

## MOVEMENT AND RANGING PATTERNS OF A TROPICAL RAT (*LEOPOLDAMYS SABANUS*) IN LOGGED AND UNLOGGED RAIN FORESTS

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Knowledge of how animals move through the environment is important for predicting effects of habitat change on faunal distributions. Logging of tropical rain forests produces habitat changes on multiple scales that may affect movement and habitat use by small mammals. To explore the effects of such habitat changes, we compared movement and ranging patterns of the long-tailed giant rat (*Leopoldamys sabanus*) in logged and unlogged rain forests in Borneo. On a small scale, movement was quantified using spool-and-line tracks; on a larger scale, movement was quantified via radiotracking. At the small scale, paths (49 tracks of  $55.2 \text{ m} \pm 20.7 \text{ SD}$  each) were relatively straight, with similar step (straight-line section) length distributions in both forest types. At the larger scale, the rats (16 individuals tracked for 4 nights each,  $\bar{X} = 1,443 \pm 991 \text{ m}$  of movement per night) moved with similar speed through both forest types (mean distance covered per 10-min interval =  $32 \pm 45 \text{ m}$ ). Based on telemetry data, mean nightly activity periods for individual rats averaged  $485 \pm 109 \text{ min}$  (areas covered =  $2,083\text{--}9,829 \text{ m}^2$ ), with no statistically significant differences between logged and unlogged forests. The large variability in individual movement parameters was not predicted by sex or forest type, suggesting that the paths taken were most likely responses to the local distribution of resources in a heterogeneous rain-forest environment. We conclude that the logged and unlogged forests did not differ with respect to features that are important to movement and ranging patterns of *L. sabanus*, suggesting that general differences associated with logging may not predict the effects of this type of disturbance on habitat use by individual species of small mammals.

Key words: foraging, forest structure, home range, logging, movement trajectories, Muridae, radiotracking

The decision rules that determine animal movement patterns are likely influenced by environmental features. Animals perceive those features and respond to them by modifying their movement patterns to optimize resource use. The resources that animals search for (e.g., food, mates, and shelter) are components of an interaction-dispersion matrix, in which a forager's movements are determined by environmental conditions and the distribution of resources in the habitat. For example, the tortuosity (divergence from a straight line movement) of movement paths is tightly linked to features of the landscape. Consequently, features such as logs, branches, and dense undergrowth that nonvolant mammals use to move through habitats may influence their progression through the habitat. Because resources in heterogeneous landscapes are often

patchily distributed (Solé and Manrubia 1995), the manner in which animals use movement to encounter those resources has generated considerable interest (Boyer et al. 2006; Fauchald and Tveraa 2003; Fritz et al. 2003; Johnson et al. 2002; Kotliar and Wiens 1990).

Understanding how animals interact with their environment requires selecting the proper scale for analysis and determining how to describe movement trajectories. In this context, the description of movement patterns using a diffusion equation modified from a Brownian motion model of independent straight-line movements (step lengths) has been successfully employed to predict dispersal over limited spatiotemporal scales (Kareiva and Shigesada 1983; Turchin 1998). However, such uncorrelated random walk models are based on the assumption of a landscape with an even distribution of resources and do not take into account structural components such as the patchy distribution of resources in a heterogeneous rain-forest matrix (Morales et al. 2004; Nolet and Mooij 2002). In tropical rain forests, the highly diverse tree assemblages that largely determine local habitat structure and resource distribution often

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vary in numbers and degrees of aggregation (Condit et al. 2000). This type of structure suggests that movement strategies consisting of long, straight-line movements of variable length interrupted by localized random motions (e.g., Lévy walk processes—Bénichou et al. 2005; Boyer et al. 2006; Shlesinger et al. 1993) are more efficient than are Brownian dispersal strategies (Boyer et al. 2006; Mårell et al. 2002; Ramos-Fernández et al. 2004; Solé et al. 2005; Viswanathan et al. 1996).

The rapid alteration and destruction of rain forests resulting from timber harvesting and agricultural land use add a major component of habitat variability to tropical environments, with as yet unforeseeable consequences for wildlife species. Logged tropical rain forests differ from unlogged forests not only in terms of floral composition, but also in type and scale of habitat heterogeneity. The former contain fewer species of trees per area than unlogged forests, and are particularly depauperate in large emergent species (Cannon et al. 1998). Animals moving through logged rain forests encounter differences in structure (e.g., denser undergrowth in combination with a reduced canopy) and resource allocation (e.g., different floral composition leading to differences in plant resource variety and abundance—DeWalt et al. 2003) that are likely to affect foraging strategies and constrain patterns of animal movements, for instance by changing movement speed, distance, and efficiency of resource encounter (Fauchald and Tveraa 2003; Johnson et al. 2002; Rettie and Messier 2000). Hence, it is important to identify how forest degradation affects movement behavior and to understand the causes of differences in movement patterns between logged and unlogged habitats.

The long-tailed giant rat (*Leopoldamys sabanus*) is present throughout the Sunda region of Southeast Asia and is a common, generalist species in local assemblages of small mammals (Lim 1970). Giant rats are mostly active on the ground with occasional forays up into the canopy. In a recent analysis of habitat utilization by *L. sabanus* based on spool-and-line-tracks, we showed that in logged forests a larger proportion of movement occurs above ground and involves shorter step lengths compared to unlogged forests (Wells et al. 2006). Further, in logged forests, the diameters of supports (e.g., branches) used by the rats are smaller and logs are more frequently used as pathways (Wells et al. 2006). Based on these data, we predicted that the differences in physical structure between logged and unlogged forest should lead to differences in the geometry of path trajectories (e.g., distribution of step lengths and path tortuosity) at small spatial scales. We further predicted that the changes in forest structure due to anthropogenic disturbance should lead to larger-scale differences in movement and ranging behavior (e.g., home-range sizes) in logged versus unlogged habitats.

## MATERIALS AND METHODS

*Study sites.*—The study was conducted in 3 logged and 3 unlogged forest sites in northern Borneo (Sabah, Malaysia). The unlogged sites consisted of 3 of the few remaining remnants of unlogged lowland rain forest in Sabah that have been designated as national parks or conservation areas. The

sites were located in the Danum Valley Conservation Area (UF1: 4°57'N, 117°48'E), Kinabalu National Park (UF2: 6°02'N, 116°42'E), and Tawau Hills National Park (UF3: 4°23'N, 117°53'E). The logged forest study sites were harvested 20–30 years before our study, resulting in the extraction of most dipterocarp and other large tree species. The logged sites were located at Luasong Field Centre (LF1: 4°36'N, 117°23'E), Kampung Monggis (LF2: 6°13'N, 116°45'E), and Kampung Tumbalang (LF3: 6°08'N, 116°53'E). Details on the logging histories of the study sites were not available, but all logged forest stands differed considerably from unlogged forests, with the former characterized by reduced canopy heights (approximately 15–25 m versus 60–70 m at unlogged sites), more frequent canopy gaps, and denser understory growth (see also Wells et al. 2007).

*Animal capture and tracking techniques.*—Rats were captured with locally made wire-mesh cage traps (280 × 140 × 140 mm) baited with banana. Trapping was conducted daily during 18 consecutive trapping sessions at the study sites between December 2002 and November 2004. All rats captured were marked with transponders (ARE 162; AEG Identification Systems, Ulm, Germany) implanted beneath the skin.

Small-scale movement patterns were quantified using spool-and-line tracking. A spool-and-line device consisting of a quilting cocoon containing approximately 120 m of nylon thread (Danfield Ltd., Lancashire, United Kingdom) and encased in a heat-shrunk plastic tube (total weight approximately 1.7 g) was glued onto the back of selected individuals with cyanoacrylate (Pattex; Henkel, Düsseldorf, Germany). One end of the thread was tied to nearby vegetation and labeled with the animal's identification number and the date of release. As the animal moved away from the point of capture, the thread was pulled from the cocoon, leaving a readily followed trace of the individual's movements. The path created by each thread was usually examined the day after the release of the animal. We used plastic poles to mark the sections of the track during which the animal had moved in a straight line, with no detectable changes in direction (i.e., no bends in the thread). The number of steps per thread was recorded and length of each straight section (step length) was measured to the nearest 0.1 m. The angle of the change in direction between steps was recorded with a sighting-compass to the nearest 2°.

Larger-scale patterns of movement were examined using radiotelemetry. Individuals that had been followed with spool-and-line tracking were recaptured and fitted with radiocollars (Biotrack, Wareham, United Kingdom). The radiotransmitters used broadcast at approximately 150 MHz and weighed <3% of an individual rat's body mass. Individual rats were tracked for at least 4 consecutive nights from dusk (1700–1830 h) until dawn (approximately 0500 h). Radiotracking was halted if an animal returned to its den during the night and remained inactive for >2 h. Some tracking nights ended before dawn because of injury or fatigue of the investigator. Radiofixes were taken at 10-min intervals. Recordings were made using a handheld Yaesu VR-500 receiver (Yaesu Musen Co. Ltd., Tokyo, Japan) with a modified handheld H-aerial antenna (Wagener Telemetrieanlagen, Köln, Germany). To estimate the

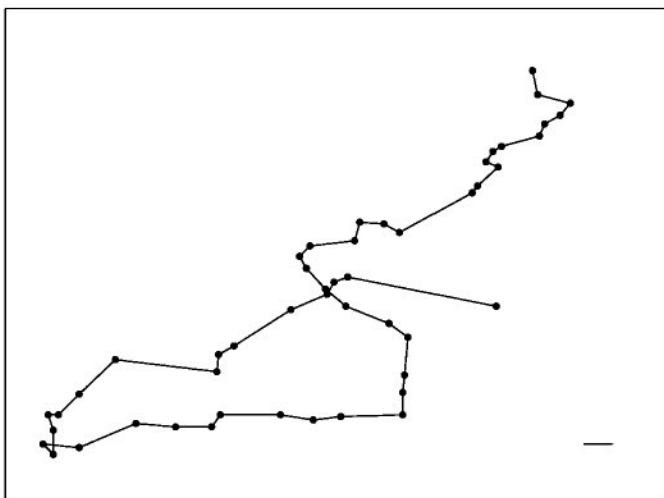
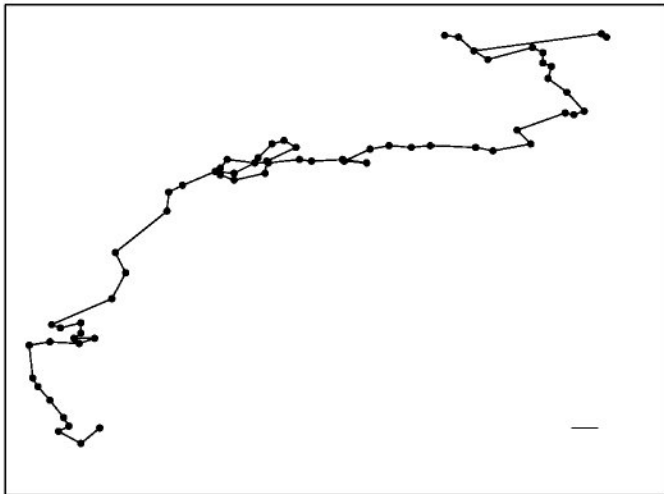


FIG. 1.—Small-scale movement tracks of 2 *Leopoldamys sabanus* obtained from spool-and-line tracking. The animal on the left was monitored in unlogged forest; the animal on the right was monitored in logged forest. Scale bars represent 1 m.

locations of rats, compass bearings were recorded relative to selected reference points marked with plastic poles; for each fix, 2 compass bearings for the same animal were taken at 1-min intervals and the actual location of the rat was triangulated from these data. To facilitate movement of the investigators between reference points, dense undergrowth vegetation was removed to create easily traversable paths between reference points; the minimal vegetation cleared to create paths should not have affected movements or space use by the study subjects.

The hilly terrain and dense vegetation at all study sites made radiotracking difficult and resulted in an estimated error of 10–30 m (determined from collars put at known locations) for our triangulated radiofixes. For a moving animal, this error increased to 40–50 m because of the 1-min time lag between consecutive compass bearings for the same fix. Although rats were occasionally spotted near reference points, there was no noticeable impact of proximity of the investigator on

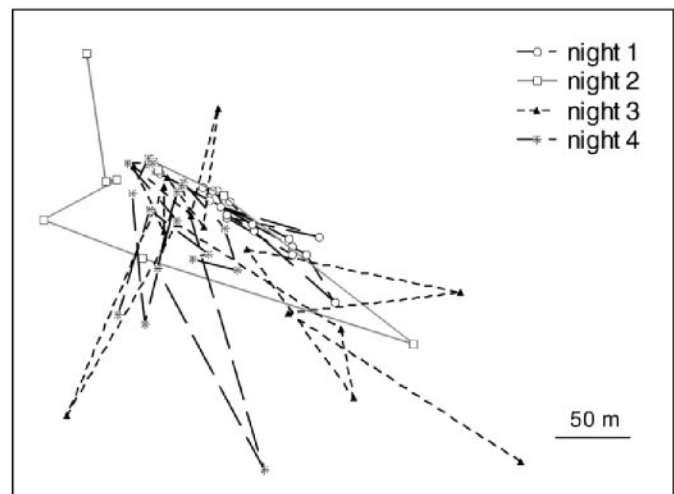
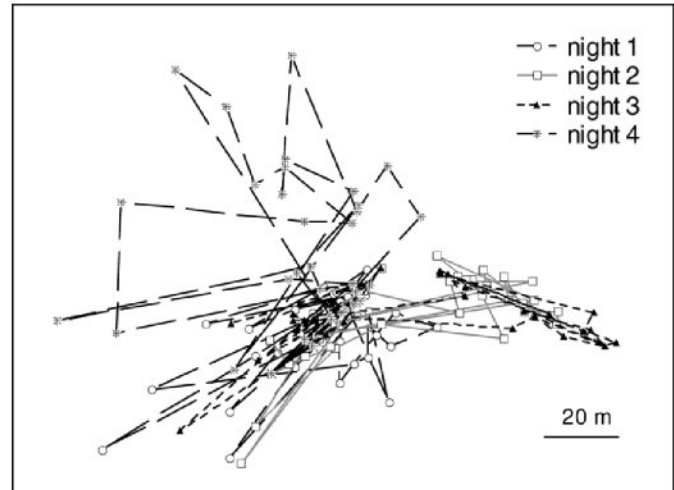
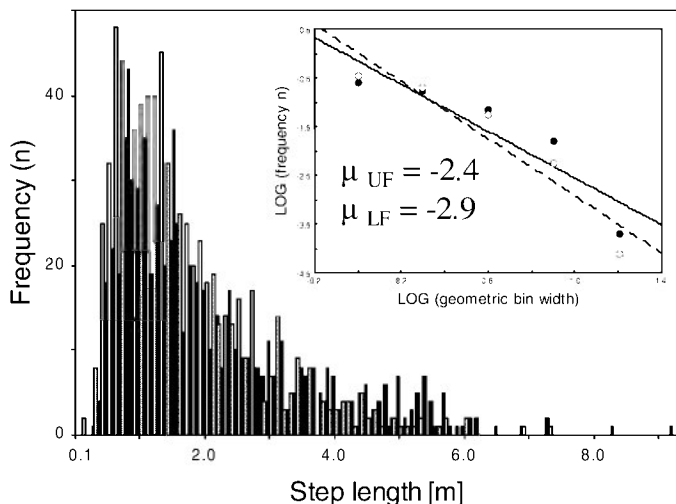


FIG. 2.—Large-scale movement paths of 2 *Leopoldamys sabanus*. Radiotracking of each individual was conducted on 4 consecutive nights, with radiofixes recorded at 10-min intervals. The animal on the left was monitored in unlogged forest; the animal on the right was monitored in logged forest.

movement patterns of rats (e.g., animals did not consistently move away from investigators). Despite the differences in forest structure and density of the undergrowth between logged and unlogged forests, to the best of our knowledge there was no consistent bias in the accuracy of tracking data from 1 habitat versus the other. At the end of the telemetry study, the rats were recaptured and their radiocollars were removed. The animals were handled following guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). The study was approved by the Economic Planning Unit at the Prime Minister's Department in Kuala Lumpur.

*Data analysis.*—Movements at both the small and large spatial scales were determined assuming that an animal walked in a straight line between consecutive bends in the thread or consecutive radiofixes (Figs. 1 and 2). Analysis of paths was



**FIG. 3.**—Distributions of step lengths from spool-and-line tracking of *Leopoldamys sabanus* in unlogged (black bars) and logged (hatched bars) forest. The inset shows a plot of the same data after logarithmic binning and transformation of the axes; estimates of  $\mu$  for both forests types are consistent with a power-law distribution. Analyses are based on 629 steps recorded from 25 animals in unlogged forest and 795 steps recorded from 24 animals in logged forest.

based on step lengths and turning angles and, for telemetry data, movement speeds. Measurements from spool-and-line tracking were made directly, as described above. For analyses of turning angles from spool-and-line tracks, we used Rayleigh's circular statistic to test the null hypothesis that the distribution of these angles was random (Batschelet 1981). Before analyzing the telemetry data, it was necessary to determine the specific locations of rats from our triangulated radiotracking data; this was done using a maximum-likelihood estimator contained in the LOAS software package (version 3.0.3, <http://www.ecostats.com/software/>). For these analyses, we excluded any points that fell  $>100$  m from all other fix locations for the same animal and that had distances  $>200$  m to neighboring point estimates.

The frequency distributions of step lengths and movement speeds were tested for a power law distribution by a plotting method based on logarithmic binning (2k) with normalization before log transformation of both axes (see Sims et al. 2007). For this, we pooled data on forest type or sex and applied a Student's *t*-test for testing differences in regression slopes (Zar 1999). We analyzed the radiotracking data by placing the distances moved per 10-min interval (movement speed) into 10-m bins; despite the estimated error of 10–50 m between fixes, many of the distances moved were larger than this and thus we considered these analyses to be meaningful. We tested for possible relationships between the physical and temporal distances between changes in movement paths using Mantel (1967) statistics, with Mantel correlograms representing the extent of spatial autocorrelation in such paths (Cushman et al. 2005). Thus, generally straight-line movements should show a high degree of correlation in contrast to more tortuous (multidirectional) paths.

Home ranges were determined using the fixed-kernel method (Worton 1989) at the 90% (median range) and 50% (core range) utilization levels. Telemetry data collected for the same animal on different nights were analyzed separately; subsequent analyses were conducted using mean or median nightly values. Estimations of home ranges were completed using the Animal Movement 2.04 extension (Hooze and Eichenlaub 1997) in ArcView 3.2a GIS (ESRI, Redlands, California). Least-squares cross validation was used to estimate the smoothing factor for these analyses; we applied a constant smoothing factor of  $h = 12.089$ . Because fixes were obtained at regular time intervals and over a standardized number of days, we assumed that the ranging behavior of individuals was most realistically described by the entire data set. Rather than estimating absolute ranges, we focused on factors potentially determining the variance in nocturnal ranges within and between individuals.

We note that our radiotelemetry data may have been subject to problems of autocorrelation because of both the time interval between fixes and the potential error associated with our estimates of animal locations. Although autocorrelation is typically expected to confound subsequent analyses of space use and movement (see Hurlbert 1984; Swihart and Slade 1985), an increasing number of studies emphasize the informative nature of nonindependent measures for some questions (see Börger et al. 2006; Cushman et al. 2005; De Solla et al. 1999). To assess the potential effects of autocorrelation on our data set, we compared the distributions of movement speeds and home-range sizes estimated from 10-min interfix intervals with those estimated using a 30-min interfix interval. Based on these analyses (see "Results"), we retained the 10-min interfix interval and did not exclude the smallest distance measures from our analyses. Although our findings should perhaps be interpreted with caution, we believe that inclusion of these data is informative regarding the behavior of our study species.

To test for the effects of forest type and sex on home-range size, movement speed, and total duration of nightly activity, we used linear mixed-effects models with restricted likelihood estimation (Pinheiro and Bates 2000), as implemented in the nlme 3.1-81 package (Pinheiro et al. 2007) for the open-source statistical software R, version 2.5.0 (R Development Core Team 2007). For these analyses, we fitted forest type and sex as fixed and random effects, respectively, while data were grouped according to study site and individuals were nested within the different sites. For estimates of the variation among consecutive measurements from individual paths, we used the coefficient of variation, which was calculated as  $CV = (SD/\bar{X}) \times 100$ . Means are given as  $\pm 1$  SD.

## RESULTS

We obtained a total of 49 spool-and-line tracks with total lengths  $> 30$  m ( $\bar{X} = 55.2 \pm 20.7$  m,  $n = 25$  individuals in unlogged forest and 24 individuals in logged forest). Sixteen individuals (9 males and 7 females) were radiotracked for at least 4 consecutive nights; 9 of these animals (3 males and 6 females) were from unlogged forest, whereas 7 (6 males and

1 female) were from logged forests. From these animals, we obtained a total of 2,829 fixes ( $\bar{X} = 177 \pm 44$  fixes per individual), with individuals located and radiofixes obtained for approximately 80% of our radiotracking efforts.

**Small-scale movement patterns.**—Distributions of step lengths followed a power-law distribution. Comparisons of slopes obtained from the regression of step-length frequencies on binning classes revealed no significant differences between logged and unlogged forests (Student's *t*-test,  $t = 0.67$ ,  $d.f. = 6$ ,  $P > 0.05$ ; Fig. 3), despite the shorter step lengths in logged forests reported previously (Wells et al. 2006). Further, step-length distributions did not differ between males and females in either habitat (both Student's *t*-test,  $t < 0.16$ ,  $d.f. = 1$ ,  $P > 0.05$ ). Although we found significant serial correlations between step length, the 2 preceding, and the 2 subsequent steps for 3 of the 49 spool-and-line tracks examined (Spearman rank, all  $R > 0.31$ ,  $P < 0.01$ ), no significant relationships between these variables were found for the remaining tracks considered. Step lengths were positively correlated with turning angles in 1 spool-and-line track ( $R = 0.79$ ,  $P < 0.01$ ), whereas a negative correlation between these variables was obtained for 6 other tracks (all  $R < -0.35$ ,  $P < 0.05$ ).

The mean turning angle recorded from spool-and-line tracks did not differ significantly between forest types (logged:  $9^\circ \pm 11^\circ$ ,  $n = 24$ ; unlogged:  $9^\circ \pm 8^\circ$ ,  $n = 25$ ; Mann-Whitney *U*-test,  $U = 274$ ,  $P = 0.60$ ). Persistence, defined as a nonrandom distribution of turning angles resulting in a relatively straight overall direction of movement, was observed in 33 (67%) of 49 spool-and-line tracks (Rayleigh's  $z > 0.322$ ,  $P < 0.05$ ); the frequency of persistent tracks did not differ between logged and unlogged forest (chi-square test,  $\chi^2 = 0.003$ ,  $d.f. = 1$ ,  $P = 0.95$ ). All spool-and-line tracks showed significant correlations between the number of steps moved and the respective straight-line distance covered (Mantel tests, all  $P < 0.01$ ). Although most tracks tended to be relatively straight in overall structure (Fig. 1), individual tracks revealed considerable variation in step lengths and turning angles, as indicated by relatively large coefficients of variation for these variables (CV for step length = 153; CV for turning angle = 59).

**Large-scale movement patterns.**—Giant rats emerged from their burrows between 1740 and 2040 h ( $\bar{X} = 1841 \pm 0033$  h,  $n = 16$ ) and were active for an average of  $485 \pm 109$  min per night ( $n = 16$ ). The shortest recorded period of nightly activity was for a male in logged forest that was only active for 138 min between 1930 and 2330 h. The longest period of nightly activity was for a female in unlogged forest that was active for more than 11 h (at least 680 min) between 1820 and 0540 h. Although the duration of activity periods varied significantly among individuals (Kruskal-Wallis analysis of variance [ANOVA],  $H = 47.5$ ,  $d.f. = 15$ ,  $64$ ,  $P < 0.01$ ; all  $3 \leq CV \leq 43$ ), no significant differences in duration were detected between forest types or sexes (mixed-effect model, forest type:  $t = -1.02$ ,  $P = 0.37$ ; sex:  $t = -1.32$ ,  $P = 0.22$ ; forest type-sex interaction:  $t = 1.15$ ,  $P = 0.28$ ). Ad libitum tracking during the daytime confirmed that giant rats were mainly inactive and remained inside their burrows during daylight hours, although

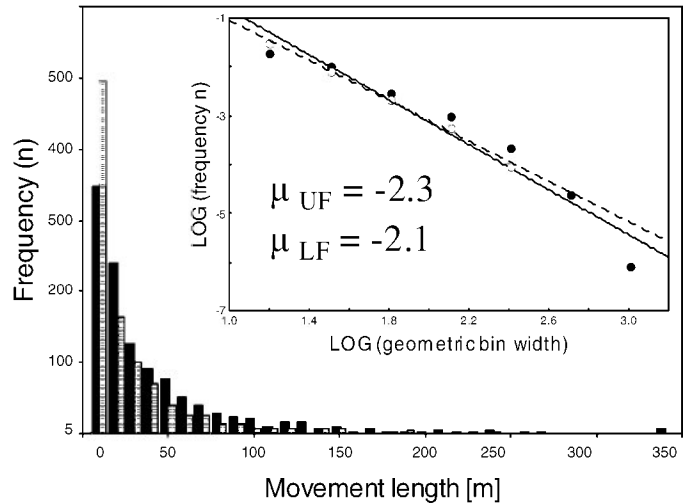


FIG. 4.—Distributions of movement speeds from radiotracking of *Leopoldamys sabanus* in unlogged (black bars) and logged (hatched bars) forest. Individuals were tracked on 4 consecutive nights, with radiofixes recorded at 10-min intervals. The inset shows a plot of the same data after logarithmic binning and transformation of the axes; estimates of  $\mu$  did not differ between forest types (Student's *t*-test,  $t_{v=8} = -0.80$ ,  $P > 0.05$ ). Analyses are based on 1,152 movements ( $n = 9$  individuals) from unlogged forest and 989 movements ( $n = 7$  individuals) from logged forest.

2 females were found to be active in the vicinity of their burrows during the daytime on a single day each.

The mean distance traveled during a single night was  $1,443 \pm 991$  m ( $n = 64$  animals). No significant differences in mean distance traveled were detected between forest types or sexes (mixed-effect model, forest type:  $t = 1.30$ ,  $P = 0.26$ ; sex:  $t = -1.02$ ,  $P = 0.33$ , fitted as fixed effects in separate models). The longest recorded average distance per night was  $4,742 \pm 1,085$  m ( $n = 4$ ) covered by a female, whereas the shortest nocturnal movement was  $618 \pm 231$  m ( $n = 4$ ) recorded for a male. A total of 2,432 movement speeds (distance covered in meters per 10-min interval) were calculated. Movement speeds did not differ significantly between forest types or sexes (mixed-effect model, forest type:  $t = 1.14$ ,  $P = 0.32$ ; sex:  $t = 0.82$ ,  $P = 0.43$ ; forest type-sex interaction:  $t = -0.99$ ,  $P = 0.35$ ). However, mean movement speeds differed significantly among individuals (Kruskal-Wallis ANOVA,  $H = 45.5$ ,  $d.f. = 15$ ,  $64$ ,  $P < 0.01$ ) and this variability may have masked effects of logging on movement patterns. The distributions of movement speeds resembled Lévy walk distributions (Fig. 4), with similar slopes for regressions of movement speed frequencies on binning classes for both forest types (Student's *t*-test,  $t = -0.80$ ,  $d.f. = 8$ ,  $P > 0.05$ ). Regression slopes did not differ between data from 10-min intervals and subset of data with 30-min intervals in either forest type (unlogged forest: Student's *t*-test,  $t = -0.97$ ,  $d.f. = 9$ ,  $P > 0.05$ ; logged forest: Student's *t*-test,  $t = 0.10$ ,  $d.f. = 6$ ,  $P > 0.05$ ). Regression slopes also did not differ when excluding binning classes with distances smaller than estimated errors (Student's *t*-test,  $t = -0.50$ ,  $d.f. = 4$ ,  $P > 0.05$ ).

**TABLE 1.**—Variation in movement and home-range attributes for *Leopoldamys sabanus* in logged and unlogged forests. Data were obtained by radiotracking 16 animals over 4 consecutive nights each. For each variable, minimum and maximum values are shown, as are estimates of nightly and total CVs. Significant correlations between variables are indicated in the 2nd column and represent Spearman's *R* correlations for which  $P < 0.05$ . Nightly CVs were calculated from data from the same individual collected over 4 different nights and reflect individual variability in movement parameters. Total CVs were calculated from means for different individuals (data averaged across different nights of monitoring) and represent the variability in trajectories among animals. *H*-statistics from Kruskal–Wallis ANOVAs reflect differences among individuals for a given variable; significant values ( $P < 0.05$ ) are marked with an asterisk (\*).

Variable	Minimum–maximum means	Correlations	Nightly CV (%)	Total CV (%)	<i>H</i> from Kruskal–Wallis ANOVA
Nightly path length (m) (PL)	278–6,328	ML, Cor, –Mr	28 ± 13	69	50.0*
Move length (10 min) (m) (ML)	5–100	PL, –Med, Cor, –Mr	34 ± 20	56	45.5*
Activity time (min) (T)	138–680	PL, Mr	14 ± 9	19	47.5*
Median range (90% kernel) (m <sup>2</sup> ) (Med)	2,083–9,829	–PL, ML, Cor, –Mr	26 ± 18	44	43.9*
Core range (50% kernel) (m <sup>2</sup> ) (Cor)	594–1,535	–PL, ML, Med, –Mr	27 ± 19	26	29.3*
Mantel <i>r</i> (Mr)	–0.11–0.49	–PL, –ML, T, –Med, –Cor	92 ± 195	89	24.2

Significant spatial autocorrelation among consecutive radiofixes for the same individual was detected for 26 (41%) of 64 nightly paths monitored (Mantel tests, all  $P < 0.05$ ), suggesting that the remaining 38 paths were relatively tortuous. Comparatively long movements occurred more often than would be expected in a normal distribution (exponent  $\mu \geq 3$ ). For all paths examined, movement speed for a given step was significantly correlated with speeds for the 1 preceding and 2 subsequent steps (Spearman rank, all  $R > 0.13$ ,  $P < 0.01$ ), indicating that individuals may reduce movement speed by making several consecutive short moves (Fig. 2). Moreover, movement speed was significantly correlated with absolute turning angles for 9 of 16 individuals (Spearman rank, all  $R > 0.19$ ,  $P < 0.01$ ). Collectively, these findings suggest that movement trajectories of radiotracked giant rats were characterized by the accumulation of shorter, slower moves in some locations and occasional very long moves in other locations, indicating that these trajectories do not fit a Brownian random walk model (Turchin 1998).

Mean sizes of nocturnal home ranges (90% kernels) varied from 2,083 to 9,829 m<sup>2</sup>. Mean nocturnal core ranges (50% kernels) varied from 594 to 1,535 m<sup>2</sup>. Median home-range sizes did not differ between forest types or sexes (mixed-effect model, forest type:  $P = 0.83$ ; sex:  $P = 0.98$ ). Median home-range sizes varied significantly between individuals (Kruskal–Wallis ANOVA,  $H = 25.8$ , *d.f.* = 15, 64,  $P < 0.05$ ), despite the relatively large variation within individual samples over 4 nights. We found no effect of forest types or sex on core range sizes (mixed-effect model, forest type:  $P = 0.39$ ; sex:  $P = 0.50$ ). Across nights, individual variation in total and core home-range sizes was high, with a mean CV of  $26 \pm 18$  for median size and a mean CV of  $27 \pm 19$  for core size. Mean nocturnal ranges and core ranges for the same individual calculated from 10-min intervals (full data set) and 30-min intervals (subset of data) were correlated (nocturnal ranges: Spearman rank,  $R = 0.85$ ,  $P < 0.01$ ; core ranges:  $R = 0.74$ ,  $P < 0.01$ ; both  $n = 64$ ). Analyses of range sizes using different data subsets revealed no effects of forest types and sex on range sizes (all mixed models  $P > 0.05$ ). Thus, overall, although both analyses of movement parameters and home-range sizes based

on telemetry data revealed substantial interindividual variation, no significant variation in these parameters was detected between forest types or sex (Table 1).

## DISCUSSION

Given the pronounced diversity of trees and other environmental features that are heterogeneously distributed in the forest matrix, tropical rain forests represent a natural mosaic of habitat patches on multiple scales. Consequently, we expected that differences in forest structure and resource allocation between logged and unlogged forest should influence the movements of animals. However, contrary to our expectations, we did not find evidence that logging affected the movements or home ranges of *L. sabanus*. Given the limits of our data set—in particular the accuracy of radiofixes obtained in a complex environment—it is possible that impacts of logging on the movement and ranging patterns of *L. sabanus* remained undetected by our analyses. However, these limitations should not have affected the results of our spool-and-line tracking studies, yet examination of these data also failed to reveal differences between logged and unlogged forests, suggesting that the apparent changes in logged habitats may not have been important to patterns of movement by the study species.

At our smaller spatial scale (spool-and-line tracking data), animal movements were mostly directed toward the burrow, presumably with little foraging activity along the way. The path tortuosity that we observed at this scale was most likely governed by physical features of the environment such as the distribution of obstructions and supports that reduce straight-line movements. Path tortuosity can be interpreted as the result of the spacing of objects that serve as target or orientation points (e.g., bushes or trees). Travel may have been directed toward such objects on a small scale, but not at a larger scale when considering movement between multiple such points (Benhamou 1990). Alternatively, tortuous paths might simply represent the most efficient way through a heterogeneous medium, as has been suggested for albatrosses (*Diomedea*), which use a tortuous path to continuously adjust their flight for optimal use of wind (Fritz et al. 2003). Similarly, the spatial

distribution of structural supports or obstructions may explain path tortuosity in terrestrial rain-forest environments. The likely impact of physical structures together with the large variability in step lengths of individuals suggest that the patchiness of local structures should have a strong influence on the movement patterns of *L. sabanus*. Marked variation in local habitat conditions may have obscured any difference between forest types, thus explaining why, despite habitat differences in step lengths (Wells et al. 2006), logging was not a strong predictor of changes in small-scale movement paths.

In contrast, larger-scale patterns (radiotracking data) are more likely determined by foraging activity, because resource distribution is central in animal movement and spacing (Mitchell and Powell 2004; Ostfeld 1990). The large variety of patchily distributed food sources in dipterocarp rain forest that are consumed by many small omnivorous mammals (Emmons 2000; Langham 1983; Lim 1970) implies that giant rats face a heterogeneous habitat with considerable variability in resource distribution in space and time. Overall, we suggest that differences in search strategies, such as changes in movement speed and nightly paths, should reflect differences in resource clumping and abundance, which may lead to differences in range size and activity time. Many tropical fruits, such as dipterocarps or figs, are spatially clumped (e.g., Condit et al. 2002) and are exploited by frugivores until all ripe fruits have been consumed. Dipterocarp seeds in particular are a key seasonal resource for rats and other vertebrates in unlogged forests but are replaced by smaller fruits of pioneer trees in logged forests (Curran and Webb 2000; Wells and Bagchi 2005).

Regardless of the specific types of food ingested, the spatial distribution of these resources should be represented in movement paths, with an increased heterogeneity and patchiness in resource allocation leading to increased tortuosity in the large-scale paths of rats. Our observed movement patterns (e.g., serial correlations and high variability in movement speeds) resemble Lévy walks (Shlesinger et al. 1993; Viswanathan et al. 1996), which are characterized by an uneven coverage of the search area that results in exploitation of distant and independent patches. The occasional longer movements of the giant rats in our study may indicate a switch in patch use, which can be seen as an adaptation for the exploration of more-profitable patches in a rain-forest habitat with rather unpredictable and mostly sparsely distributed resources (see Ramos-Fernández et al. 2004). However, our findings regarding path trajectories do not fully correspond to Lévy walks because the rats regularly revisited sites and returned to the same burrows. Such discrepancies of movement traits in a single model are expected, because models only deal with select, simplified aspects of complex movements. As a generalist species, giant rats might change their search behavior (e.g., searching for fruits versus invertebrates) or exhibit distinct individual search strategies (attributable to local variations in resource availability or differences in individual energetic requirements), as has been suggested for other vertebrates (Austin et al. 2004; Mårell et al. 2002; Morales et al. 2004).

Although our study design did not permit us to directly compare movement trajectories across spatial scales, the impact

of physical structure on small-scale trajectories may be associated with the effects of resource availability on large-scale trajectories. For example, undergrowth is usually more open near large and shady fruiting trees, whereas it is denser and faster growing in tree-fall gaps or near streams (Newbery et al. 1999). Given more light and different vegetation, the arthropod prey of rats may be more common in tree-fall gaps (Davis et al. 2001; Hill et al. 2001), thereby influencing both small- and large-scale movement patterns with respect to habitat type. Specifically, rats may have to spend more energy in logged than in unlogged forest for the same net movement distance because of the increased density of undergrowth and obstructions. Alternatively, increased density of undergrowth in logged forests might facilitate locomotion of rain-forest dwellers by providing more supports, as has been suggested for the arboreal tarsier *Tarsius* (Merker et al. 2005). Thus, although the specific effects of habitat structure on movement remain unknown for most small mammals, it seems logical that differences in forest structure and resource distribution would simultaneously affect movement on multiple spatial scales.

In summary, examination of our data suggests that movement patterns are highly variable among individual giant rats and may reflect heterogeneity in habitat structure and resource availability. Our analyses do not provide strong evidence that logging affects movement by *L. sabanus*. Although these findings may in part reflect the ability of our data-collection techniques to detect changes in movement and activity, they also may indicate that logging does not alter forest structure in ways that are critical to movements by small mammals such as *L. sabanus*. Our results support the hypothesis that some common small mammals are able to persist in logged forests provided that a certain level of environmental diversity and resource availability are maintained after logging (Lambert et al. 2005; Wells et al. 2007). Plasticity in movement and searching behavior are essential prerequisites for adaptation to an anthropogenically altered landscapes and may obscure differences in movement trajectories between logged and unlogged forest. In logged rain forests, those species that are unable to cope with altered resource availability, or that fail to adapt their search and dispersal strategies, likely face reduced survival and dispersal. Understanding how individual species will respond to such changes is critical to preserving tropical forest faunas. The disappearance of intact rain forest is increasing rapidly, with the result that there is little time left to improve our understanding and, hence, ability to manage these habitats in a meaningful way.

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