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Population Survey of the Spider Monkey *Ateles geoffroyi* at Tikal, Guatemala

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ABSTRACT. Intensive strip census methods were used to estimate population density and age-sex composition of a natural population of the spider monkey *Ateles geoffroyi*, in seasonally dry forest at Tikal, Guatemala. An objective procedure for determining effective strip width is discussed, and various census methods, including direct count and strip census, are evaluated as to merits and disadvantages

INTRODUCTION

Spider monkeys are important subjects for field study because of their unusual social organization and unique form of locomotion. Traditionally they have been classified in four species however HERSHKOVITZ (1972) considers the forms subspecies of a single species *Ateles paniscus*. For present purposes a taxonomic decision is not vital and I treat the four forms of *Ateles* as though they are valid species. Studies of natural populations of *Ateles* include CARPENTER's (1935) early work on *A. geoffroyi* in Panama, DURHAM's (1971, 1975) investigation of *A. paniscus* in Peru, and an excellent study of *A. belzebuth* in Colombia by L. and D. KLEIN (KLEIN, 1971, 1972, 1974; KLEIN & KLEIN, 1975, 1976). More limited amounts of field data are presented by COELHO et al. (1976), EISENBERG and KUEHN (1966), and WAGNER (1956). R. A. MITTERMEIER is currently studying spider monkeys in Surinam.

Throughout most of the generic range from southern Mexico to southern Brazil, *Ateles* is disappearing from the usual causes of habitat destruction, exploitation for food, export, and local pet trade. Fortunately an adequate sized population of *A. geoffroyi* is protected in lowland Guatemala and in 1975–1976 I conducted a 14-1/2 field study of ecology, locomotion, and social organization at Tikal National Park. In this paper I report on population density and age-sex structure.

Censusing of primates is receiving increasing attention because of the need to obtain, preferably with a reasonable amount of effort, population estimates to be used in planning conservation programs. One method, the strip-census, is strongly advocated by WILSON and WILSON (1975) who believe it is both more rapid and more objective than other methods. I used a form of strip-census based on a procedure of determining strip width that has not been used previously in censusing primates. Following the results of the census I discuss merits and disadvantages of strip-censuses.

STUDY AREA AND METHODS

Tikal National Park is a square of 576 km^2, located in northern Guatemala at an average elevation of about 225 meters. The park is centered on substantial Maya ruins. Ten incomplete years of rainfall data from 1960–1975 indicate annual precipitation of approximately 1,350 mm, and there is a distinct dry season, usually January to early June. Three plant associations predominate: (1) upland forest in well-drained areas, on ridges and hills, (2) *escobal* in poorly drained depressions, containing trees generally lower than those of upland forest, and (3) *tintal* of broad seasonally inundated depressions where vegetation is low, less than 15 meters in height (SMITHE, 1966). Data of PULESTON (1973) indicate that the three associations occupy about 55%, 29%, and 16% of the park, respectively. Local informants state that spider monkeys are absent from *escobal* and *tintal*. I spent relatively little time in these types of vegetation. I think it unlikely that monkeys utilize *tintal* but believe they may use *escobal* as some trees of upland forest that are preferred food sources are also present in *escobal*.

CENSUS METHODS

Between June 1975 and May 1976 I conducted strip censuses on foot for a total of 59 hours, during early morning and late afternoon, along 9.4 km of narrow roads and trails. Speed averaged 1.8 km/hr. Most of the census routes are in the central part of the ruins enclosing and meandering through a roughly triangular area of about 150 hectares. One route of 1.5 km begins 1.5 km southeast of the main plaza of the ruins and proceeds southeast. THORINGTON (1972) notes that roads are sometimes located on ridges and this may introduce bias in a strip census, depending on the heterogeneity of the habitat. I doubt the routes I used are biased in this manner because the upland forest of the census includes 3.5% area that might be considered transitional *escobal*, using the 200 meter contour as the criterion, and the routes are in close agreement at 3%. Although the roads had done very little to alter original vegetation, archaeological activities involved some clearing and subsequent development of second growth.

I recorded all contacts with mammals and some birds, using a simple version of methods recommended by EMLEN (1971) and ROBINETTE, LOVELESS, and JONES (1974), according to which the observer records for every sighting the perpendicular distance from the contact to the census route. Strip width is derived from the detection distances by grouping them in frequency classes. The class frequencies are then examined for a distance within which detection appears more or less uniform: naturally one expects detection to drop off with increasing distance from the path of travel but hopefully an initial plateau will be present. When density is calculated only those contacts within that distance are used and the distance is doubled to obtain strip width. The area of the census is simply strip width multiplied by transect length. When more than one species of animal is censused strip width must be determined separately for each species.

METHODS FOR AGE-SEX COMPOSITION

The social organization of *A. geoffroyi* at Tikal appears similar to that of *A. belzebuth* studied in Colombia by KLEIN (1972). All members of a social group are seldom together and individuals associate in temporary "parties" of variable size. The fluid nature of *Ateles* spatial relations creates problems in the determination of age-sex composition. It is possible to age and sex a group only if one recognizes individually all members of a group. Even when this can be achieved, sample size is limited, and sample size is extremely important when estimating sex ratios.

When censusing I attempted to determine the age and sex of party members. This was possible except in the case of large parties when I could only obtain a count. In addition I determined age and sex of monkeys in initial contacts with parties during other phases of fieldwork. An initial contact is any contact made when I was not already following a party. This restriction is necessary because there is a tendency for adults to associate with other adults of the same sex. Thus the age-sex composition of parties joined by the party being followed may be biased.

The age-sex determinations obtained in this manner are not independent observations. An unknown number are repeats of the same animals. This should not bias the composition of the determinations because spider monkeys travel extensively and the censuses and initial contacts cover a large area.

There is no single perfect way to classify animals in age classes by size and consequently the classification schemes for primates vary among investigators. I did not create a subadult class as it is a biologically dubious concept for females, and is appropriate for males only if males take longer to mature than females, as is true in dimorphic species. Authorities have contended that *Ateles* either lacks sexual dimorphism in size or females are slightly larger than males (KLEIN, 1972; SCHULTZ, 1956, 1960). Visual observations at Tikal gradually convinced me that maximum adult size of males is greater than that of females, certainly in weight if not in total length. EISENBERG (1976) concludes that the male: female weight ratio is about 1.17: 1.00 and very limited data of MURIE (1935) indicate a similar relation. Statistically adequate data of weights and measurements, with females separated according to whether they are pregnant, have not been published for any population of *Ateles*, but it appears there is dimorphism in the common direction, albeit less than in some other primates.

The dividing line between infants and juveniles is relatively clear: while an older infant progresses independently only during short moves, a small juvenile is rarely or never carried by an adult. Juvenile categories are less simple and I tried to envision the size range of animals that were not infants and not adults, and divide that range into three size classes. When ambiguity arose it usually was in deciding whether to record a male as a large juvenile (J3) or as an adult, and J3 males were seldom in association with adult females for comparison. The result is that older J3 males are larger than J3 females and would constitute a subadult class in other classifications. I assigned age in months to my size classes by comparing size estimates and behavioral indicators with those of EISENBERG (1976). Consequently the age entries of Table 4 for the present study do not constitute an addition to knowledge of *Ateles* maturation rates.

POPULATION DENSITY

RESULTS

During 59 census hours I contacted spider monkeys 52 times in parties of 1 to 28 ($\bar{x} = 4.3$; s.d. $= 4.2$). Party counts include both independently locomoting animals and dependent infants. Perpendicular detection distances ranged from 0 to 55 meters ($\bar{x} = 23.1$; s.d. $= 13.2$) and are shown in Table 1. The distances do not present as smooth a picture as might be desired. There is a marked peak at 25–30 meters. I think this is simply a result of sample size, and certainly does not indicate that monkeys closer to the route "froze" and went undetected. In most of the census area spider monkeys have long been habituated, and the response of those that are not is flight, often preceded by mobbing the observer.

On the basis of the data in Table 1, I use a strip width of 72 meters (perpendicular distance 36 meters). Census routes were patrolled an unequal number of times, minimum 10 and maximum 14. Accordingly I calculated a mean density estimate for each route and combined the estimates in a weighted mean using route lengths for weights. The density estimates for the individual routes range from 14.2 to 41.6 spider monkeys per km^2. The overall weighted mean is 27.8/km^2.

I now consider two separate sources of potential error in this estimate: (1) some animals may have escaped detection in the census strips, and (2) sampling error, a function of the monkeys' dispersion in space and sampling intensity. Ideally one would estimate the efficiency of detection by conducting in the same area a census by some other more reliable method. NEVILLE, CASTRO, & MARMOL (1976) call this "calibration". COELHO et al. (1976), worked at Tikal and give an estimate of 45/km^2. They consider this a maximum estimate and I discuss later a source of bias in their determination. Thus the difference between 28 and 45/km^2 is not a good indicator of animals missed in the census strips. There is, however, an indirect way to check detection. If the number of undetected animals is large it is logical to expect that small parties will be detected with decreasing frequency as distance from the census routes increases. To determine if this relation exists I take party sizes and group them according to the number of independently locomoting animals they contain and test

Table 1. Perpendicular detection distances.

Distance (meters)	Number of contacts
1–6	8
7–12	2
13–18	9
19–24	6
25–30	15
31–36	7
37–42	1
43–48	0
49–54	3
55–60	1

Table 2. Relation between party size and distance.

	Number of parties detected at distances	
Party size*	<25 m	≥25 m
1–2	11	10
3–25	14	17

*Independently locomoting individuals.

Table 3. Census data for ten complete patrols.

	All parties per patrol, including beyond 36 m	Parties per patrol, within 36 m	Animals per patrol*	Density estimate per patrol (per km²)*
Range	2–11	2–7	7–47	10.4–69.8
$\bar{X}$	4.7	4.3	17.30	25.67
s.d.	2.98	1.83	12.49	18.55
C.V.	63.5%	42.6%	72.2%	72.2%

*Entries computed from data of second column, "Parties per patrol, within 36 m".

for association with distance (Table 2). Analysis by chi-square shows no significant association ($\chi^2 = .268$; $p > .5$). This supports the view that not many animals were missed.

The second source of error refers to the internal reliability of the census. Because I did not census all routes the same number of times it is not possible to include all data when computing traditional measures of variation. This can be done, however, for the ten complete patrols of the 9.4 km route system, thereby using 86% of total censusing measured in distance walked (Table 3). The 95% confidence limits for the mean density estimate of 25.7/km² are 12.4 and 38.9.

BIOMASS

In the absence of good weight data the calculation of biomass can be only a rough approximation. EISENBERG and THORINGTON (1973) use 5 kg for mean weight of *Ateles* and the Tikal density of 28/km² implies 140 kg/km². The estimates of body weight for various age-sex classes of COELHO et al. (1976), yield biomass 156 kg/km², using the age-sex composition of the present study.

DISCUSSION

In the summer of 1973 COELHO et al. (1976), conducted an investigation of spider and howler monkeys at Tikal. Their census method is most easily described in their own words: "A second form of observation technique consisted of 13 hour picket or census stake outs. During each of these census gathering periods, all researchers were situated at known crossing and travel areas leading into known feeding and congregation sites (such as Palace Reservoir, Fig. 1, quadrant D2-56)." This method yielded a maximum density estimate of 45/km², considerably higher than my overall estimate of 28/km². We do not know the standard error of COELHO et al.'s estimate and it is also possible that population density decreased from 1973 to 1975. I believe, that most or all of the difference can be explained by the fact that Palace Reservoir is normally an unusually favorable area for spider monkeys. This is implied by COELHO et al.'s choice of "known feeding and congregation sites". During my analysis the first step was to treat the data by route, and the estimate for the route passing by the reservoir is 39/km².

KLEIN and KLEIN (1976) estimate that *A. belzebuth* existed at a density between 11.5 and 15.5/km² at their Colombian study site. They used a very different method, home range mapping, that I discuss in the final section of this report.

AGE-SEX COMPOSITION

Results

Data on age-sex composition from the present study and from the investigations of Coelho et al. (1976) and Klein (1972, 1974) are summarized in Table 4. There are several problems in interpreting proportions of age classes, and sex ratios within age classes. There is individual variation in the size of fully grown adults and the assignment of a non-adult to an age class is plagued by the lack of clear divisions between the classes; animals do not grow in leaps and bounds. The subjectivity of determinations is yet more vexacious when results of different observers are compared, even if their systems of size classes and criteria appear the same.

Another problem arises when the proportions of classes and sexes are derived not from animals *per se* but from non-independent observations, as are my results and those of Coelho et al. (1976). The lack of independence prohibits statistical tests of the observations. When the form of the data permits statistical procedures, considerable sample size is often necessary to demonstrate that a ratio is significantly different from 1:1.

Table 4. Age/sex compostion.

				Sex composition within class[3]			
				Relative frequency		Sex ratio	
Age class	Estimated age (mo.)[1]	Absolute frequency[2]	Relative frequency	♂	♀	♂ : ♀	"Reproductive rate" Infants: Adult females
A. geoffroyi							
From present study							
Adult	56,48	338	.50	.36	.64	1:1.76	
J3	36	109	.16	.68	.32	1:0.47	
J2	20	91	.14	.46	.54	1:1.17	
J1	12	50	.07	.31	.69	1:2.20	
Infants[4]		82	.12				.375
		670	.99				
All J		250	.37	.53	.47	1:0.89	
Ad +J3		447	.67	.44	.56	1:1.28	
Ad + all J		588	.88	.43	.57	1:1.31	
From Coelho et al. (1976)[5]							
Adults			.48	.31	.69	1:2.23	
All J			.30				
Infants			.22				.676
A. belzebuth							
From Klein (1972, 1974)[6]							
Adults	48	40	.70	.25	.75	1:3.0	
All J	12	11	.19	.36	.64	1:1.75	
Infants		6	.11				.200
Ad + J		51	.89	.27	.73	1:2.64	

1) Lower class boundary. See text for procedures used to estimate ages for present study; the two figures for adult are for male and female. Klein (1972) gives the estimated ages for *A. belzebuth*. 2) Observations for *A. geoffroyi*, individuals for *A. belzebuth*. 3) Relative frequencies and sex ratios present the same information in different format. 4) Most infants were not sexed. 5) Sex ratios for classes other than adult not presented. 6) Kiein (1974) presents estimated composition for 57 individuals of three social groups, listing adults by sex, and juveniles and infants without reference to sex. I derived sex ratio for juveniles from his (1972) data for the two better known groups.

In spite of these obstacles it is profitable to examine the entries of Table 4 in some detail. I believe that Klein and I used the same criteria for defining infants and our proportions are .11 and .12, respectively. Coelho et al.'s (1976) figure of .22 is higher than the proportion of infants that I found in any month. Coelho and his coworkers and I are in close agreement on the proportion of adults, about .50, while Klein (1974) found a much higher proportion (.70) in *A. belzebuth*. Part of the apparent difference may be due to different criteria for the adult class as Klein (1972) distinguished for both sexes two sizes within the adult class. At Tikal I think it would have been possible to do so only for males, a few individuals appearing exceptionally robust.

It is impossible to determine directly if the sex ratios I derive for *A. geoffroyi* are statistically different from equality because the sample sizes underlying the nonindependent observations are unknown. To obtain some notion of whether the ratios represent differences from equality, I postulated various hypothetical "real" sample sizes and tested the proportions of males and females in the various classes by chi-square (Table 5). Hypothetical sample size (HSS) is the minimum size at which the class sex ratio would be different from 1:1 at the .05 level of significance.

Note that for the J1 class HSS must be at least 52% of the number of observations for the sex ratio to differ from equality. This means that the observations could have involved, on the average, no more than slightly less than two per individual J1 that I ever saw. I believe there were probably more repeats and thus conclude that real sample size was less than 26. Accordingly it is unlikely that the sex ratio of J1's is significantly different from 1:1.

The same method of reasoning indicates that the sex ratio for J3's is probably different from equality, for adults it is almost certainly different, and for adults and J3's combined it is not different. To summarize, I think there are equal or nearly equal numbers of males and females in J1 and J2 classes, more males than females among J3's, and more females than males among adults. When adults and J3's are combined, males and females are about equal. These proportions are similar to those found in more dimorphic species such as savanna baboons (DeVore & Hall, 1965, Table 2–6) and red howlers (Neville, 1976, Table 3). The explanation for this pattern is that at the age when females reach full adult size, males are still subadults or large juveniles, depending on the investigator's categories. Thus there should be more males than females in the class immediately before adult, and the opposite for adults, because males spend longer in the pre-adult class and females reach adult size sooner. This is to be expected even when there is no differential mortality of the sexes. The approxi-

Table 5. Sex ratios and hypothetical sample sizes.

Age class	Ratio from Table 4	Hypothetical sample size (HSS)*	HSS as % of observations in age class	χ^2 calculated ‡
J1	1:2.20	26	52%	3.846
J3	1:0.47	30	28%	3.888
Adult	1:1.76	50	15%	3.920
Ad + J3	1:1.28	275	62%	3.960

*See text for explanation. ‡ For all tests $d.f.=1$, χ^2 .95=3.841.

mately equal proportions of combined adults and J3's argue against differential mortality in *A. geoffroyi* at Tikal.

In *A. belzebuth* the adult ratio of 1: 3.0 differs significantly from 1: 1 ($\chi^2 = 10.0$; $p < .005$), the 1: 1.75 ratio for juveniles does not ($\chi^2 = .818$; $p > .3$), and the ratio 1: 2.64 for combined adults and juveniles does differ from equality ($\chi^2 = 10.79$; $p < .005$). It is not possible to compare statistically sex ratios of *A. geoffroyi* with *A. belzebuth.*

CARPENTER (1935) did not have sufficient data to derive sex ratios for *A. geoffroyi* in Panama.

EVALUATION OF STRIP-CENSUSING

Census techniques, particularly the strip method, have been discussed by NEVILLE, CASTRO, and MARMOL (1976), STRUHSAKER (1975), and WILSON and WILSON (1975). For purposes of the present discussion it is useful to classify census techniques in three categories:

(1) *home range mapping* in which the investigator calculates the home range of one or more groups and divides by the number of animals in the group(s);
(2) *delimited area* method wherein the number of groups and their average size are determined by direct count in a naturally or arbitrarily delimited area; and
(3) *strip-censusing* in which the observer counts the animals in a strip of known or estimated width.

Objections to method 1 include home range overlap, which must be estimated, and the probably small area of habitat that is sampled. Problems of method 2 relate to the boundary of the area. If the boundaries are created by the habitat itself, e.g., a patch of forest surrounded by grazing land, it is likely that the population density of the species in question will not be typical of larger tracts. On the other hand, when the investigator sets arbitrary boundaries in more homogenous habitat he must somehow deal with groups of animals that spend part of their time in the census area and part of their time outside it.

Repeated strip-censusing on sufficiently long routes avoids the foregoing pitfalls. How long the transects should be is partly a matter of subjective evaluation, taking account of population density, habitat heterogeneity, and habitat choice. The last two factors will seldom be known in advance but the strip censuses themselves are an excellent way to obtain relevant data. How many repeats are necessary can be assessed by calculating a confidence interval for the individual density estimates as I have described for the first ten patrols at Tikal. Depending on species-specific ranging habits, more repeats should be necessary the scarcer the groups of the animal are, because of expected greater variation in the number of contacts per census. This is shown clearly by STRUHSAKER's (1975) data. STRUHSAKER conducted repeated strip censuses in Kibale Forest, Uganda, in which he recorded sightings of various primates, and his Table 55 gives the coefficient of variation of the number of contacts per patrol by species, and the estimated number of groups per km^2 derived from the censuses. I calculated rank correlation coefficients for c. v. and density, for Compartment 30 and combined Compartments 12, 13, and 17. There is a significant inverse relation between variation and density in both cases ($r_s = -.964, p < .01$; $r_s = -1.0$, $p = .01$).

The determination of effective strip width is crucial to the accuracy of the density estimate and the method of EMLEN (1971) and ROBINETTE, LOVELESS, and JONES (1974), used at Tikal, is excellent because it uses every contact for information on detection. One of the interesting results of the *Ateles* census is that effective detection distance (36 meters) is considerably less than other investigators have estimated subjectively for animals of comparable size.

Strip-censusing assumes 100% detection within some distance of the path of travel. Every time an animal is missed in the determined strip, the resulting estimate receives a downward error. This is not the case in methods 1 and 2 where the investigator gradually builds up knowledge of definite groups and it does not matter if a group is not detected on a particular day. Obviously one should census when animals are most active, but beyond that the ultimate solution is a more accurate census by some other method to determine the detection error. The problems associated with methods 1 and 2 raise doubts about their greater accuracy and considerations of manpower usually prohibit extensive censuses by two procedures.

A final point regarding density estimates from strip censuses is that some workers have stated that the results can be used as relative estimates even if unsuitable for estimates of absolute density. This is not as encouraging as it sounds for we have to ask relative to *what*? Likely differences in the detection error between species, and between sites for the same species, lead me to conclude that strip census estimates are best considered estimates, perhaps faulty, of absolute density except when comparing censuses of the same species at one site at different times. In the latter situation it is proper to describe relative changes in population density without the burdon of claiming absolute estimates.

Density estimates are not the sole product of censuses. Age-sex structure is very important for a conservation survey as well as for questions of population biology. Strip-censusing has positive and negative aspects. It is more likely to account properly for solitary males than methods 1 or 2 but proportions cannot be tested statistically. This might be a serious drawback if one is concerned with assessing reproductive rates by means of infant proportions.

Perhaps this debate over the relative merits of census methods will usually be decided in favor of the strip census because it is less time-consuming, particularly when several species are to be censused, even though repeated patrols are necessary. For spider monkeys, with their fragmented social structure, it is clearly the best method. Density estimates, regardless of their provenance, can be and have been misused in facile comparisons with no regard for sampling error. I would urge that greater attention be directed to estimating the magnitude of errors in censusing, and that the potential advantage of the strip method for assessing internal reliability be exploited.

SUMMARY

A strip census method wherein strip width is determined by the detection distances for all contacts was used to derive a density estimate of 28/km^2 for *Ateles geoffroyi* in upland forest at Tikal, Guatemala. The 95% confidence limits are 12.4 and 38.9 for a density estimate of 26/km^2, for 86% of the census patrols. It was estimated that

adults comprise 50% of the population, juveniles 37%, and infants 12%. Sex ratios for small and medium juveniles are probably not different from equality while males outnumber females in large juveniles, and females outnumber males among adults. These ratios are expected in a species with some sexual dimorphism in size. Ratios indicate that the sexes experience little or no differential mortality.

Census methods are critically evaluated, and the strip method's advantage of enabling sampling error calculations is advanced as a major point in its favor.

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