.f. = 4$, $P < 0.01$), $a = 1.749$ ($r^2 = 0.98$, $d.f. = 4$, $P < 0.01$). For the 20-min interval data, $c = 1.259$ (time $t \leq 100$ min; $r^2 = 0.93$, $d.f. = 4$, $P < 0.01$), $a = 1.866$ ($r^2 = 0.96$, $d.f. = 6$, $P < 0.01$). These exponents are summarized in Table 2.

For the 10-min interval data $2 < a \leq 3$, so the expected values for c from equation 2 are $c^* = 2 + \min(b, 2) - a = 1.204$ (Table 2). For the 15-min interval and the 20-min interval data $1 < a \leq 2$, and so $c^* = 2 + \min(b, 2) - a = 1.818$ and $c^* = 1.701$, respectively.

During all 3 sampling intervals, the observed net squared displacements $\bar{R}^2(t)$ did not continuously grow monotonically with number of steps (Fig. 3). The $\bar{R}^2(t)$ peaked at ~ 0.75 km (~ 60 min) for the 10-min interval paths, at ~ 1.25 km (~ 75 min) for the 15-min interval paths, and at ~ 0.75 km (~ 100 min) for the 20-min interval paths. The $\bar{R}^2(t)$ returned to a minimum value close to the origin at 180 min for the 10-min paths, at 150 min for the 15-min paths, and at 180 min for the 20-min paths.

DISCUSSION

The distances moved over all 3 time intervals were predominantly less than 100 m and thus the herd moved mainly over short distances before changing direction. When moving

TABLE 2.—Summary of the exponents required for a Lévy walk (see text for details).

Time interval	A	b	c	Predicted c^*
10 min	2.363		1.215	1.204
15 min	1.749	1.567	1.488	1.818
20 min	1.866		1.259	1.701

they tended to keep to the existing direction and did not show any preference between left and right turns.

The lack of correlation between movement angle, turning angle, and movement length indicate that, in general, the herd did not have a tendency to turn more or less when they moved over a short distance than when they moved over a long distance. Also, the length and turning angle of one move was independent of its absolute direction, indicating a lack of bias in any particular direction. However, consecutive lengths ≥ 100 m were more direct (turning angles more concentrated around 0°). This result is most likely because movements between food patches were more direct than movements within food patches.

Autocorrelations between sequential movement lengths and sequential movement angles indicate that the length and direction of a given move depends on that of the previous move, which suggests oversampling (Turchin 1998). For the 10-min and 15-min intervals, autocorrelations show that these were oversampled and that 20-min intervals were sufficient for understanding the herd's path structure. Oversampled data where the turn angles concentrate near 0° should result in autocorrelations between sequential turn angles, which was true for the 10-min intervals.

As predicted, short-duration movement of this herd can be characterized by Lévy processes. The frequency distributions of movement lengths, waiting time intervals, and mean squared displacements follow the required power laws for a Lévy walk. The observed c of the mean squared displacement power law is in the range $1 < c < 2$ and in addition is reasonably close to the c^* predicted by equation 2. Also, as predicted, directional persistence (turning angles around 0°) characterizes the herd paths. Movements can therefore be modeled using a combination of correlated and Lévy random walk theory (Lévy-modulated correlated random walk).

Viswanathan et al. (1999) show that for a Lévy distribution an exponent $a \approx 2$ is an optimal value for a search in sparsely and randomly distributed resource targets. For nondestructive foraging this success is increased with an increase in directional persistence (Bartumeus et al. 2005). Previous work in Pongola Game Reserve suggests that forage is sparsely and randomly distributed in different vegetation types (Duffy et al. 2002; Shannon et al. 2006). In our study, a values are close to the optimal value 2. These results suggest the possibility that this herd uses a combination of correlated and Lévy walks to locate food. For Lévy movement strategies, previously visited food sources are revisited after longer periods (Viswanathan et al. 1999), which could facilitate the recovery of utilized vegetation.

It has been postulated that Lévy walks could be a response to scale invariance of food in the landscape (Atkinson et al. 2002;

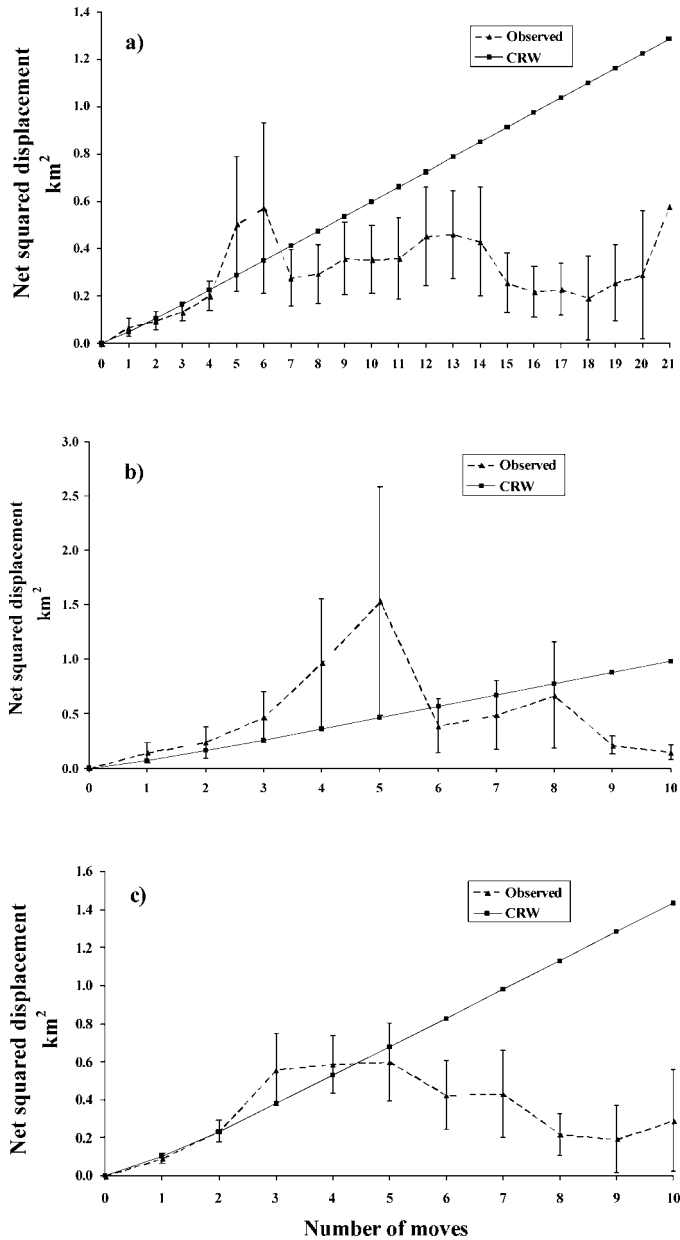


FIG. 3.—Comparisons of the observed net squared displacement $\overline{R_n^2}$ and those predicted by a correlated random walk model (CRW). Error bars are 1 SE. Time intervals: a) 10 min, b) 15 min, and c) 20 min.

Ramos-Fernández et al. 2004). Our results suggest that this could be the case in Pongola Game Reserve.

A peak followed by a fall in observed $\overline{R_n^2}$ indicates a tendency to loop. Looping occurred at scales between 0.5 km and 1.5 km and between 60 min and 100 min. For example, in one typical path (Fig. 4) the herd reached a maximum displacement of about 1.0 km after 90 min and then looped back returning close to the original location. These distances correspond to roughly the cross-sectional distances of habitat patches in the Pongola Game Reserve (Shannon et al. 2006). Looping by the herd probably occurs to stay within patches when selecting for them and is likely to characterize the movement of all elephant herds. Thus, elephant movement models also should include looping.

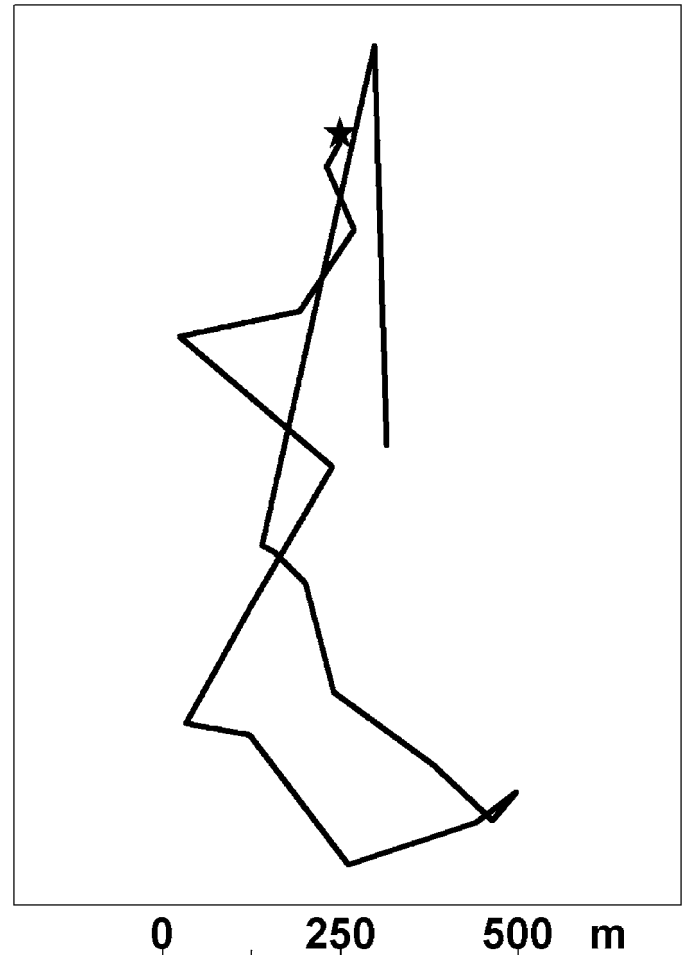


FIG. 4.—An example of a movement path of the group. A star shows the point where sampling began. Intervals between turns are 10 min.

African elephants have large effects on vegetation and high numbers can lead to extensive habitat modification (Skarpe et al. 2004). Driven by the need to manage these impacts several models have been developed to better understand the interaction between elephants and trees (Baxter and Getz 2005; Caughley 1976; Dublin et al. 1990; Duffy et al. 1999, 2000; Pellwe 1983). None of these models have considered the effects of elephant movements, which should influence the impact of elephants on trees. In this study, a combination of correlated random walk, Lévy walk, and looping described the short-duration movements of an elephant herd. The consequences of combined Lévy processes and correlated random walk (increased search efficiencies and reduced return times) and of looping (higher occupancy of some patches) emphasizes the importance of including movements in elephant–tree models.

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