REVIEW ARTICLE

Spatial Patterning in Nocturnal Prosimians: A Review of Methods and Relevance to Studies of Sociality

ELEANOR J. STERLING[1]*, NGA NGUYEN[2], AND PETER J. FASHING[3]
[1]*Center for Biodiversity and Conservation, American Museum of Natural History, New York, NY*
[2]*Department of Biological Sciences, Barnard College, Columbia University, New York, NY*
[3]*Department of Anthropology, Columbia University, and the New York Consortium in Evolutionary Primatology (NYCEP), New York, NY*

Patterns of home range overlap between individuals are key parameters used in discussions of sociality in nocturnal prosimians. Despite the importance of space use variables in defining social structure in nocturnal prosimians, researchers have yet to reach a consensus concerning the most reliable techniques for measuring patterns of home range use. In this paper, we review the methods used in 27 studies of nocturnal prosimian ranging behavior published since 1977. We discuss the usefulness and limitations of the various methods of data collection (radio tracking, trap mark, and identification of sleeping site locations) and data analysis (minimum convex polygon method, minimum concave polygon method, and quadrat analysis) used in these studies. We conclude that the most effective method for gathering data on individual movements and social interactions is direct observation of individual radio tagged animals during all-night follows. In those cases where radio tracking and/ or all-night follows are not possible, trap mark techniques can be used, although they tend to greatly underestimate home range size. We recommend that data collected on nocturnal prosimian ranging behavior be analyzed using the minimum convex polygon method, quadrat analysis, and, perhaps, one other of the more mathematically sophisticated techniques popular in studies of non-primate mammals. Finally, we urge researchers to employ standardized methods of data collection and data analysis in future studies of range use in nocturnal prosimians. Without standardization of methods, quantitative comparisons of the findings from different studies are biologically meaningless and prevent cross-species comparisons of space use and its relation to sociality. Am. J. Primatol. 51:3–19, 2000.   © 2000 Wiley-Liss, Inc.

*Correspondence to: Eleanor Sterling, Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at West 79th Street, New York, NY 10024. E-mail: sterling@amnh.org

INTRODUCTION

Since 1965, when the first compendium was published summarizing research on wild primate populations [De Vore, 1965], field studies of diurnal primates have flourished. Studies of nocturnal primates, on the other hand, have not. In the 1960s, however, a small cadre of pioneering researchers developed and maintained interest in these elusive species. The work of these researchers and that of their students has served as a strong foundation for all subsequent research on nocturnal prosimians [Martin, 1972; Charles-Dominique, 1977; Petter et al., 1977; Doyle & Martin, 1979]. A new wave of studies on nocturnal primates began in the 1990s, facilitated in part by advances in radio tracking technology [Sterling, 1993; Warren & Crompton, 1997; Gursky, 1998; Fietz, 1999a, b; Müller, 1999]. The individual–level research made possible by radio tracking technology provided new insights into the behavior and ecology of a number of previously little known nocturnal species. Despite the fact that several nocturnal taxa remain largely unknown today, our understanding of the diversity of social structures found among both diurnal and nocturnal primate communities is far more sophisticated now than it was several decades ago. We are now better able to analyze and explain the patterns of social structure found within and between primate species [Wrangham, 1980; Bearder, 1987; Van Schaik, 1989; Kappeler, 1997; Sterck et al., 1997].

Social structure can be defined as the content and quality of relationships among all the members of a group of regularly interacting animals [Richard, 1985]. While the social structures of most diurnal primates can be discerned with study, relationships and interactions between nocturnal primates are often difficult for human observers to perceive. This difficulty is due to the poor observational conditions at night, the cryptic behavior of some species, and the fact that interactants are often displaced from each other in space and time [Sterling & Richard, 1995]. For example, many nocturnal primates rely on long distance vocalizations and long lasting chemical signals to communicate with other members of their species [Charles-Dominique, 1978; Clark, 1985]. These modes of communication are difficult for human observers to detect and measure. Consequently, variables related to space use, such as home range overlap between and within the sexes, have often been relied on to infer aspects of the social structures of nocturnal primates [Bearder & Martin, 1980b; Bearder, 1987; Harcourt & Nash, 1986; Müller, 1998; Radespiel, 2000].

Although the importance of space use variables in defining social structure is well accepted, researchers have yet to reach a consensus concerning the most reliable techniques for measuring patterns of home range use. Over ten years ago, Bearder [1987] noted that the values for home range size reported from different studies in the literature could not be easily compared because different methods of measuring space use may yield different patterns of home range use. Despite the recent rise in the number of studies on nocturnal primates, Bearder's plea for the standardization of methods for measuring space use has generally been ignored.

In this article, we review the methods of data collection and data analysis most commonly used in studies of the ranging behavior of nocturnal prosimians. We limit our analysis to only those studies published since 1977, when the first study of nocturnal prosimians using radio tracking techniques was published [Charles-Dominique, 1977]. Although many good studies of nocturnal primates have been undertaken without the use of radio telemetry, we concentrate our review on those studies that use radio tracking, as it has

greatly modified the quantity and quality of the data that can be collected [Charles-Dominique, 1977].

The studies included in this review represent all field studies of nocturnal prosimian ranging behavior published since 1977 in six journals (*American Journal of Primatology*; *Ethology*; *Folia Primatologica*; *International Journal of Primatology*; *Journal of Zoology, London*; and *Primates*) and seven books (*Ecology and Behavior of Nocturnal Primates* [Charles-Dominique, 1977]; *A Handbook on Biotelemetry and Radio Tracking* [Amlaner & MacDonald, 1980]; *The Study of Prosimian Behaviour* [Doyle & Martin, 1979]; *Nocturnal Malagasy Primates: Ecology, Physiology and Behavior* [Charles-Dominique et al., 1980]; *Biology of Tarsiers* [Niemitz, 1984]; *Lemur Social Systems and Their Ecological Basis* [Kappeler & Ganzhorn, 1993]; and *Creatures of the Dark: The Nocturnal Prosimians* [Alterman et al., 1995]. The books represent the major edited volumes published since 1977 that contain papers on nocturnal prosimian ranging behavior. We address the methods used to record animal locations and to estimate home range area as they are described in these studies, and discuss the usefulness and limitations of these methods.

CRITIQUE OF METHODS

Home range size is perhaps the most fundamental measure of an animal's use of space, and overlap in home ranges between individuals is a key parameter used in discussions of sociality in nocturnal primates [Bearder & Martin, 1980b]. An animal's home range can be defined as "that area traversed by [an] individual in its normal activities of food gathering, mating and caring for young" [Burt, 1943]. Home range area can be computed with location data obtained from trapping or tracking techniques [Nash & Harcourt, 1986]. Both the shape and size of the home range area depend on the type of data collected, method of data collection, and method of home range analysis. Home range shape and size are also strongly influenced by artificial and natural barriers to dispersal.

For every field study of nocturnal prosimian ranging behavior, decisions must be made concerning the method(s) of data collection and the method(s) of data analysis. Because different methods of data collection and data analysis may yield different estimates of home range use [Harcourt & Nash, 1986; Bearder, 1987; Quin et al., 1992], researchers should be aware of the costs and benefits of each method and should aim to use the most reliable methods to meet their study objectives.

In the following sections, we examine the limitations and benefits of different methods of data collection and data analysis used in most studies of nocturnal prosimian ranging behavior.

Methods of Data Collection

Most studies of nocturnal prosimians use either radio tracking devices, trap mark techniques, or a combination of both, to collect data on the ranging behavior of a study population of animals. Of the 27 studies reviewed here, both radio tracking and trap mark were used in 12 cases (see Table 1). Radio tracking was the sole method used in seven. Trap mark was the sole method used in four studies. Neither method was used in the four remaining studies. These studies relied only on the aid of a headlamp to relocate individually marked animals. The difficulty involved in capturing some species of nocturnal prosimians precludes the use of telemetry techniques. This makes it difficult to achieve

TABLE I. Details on the Methods Used to Collect and Analyze Data in the 27 Studies of Nocturnal Prosimian Ranging Patterns Reviewed in this Paper

Study	Author	Study species	Duration and dates of study	Methods of data collection[a]	Methods of home range analysis[b]
1	Atsalis [2000]	*Microcebus rufus*	16 mo; Feb 1993–May 1994	T-M	Range size not calculated
2	Bearder and Martin [1980a,b]	*Galago senegalensis*	2 yrs; Aug 1975–Aug 1977	ANF T-M SSL	MCP
3	Charles-Dominique [1977]	*Galago demidovii*	Not specified. 1968–1973	T-M	Not specified
4	Charles-Dominique [1977]	*Galago alleni*	Not specified. 1968–1973	PNF T-M	Not specified
5	Charles-Dominique [1977]	*Perodicticus potto*	Not specified. 1968–1973	PNF T-M	Not specified
6	Charles-Dominique and Petter [1980]	*Phaner furcifer*	Not specified. Oct–Dec 1973, Jan–Feb 1974, May–Jun 1974	PNF[c]	Not specified
7	Clark [1985]	*Galago crassicaudatus*	Not specified. Jan 1976–Jul 1977	PNF[c]	Not specified
8	Crompton and Andau [1987]	*Tarsius bancanus*	Not specified	ANF SSL	(a) MCP (b) Quadrat Analysis
9	Fietz [1999a]	*Microcebus murinus*	2 mo; Aug–Oct 1993	NL[d] T-M	MCP
10	Fietz [1999b]	*Cheirogaleus medius*	Not specified. Nov 95–May 96, Oct 96–Apr 97, Dec 97–Mar 98	NL[d] T-M SSL	MCP
11	Gursky [1998]	*Tarsius spectrum*	442 nights; 1994–1995	ANF	Min. concave polygon
12	Harcourt [1987]	*Microcebus rufus*	Jun–Jul; no year provided	T-M	Range size not calculated
13	Harcourt [1991]	*Avahi laniger*	1 mo; Aug 1987	ANF SSL	MCP
14	Harcourt and Nash [1986]: Diani study site	*Galago zanzibaricus*	Not specified; Mar 79–Nov 80, Jan 81–Nov 82.	ANF T-M SSL	MCP
15	Harcourt and Nash [1986]: Gedi study site	*Galago zanzibaricus*	Not specified; Mar 79–Nov 80, Jan 81–Nov 82	ANF T-M SSL	MCP

16	MacKinnon and MacKinnon [1980]	*Tarsius spectrum*	15 mo; Nov 77–Jan 79	PNF[c]	Not specified
17	Muller [1998, 1999]	*Cheirogaleus medius*	20 mo; Nov 95–Jun 96, Sep 96–Jun 97	PNF[e] T-M	MCP
18	Nash and Harcourt [1986]; Diani study site	*Galago garnettii*	Not specified; Mar 79–Nov 80, Jan 81–Nov 82.	ANF T-M SSL	MCP
19	Nash and Harcourt [1986]: Gedi study site	*Galago garnettii*	Not specified; Mar 79–Nov 80, Jan 81–Nov 82.	ANF T-M SSL	MCP
20	Nash and Whitten [1989]	*Galago senegalensis*	17 days; July–Aug 1984	PNF[e]	Not specified
21	Niemitz [1984]	*Tarsius bancanus*	Not specified; Dec 71–73	T-M	Not specified
22	Pages [1980]	*Microcebus coquereli*	Not specified. Jun–Jul 1974	PNF	Not specified
23	Pages-Feuillade [1988]	*Microcebus murinus*	6 weeks; Sep–Nov 1985.	PNF	Not specified
24	Radespiel [2000]	*Microcebus murinus*	At least 4 mo; Aug–Oct 95; Sep–Nov 96	NL[d] T-M	MCP
25	Schwab [2000]	*Microcebus myoxinus*	At least 16 mo; Sep 94–Oct 94, Sep 95, Apr–May 95, Jan-Mar 96, Jun 96–May 96	T-M SSL[d]	MCP
26	Sterling [1993]	*Daubentonia madagascariensis*	497 hrs; Nov 89–Feb 91	ANF	MCP
27	Warren and Crompton [1997]	*Avahi occidentalis, Lepilemur edwardsi*	18 mo; May 92–Oct 93	ANF	(a) MCP (b) Quadrat Analysis

[a]Methods of data collection include: follows (ANF, PNF), nightly locations (NL; estimated from triangulation), sleeping site locations (SSL) and trap-mark (T-M) techniques. Follows of, on average, less than 6 hrs are considered partial night follows (PNF). Follows averaging greater than 6 hrs each night are considered all night follows (ANF).

[b]Methods of home range data analysis (where specified) include: minimum convex polygon (MCP), quadrat analysis, and minimum concave polygon.

[c]All partial and all night follows were conducted on radio-tagged animals, except where noted.

[d]Location data achieved by triangulation.

[e]In addition to follows, the positions of radio-collared animals were located sequentially. It is unclear whether Müller [1998, 1999] achieved these localizations by direct observation or by triangulation.

resightings of individuals and to collect systematic data on them, except in the best of observational conditions (flat terrain, relatively open forest, etc.) [Charles-Dominique, 1977]. This technique will not be one of the methods discussed in detail in this review because it is generally difficult to collect systematic data using only a headlamp.

Radio tracking. Radio tracking is a technique commonly used to collect data on the location, patterns of range use, and behavior of a study population of animals [Harris et al., 1990]. Radio transmitters, each with a unique identifying frequency, are attached to a number of study animals. The signals from these transmitters are then used to locate and follow individual animals to obtain data on their behavior and ecology. These data are then used to determine home range size and patterns of range use.

Radio tracking was first adapted for biological research in the 1960s [Cochran & Lord, 1963] and has since been used in many ecological studies [for a recent review, see Harris et al., 1990]. Since its introduction, biologists have realized that tracking radio collared animals was a more efficient and predictable method of collecting data on an animal's behavior and ecology than observations from opportunistic resightings of individually marked animals [Charles-Dominique, 1977; Lance & Watson, 1980]. In addition, radio tracking allows researchers to go beyond group level analyses to the analysis of variation between individuals. Data collection is possible even when members of the group disappear for hours or days.

Radio tracking has proven to be especially useful in the study of nocturnal animals and has been employed in at least 19 studies of nocturnal prosimians over the past 25 years (Table 1). In recent years, transmitter life span has increased and transmitter size has decreased. These changes have greatly facilitated use of telemetry with nocturnal prosimians, all of which weigh 3 kg or less.

Unfortunately, comparisons among the findings of various published radio tracking studies are problematic, as differences in the procedures used to collect and analyze radio tracking data have provided very different home range estimates [Harcourt & Nash, 1986; Crompton & Andau, 1987; Quin et al., 1992]. In fact, despite the increasing popularity and intensive use of radio tracking in many ecological studies (including studies of nocturnal prosimians) in the past two decades, the reviews of the publications from the second [Lance & Watson, 1980] and the third [Harris et al., 1990] decades of radio tracking both call for a greater standardization of the methods used to collect and analyze tracking data.

Collecting location data. Radio tracking is commonly used to collect data on the ranging behavior of free ranging animals. The two methods used to obtain location records for radio tagged nocturnal prosimians are: 1) homing in on the animal, or direct observation; and 2) distance localization, or triangulation. Direct observation involves following a transmitted signal's increasing strength until the radio tagged animal is actually sighted. Direct observation is most easily achieved with animals that are relatively sedentary, slow moving, and well habituated, or with animals that occupy open habitat [White & Garrott, 1990]. Because animals are actually seen, direct observations should generally provide more accurate location estimates than triangulation location techniques. The main disadvantage with this method, however, is that it is time consuming and thus limits the number of animals that can be simultaneously studied.

Triangulation is "the process of estimating the location of a transmitter by using two or more directional bearings obtained from known locations remote from the transmitter's position" [White & Garrott, 1990]. The location of the radio tagged animal is the point of intersection between two or more bearings

taken from known locations [White & Garrott, 1990]. This method is particularly useful for the simultaneous study of a large number of animals. This method does not, however, result in the precise location of an animal because bearings are approximated rather than measured exactly. The accuracy of the point estimate obtained from triangulation depends on the precision of the bearings from the receivers to the transmitter, the distance between the receiver and the transmitter, and the angle of intersection between the two bearings [White & Garrott, 1990]. Accuracy can also be influenced by inter-observer differences [Radespiel, personal communication]. Although few researchers test the accuracy of their triangulation procedures [White & Garrott, 1990], several studies have found that bearing errors of more than 10 degrees can result in location estimates that are far from the known locations of transmitters [Lee et al., 1983; Garrott et al., 1986]. Therefore, triangulation should not be used to collect accurate location data on an individual animal, but is instead useful for collecting data on the approximate locations of several individuals simultaneously. It is perhaps the most effective method to use for studies of home range overlap and access to social partners and mates, and, therefore, is useful for analyses of sociality in nocturnal prosimians.

Four of the 19 radio tracking studies reviewed here [Fietz, 1999a, b; Radespiel, 2000; Schwab, 2000] used triangulation, while 15 studies used direct observation to obtain ranging data on tagged animals [Table 1]. During radio tracking sessions, location records for each animal were obtained at their nests, sleeping site locations, and/or during nightly follows. Nightly location records were collected either by interval sampling, where the location of an animal at regular (spatial or temporal) intervals is recorded, or by continuous monitoring, where movement of an animal is recorded continuously [Kenward, 1992]. Two of the four studies that used triangulation recorded location data by interval sampling [Fietz, 1999a; Radespiel, 2000], one recorded data by continuous monitoring [Fietz, 1999b], and one triangulated sleeping site locations during the day [Schwab, 2000]. Of the 15 studies that used direct observation: nine used interval sampling [Bearder & Martin, 1980a, b; Harcourt & Nash, 1986: Gedi study site; Nash & Harcourt, 1986: Gedi study site; Crompton & Andau, 1987; Harcourt, 1991; Sterling, 1993; Warren & Crompton, 1997; Müller, 1998, 1999; Gursky, 1998]; two used continuous monitoring [Harcourt & Nash, 1986: Diani study site; Nash & Harcourt, 1986: Diani study site]; three did not report what method they used [Charles-Dominique, 1977, for *G. senegalensis* and *G. alleni*; Pagés-Feuillade, 1988]; and one used both interval sampling and continuous monitoring to collect ranging data on tagged animals during partial or all-night follows [Pagés, 1980].

If the time between samples for a single animal is large enough, interval sampling can be used to simultaneously study a large number of animals [Harris et al., 1990]. However, when certain conditions (such as uneven terrain, shy study subjects, thick vegetation, and consequent poor visibility), make locating animals difficult, continuous monitoring may be the only practical means of tracking radio tagged animals [Harcourt & Nash, 1986; Nash & Harcourt, 1986]. Researchers using continuous sampling should be specific about how they define a movement, as this definition is critical to understanding how they plot their data.

Plotting location data. Once an animal is located, its position within the study area is determined and then plotted on a map of the area. Mapping animal locations requires extreme care as errors in plotting animal locations in the field could influence home range estimates and overlap later on. Location records obtained in the field have to be transformed into coordinates that can be plotted on

a two dimensional map of the study area. The accuracy with which location records obtained from direct observation and triangulation are plotted are influenced by the quality of the maps or aerial photos used, and by the investigator's ability to estimate the location of the animal on the map [White & Garrott, 1990].

An established grid system of trails, or any accurately measured system of regular trails, helps ensure the accuracy with which animal locations are geo-referenced and plotted on a map of the study area. Most researchers established a grid system at their study sites to facilitate locating and following radio tagged animals. Locations were then measured with reference to the established grid system [Charles-Dominique & Petter, 1980; Harcourt & Nash, 1986: Gedi study site; Nash & Harcourt, 1986: Gedi study site; Crompton & Andau, 1987; Warren & Crompton, 1997; Müller, 1998; Fietz, 1999a, b; Radespiel, 2000]. Because nocturnal prosimians are found in a variety of habitats that vary in the steepness of the terrain and in the thickness of the vegetation, from the savanna woodlands of southern Africa to the rugged tropical rainforests of Madagascar, the logistics of setting up a grid system can vary from site to site. A grid system of trails is more difficult to install with precision at sites with steep terrain and dense vegetation. In addition, poorer visibility in sites with steep terrain and dense vegetation can hinder the sighting of grid line markers.

In the papers we reviewed, grid cell sizes ranged from 10×10 m to 50×50 m. The smaller the grid used, the more accurate the estimates of an animal's location within the study site can be. The possibility of making errors in plotting grid cell lines may, however, increase with decreasing grid cell sizes [Crompton & Andau, 1987], especially at sites with steep terrain and dense vegetation (Sterling, personal observation). Choice of grid cell size at a particular site should reflect both considerations to maximize the precision of plotting animal locations.

Alternatively, researchers have placed flagging tape along an animal's nightly path and subsequently returned during daylight hours to measure and plot the animal's activity for the previous night. Six studies used this method to obtain data on the nightly ranges of the study subjects [Bearder & Martin, 1980a, b; Crompton & Andau, 1987; Harcourt, 1991; Sterling, 1993; Warren & Crompton, 1997; Gursky, 1998].

The difficulty with any system that does not involve grid lines laid out along a trail system is determining how the locations are geo-referenced when plotting the data. Researchers should be specific in their methods regarding whether or not grid lines were cut along trails or merely flagged. The former lend themselves to much more accurate locality estimates than the latter.

Trap mark. Grid trapping has been used since the 1940s [Burt, 1943; Manville, 1949] to determine patterns of home range use in small mammals. Most studies of home ranges have relied heavily on the use of trap mark methods with grid trapping data, despite the fact that it has long been suspected that trap revealed home ranges differ markedly from true home ranges [Trevor-Deutsch & Hackett, 1980; Harcourt, 1987; Quin et al., 1992]. Reliance on grid trapping may be related to the considerable funds and effort required to tag animals for individual identification and to conduct follows on as many study subjects as possible in studies using radio tracking.

Trap mark studies use traps placed at specified locations in a study area to recapture marked animals. The number of different trap locations where each animal is caught is recorded. These data are then plotted on a map of the study area and are used to estimate home range area and patterns of range use. Sixteen studies used trap mark to record data on the ranging behavior of individual animals (Table 1).

Home range estimates may be affected by trap locations, size and shape of grids, and frequency of trapping sessions [Bergstrom, 1988; Quin et al., 1992]. Researchers should always report these factors when reporting home range values calculated from trapping data. Descriptions of the methods for determining the locations chosen were lacking when studies did not provide complete details regarding the frequency of trapping sessions and when capture locations were not distributed evenly at the intersections of grids [Harcourt & Nash, 1986; Nash & Harcourt, 1986; Müller, 1998, 1999]. These values were provided in only six of the 16 trap mark studies under review here [Harcourt, 1987; Fietz, 1999a, b; Atsalis, 2000; Radespiel, 2000; Schwab, 2000]. All five authors distributed their traps evenly at the intersections of a grid system of trails or along regular trap lines and most traps were reported to be in operation at least three consecutive nights each month.

Sleeping site locations. Researchers often gather substantial information on sleeping site locations for nocturnal prosimians. All-night follows usually start and stop at sleeping sites, possibly offering two data points in one night if an animal sleeps in a different site from where it starts. Seven of the studies reviewed in this paper provided home range estimates using only sleeping site location data [Bearder & Martin, 1980a, b; Harcourt & Nash, 1986: Diana and Gedi sites; Crompton and Andau, 1987; Schwab, 2000]. Most of these studies also provided home range estimates using data collected by tracking or trapping as well.

Comparison of home range estimates based on trapping, tracking, and sleeping site location data. In this section, we focus on the variation in home range estimates obtained from the sources of data most often used to compute home range size in nocturnal prosimians: grid trapping data (trap-revealed), radio tracking data (track-revealed), and sleeping site location data (sleeping site location-revealed).

It has long been speculated that track-revealed home range sizes represent more accurate approximations of an animal's true home range size than do trap-revealed home range sizes [Waser & Wiley, 1979; Harcourt, 1987; Quin et al., 1992], probably because the former are not constrained by trapping site locations. Similarly, track-revealed home ranges are believed to represent more accurate approximations of an animal's true home range size than range estimates derived from sleeping site locations alone [Crompton & Andau, 1987]. The contention that track-revealed home ranges represent the best approximations of an animal's true home range can best be evaluated by comparing track-, trap- and sleeping site location-revealed home ranges for a study population of animals and examining the extent to which these values differ from each other.

Harcourt and Nash [1986] compared track-, trap- and sleeping site location-revealed home ranges (computed as minimum convex polygons around the outermost location records from all-night follows, trapping, and sleeping site locations, respectively) for two study populations of *Galago zanzibaricus*. They found that track-revealed home ranges were almost always several orders of magnitude greater than those calculated from trapping data (mean=4.6 times greater, n=14), or from sleeping site locations (mean=2.8 times greater, n=16) for a study population of 16 *G. zanzibaricus*. Crompton and Andau [1987] similarly found that home range areas (computed as minimum convex polygons) calculated from sleeping site locations for *Tarsius bancanus* (n=4) were 5 to 29 times smaller (mean=13.4) than those calculated from direct observations.

When Nash and Harcourt [1986] compared track-, trap- and sleeping site location-revealed ranges for two study populations of *G. garnettii*, they did not find that track-revealed home ranges were always larger than those computed

from sleeping site locations. They did find that track-revealed ranges were always larger than trap-revealed ranges (mean=2.5 times greater, n=7). In some cases, home range areas plotted from sleeping site locations were slightly larger (1.3 to 1.5 times larger, n=3). In other cases they were about the same (n=2), or slightly smaller (1.4 to 1.8 times smaller, n=2), than those plotted from tracking data. These differences between track- and sleeping site-revealed home ranges are small and thus cannot be regarded as definitive evidence against the hypothesis that track-revealed home ranges are closest in value to an animal's true home range.

Though it would be best to apply these tests to other species as well, the wide disparities between track-revealed home ranges and trap- and sleeping site location-revealed home ranges in the studies by Harcourt and Nash [1986] and Crompton and Andau [1987] clearly show that the latter two techniques tend to underestimate the size of an animal's range.

It is not surprising that tracking data tend to provide more accurate estimates of home range area than do trapping or sleeping site data. First, and most importantly, sleeping sites and trapping sites provide one locational data point per animal each night, while tracking allows an observer to gather locational data points throughout the night for a focal animal. Many more locational points can be gathered during a night of tracking than during a night in which only the sleeping site location or trap site location is identified. This suggests that tracking should provide the most accurate approximation of an animal's true home range size. Second, sleeping sites are often chosen for particular characteristics, such as proximity to food resources, quality of shelter, or safety from threats. Animals are, therefore, likely to enter sections of their home range during the night for purposes other than sleeping. Similarly, animals appear to be easier to trap in some parts of their range than in other parts, due to differences in attractiveness to the study animals between locations where traps have been set (Radespiel, personal communication). If direct observations are complemented by trap mark and/or sleeping site location records, then an even more complete estimate of home range area can be achieved [Harcourt & Nash, 1986]

Methods of Home Range Analysis

Home range refers to both the shape of the map of an animal's locations obtained by direct observation or by triangulation and to the size of the area used by the animal [White & Garrott, 1990]. The accuracy of both the shape and size of the home range estimate is a function of the precision of the location data and the accuracy with which these data points are plotted [White & Garrott, 1990]. Both the shape of the map of locations and the numerical estimation of the area used by an animal depend on the number of independent data points used to make the calculation or the length of the study and the method of home range analysis chosen.

The time scale over which a study is conducted can affect the size of home range estimates [Waser & Wiley, 1979]. As length of sampling time increases, the number of data points collected generally increases, and an animal's cumulative range size tends to approach an asymptote [Waser & Wiley, 1979]. However, most studies of nocturnal prosimians achieve so few hours of direct observation that an asymptote may only rarely be reached. Home range sizes of nocturnal prosimians, therefore, are probably only rarely fully estimated. The cumulative ranges of some animals may also pass through several successive asymptotes as observation time increases [Waser & Wiley, 1979]. For example, some animals

may concentrate their activities successively in different parts of their ranges or show strong seasonality in the use of different parts of their ranges [Waser & Wiley, 1979]. Thus, range estimates based on short term study may not be accurate even when an initial asymptote has been reached.

The number of data points or length of study are not the only factors that can influence home range estimates. Different methods of home range analysis have been demonstrated to yield different range use estimates [Trevor-Deutsch & Hackett, 1980; Quin et al., 1992]. It is unclear as to what extent the lack of concordance between the results derived from different methods of home range analysis is due to inadequate sampling. Researchers should test whether or not larger data sets would even out the differences between the results provided by the different methods. An animal's uneven use of space, including occasional forays outside the usual area and any temporary shifts in habitat use, make it virtually impossible to propose any one universally applicable and appropriate method of home range analysis [Waser & Wiley, 1979].

Various methods of home range analysis have been previously described and evaluated [Macdonald et al., 1980; Jaremovic & Croft, 1987; Worton, 1987; Harris et al., 1990; White & Garrott, 1990]. In this section, we examine the methods of home range analysis most commonly used in studies of nocturnal prosimian ranging behavior: minimum convex polygons, minimum concave polygons, and quadrat analysis. We also briefly discuss other methods of home range analysis used by other biologists. Of the 27 studies included in this review that specified their method of home range calculation: 12 used only minimum convex polygons; two used both minimum convex polygons and quadrat analyses; one used minimum concave polygons; 10 did not report the method(s) used to analyze ranging data; and two did not calculate home range size at all.

Minimum convex polygon. Home range size in nocturnal prosimians has traditionally been quantified as the area enclosed by a convex polygon of an animal's known locations [Bearder & Martin, 1980b; Harcourt & Nash, 1986; Warren & Crompton, 1997]. The minimum convex polygon method is the oldest and most widely used method of home range analysis [Harris et al., 1990; White & Garrott, 1990]. Minimum convex polygons are constructed by connecting the outermost known location records of an animal to form a convex polygon [Mohr, 1947; Southwood, 1966] with a quantifiable area. Minimum convex polygons are easy to construct and calculate. They can also be compared between studies [Harris et al., 1990] if a similar number of data points is used to generate them in each study [White & Garrott, 1990]. This method should be included as one of two or more methods of home range estimation in any study because minimum convex polygons permit home range shape and area comparisons between different studies [Harris et al., 1990].

Despite its usefulness and popularity, the minimum convex polygon method suffers from three major limitations. First, the size of the home range increases as the number of location records increases because minimum convex polygons measure only the total area used and not the specific area used during an animal's normal activities. As the number of location records for an animal increases, so does the probability of obtaining a location record outside of the animal's normal range [White & Garrott, 1990]. Home range estimates computed with significantly different numbers of data points may, therefore, not be directly comparable [White & Garrott, 1990]. Second, this method may include areas in an animal's range that the animal never actually entered, thereby overestimating its home range. This problem occurs when infrequent forays to locations outside of the normal range of an animal contribute outlying points that must then be

connected by lines to the outermost points in the animal's normal range [Harris et al., 1990]. Third, this method completely ignores differences in intensity of use of certain parts of an animal's range.

Several software programs (Calhome, Home Range, RANGES IV and V, and Tracker) have been designed to correct for some of the problems with the minimum convex polygon method by eliminating 5%, 25%, or even 50% of the outlying locational data points. Unfortunately, a recent analysis of a dataset of moose (*Alces alces*) ranging patterns that used these software programs found that there was little concordance between the home range estimates produced by the programs when the same number of outlying locational data points was excluded for each program [Lawson & Rodgers, 1997].

Minimum concave polygons. Of the studies reviewed, only one, Gursky [1998], employed the minimum concave polygon method [Stickel, 1954] for home range estimation. Minimum concave polygons can be constructed by connecting all location points for each animal to form a closed concave polygon [White & Garrott, 1990], or by connecting only those location points for each animal that are not judged to be outliers to form a closed concave polygon [Kenward, 1987]. The usefulness of the minimum concave polygon method for estimating home range size has yet to be assessed. While the minimum concave polygon method is less likely to produce home range overestimates than the minimum convex polygon method, an objective procedure for constructing a concave polygon around an animal's location records does not exist [White & Garrott, 1990]. For this reason, minimum concave polygons, in contrast to minimum convex polygons, may not be comparable between studies.

Quadrat analysis. Because both of the previously described measures of home range analysis ignore differences in the intensity of use of parts of an animal's range, some authors have also used quadrat analysis to measure the pattern of home range use in nocturnal prosimians [Crompton & Andau, 1987; Warren & Crompton, 1997]. This method of home range analysis is frequently used in studies of day-active primates [Olson, 1986; Kool, 1989].

Quadrat analysis [Siniff & Tester, 1965; Adams & Davis, 1967; Clutton-Brock, 1974] uses the frequency of an animal's locations within a uniform grid system of cells to estimate home range shape and size [Adams & Davis, 1967], instead of drawing a single contour around the boundary of a home range. The area over which an animal moves, or in some cases the entire study site, is dissected by a grid of cells. These cells are either established by a grid system of trails or are superimposed over a map of the study site. The number of times an animal enters a particular cell or the percentage of an animal's total observation time spent in each cell is then tabulated. The home range size is calculated as the number of cells entered or occupied by an animal or group at least once, multiplied by the area of a cell. Cells of intensive use [Struhsaker, 1975; Oates, 1977] or core areas [Kaufmann, 1962] of frequently used cells are identified as those cells containing at least some particular percentage [Warren & Crompton, 1997] of the location records.

The quadrat analysis method of estimating range size, based on the number of cells entered, can overestimate an animal's or group's range size because parts of some cells are never actually entered [Oates, 1977]. In fact, the choice of grid cell sizes can significantly influence the magnitude of home range size overestimation [Olson, 1986; Kool & Croft, 1992]. Larger cell sizes may yield greater overestimates of home range size than do smaller cell sizes since the entire area of a larger incompletely entered cell contributes a greater area to the estimate of an animal's home range than does the area of a smaller incompletely entered cell

[Oates, 1977; Kool & Croft, 1992]. Smaller grid cells can reduce the error in home range calculations [Kool & Croft, 1992] but are prone to errors in plotting when they are superimposed on a map of the study area: the smaller the grid cell used, the greater the chance that a small error in plotting will place an animal's location in the wrong cell.

Other methods of home range analyses. Most field studies of primates have relied on the minimum convex polygon method or quadrat analysis to analyze home range data, although a variety of other methods have long been used for home range studies in other mammals [Macdonald et al., 1980; Trevor-Deutsch & Hackett, 1980]. Other methods include: various normal ellipsoid home range estimating techniques, such as the Jenrich-Turner estimator; several contour methods, such as the harmonic mean method; and cluster analysis. For a review of these methods, see Harris et al., 1990; Macdonald et al., 1980; White and Garrott, 1990; and Kenward, 1992. There is little consensus as to which of these mathematically sophisticated methods best estimates home range size [Harris et al., 1990].

Given the many limitations of the traditional methods for calculating home range, it is clear that we need to explore alternative methods. We encourage nocturnal prosimian researchers to estimate home range sizes using some of these newer methods to determine how the estimates provided by these methods compare to those provided by the more traditional methods of data analysis. Regardless of which newer techniques are employed, we feel it is important to include at least one traditional method of data analysis in order to facilitate comparisons with results from previous studies [Voigt & Tinline, 1980; Harris et al., 1990].

Comparison of home range estimates based on different methods of data analysis. Each method of home range analysis has its own advantages and disadvantages and each method meets certain study requirements. The choice of method has been shown to affect home range estimates for two non-primate mammal species [Trevor-Deutsch & Hackett, 1980; Quin et al., 1992]. A comparison of range estimates computed from *tracking* data for a study population of 12 sugar gliders (*Petaurus breviceps*) using two different methods of data analysis (the minimum convex polygon method and the harmonic mean method, 95% isopleth [Dixson & Chapman, 1980]), found that mean home range estimates derived from the latter method were, on average, 65.7% of those determined by the former method [Quin et al., 1992]. In addition, Quin et al. [1992] computed home range sizes from *trapping* data for the same population using nine different methods of data analysis. The nine estimates, all computed with the same set of trapping data, also varied greatly. Similarly, Trevor-Deutsch and Hackett [1980] produced widely varying home range estimates using several different methods of analysis on a single data set of eastern chipmunk (*Tamias striatus*) ranging patterns.

The effect of method of data analysis on home range estimates has not yet been evaluated for nocturnal prosimians. However, data from two studies provide some preliminary comparisons. Crompton and Andau [1986] calculated home range size for *Tarsius bancanus* (n=4) using the minimum convex polygon method. They also provided a map of each tarsier's range divided into 20 × 20 m grid squares. From the information provided, we were able to calculate home range size using quadrat analysis. We were then able to compare the estimates derived from both methods. As with the studies of non-primate mammals described above, we found that home range estimates derived from different methods of data analysis varied considerably. Mean home range estimates for Crompton & Andau's tarsiers derived from the quadrat analysis method were, on average, 67.7% of those determined by the minimum convex polygon method. However, a similar

comparison of home range data for *Avahi occidentalis* (n=4) and *Lepilemur edwardsi* (n=4) from a study by Warren and Crompton [1997] failed to reveal substantial differences between home range estimates derived from the minimum convex polygon and the quadrat analysis methods. With such a paucity of available data on the topic, further studies of nocturnal prosimian ranging patterns employing more than one method of data analysis are needed to examine the variation in home range estimates produced by different methods of data analysis.

CONCLUSIONS

1. We have demonstrated in this review that the methods used to collect and analyze data on the ranging patterns of nocturnal prosimians have profound effects on the sizes and shapes of the home range estimates that are produced. Direct observations facilitated by radio tracking during all-night follows appear to be the most effective method for gathering data on individual movements. Triangulation techniques seem to yield the most data relevant to home range overlap and access to social partners and mates. A combination of triangulation and all-night follows would yield data on the macro (overlap in space use) and micro (direct social interactions between individuals) levels, both of which are important to studies of sociality. In those cases where radio tracking and/or all-night follows are not possible, trap mark techniques can be used though they appear to greatly underestimate home range size and will not yield data that is easy to analyze for studies of sociality.

2. To facilitate comparisons between studies, we urge researchers to include in their publications the specifics of their data collection methods, including, but not limited to: total number of hours sampled per animal; number of full-night follows; explanation of how movements are defined and recorded; and method of plotting the data (including geo-referencing). For trap mark studies, specification of trap locations, size and shape of grids, and frequency of trapping sessions are important.

3. Data collected on nocturnal prosimian ranging patterns should be analyzed using more than one method of data analysis. We agree with Voigt and Tinline [1980] and Harris et al. [1990] that at least one of the methods used for data analysis should be a widely used method, such as minimum convex polygon and/or quadrat analysis, to facilitate comparison with previous studies. Quadrat analysis is particularly effective because it provides data not only on home range size, but also on intensity of use of different areas of an animal's range. We recommend that primatologists explore the more mathematically complex methods of data analysis available in the non-primate literature [White & Garrott, 1990; Harris et al., 1990]. Researchers should bear in mind, however, that the more sophisticated methods do not necessarily provide more accurate or useful results [Macdonald et al., 1980].

4. Although patterns of home range use are used to infer social structure in nocturnal prosimians (e.g., Fietz's 1999b inference that because male and female *Cheirogaleus medius* maintain completely overlapping home ranges and share the same sleeping sites, they must live in monogamous pairs), the accuracy of this approach for measuring social structure remains largely untested. Of the 27 studies reviewed in this paper, not one provides evidence for evaluating the validity of inferring social structure from ranging data. We believe that this and other unexplored topics provide a rich opportunity for further research into the social lives of nocturnal prosimians.

ACKNOWLEDGMENTS

REFERENCES

Adams L, Davis SD. 1967. The internal anatomy of home range. J Mamm 48: 529–536.

Alterman L, Doyle GA, Izard MK, eds. 1995. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press.

Amlaner CJ, MacDonald DW, eds. 1980. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press.

Atsalis S. 2000. Spatial distribution and population composition of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar, and its implications for social organizations. Am J Primatol 51:61–78.

Bearder SK. 1987. Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 11–24.

Bearder SK, Martin RD. 1980a. *Acacia* gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). Int J Primatol 1:103–128.

Bearder SK, Martin RD. 1980b. The social organization of a nocturnal primate revealed by radio tracking. In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press. p 633–648.

Bergstrom BJ. 1988. Home ranges of three species of chipmunks (*Tamias*) as assessed by radio-telemetry and grid trapping. J Mamm 69:190–193.

Burt WH. 1943. Territorial behavior and populations of some small mammals in southern Michigan. Miscellaneous publications of the Museum of Zoology, University of Michigan No. 45.

Charles-Dominique P. 1977. Ecology and behavior of nocturnal prosimians. London: Duckworth.

Charles-Dominique P. 1978. Solitary and gregarious prosimians: evolution of social structures in primates. In: Chivers DJ, Joysey KA, editors. Recent advances in primatology, vol. 3. Evolution. London: Academic Press. p 139–149.

Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pagés E. Pariente GF, Petter-Rousseaux A, Schilling A, Petter J-J. 1980. Nocturnal malagasy primates: ecology, physiology, and behavior. New York: Academic Press.

Charles-Dominique P, Petter JJ. 1980. Ecology and social life of *Phaner furcifer*. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pagés E, Pariente GF, Petter-Rousseaux A, Schilling A, Petter J-J, editors. Nocturnal malagasy primates: ecology, physiology, and behavior. New York: Academic Press. p 75–95.

Clark AB. 1985. Sociality in a nocturnal "solitary" prosimian: *Galago crassicaudatus*. Int J Primatol 6:581–600.

Clutton-Brock TH. 1974. Activity patterns of red colobus (*Colobus badius tephrosceles*). Folia Primatol 21:161–187.

Cochran WW, Lord RD. 1963. A radio-tracking system for wild animals. J Wildl Manage 27:9–24.

Crompton RH, Andau PM. 1987. Ranging, activity rhythms, and sociality in free-ranging *Tarsius bancanus*: a preliminary report. Int J Primatol 8:43–71.

DeVore I. 1965. Editor. Primate behavior: field studies of monkeys and apes. New York: Holt, Rinehart, and Winston.

Dixson KR, Chapman JA. 1980. Harmonic mean measure of animal activity area. Ecology 61:1040–1044.

Doyle GA, Martin RD, eds. 1979. The study of prosimian behavior. New York: Academic Press.

Fietz J. 1999a. Mating system of *Microcebus murinus*. Am J Primatol 48:127–133.

Fietz J. 1999b. Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. Ethology 105:259–272.

Garrott RA, White GC, Bartmann RA, Weybright DM. 1986. Reflected signal bias in biotelemetry triangulation systems. J Wildl Manage 50:747–752.

Gursky S. 1998. Conservation status of the spectral tarsier *Tarsius spectrum*: population density and home range size. Folia Primatol 69(suppl):191–203.

Harcourt C. 1987. Brief trap/retrap study of the brown mouse lemur (*Microcebus rufus*). Folia Primatol 49:209–211.

Harcourt C. 1991. Diet and behavior of a nocturnal lemur, *Avahi laniger*, in the wild. J Zoolog Soc Lond 223:667–674.

Harcourt C, Nash L. 1986. Social organization of galagos in Kenyan coastal forests: I. *Galago zanzibaricus*. Am J Primatol 10:339–355.

Harris S, Cresswell W.J, Forde PG, Trew-

hella WJ, Wollard T, Wrary S. 1990. Home range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. Mamm Rev 20:97–123.

Jaremovic RV, Croft DB. 1987. Comparison of techniques to determine eastern grey kangaroo home range. J Wildl Manage 51:921–930.

Kappeler P. 1997. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemur. Biol Rev 72:(1) 111–151.

Kappeler PM, Ganzhorn JU, eds. 1993. Lemur social systems and their ecological basis. New York: Plenum Press.

Kaufmann JH. 1962. Ecology and social behavior of the Coati, *Nasua narica*, on Barro Colorado Island, Panama. Univ Calif Publ Zool 60:95–222.

Kenward RE. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. New York: Academic Press.

Kenward RE. 1992. Quantity versus quality: programmed collection and analyis of radio-tracking data. In: Priede IG, Swift SM, editors. Wildlife telemetry: remote monitoring and tracking of animals. New York: Ellis Horwood. p 231–246.

Kool KM. 1989. Behavioral ecology of the silver leaf monkey, trachypithecus auratus sondaicus, in the Pangandaran Nature Reserve, West Java, Indonesia. Ph.D. dissertation. University of South Wales, Sydney, Australia.

Kool KM, Croft DB. 1992. Estimators for home range areas of arboreal colobine monkeys. Folia Primatol 58:210–214.

Lance AN, Watson A. 1980. A comment on the use of radio tracking in ecological research. In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press. p 335–359.

Lawson EJG, Rodgers AR. 1997. Differences in home-range size computed in commonly used software programs. Wildl Soc Bull 25:721–729.

Lee JE, White GC, Garrott RA, Bartmann RM, Alldredge AW. 1983. Assessing the accuracy of a radiotelemetry system for estimating mule deer locations. J Wildl Manage 49:658–663.

Macdonald DW, Ball FG, Hough NG. 1980. The evaluation of home range size and configuration using radio tracking data. In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press. p 405–424.

MacKinnon J, MacKinnon K. 1980. The behavior of wild sprectral tarsiers. Int J Primatol 1:361–371.

Manville RH. 1949. A study of small mammal populations in northern Michigan. Ann Arbor: University of Michigan Press.

Martin RD. 1972. A preliminary field study of the lesser mouse lemur (*Microcebus murinus* J.F. Miller 1777). Zeitschrift Fuer Tierpsychologie Beiheft 9:43–89.

Mohr CO. 1947.Table of equivalent populations of North American small mammals. Am Midland Nat 37:223–249.

Müller AE. 1998. A preliminary report on the social organisation of *Cheirogaleus medius* (Cheirogaleidae; Primates) in northwest Madagascar. Folia Primatol 69:160–166.

Müller AE. 1999. Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): infrerences from body weights and trapping data. Am J Primatol 49: 265–280.

Nash LT, Harcourt CS. 1986. Social organization of galagos in Kenyan coastal forests: II. *Galago garnettii*. Am J Primatol 10:357–369.

Nash LT, Whitten PL. 1989. Preliminary observations on the role of Acacia gum chemistry in *Acacia* utilizations by *Galago senegalensis* in Kenya. Am J Primatol 17:27–39.

Niemitz C. 1984. Editor. Biology of tarsiers. Stuttgart: Gustav Fischer Verlag.

Oates JF. 1977. The guereza and its food. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behavior in lemurs, monkeys, and apes. London: Academic Press. pp 275–321.

Olson DK. 1986. Determining range size for arboreal monkeys: methods, assusmptions, and accuracy. In: Taub DM, Kay FA, editors. Current perspective in primate social dynamics. New York: Van Nostrand Reinhold Co. p 212–227.

Pagés E. 1980. Ethoecology of *Microcebus coquereli* during the dry season. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pagés E, Pariente GF, Petter-Rousseaux A, Schilling A, Petter J-J, editors. Nocturnal Malagasy primates: ecology, physiology, and behavior. New York: Academic Press. p 97–116.

Pagés-Feuillade E. 1988. Modalités de l'occupation de l'espace et relations inter-individuelles chez un prosimien nocturne malgache (*Microcebus murinus*). Folia Primatol 50:204–220.

Petter J-J, Albignac R, Rumpler Y. 1977. Mammiferes lemuriens (primates prosimiens). Faune de Madagascar 44. Paris: ORSTOM-CNRS.

Quin DG, Smith AP, Green SW, Hines HB. 1992. Estimating the home ranges of sugar gliders (*Petaurus breviceps*) (Marsupialia: Petauridae), from grid-trapping and radio-telemetry. Wildl Res 19:471–487.

Radespiel U. 2000. Sociality in the gray mouse lemur (*Microcebus murinus*) in

northwestern Madagascar. Am J Primatol 51:21–40.

Richard AF. 1985. Primates in nature. New York: W.H. Freeman and Company.

Schwab DA. 2000. A preliminary study of the social and mating system of pygmy mouse lemurs (*Microcebus myoxinus*). Am J Primatol 51:41–60.

Siniff DB, Tester JR. 1965. Computer analysis of animal movement data obtained by telemetry. Bioscience 15:104–108.

Southwood TRE. 1966. Ecological methods: with particular reference to the study of insect populations. London: Chapman & Hall.

Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behav Ecol Sociobiology 41:291–309.

Sterling EJ. 1993. Patterns of range use and social organization in aye-ayes (*Daubentonia madagascariensis*) on Nosy Mangabe. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 1–10.

Sterling EJ, Richard AF. 1995. Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. In: Alterman L, Doyle GA, Izard MK, editors. Creatures of the dark: the nocturnal prosimians. New York: Plenum Press. p 439–451.

Stickel LF. 1954. A comparison of certain methods of measuring ranges of small mammals. J Mamm 35:1–15.

Struhsaker TT. 1975. The red colobus monkey. Chicago: The University of Chicago Press.

Trevor-Deutsch B, Hackett DF. 1980. An evaluation of several grid trapping methods by comparison with radiotelemetry in a home range study of the eastern chipmunk (*Tamias striatus* L.) In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press. p 375–386.

Van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology: the behavioral ecology of humans and other mammals. Oxford: Blackwell. p 195–218.

Voigt DR, Tinline RR. 1980. Strategies for analyzing radio tracking data. In: Amlaner CJ, MacDonald DW, editors. A handbook on biotelemetry and radio tracking. Oxford: Pergamon Press. p 387–404.

Warren RD, Crompton RH. 1997. A comparative study of the ranging behavior, acitivity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indridae) at Ampijoroa, Madagascar. J Zool Soc Lond 243:397–415.

Waser PM, Wiley RH. 1979. Mechanisms and evolution of spacing in animals. In: Marler P, Vandenbergh JG, editors. Handbook of behavioral neurobiology. vol 3. Social behavior and communication. New York: Plenum Press. p 159–223.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data. New York: Academic Press.

Worton BJ. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277–298.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262–300.