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Population Density of the Mantled Howler Monkey (*Alouatta palliata*) at La Selva Biological Reserve, Costa Rica: A New Technique to Analyze Census Data¹

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ABSTRACT

Broad survey census data for mantled howler monkeys, *Alouatta palliata*, from La Selva Biological Reserve, northeastern Costa Rica, are analyzed with an agglomerative hierarchical clustering method to estimate minimum number of troops. The estimate of 15 troops (7-15 howlers/km²) provided by the cluster analysis is similar to an independent census of the same population using the triangulation technique. These data indicate the potential usefulness of cluster analysis methods to estimate minimum number of primate troops within an area. Cluster analysis has several advantages over more traditional primate census techniques: the assumption that it is necessary to achieve reliable estimates from line transect sampling is not required (*i.e.*, points directly on the line will never be missed); census data can be collected by one person making it easier logistically than conducting a census with the triangulation technique which requires many people; census data collected over a brief period of time can be used to provide quantitative estimates of population density; and observations provided by others in the survey area during the time period of the census may be used. Cluster analysis is recommended when attempting to estimate population densities of primates in tall evergreen forests where visibility is poor, when animals have long inactive periods, few or unpredictable vocalizations, and/or occupy the top of the canopy. The cluster method of analyzing broad survey data may also be applicable to other territorial mammalian populations that are difficult to census by other means.

RESUMEN

Los datos obtenidos en un censo general de monos cónegos, *Alouatta palliata*, en La Estación Biológica La Selva, Costa Rica, fueron analizados con el método estadístico de agrupación jerárquica de datos para estimar el número mínimo de tropas. Los resultados obtenidos a través de dicho análisis indican que existen aproximadamente 15 tropas de cónegos (7-15 animales/km²). Este resultado es semejante al obtenido por el método de triangulación en un censo independiente de la misma población, por lo tanto se puede considerar que el método de agrupación jerárquica es válido para estimar el número mínimo de grupos de primates dentro de un área. El método de agrupación jerárquica tiene algunas ventajas en relación a las técnicas tradicionales para estimar poblaciones de primates: no se requiere la suposición necesaria utilizada por el método de transectos (*i.e.*, los monos sobre el transecto son absolutamente evidentes); una sola persona puede realizar los censos, lo que conlleva ventajas logísticas; se pueden usar datos obtenidos en un período corto para obtener estimaciones cuantitativas de densidad poblacional. Además, pueden usarse observaciones hechas por otras personas presentes en el área estudiada al tiempo que se realizó el censo. Se recomienda el uso del método de agrupación jerárquica para estimar densidades poblacionales de primates en selvas de copa alta donde la visibilidad es reducida, y cuando los primates tienen períodos prolongados de inactividad, vocalizan poco o de manera impredecible, y/o se encuentran principalmente en las partes altas del dosel. Este método podría ser utilizado también para poblaciones de otros mamíferos territoriales, que suelen ser difíciles de contar.

Key words: *Alouatta palliata*; census techniques; cluster analysis; Costa Rica; howler monkey; La Selva; population density; primate density.

THE ABUNDANCE OF NONHUMAN PRIMATES has rapidly declined throughout the Neotropics in the last few decades. Human interference from hunting, illegal

trade, and habitat destruction threatens the survival of most populations of wild monkeys. Habitat destruction due to deforestation is by far the most serious threat to wild primates in the Neotropics (Thorington & Heltne 1976; Robinson & Ramirez 1982; Mittermeier *et al.* 1986; Mittermeier 1987, 1991). Information on population densities in protected areas may be used to recognize declining primate populations in areas where conservation efforts are most needed. Data on population densities

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of primates will assist policy makers in developing conservation laws and long-term management plans (Thorington & Heltne 1976, Defler & Pintor 1985, Marsh & Mittermeier 1987, Chapman *et al.* 1988). Finally, primate census data are important for a better understanding of the population ecology of these long-lived mammals.

In Costa Rica the current rate of deforestation outside of protected areas has been estimated as greater than 7 percent of the total remaining forest per year (Sader & Joyce 1988). Therefore, obtaining estimates of population densities of endangered species is particularly important to determine if diminishing habitats will be sufficient to maintain these populations.

Population sizes of mantled howler monkeys (*Alouatta palliata*) have been estimated in several dry forest areas in Costa Rica, including Santa Rosa National Park (Freese 1976, Fedigan *et al.* 1985, Clarke *et al.* 1986, Chapman *et al.* 1988) and La Pacifica (Heltne *et al.* 1976, Glander 1978, 1980; Clarke *et al.* 1986). However, with the exception of one ten-day broad survey that provided a preliminary estimate of primate populations (Fishkind & Sussman 1987), no information has been collected on primate populations in the Atlantic lowland wet tropical forests of Costa Rica. I conducted a census of mantled howler monkeys at La Selva Biological Reserve in Costa Rica, as part of a sixteen-month ecological study of the foraging behavior of howler monkeys.

Several techniques have been used to estimate primate population densities with variable success (Green 1978, Marsh & Wilson 1981, NRC 1981, Defler & Pintor 1985, Koster & Butynski 1985, Brockelman & Ali 1987, Chapman *et al.* 1988). Undoubtedly, the most accurate method of estimating primate population densities is the long-term monitoring of specific groups (NRC 1981), but this technique is not always an option.

The most commonly used technique for estimating primate population densities in the Neotropics is one of the various line transect methods (Brockelman & Ali 1987, Chapman *et al.* 1988). Line transects, however, show much variation, making it difficult to reliably compare estimates between sites. Furthermore, one of the basic assumptions for line transects is that animals directly on the line will never be missed (Burnham *et al.* 1980). This assumption is difficult to fulfill when censusing howler monkeys in tall evergreen forests with limited visibility (Freese *et al.* 1982). In addition, the activity pattern of howlers, which may spend as much as 79 percent of the daytime resting (Crockett & Ei-

senberg 1987; Stoner 1993), further complicates recording their presence on a transect line. In sum, line transect methods frequently underestimate the density of *Alouatta* in tall evergreen rain forests.

The main objectives of this research were to develop a reliable and reproducible method for censusing populations of *Alouatta* in dense evergreen tropical forests and to obtain an estimate of the population density of *Alouatta palliata* in the Atlantic lowlands of Costa Rica.

STUDY SITE

La Selva Biological Reserve is located at the confluence of the Sarapiquí and Puerto Viejo rivers in the Atlantic lowlands of northeastern Costa Rica in the province of Heredia (10°26'N, 83°59'W) (Hartshorn 1983). This area contains two major Holdridge life zones—Tropical Wet Forest on the west side, and Tropical Premontane Wet Forest to the east (Holdridge 1967), and can be defined as wet tropical forest. La Selva is composed of approximately 56 percent primary forest and 23 percent regenerating secondary forest of various ages; the remainder of the reserve consists of pastures and managed areas (Clark 1990). The 1500 ha La Selva Reserve is connected to a much larger protected area, Braulio Carrillo National Park, on the south side via the Zona Protectora. These two areas together encompass an area of over 52,000 ha of protected rain forest and span an altitudinal range of 35–2900 m.

Although no formal surveys of any primates were conducted at La Selva prior to 1986 (Fishkind & Sussman 1987), local residents and researchers from La Selva noted a scarcity of primates in the 1960s and 1970s (Timm *et al.* 1989). It was believed that the nonhuman primate populations were greatly reduced as a result of a human yellow fever epidemic which swept through Central America in the early 1950s (Galindo 1971, Downs 1982, Yuill 1983, Fishkind & Sussman 1987).

METHODS

Two census techniques for estimating the minimum number of howler monkey troops were used: a two-month broad survey which used a centroid method of agglomerative clustering to estimate minimum number of troops (Johnson & Wichern 1982, SAS 1990); and a standard triangulation method (Cochran 1980, Brockelman & Ali 1987).

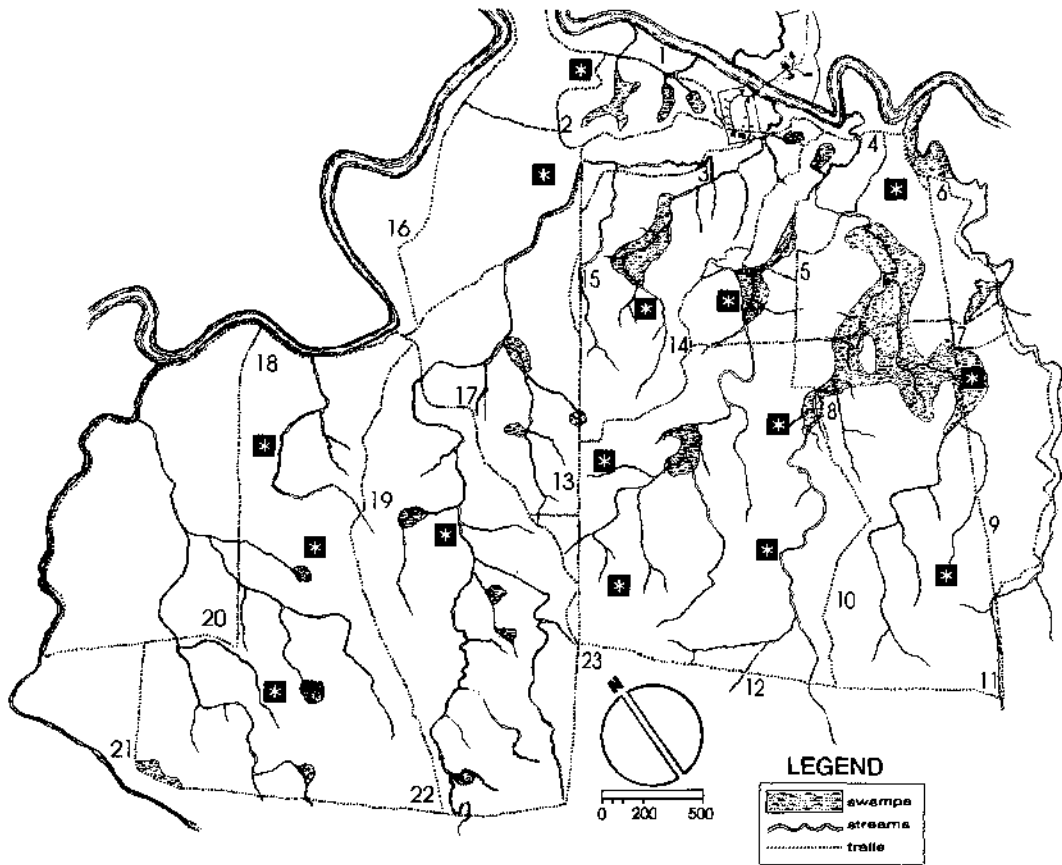


FIGURE 1. Results of *A. palliata* census 19 July 1992 using triangulation technique to estimate minimum number of troops. Each asterisk indicates the approximate location of howler troops based on the overlap of 3 different observation groups. The numbers represent the locations of the 23 volunteer groups recording the howls. (Map based on the Organization for Tropical Studies visitor's map, Carlos A. Camacho, 1987.)

DATA COLLECTION FOR CLUSTER ANALYSIS TECHNIQUE.—All observations of howler monkeys were recorded during a broad survey conducted from 4 June through 31 July 1990. The census was performed 6 days a week from existing trails between 0500 and 0900 hr and between 1400 and 1800 hr. The precise locality and the time of observation were recorded for all troops. Members of troops encountered were counted, and identified by age (adult, subadult, and infant) and sex classes when possible (NRC 1981). In addition to my observations, information on howler sightings from naturalists and researchers at La Selva during this period were added to the data base.

ESTIMATING MINIMUM NUMBER OF TROOPS WITH CLUSTER ANALYSIS.—To estimate the minimum number of howler troops using the data from howler

sightings over an eight-week period, average home range size was first estimated and then the centroid method of agglomerative hierarchical clustering was used to determine which observations were likely to be from the same troop (SAS 1990). In the centroid cluster analysis method, the distance between two clusters is defined as the (squared) Euclidean distance between their centroids or means (Massart & Kaufman 1983). To use this method, the data on troop observations were first converted to X and Y coordinate data and distances between groups were recorded in meters. The cluster analysis begins by considering every point a separate cluster and then points are grouped together based on similarities of distances (SAS 1990). For example, the two closest observations of troops would first be combined into a cluster and the average is calculated, then the next closest observation is added and

TABLE 1. Home range sizes and densities reported for howler monkeys at various study sites. NA: Data not available from publication.

Study site	Home range (ha) ^a		Density/km ²	Source
	$\bar{x} \pm \text{SD}$	N		
Mexico, Los Tuxtlas ^b	60 ± NA	3	23	Estrada 1982
Costa Rica, La Pacifica ^b	10	1	77	Glander 1978
Panama, Chiriquía ^b	5 ± 2	7	1067	Baldwin & Baldwin 1976
Panama, Barro Colorado ^b	31 ± 1	2	92	Milton 1980
Belize ^c	18 ± 7	3	12	Horwich & Gebhard 1983
Colombia, Finca Merenberg ^d	22	1	NA	Gaulin & Gaulin 1982
Colombia, El Tuparro ^d	24 ± 2	5	27	Defler 1981
Colombia, El Tuparro ^d	13 ± 6	3	23	Defler 1981
Peru, Cocha Cashu ^d	25 ± NA (range 20–30)	NA	30	Terborgh 1983
Surinam, Raleighvallen- Votzberg Park ^d	9 ± NA (range 6–11)	NA	17	Mittermeier 1977
Trinidad, Bush Bush Island ^d	6	1	NA	Neville 1972

^a 95% confidence interval based on mean home ranges reported for all sites is 5–29 ha.

^b *Alouatta palliata*

^c *A. pigra*

^d *A. seniculus*

the average is calculated again. The distance between two clusters is then calculated based on the average within the clusters. In my analysis, howler monkey home range size was used to define the size of the clusters.

DATA COLLECTION FOR TRIANGULATION TECHNIQUE.—The howlers' unique behavior of making loud territorial calls at sunrise (Crockett & Eisenberg 1987) allowed a triangulation method to be used to estimate minimum number of troops. With the assistance of 70 volunteers, a survey of the entire reserve was conducted 18 July 1992. Volunteers included local naturalists and field assistants with considerable experience in the forest, as well as local high school students and visiting students and researchers at La Selva. The more experienced naturalists and field assistants were matched up with 2–3 others to form a group. Each group arrived at designated sites (Fig. 1) within La Selva forming a triangle among three different volunteer groups; data were collected between 0400 and 0700 hr. Each

group recorded the compass direction of the howl, the time, the approximate distance of the group, and if one or more than one individual was calling. The distance was a subjective estimate of close (<100 m), medium (100–1000 m), or far (>1000 m). I relied upon the more experienced volunteers to determine the distance, and worked with them the week before the survey providing examples in order to attain consistency for this estimate.

RESULTS

Home range size was estimated using a representative sample of howler troop home range sizes from the literature, which includes various countries, habitats, and densities (Table 1). Based on these data, a ninety-five percent confidence interval for the mean home range size of howler troops was calculated as 5–29 hectares. In order to be conservative and to avoid overestimating troop density, the top of the ninety-five percent confidence interval was used as the estimated home range size of howlers at La Selva

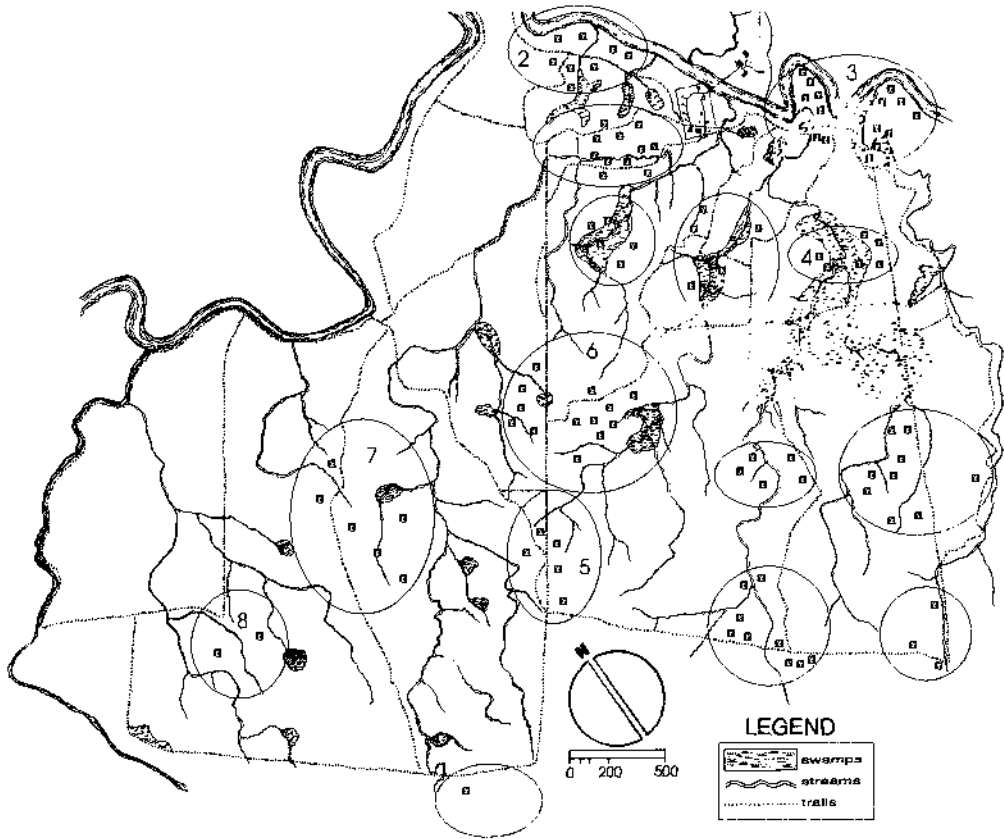


FIGURE 2. Results of centroid cluster analysis for *A. palliata* census data encircling observations which likely represent the same troop, but do not indicate actual ranging patterns. Numbers represent groups which were counted (Table 2) or are referred to in the text. Each X represents an observation of a howler troop on a different day during the two-month survey period. (Map based on the OTS visitor's map, Carlos A. Camacho, 1987.)

during the census period. Furthermore, data from ranging patterns of two howler troops at La Selva over a 16-month period indicate that the troops utilized only a portion of their home range during any two-month period (K. Stoner, pers. obs.). The area used during a two-month period varied depending on the season, but the range was 10–30 ha. Therefore, an estimated home range of 29 hectares for howler troops at La Selva during a two month period appears to be consistent with the observed ranging patterns.

Using a home range size of 29 ha, the centroid cluster analysis estimated a minimum of 15 howler troops within La Selva (Fig. 2). Similar results were obtained from the triangulation method which recorded the vocalizations of at least 15 different troops (Fig. 1). All vocalizations recorded on the census day consisted of the howls of two or more individ-

uals, and thus did not represent lone males, but most likely troops.

To avoid artificial groupings of clusters that did not reflect the same troop, I compared the quantitative cluster analysis with my qualitative observations of troop identifications. For example, Figure 2 demonstrates that groups one and two, as recognized by the cluster analysis, were very close and thus one may doubt the validity of recognizing two groups. However, the group composition was different between these two troops (Table 2) and group one had a female with a naturally occurring unique color mark. Another example of comparing the quantitative results of the cluster analysis with qualitative observations is found for groups seven and eight. Group seven was initially encountered close to the trail and I was able to accurately count the group (Table 2). Group eight was heard howling

TABLE 2. Census data for *Alouatta palliata* troops June 4–July 31, 1990 at La Selva Biological Reserve.

Group	Male	Female	Subadult	Infant	$N (\bar{x} = 11 \pm 4)$
SURA (1)	4	4	2	1 ^a 1 ^b	12
CES (2)	4	6	2	1 ^a 1 ^b	15
SOR (3)	1	4	0	1 ^a	6
SHO (4)	3	3	2	0	8
LOC (5)	5	4	4	1 ^a 1 ^b	15
SSO (6)	4	4	3	1 ^a 1 ^b	13
SSA (7)	2	3	3	0	8

^a Infant carried on mother's back.

^b Infant carried on mother's stomach.

shortly after I had left group seven and thus represents another group. In sum, all possibilities of comparing qualitative observations with the results from the cluster analysis, supported the groupings the cluster analysis produced.

Census data from the two-month survey in 1990 indicate an average group size of 11 ± 4 (Table 2), which estimates population density to be 7–15 howlers/km² within the 1500 ha reserve. This density is considerably lower than has been reported for howlers at most other sites (Table 1).

DISCUSSION

The similar estimates provided by the cluster analysis and the triangulation method indicate the usefulness of cluster analysis for estimating minimum number of troops of *Alouatta* and possibly other species of primates and mammals for which broad survey data are available. The triangulation method and the cluster analysis both estimated 15 troops to be within the reserve even though they were conducted almost two years apart. These results are not surprising given the low rate of population growth (Glander 1980) and group fission in howler monkeys. It is unlikely that the density and distribution of troops changed significantly in two years.

POTENTIAL SOURCES OF ERROR IN THE TRIANGULATION METHOD AND CLUSTER ANALYSIS.—Some factors may have limited the accuracy of the methods used in this study. The triangulation technique may have missed troops that did not howl on the census day or troops that were out of detectable range and thus may have underestimated the population density. However, it has been well-documented that howler monkeys howl most mornings (Chivers 1969), and the triangulation method has been successfully used at other sites to estimate minimum number of howler troops (Milton 1982).

Factors which may have affected the estimate of population density provided by the cluster analysis include the estimate of home range size and the assumption of non-overlapping home ranges. If home range size was overestimated, the number of groups would have been underestimated; if home range size was underestimated, the number of groups would have been overestimated. However, as described in the methods section, the home range estimate of 29 ha during a two-month period was confirmed during a 16-month ecological study of *Alouatta palliata* at La Selva (K. Stoner, pers. obs.). Therefore, home range size is an unlikely source of error for the estimate provided by the cluster analysis in this study.

Cluster analyses assume that clusters are exclusive and non-overlapping (Johnson & Wichern 1982). Although this assumption does not apply to howler monkey home ranges over an entire year, especially where there is a high population density (Baldwin & Baldwin 1976, Milton 1980, Sekulic 1982), it is likely to be true over some shorter time period. During the eight-week survey period several groups could be identified accurately based on group composition (Table 2) and/or characteristic marks of individuals; however, groups were never observed in overlapping areas. In addition, a 16-month ecological study of *Alouatta palliata* provides further evidence that howler troops do not have overlapping ranges at this site during a two-month period (K. Stoner, pers. obs.). Several other studies have reported non-overlapping home ranges to characterize howler monkeys during periods of less than three months (Chivers 1969, Schlichte 1976, Braza *et al.* 1981, Estrada & Coates-Estrada 1984). In sum, the assumption of non-overlapping home ranges appears to be a valid assumption and an unlikely source of error in this study.

APPLICATIONS AND ADVANTAGES OF CLUSTER ANALYSIS.—The technique of cluster analysis can be

used if it is assumed that home ranges are not overlapping during the census period. Under conditions of high density, cluster analysis can be used to estimate minimum number of groups, but the census period must be shorter. Clusters must be calculated before the groups' home ranges overlap. The length of the census period will be determined by the shortest time period in which one group enters the area of another. Cluster analysis may be performed on multiple census periods. In this way, sequential estimates of minimum number of troops may be calculated as well as patterns of home range use. The clusters will likely be in a different area, but the number of clusters should be the same.

The broad survey is the most common method applied when attempting to survey a large area in a short time period (Scott *et al.* 1976, NRC 1981); however, broad surveys provide qualitative estimates only. In contrast, cluster analysis provides a quantitative method in which to analyze broad survey census data. Furthermore, cluster analysis has several advantages over more traditional primate census techniques: the assumption that is necessary to achieve reliable estimates from line transect sampling is not required (*i.e.*, points directly on the line will never be missed); census data can be collected by one person making it easier logistically than conducting a census with the triangulation technique which requires many people; census data collected over a brief period of time (as little as two weeks depending on the size of the area sampled and the density) can be used to provide quantitative estimates of population density; and, observations provided by others in the survey area during the time period of the census may be used. Local people often have more information about primates in the area than investigators can obtain during a survey of short duration (Colvin 1992).

Cluster analysis is particularly recommended when attempting to estimate population densities of primates that have long inactive periods, few or unpredictable vocalizations, and/or occupy the top of the canopy; conditions which render line transect methods inappropriate (Burnham *et al.* 1980). The cluster method of analyzing broad survey data may also be applicable to other territorial mammalian populations which are difficult to census by other means.

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