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CENSUSING OF DIURNAL RAPTORS IN A PRIMARY RAIN FOREST: COMPARATIVE METHODS AND SPECIES DETECTABILITY

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ABSTRACT.—No reliable method has ever been proposed to census a rain forest raptor community. I investigated 4 methods in primary forest of French Guiana and compared results; 1) Mapping territorial pairs, displaying over canopy and followed from dominant lookouts, gives the most complete data on regularly soaring species (*Harpagus, Buteogallus, Spizaetus, Spizastur*); 2) mean instantaneous number of birds flying over a definite area in optimum conditions may be a reasonable density estimate for vultures (Cathartidae); 3) mapping of individuals recorded along a regular network of trails in the understory was only successful for the highly conspicuous Red-throated Caracara (*Daptrius americanus*); 4) density estimates from understory strip transects were consistent with those obtained by other methods for 6 of 8 species. Specific detectability, soaring behaviors and frequencies of display flights varied widely among species and so did time required to assess the existence of a territorial pair (1-7 d). Marking, radiotracking and playback of vocalizations are promising techniques but are very time consuming and more appropriate for a detailed study of particular pairs than for survey of a whole community. Use of an abundance index, with a distinct technique for each species, may avoid biases of density estimates.

Birds of prey are notoriously difficult to survey in tropical forests, especially in tall, dense, large unbroken tracts of humid lowland forest. No complete census of a rain forest raptor community, with density estimates over a significant area, has ever been published and no appropriate methodology has even been proposed. However, many rain forest raptors are now threatened by habitat destruction, disturbance or fragmentation (Thiollay 1985b). Raptors may be suitable indicators of optimum size of a forest reserve, because raptors are likely to require areas larger than most other species. Yet, there is still an urgent need of basic data on natural distribution and density of rain forest raptors because of a concern about the suitability of many reserves or even national parks which may well prove to be too small for long term survival of some raptor species supported originally.

As part of a larger study on design of a national park in French Guiana, I assessed the distribution and relative abundance of raptors over the country's 80 000 km^2 rain forest area, and I estimated the density of every species within a representative 100 km^2 sample quadrat (Thiollay 1989).

Life history and behaviour of most rain forest raptor species are very poorly known, if at all (Thiollay 1985a). Often only scant information comes from marginal habitats, rather open woodlands or edges where a species' biology may be atypical. After 20 yrs of personal experience in both New and Old World tropical forests, I can testify that nests of many species are almost impossible to find in primary forest, except under extraordinarily lucky circumstances. In fact, for many species, the nest has never been described. Several species, including some of the most common neotropical forest raptors, seem to never soar(?) nor even fly over the canopy and very rarely venture outside the understory. Although not particularly shy, most species are very secretive and spend long periods perched motionless. Many are very vocal, but others are usually silent. Density is often low and distribution very patchy, which further decreases rate of encounters.

Thus, most raptor-specific census methods (see review in Fuller and Mosher 1981), devised for temperate species, cannot be applied directly to tropical forest species. Nevertheless, I have tried to adapt classical concepts to propose empirical methods that need further improvement and testing in similar situations. My attempts are preliminary, and as such, voluntarily unsophisticated. No single method can be appropriate for every species, and 2 or more different techniques should always be used concurrently.

In this paper I concentrate only on comparative results of complementary methodologies. Biological and conservation significance of the data are developed elsewhere (Thiollay 1989).

STUDY AREA AND METHODS

After 5 yrs of raptor surveys throughout French Guiana, I tried to obtain a quantitative estimate of the density of every raptor species within as large a representative area as possible.

Around the Nouragues field station, in north-central French Guiana (4°05'N, 52°41'W), a 100 km^2 quadrat of primary forest was chosen within a much larger expanse of similar unbroken lowland rain forest. The area was hilly, crossed by small rocky watercourses, and ranged in altitude from 27–413 m. Also included were sizeable tracts of every forest type encountered in Guiana, except cloud forest. The quadrat was centered around 2 large natural openings, with small field stations nearby: a medium-sized river in the south and a large granitic inselberg in the northern part provided the most convenient observation sites (Fig. 1).

The survey took place in the driest season, from early September to mid-October 1986 and 1987 over a total of 73 d of intensive field work with unusually fine weather conditions. From the little information available (Haverschmidt 1968 and pers. obs.), most raptors were either breeding or ending their reproductive cycle (feeding fledged young). All were assumed to be sedentary with an extended period of breeding activity and a permanent pair bond and territory occupancy.

Different census methods have been adapted to the behavior of individual species. Methods are here proposed as preliminary suggestions. Comparative results will be used as a test of reliability. As the coverage was better, more intensive and frequent around field stations and large openings, 2 better known areas were distinguished (Fig. 1). *Zone I* (6 km^2) included the inselberg and its lookouts, the main field station and its clearing as well as a dense network of trails. Every species present was assumed to be recorded and reasonably well mapped (no new data during the last 30 d.). *Zone II* (42 km^2 including Zone I) was centered around the inselberg and covered a 3-km rad area around the 4 outmost lookouts of the mountain top from which only soaring species were mapped. A 3-km rad was the maximum distance at which large raptors were accurately identified and located with 10 × 40 binoculars and 11–33× telescope.

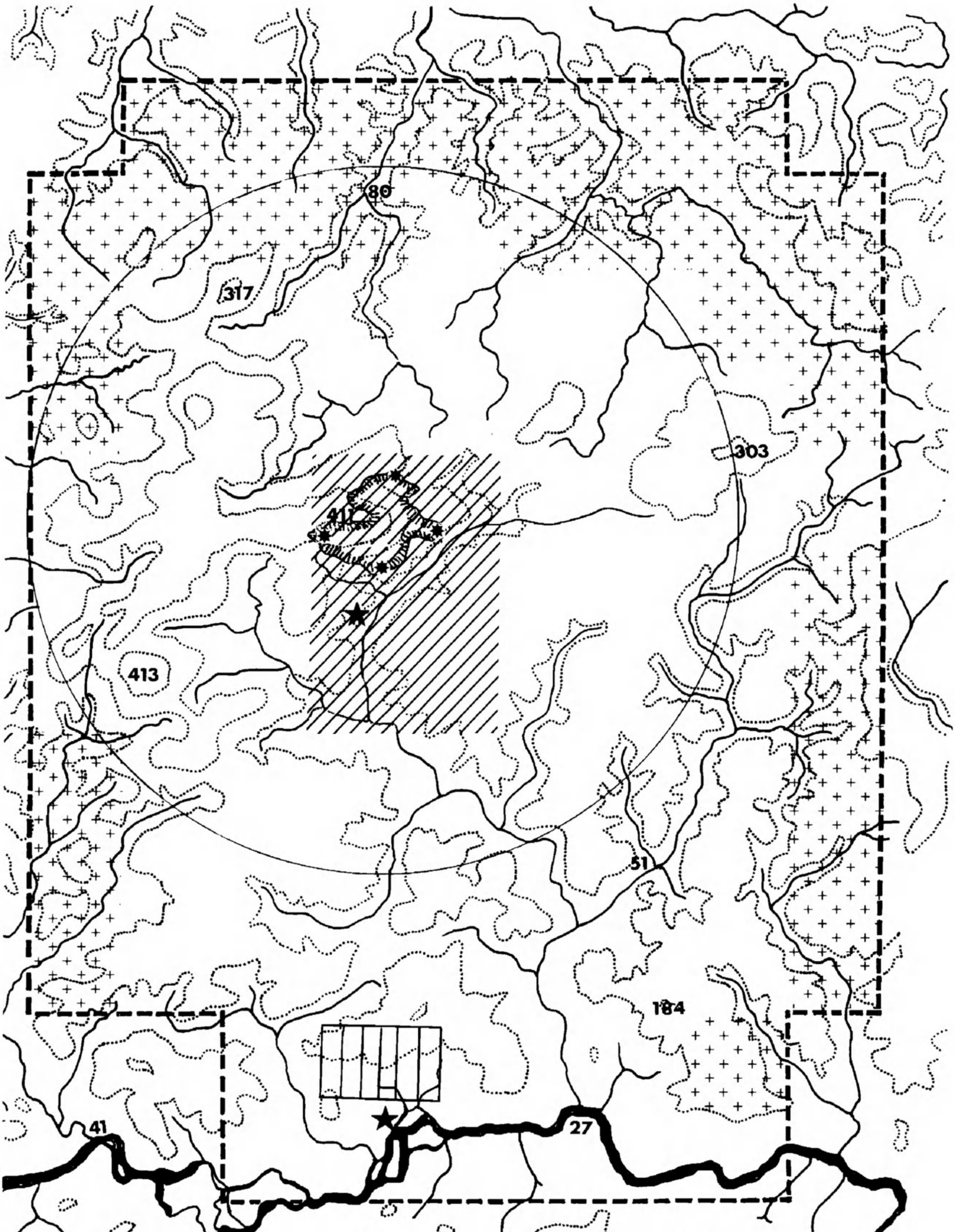
The entire study area (100 km^2) was visible from the top of the inselberg but only the largest raptors could be seen beyond Zone II. However, most outer regions were in sight above canopy within 2.5 km of 9 additional lookouts (riverbanks and large treefall gaps on ridges or steep slopes). The quadrat was divided into 1 × 1 km squares, of which 70 were crossed by foot at least twice, including 35 outside Zone II.

Mapping of Soaring Birds. One group of species regularly soar above canopy and may then be easily detected from outside the forest or through large openings: Gray-headed Kite (*Leptodon cayanensis*), Hook-billed Kite (*Chondrohierax uncinatus*), Rufous-thighed and Double-toothed Kites (*Harpagus diodon* and *H. bidentatus*), Tiny, Bicolored and Gray-bellied Hawks (*Accipiter superciliosus, A. bicolor* and *A. poliogaster*), White Hawk (*Leucopternis albicollis*), Great Black Hawk (*Buteogallus urubitinga*), Crested Eagle (*Morphnus guianesis*), Black and White Eagle (*Spizastur melanoleucus*), Black and Ornate Hawk Eagles (*Spizaetus tyrannus* and *S. ornatus*). Soaring behavior performed by adults on their breeding grounds has mainly a territorial function (surveillance and maintenance of pair bond or territorial limits, Newton 1979). Soaring is often accompanied by loud calling, nuptial display or instraspecific aggression. I assumed that adults, especially when displaying, flew mostly, if not only, over their own territory.

A large, bare, rocky outcrop protruding 200 m over the surrounding forest offered an ideal vantage point. Four convenient lookouts were chosen on the outermost parts of the inselberg, each offering an unrestricted 180° view. A total of 167 hr was spent overlooking the forest in fine weather and mainly during the optimal morning hours (0900 H–1200 H). The marked relief facilitated the location of flying birds.

All raptors seen flying over the forest (or perched on emergent dead trees) were followed and their itinerary carefully mapped (1/50 000 scale). Day after day, the data were superimposed, soon giving a picture of clearly separated ranges for most species So-called territories were derived by the minimum convex polygon method (Ford and Myers 1981; Southwood 1966) connecting the outermost points reached by birds under observation. Territory size was determined using a planimeter and correcting for small sample size biases by the method of Jennrich and Turner (1969). Adjacent territories were discriminated by simultaneous observation of the 2 pairs involved.

Over 20 complete flight circuits were drawn for at least 1 pair of the 5 most common and conspicuous species (*H. bidentatus, L. albicollis, B. urubitinga, S. melanoleucus* and *S. ornatus*). Each pair yielded rarely more than 1 circuit/d. No new information was


80
317
303
411
413
51
184
41
27

obtained after the 5–10 circuits plotted initially. Thus, sample size was probably large enough to avoid an underestimation of territory size (Ford and Myers 1981).

Population Estimates of Species Hunting Over the Forest. Another group of raptors fly above canopy to search for carrion (vultures) or hunt for insects (kites) and birds (falcons). Each group is easily detected but wide ranging and may be occasionally gregarious.

The most common species in the group is the Greater Yellow-headed Vulture (*Cathartes melambrotus*) which wanders throughout the area and temporarily concentrates around carcasses. Particular pairs could not be separated. For want of a more accurate estimate, I have recorded during 20 hr in the late morning (0900 h–1200 H) period, the mean number of individuals crossing a 10 km^2 area/hr. The 20-hour data, extrapolated to the larger study area, are in good agreement with the largest concentration of birds seen during the course of the study.

A similar estimate has been computed for the King Vulture (*Sarcoramphus papa*) and the Swallow-tailed Kite (*Elanoides forficatus*), both of which wander great distances; the former solitarily or in pairs and the latter in flocks. Additionally, resident families were recognizable and their roost sites located.

The Plumbeous Kite (*Ictinia plumbea*) is well distributed over the area in isolated pairs which occasionally join nomadic groups of *Elanoides* but are otherwise rather territorial. Plumbeous Kites have been mapped according to the previous method and a small floating population, inferred from rare concentrations observed, has not been considered. One pair of Orange-breasted Falcon (*Falco deiroleucus*) was attached to the only suitable cliff.

Specific Daily Soaring Activity. Each species had its own pattern of soaring behavior and hence a different detection probability. To assess daily flight pattern and time during which each species was visible, I define a fixed 10 km^2 area (i.e., a 2.5 km rad on a 180° field, the largest area manageable for this purpose), from the western lookout of the inselberg. I divided daylight hours (between sunrise and sunset) into 4 periods. Each period was covered during 17–20 hr. (fine weather only). Within each hour observation, the following parameters were recorded: 1)minimum number of different individuals seen; 2) total time (min) where at least 1 bird was flying over the area; and 3) behavior of each individual (soaring, hunting, displaying, . . .). Besides vultures, whose home ranges were difficult to define, all 12 soaring species were represented by 1 resident pair on the 10 km^2 area (either >50% of their territory included in the area or a larger territory covering >50% of the area).

The number of flying raptors slowly increases from sunrise to 0900 H, then quickly reaches a maximum between 1000 and 1100 H, and decreases almost continously after noon. However, vultures remained very active up to about 1600 H and kites were even most active in mid and late-afternoon when no rain had occurred.

Understory Censuses. The Forest Falcons (*Micrastur*), the Black-faced Hawk (*Leucopternis melanops*) and, to a lesser extent, the Red-throated Caracara, rarely fly high over the canopy. Caracaras are very noisy but Forest Falcons usually call mostly at dawn and *Leucopternis* is not often heard. The Harpy Eagle (*Harpia harpyja*) is only conspicuous when sun-bathing on emergent dead trees in early morning. Since it was necessary to scour the forest to find these species, I tried to use sightings in 2 different ways. For soaring species understory records were compared to results of the above mapping method.

I first walked along a network of trails in the understory, 100 km long, designed to pass within 500 m of every point. Thirty km were already laid out through the undergrowth, mostly in Zone I. Remaining "trails" were only outlined by a white thread at breast height. I moved slowly, focusing my attention exclusively on raptors and recording every

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Figure 1. Topography of the 100 km^2 study area: main watercourses (unbroken lines), 100 m contour lines (dotted lines), maximum and minimum altitudes (meters asl), little wooded part of the rocky inselberg (hatched contour). The circle features the 42 km^2 area covered by a 3 km-rad around the 4 outmost observation points around the inselberg's summit (asterisks). The hatched rectangle is the 6 km^2 most intensively surveyed area. Stars indicate the field stations and the rectangular network is the intensive study trails near the southern station. Peripheral stippled squares have been crossed by foot only once, if ever.

observation on a map at the nearest 100 m. The area to be covered was too large and the density of birds was too low to obtain enough records and an accurate mapping of territorial pairs outside the most intensively searched area.

The second method was to use the data for a tentative density estimate of all individuals. The most rigorous technique should have been a line transect sampling [i.e., recording along a straight line sighting and perpendicular distances, as well as sighting angles, of every bird seen]. A density estimate may then be derived through a probability function at zero distance from the line. This is obtained by fitting, to the perpendicular distance data collected, Fourier series models which best meet the estimator shape and goodness of fit criteria (Burnham et al. 1980; Brennan and Block 1986). Unfortunately, the first assumption of line transect theory, that all birds on the line must be seen with probability 1, is not always met since raptors initially perched just along the transect can escape undetected well ahead of the observer. Most of all, no reliable density can be statistically estimated without at least 40–60 observations, a sample size which for most raptors can hardly be obtained within several months (see Results). Probability of detecting a bird could not be estimated. Hence any technique based on such an estimation (Cochran 1977) could not be used. Individuals were not distinguishable and time was too short to make repeated counts on most transects, thus preventing another method for estimating probability of detection (Seber 1982) to be used. My survey was not devised to calculate proportion of the area occupied (Geissler and Fuller 1986), a promising technique especially if birds are detected by responses to playbacks of their calls.

Therefore, the alternative method used was a strip transect census which gave the best compromise between efficiency and biases (Burnham et al. 1985; Verner 1985) and used the traditional concepts of detectability and effective area surveyed (Emlen 1971; Ramsey and Scott 1981). Strip transect census is equivalent to a long narrow quadrat within which all birds are assumed to be recorded. The transect was unbounded, drawn randomly, and transect width was not adjusted to varying density of vegetation which changed constantly but within rather narrow limits at mid- or upper-levels. Daily sections covered were of unequal size and many were traced 2 or more different d. There is a distance from the observer under which the species studied almost always move, fly or call and thus can be detected. Large terrestrial game birds and macaws (*Crax, Psophia, Ara* spp.) were also included in the survey and were almost always first detected by calls. Flushing or detection distance is a critical parameter which has proved, from my experience in Guiana, to be rather constant for a given species in primary, not hunted, forest. Detection distance is also lower than maximum distance (both vertically and horizontally) at which birds are visible in undergrowth of high primary forest, ensuring that most birds do not flee when out of sight. Any departure from basic assumptions leads to an underestimation of density.

Such specific detection distance (d) is used here as the radius of a circle moving with the observer at its center and whose dia is the effective minimum width of the strip transect. Sighting angle or perpendicular distance are no longer involved since birds become conspicuous in any quarter as soon as the observer is closer than d. Then density estimate is

$$\hat{D} = n/2dL$$

where n is the number of birds detected within the 2 d-wide strip and L is the length of the transect.

From all individual detection distances obtained, d will be the shortest distance at, or interval within which the largest number of birds were recorded [i.e., width maximizing the density estimate (highest n/d ratio)]. Thus, detections further than d are not used. Sampling variance of the density estimate is dependent on sampling variance of n which could be estimated from replicated counts. However, sample size was so small that the variance was inevitably large and not very meaningful.

Data Collection on Strip Transect. Field counting procedure, or search method, was carefully devised to meet as much as possible the prerequisite assumptions of the strip census (all objects must be detected within the limits and have a fixed initial position; all sightings must be independent events and their distance must be accurately measured). I walked very slowly (<1 km/hr), making as little noise and movement as possible, along narrow trails or through undisturbed undergrowth and randomly crossing every forest type. Attention was focused exclusively on raptors and large game birds (*Crax, Psophia, Ara*). Only periods between sunrise and sunset, without rain, fog or strong wind, were taken into account.

I recorded every bird either sitting, walking or flying, from ground level to top of the canopy, but not above. Distances between the observer and first sighting were measured with a range finder (Optimeter 620) then controlled with the number of steps and rounded to the upper 5 m-interval. Although not used subsequently, angle deviation from the transect was read through the sighting mirror of a liquid filled compass. For each observation I also recorded the number of individuals, their age, sex, height, behavior, location on the map, direction of flight, as well as habitat type and vertical structure of the vegetation (estimated index of density, ranked from 1–4 in the 0–2, 3–14, 15–25, 26–36 and >36 m strata).

Birds were often detected when taking flight or alighting. Those calling were recorded only if they were within sight distance. Only Caracaras, which almost always utter their loud alarm calls when seeing an observer, were sometimes noted further away, but never at more than 100 m. Some birds were seen in or from a tree-fall gap and their detection distance may have been higher than in closed understory. Transect length was measured daily on a 1/50 000 scale map and monitored using a pedometer. Total distance walked in good censusing conditions through the 100 km^2 study area in 1986–1987 was 517 km in 498 hr.

Similar censuses were performed from 1981–1986 in 8 other study areas throughout French Guiana (total: 1188 km in 1135 hr). Being often associated with the survey of other species, these censuses could not be as accurate (uneven speed, attention distracted) and results may sometimes underestimate raptor densities.

Additional Techniques. Other methods are promising for application to the most secretive species but are time consuming with limited results (Thiollay and Tostain unpubl. data), as far as population estimate over a large area is concerned.

Trapping and marking. Forest Falcons and Bicolored Hawk are not infrequently caught in mist nets or traps baited with live birds, but few other species have been caught in this way. Yet, only an unknown fraction of the population is likely to be captured, which does not fit our purpose. Subsequent radiotracking of tagged birds has proved to be invaluable to assess home range and foraging patterns of individual species but can hardly be considered for a relatively short period multispecies survey. Radiotracking could also be an elegant method to find occupied nests. Sightings and recaptures are so rare that visual marking and banding are of limited interest for secretive species.

Vocalisations. Fortunately, several species have loud calls which helps in detection and location. First of all, the very noisy groups of Red-throated Caracara and Black Caracara (*Daptrius ater*) are easy to follow and cannot be missed if one moves a few hours through their home range. Around their nest, the Orange-breasted Falcon and Bat Falcon (*Falco rufigularis*) are aggressive and vocal even when not breeding but may be silent and unobtrusive a few hundred meters away. Black and the Ornate Hawk Eagles, as well as, to a lesser extent, the Great Black Hawk, rarely fail to perform display flights above canopy with loud calling nearly every day if the weather is fine, but usually during a short time (5–15 min) and only once-a-day in mid- or late-morning. Thus, territorial pairs can be located from inside the forest.

The 4 sympatric Forest Falcons (*Micrastur ruficollis, M. gilvicollis, M. mirandollei* and *M. semitorquatus*) are all very vocal but mainly during a short time at dawn when it is usually too dark to see them in the understory. Most stop calling before sunrise and in Guiana during the dry season only *M. mirandollei* and *M. semitorquatus* are likely to be heard with some frequency later in the morning and around sunset. However, calls (which are probably true songs) are quite variable, rather similar to each other and not always easy to determine. Unfortunately, playback experiments conducted so far rarely elicited a response (outside the dawn chorus) and failed to attract birds. Many more attempts are still necessary to define which part of their call repertoire may be most efficiently broadcasted, at what time and at what distance. Population density of the 6 km^2 central zone has been drawn from distribution of calling birds, assuming that both sexes were vocal (often 2 birds close to each other seemed to call in turn or together).

Other techniques such as audio-luring utilizing prey calls are being developed in the northern Neotropics and have already produced some very promising results (J. Vannini, pers. comm.). Playback of conspecific calls to attract birds or elicit a vocal response is certainly worth additional study although some species may not be lured. Flushing canopy birds or searching for nests using a low flying helicopter has been attempted repeatedly in French Guiana with disappointing results. Specific trapping methods also remain to be investigated.

RESULTS

I am only concerned here with applicability of census methods actually used. More details about densities and distribution patterns are given elsewhere (Thiollay 1989).

Understory Mapping. The Red-throated Caracara alone provided enough records to construct comprehensive home ranges, not only from >200 sightings but from the movements of noisy flocks followed out of sight and the location of roosting places (Fig. 2). Limits between group territories have been checked by simultaneous records of contiguous flocks. Outside the 6 km^2 intensively surveyed core area, all other species were seen or heard too infrequently to accurately map territories, and no individual was marked. Nevertheless, data were useful in assessing overall distribution of non-soaring species and to check from the ground the exact location of birds displaying over the canopy far from any lookout.

Strip Census. Notwithstanding the low number of records on strip transects, density estimates obtained on strip census through the 100 km^2 study area are remarkably close to those derived from mapping of soaring birds on the restricted 42 km^2-circle. The 2 estimates are within a range of ±40% for 6 of the 8 species available for comparison (Table 1). Significantly, lower densities are given by strip census for species either very shy, secretive and unevenly distributed (*A. bicolor*) or restricted to tree tops and openings (*L. albicollis*). At least 2 pairs of Lined Forest Falcon (*Micrastur gilvicollis*) were found on 300 ha in the Central zone; the strip census slightly underestimates the overall density of this secretive species.

The Red-throated Caracara, according to our results, is the most abundant raptor. On the study area the Caracara lives in flocks of 4–7 birds. Mean number of individuals recorded per flock encounter on the ≤200 m wide strip transect (3.43 ± 0.91) is lower than actual size of groups occurring on the study area (5.50 ± 0.90, N = 12). Yet overall density obtained by the strip census method is markedly higher than that derived by plotting the flock home ranges (Table 1 and Fig. 2). Frequency and length of the Caracaras' movements violate the basic assumption underlying computation of density using the strip method and probably leads to the overestimation found here.

Mean Density of Aerial Hunters. Raptors hunting over the canopy are usually seen on line transects only in flight and where the canopy is rather open. Such records would violate the main assumptions of the strip census method and thus cannot be used except to map species distribution. Mean number of individuals seen per hour over a given area has a high variance and can rarely be extrapolated to a much larger area. Only instantaneous densities would be reliable but are feasible only if almost all birds are in flight at the same time over a large area. This assumption is met only for vultures during the best hours and it has been used as a minimum estimate of the total population (Table 2). Kites, on the other hand, are not on the wing for such long and predictable periods. Therefore, the basic estimate of mean number of birds seen in flight over a given area may be biased and must be complemented by maximum flock size and the localisation of pairs.

Mapping of Soaring Birds. Mapping is by far the easiest and probably the most accurate technique when suitable lookouts are available (Fig. 3). However, any method relying on occurrence of raptors soaring over the forest is very sensitive to activity pattern of the species involved. Detectability of most forest species may be very low, even when the observer overlooks the whole territory of a pair in fine weather. The probability to contact a species at least once during any 1-hr observation bout is <50% for 10 of 14 species and ≤30% outside the 0900–1200 H period (Table 3). There is >85% chance of encounter only for 2 species and during the midday period. At the other extreme, 5 of 14 species have been recorded in <15% of any hour.

If one takes into account the actual time spent in flight, 11 of 14 species are visible <5% of the daylight period whereas the 2 most conspicuous (*Cathartes* and *Ictinia*) were seen an overall 14–16% of the time. From mid-morning to mid-afternoon (peak of activity), the last 2 species were visible during 20–25% of the time against <10% for all others and even <1% for 5 species.

It is not known how the time budget of these

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Figure 2. Distribution of groups of Red-throated Caracaras (*Daptrius americanus*) over the 100 km^2 study area Dashed lines: see Figure 3. Open limits: uncertain boundaries due to lack of records because of an insufficient survey in marginal areas.

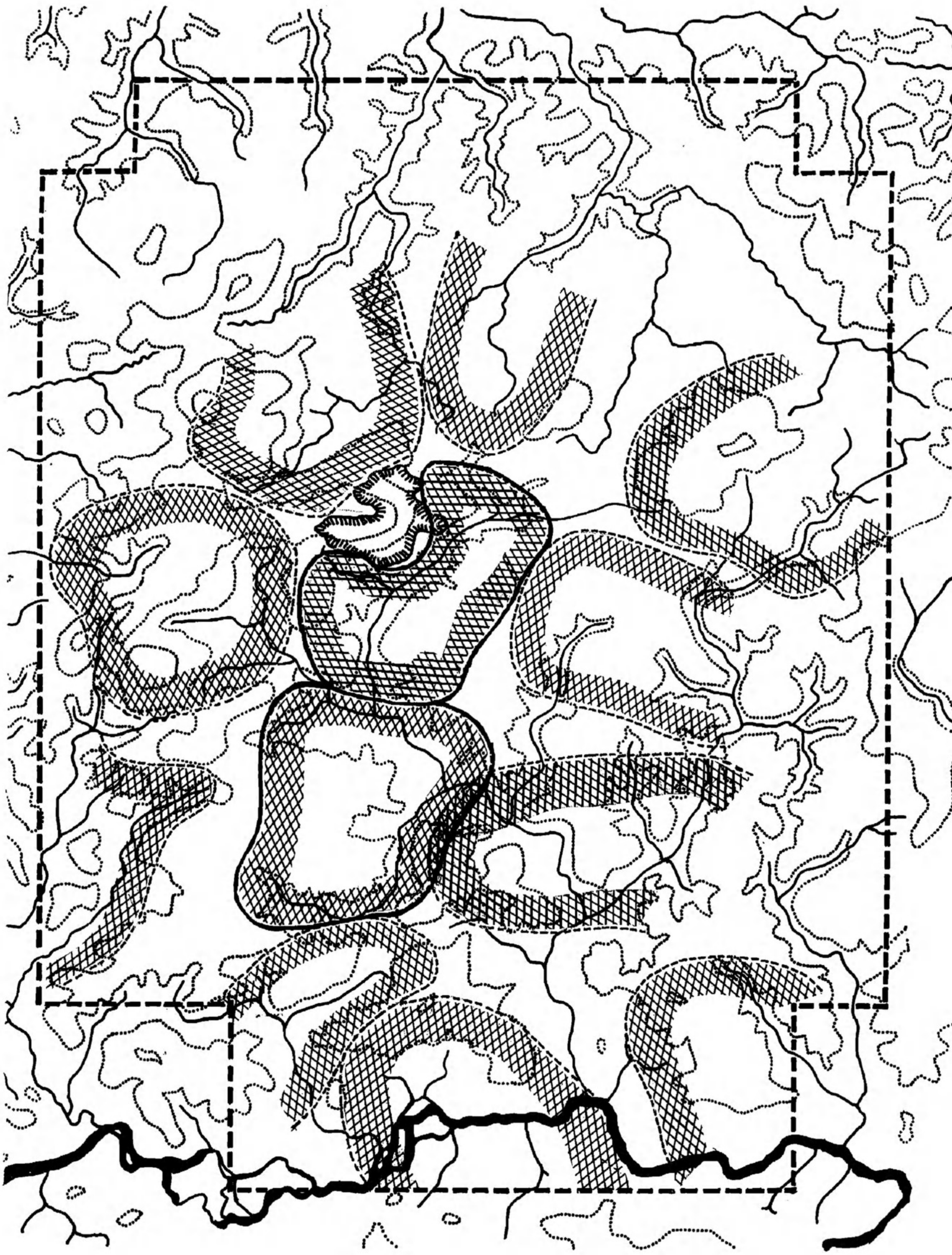

Table 1. Comparative results of quantitative surveys of territorial raptors in primary rain forests of French Guiana **Zone I**: intensive soaring bird census and understory mapping on 6 km^2 (see text). **Zone II**: mapping of soaring birds on 42 km^2. Total area: minimum population estimate, combining both methods, on the 100 km^2 study area. Data are numbers of individuals (i.e., ≥ 2 times the number of pairs). Strip censuses· N = number of birds recorded within 100 m on either side of cumulative line transects (517 km for the main study area and 1188 km for other localities). d = detection distance (m) maximizing the density estimate $\hat{D}$ (in number of individuals/100 km^2).

Species[a]	Main Study Site						8 Other localities		
	Zone I	Zone II	Total Area	Strip Census N	Strip Census d	Strip Census $\hat{D}$	Strip Census N	Strip Census d	Strip Census $\hat{D}$
Leptodon cayanensis	0	0	≥2	1	30	3.2	1	25	1.7
Harpagus diodon	≤1	±2	≥2	1	25	3.9	2	25	3.4
Harpagus bidentatus	≤2	±6	>8	3	20	14.5	9	25	15.1
Accipiter bicolor	≤2	±4	≥6	1	25	3.9	2	20	4.2
Leucopternis melanops	≤2	—	≥2	1	25	3.9	8	30	11.2
Leucopternis albicollis	±3	±10	15	5	50	9.7	10	35	12.0
Buteogallus urubitinga	±3	≤12	≤20	10	45	17.2	9	40	9.5
Morphnus guianensis	≤1	2	≥2	2	40	4.8	3	35	3.6
Spizastur melanoleucus	<2	<4	≥6	3	30	6.4	5	30	7.0
Spizaetus ornatus	<2	4	≤10	9	45	12.9	15	50	10.1
Micrastur semitorquatus	≤2	—	≥10	3	25	11.6	10	25	13.4
Micrastur ruficollis	≤2	—	>8	2	20	9.7	3	20	6.3
Micrastur gilvicollis	≥4	—	>30	22	20	72.5	31	20	63.0
Micrastur mirandollei	≤2	—	≥6	1	25	3.9	4	25	5.0
Daptrius americanus	±6	—	≥66	206	100	199.2	395	100	166.2

[a] Additional species: *Accipiter superciliosus*, *A. poliogaster*, and *Spizaetus tyrannus* (one pair of each recorded on the main study area) and *Harpia harpyja* (3 records, only outside the main study area, $\hat{D}$ = 3.1).

Table 2. Population estimate of vultures and kites hunting in flight above the canopy. Number of individuals crossing a 10 km^2 sample area (mean of 20 hr between 0900 and 1200 H); number of territorial pairs or families settled within the 100 km^2 study area; highest number of birds seen together; total population (i.e., resident adults + fledged young + estimated additional birds).

	Mean Number of Birds/hr/10 km^2 ±S.D.	Number of Resident Pairs Located/100 km^2	Highest Concentration Recorded	Average Population (Ind/100 km^2)
Cathartes melambrotus	1.95 ± 1.50	?	12	19
Sarcoramphus papa	0.90 ± 0.96	2	7	9
Elanoides forficatus	0.60 ± 1.09	2	30	≥10
Ictinia plumbea	1.90 ± 0.97	3	7	9

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Figure 3. Distribution of territorial pairs of the Great Black Hawk (*Buteogallus urubitinga*) over the 100 km^2 study area of primary rain forest. Home ranges shown here are mostly areas covered by displaying adults. Dashed lines are provisional limits based on too small a number of records or on observations that could not be accurately located.

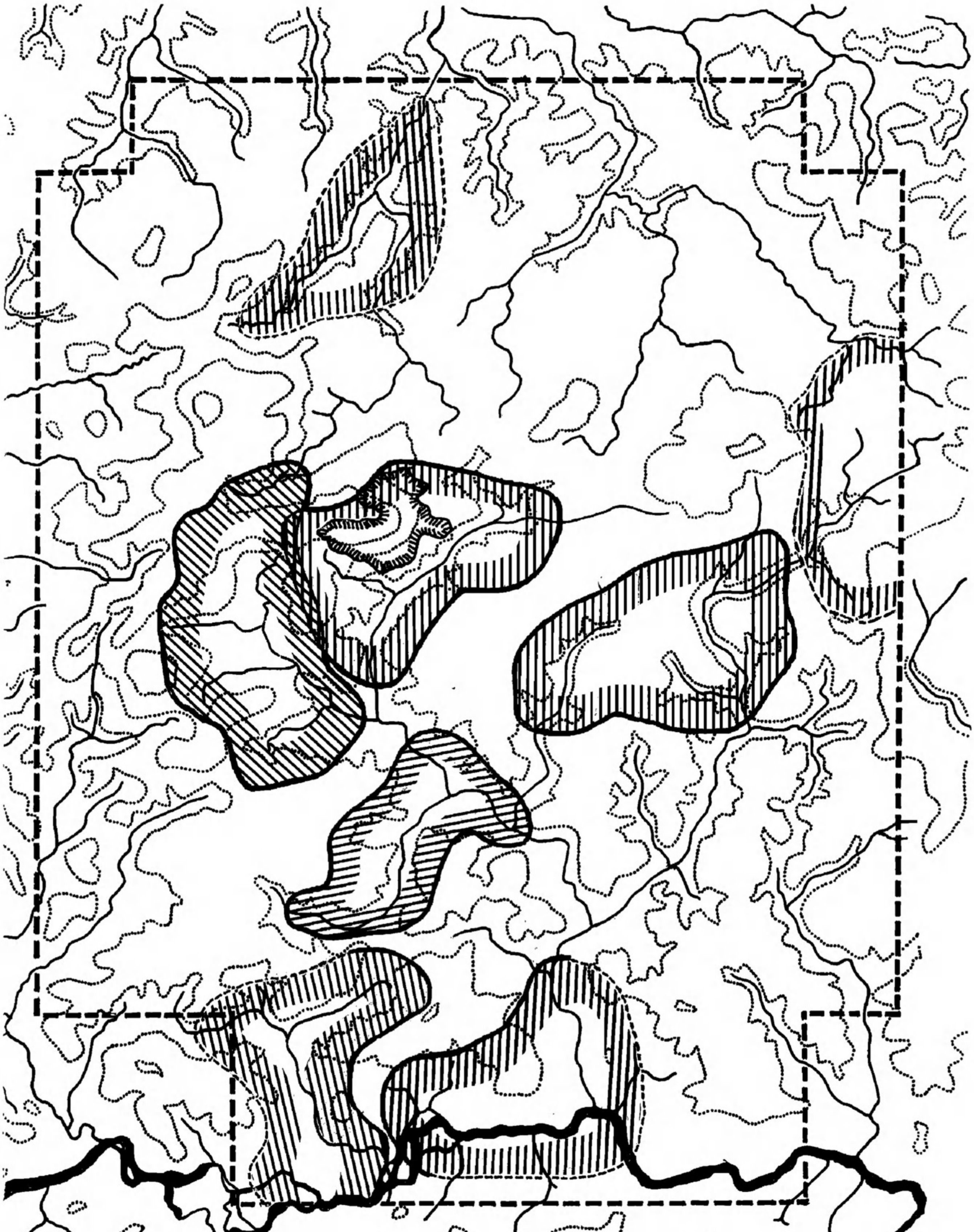

Table 3. Occurrence of soaring raptors over a 10 km^2-area of primary forest. Proportion of time 1 or more birds spent in flight, then probability to record the species during 1 hr and number of birds counted within each hour. Observation periods: A = 0630–0900 H; B = 0900–1130 H; C = 1130–1530 H; D = 1530–1800 H Sample sizes (hours): A = 17; B = 20; C = 17; D = 17.

Species	Percent of Observation Time where ≥1 Bird Was Flying over the Forest				Percent of 1-hr Periods where the Species Was Recorded				Minimum Number of Individuals Seen/hr (Range)			
	A	B	C	D	A	B	C	D	A	B	C	D
Cathartes melambrotus	1.3	27.9	22.1	5.1	18	85	100	47	1–2	1–6	1–6	1–5
Sarcoramphus papa	0.7	12.3	4.5	2.1	6	55	24	30	1	1–3	1–2	1–2
Elanoides forficatus	5.9	5.5	6.5	10.6	24	30	30	30	1–7	1–3	1–15	1–17
Harpagus diodon	—	0.7	0.9	—	—	5	6	—	—	1	1	—
Harpagus bidentatus	1.0	3.3	—	—	12	40	—	—	1	1–3	—	—
Ictinia plumbea	9.5	22.8	17.1	17.2	47	100	77	71	1–4	1–4	1–3	1–7
Accipiter superciliosus	—	0.3	—	—	—	5	—	—	—	1	—	—
Accipiter bicolor	—	0.9	—	—	—	10	—	—	—	1	—	—
Leucopternis albicollis	0.1	7.7	0.2	—	6	45	6	—	1	1–4	1	—
Buteogallus urubitinga	0.7	9.2	4.5	0.1	41	75	47	6	1–2	1–4	1–2	1
Morphnus guianensis	—	1.3	—	—	—	15	—	—	—	1	—	—
Spizastur melanoleucus	0.4	0.8	—	1.8	12	10	—	12	1	1	—	1
Spizaetus ornatus	—	3.6	0.6	—	—	25	6	—	—	1–2	1	—
Falco deiroleucus	1.3	4.3	1.6	5.1	30	50	24	24	1–2	1–2	1–2	1–2

species, and hence their detectability, may vary over the seasons. Obviously, long periods of time with good observational and weather conditions are necessary to assess the presence of some species, let alone their spatial distribution. However, several very territorial species (*H. bidentatus*, *B. urubitinga*, the 2 *Spizaetus* and, to a lesser extent, *L. albicollis* and *Spizastur*) performed their display flight once nearly every day, mostly in late morning when soaring conditions were suitable. Displays often lasted 5–15 min but proved to be a fairly reliable indication of an occupied territory. Thus, concentrating most research during the favorable hours may save much time and, for such species, most information may be obtained within only 1–2 d. Conversely, to assess confidently the presence or absence of the most secretive species (*H. diodon* and *Accipiter* sp.), which are more occasionally soaring, it is necessary to repeat the above observation from a vantage point for at least 6–7 d. (Table 3). Indeed, a complete mapping of their territory may require much more time.

Discussion

Reliability of results rests with the detectability of each species. Therefore, specific behavioral traits determine the most appropriate census methods (Table 4).

Mapping of soaring birds was the most accurate technique. Territorial species regularly displayed above the canopy and easily provided a fairly convenient set of data within a rather short time. For many pairs, almost no additional information was accumulated after 2–3 d of fine weather. However, most territory sizes may be very conservative estimates because of potential biases: 1) some species (e.g., *Accipiter*) perform relatively short flights and may not display over their entire home range; 2) it is not known whether the area flown coincides with defended territory and/or hunting range; 3) a few exceptional flight circuits of individuals not surely identified, or long pursuits of a neighbor, were ignored; 4) the exact position of birds too far away was not precise and always conservatively estimated. There was a substantial floating population, either transient birds or members of temporary or permanent trios.

Conversely, an accurate mapping of non-soaring species is difficult without the help of time consuming radio-tracking. First of all, unmarked birds cannot be assigned to a particular pair or territory. More

Table 4. Behavior and most suitable census methods of forest raptors in French Guiana. MS = mapping movements of soaring territorial pairs; TP = minimum estimate of total population. Extrapolation of the mean number of individuals soaring over a given area; MU = mapping location and movements of birds seen or heard in the understory; DE = mean density estimate from understory strip census.

		METHODS			
BEHAVIOR	SPECIES	MS	TP	MU	DE
Soaring—regular:					
Mid-late morning: loud calls rarely heard	*Buteogallus, Spizaetus*	+		+	+
	Leucopternis albicollis	+			
	Harpagus bidentatus	+		+	+
Mid-morning to mid-afternoon	*Cathartes melambrotus*		+		
	Sarcoramphus papa	+	+		
Morning to evening	*Elanoides forficatus*	+	+		
	Ictinia plumbea	+			
	Falco (2 sp)	+			
Soaring—Occasional:					
Mid-late morning	*Leptodon, Morphnus*	+		+	+
Morning and afternoon	*Accipiter, H. diodon,*	+			
	Spizastur	+		+	+
Non-soaring—silent:					
Sometimes conspicuous	*Harpia harpyja*			+	+
secretive (undergrowth)	*Leucopternis melanops*			+	+
Non-soaring—calling:					
Early morning	*Micrastur* (4 sp)				+
All day	*Daptrius* (2 sp)			+	

importantly, frequency of encounters with secretive and/or rare species is extremely low. Even the Lined Forest Falcon, by far our most common solitary raptor, was sighted at best once every 2 or 3 d, whereas most other species were spotted as a mean only once every 13–56 full d (>10 hr/d) spent actively searching the forest. Only species often flying low over the canopy (kites, vultures, *Buteogallus, Leucopternis, Spizaetus*) were seen once every 3–10 d. I met with 1–3 groups of Caracaras nearly each day along a 10 or more km line transect. A low rate of raptor encounters seems to be more a consequence of very low density, uneven distribution or too confiding a behavior rather than of shyness, since some perched birds allowed a surprisingly close approach or did not take flight when they were in the upper canopy. The possibility that some species or pairs may be overlooked is suggested by the following examples. *Accipiter poliogaster* was identified here for the first time in French Guiana even though 10 other similar areas had been carefully surveyed in previous years. A pair of *Chondrohierax uncinatus* was found breeding in March 1989 in the study area where it was never seen before.

The strip census method, or any technique adapted from it to the conditions of the rain forest, remains to be encouraged, provided that underlying assumptions are carefully respected. Good results have been obtained with large terrestrial birds [the Trumpeter (*Psophia crepitans*) and the Curassow (*Crax alector*)]. Each lives in small flocks, slowly moving in the undergrowth and always giving a soft alarm call without fleeing, allowing the observer to detect their presence.

The overall consequence of possible biases is an underestimation of the density of most species, especially when large areas (>10 km^2) and small species are involved. The density estimate of the 100 km^2 area is lower than that of the intensively surveyed 6 km^2 core area for 11 of 14 species (Table 1). However, the greatest care must be taken in extrapolating density of a small area to a larger area, because many species are patchily distributed and territories are far from being contiguous. An overall density estimate is meaningful only if drawn from an area including >2 pairs. Such an area is necessarily large for most species and difficult to survey.

CONCLUSION

To obtain a reliable density estimate of breeding raptors in a primary rain forest, the best strategy should be the design of a particular census method for almost each species separately (i.e., a specific mixture of several techniques complementing each other). Moreover, following radio-tagged birds should be strongly encouraged and is currently the only way to confirm the actual territory size of most species.

When the aim is only to compare the raptor population of different forest areas, it may be advisable to use a specific abundance index. Such an index may be the highest frequency (e.g., mean number of individuals recorded/hour) given by the most rewarding method for the species involved. Indeed, any index is comparable within but not between species. The same technique should be used for a given species over different study sites (including season, time of day and sighting radius). So, the method would avoid the biases of density estimates coming from different specific detectabilities and the more difficult assessment of actual density.

Time is more accurately and easily measured than area or distance and is a more constant unit. I have found here better correlations between number of birds detected and time spent than with distance travelled (all specific $r = 068\text{–}0.92$; $P < 0.01$), either inside or outside the forest.

Results are encouraging but we are far from mastering reasonably easy and accurate census methods appropriate for most raptor species within large areas of dense rain forest. Always necessary will be the use of several censusing methodologies in conjunction, including audio-luring, in order to minimize biases inherent in all. To work out and test such methodologies remains an urgent challenge with regard to rapidly declining tropical forest raptors.

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