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RAPTOR COMMUNITIES IN FRENCH GUIANA: DISTRIBUTION, HABITAT SELECTION, AND CONSERVATION

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ABSTRACT.—French Guiana still has a full gradient of natural habitats, from coastal mangroves, marshes, and savannas (ca. 3700 km²), to swamp and *terra firme* lowland primary rain forest (ca. 80 000 km²). Thirty-two study sites, >2000 ha each, were surveyed throughout the country, including all major vegetation types from 1981 to 2003 during >5472 hr of effective daylight raptor searches. Census techniques took into account the behavior and detectability of every species to assess their abundance and habitat associations. The French Guiana raptor community included 27 forest species, five species restricted to forest edges and large gaps, five species of wetlands and mangroves, eight coastal grassland specialists, four nearctic migrants, and seven occasional taxa of unconfirmed status. In the 19 undisturbed primary forest sites, the most common raptor was the Lined Forest-Falcon (*Micrastur gilvicollis*). Many species were rare or patchily distributed: 15% of all species were found in only 5–11% of the 32 localities sampled and <30% were present in almost all of them. The abundance index was correlated with site occupancy frequency. There was no significant difference in species richness among parts of the country. Some taxa widespread in Latin America (*Cathartes*, *Accipiter*, *Micrastur*) were comparatively rare and local in French Guiana, where more typical Amazonian species were present. Mean abundance of forest vultures, eagles, and caracaras decreased with hunting and logging activities. Country-wide population estimates of forest species ranged from fewer than 100 pairs for habitat specialists such as Orange-breasted Falcon (*Falco deiroleucus*) and Black Caracara (*Daptrius ater*) and 400–500 pairs for the largest and widespread Harpy (*Harpia harpyja*) and Crested (*Morphnus guianensis*) eagles, to >10 000 pairs for the common Lined Forest-Falcon.

KEY WORDS: *distribution*; *French Guiana*; *habitat use*; *population size*; *rainforest*; *raptor community*.

COMUNIDADES DE RAPACES EN LA GUAYANA FRANCESA: DISTRIBUCIÓN, SELECCIÓN DE HÁBITAT Y CONSERVACIÓN

RESUMEN.—La Guayana Francesa todavía presenta un gradiente completo de ambientes naturales, desde los manglares de la costa, humedales y sabanas (ca. 3700 km²), hasta pantanos y bosques lluviosos primarios no inundables de tierras bajas (ca. 80 000 km²). Durante más de 5472 horas diurnas de búsqueda efectiva de rapaces acumuladas entre 1981 y 2003, realizamos censos en 32 sitios de estudio de más de 2000 ha ubicados por todo el país, incluyendo todos los tipos de vegetación principales. Las técnicas de censo consideraron el comportamiento y la detectabilidad de cada especie para estimar su abundancia y las asociaciones de hábitat. La comunidad de rapaces de la Guayana Francesa incluyó 27 especies de bosque, cinco restringidas a bordes de bosque y grandes claros del bosque, cinco de humedales y manglares, ocho especialistas de pastizales costeros, cuatro migrantes neárticos y siete taxa ocasionales de estatus no confirmado. En los 19 sitios de bosque primario no disturbado, la rapaz más común fue *Micrastur gilvicollis*. Muchas especies fueron raras o se presentaron distribuidas en parches: el 15% de todas las especies se encontraron en sólo el 5 al 11% de las 32 localidades muestreadas y menos del 30% estuvieron presenten en casi todos los sitios. El índice de abundancia se correlacionó con la frecuencia de ocupación de los sitios. No hubo una diferencia significativa en la riqueza de especies entre las partes del país. Algunos taxa distribuidos ampliamente en América Latina (*Cathartes*, *Accipiter*, *Micrastur*) fueron comparativamente raros y de distribución local en la Guayana Francesa, en donde se observó una comunidad de rapaces más afín a las comunidades de la Amazonía. La abundancia media de los buitres, águilas y caracaras de bosque disminuyó con la cacería y las actividades de extracción de madera. Las estimaciones poblaciones de las especies de bosque para el país variaron entre menos de 100 parejas para los especialistas de hábitat como *Falco deiroleucus* y *Daptrius ater*, a 400–500 parejas para las águilas más grandes y ampliamente distribuidas como *Harpia harpyja* y *Morphnus guianensis*, a más de 10 000 parejas para la especie común *M. gilvicollis*.
[Traducción del equipo editorial]

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Whole tropical forest raptor communities are rarely surveyed because of the difficulty in such a dense habitat to detect and census many secretive species, most of them little known (Thiollay 1985a, 1989a). The northern half of South America has the highest average local bird species richness in the world and its raptor assemblages are also the richest (del Hoyo et al. 1994). However, the number of species is strongly dependent upon the size of the study area and its diversity of vegetation cover types.

To assess a species' population and its conservation status, presence records and geographical distribution data should be supplemented by estimates of density across the gradient of optimal to suboptimal habitats, and an evaluation of the availability of suitable habitats in the landscape. Distribution patterns are also affected by a complex array of factors including interspecific competition, predation, and availability of nest sites and food resources, which may result in local absences in otherwise suitable habitat patches. Distributional gaps or unexpected local rarity have been commonly found among tropical forest birds, including raptors (Diamond 1980, Thiollay 1989b, 1991). Observed habitat use of a species, within a gradient of natural habitats, is a predictor of its expected distribution over a mosaic of modified habitats. Large pristine tropical forest landscapes which may be used to assess such natural distributions are increasingly rare, and so is the opportunity to know which taxa are true forest species and what is the relative importance of marginal, open, edge, or successional habitats compared to continuous mature forest.

French Guiana still provides this opportunity and has a natural raptor community distributed over the full range of natural vegetation cover types. After more than 20 yr of systematic and intensive raptor surveys throughout this country, my objectives were to sum up all records from a wide array of representative localities to assess the composition of diurnal raptor communities, their geographical variation among sites, the frequency distribution and habitat associations of every species according to landscape patterns, and their country-scale conservation status.

METHODS

Study Area. At the northeastern edge of the Guiana Shield, between Amapa (NE Brazil) and Surinam, French Guiana, is the smallest (84 000 km^2), but one of the most pristine countries in South America. It can be divided into a coastal alluvial plain (3700 km^2) and an upland, hilly, entirely forested interior (>80 000 km^2). Its physical and ecological features were described in Anonymous (1979) and Jullien and Thiollay (1995). Almost all urban areas and 95% of the <200 000 inhabitants (in 2004) are concentrated within 20–40 km from the coast and all logging operations within 50–70 km, leaving a 200–300% 200–250 km roadless area of primary forest almost free of settlement. Villages, towns, and cultivated areas cover 300 km^2 and an additional 10 000 km^2 of forest have been, or are scheduled to be logged (Office National des Forêts unpubl. reports). However, in recent years (2000–06), widespread and mostly illegal goldmining activities have disturbed several forest areas (openings, hunting, river pollution) and may have affected some of the pristine ecosystems and animal communities previously sampled in this study.

The 20–40-km-wide coastal lowlands are covered from the sea to the interior by a belt of young mangroves (6–23 m high, dominated by *Avicennia*, often regenerated by cycles of erosion and siltation), then a taller (25–35 m) mature mangrove (*Rhizophora*, progressively mixed with *Pterocarpus*, *Virola*, and *Symphonia*) region and large palm swamps (*Euterpe*, *Mauritia*) or marshes of dense *Typha*, *Cyperaceae*, or *Montrichardia*, dotted with bushes (*Mimosa*, *Chrysobalanus*). Further inland are extensive savannas (750 km^2), burnt in the dry season, often inundated during the rainy season, and also plantations, pastures, dense woodlots, and forests on white sand. In the east, the primary rain forest extends continuously down to the coast.

South of this low coastal belt (2°30–5°N), the country is covered continuously by rainforest on hills (maximum elevation: 850 m), criss-crossed by numerous streams, some of them with seasonally flooded plains. The northern part of the forest zone is disturbed by roads, logging, hunting, and gold mining, but the larger southern part is only hunted locally around a few settlements.

The rich (>1000 tree species), lowland (50–700 m) rainforest (mean height of 30–40 m, with emergent trees >50 m) is a heterogenous vegetation mosaic, from palm swamps in valley bottoms to dense vine-laden forest on disturbed slopes and high mature forest on well drained plateaus. Tree-fall gaps and multiple watercourses of varying size, and their associated successional vegetation provide a variety of natural openings. Bare granitic outcrops (inselbergs) with their patches of spiny bromeliads (*Pitcairnia*) and *Clusia* woodlots, and some dense stands of monospecific bamboo-like *Gadua macrostachya* provide other distinctive cover types breaking the otherwise uniform forest cover.

From northeast to southwest, the mean annual rainfall decreases from 350 to 200 cm. The mean daily temperatures are lowest during the rainy season (21–22°C; December–June) and highest during the drier season (29–30°C; August–November). In spite of the rainfall gradient, there is no obvious change in forest structure and composition, nor in the proportion of habitat types, from north to south. The central Inini-Camopi range, that includes all the summits (680–850 m), is not high enough to have a true submontane bird community (Thiollay 2002a). The southern part of the country has the lowest average elevation, large seasonally flooded flats, and includes 67% of the >80 large inselbergs scattered throughout the forest zone (Thiollay 2002a, 2002b).

Two natural reserves in the coastal lowlands (Kaw and Amana, 1095 km²) and three in the northern part of the forest interior (Nouragues, Trinité, and Matoury, 1787 km²) are the only protected areas, along with a national park (>20 000 km²) created in 2007 in the south.

Site Selection. A comprehensive network of 32 sample sites covering all natural regions was surveyed. Sites were chosen without prior knowledge of the local habitats or fauna as most of them had never been visited by a scientist. They were selected arbitrarily on the basis of logistical constraints, determined on a 1:50 000 map or aerial photographs, i.e., accessibility by car (road, 10 sites in coastal zone), plane (airstrip, four sites), boat (river, eight sites), or helicopter (inselberg, 10 sites). Thus, the selection of study sites was random with respect to the forest types and raptor assemblages that occurred at the local scale. However, at the country scale, survey areas were rather evenly distributed, so as to sample every significant area of French Guiana (Fig. 1). Together, the study sites covered all habitat types, microclimates, and disturbance regimes found in the country. They were divided into three categories (a, b, and c, respectively, in Table 1): (1) four coastal sites with mostly open habitats, forest patches, palm swamps and mangroves; (2) nine continuous forest areas, near the coastal savannas or around villages along rivers, partially opened by shifting cultivation, roads, or logging (hereafter, disturbed or forest edge); and (3) nineteen sites within unbroken primary undisturbed forest in the interior of the country.

Study sites may be considered as independent units (>10 km between the nearest sites). Each of them included an array of the forest types, albeit in different proportions. They differed mostly by the presence or absence of the larger gaps (i.e., wide river or inselberg). All sites were also surveyed by botanists and overall tree species composition was not found to vary substantially across the country (J. de Granville pers. com.), as already found within such limited regions of Amazonia (Terborgh and Andresen 1998).

Habitat Types. Large sparsely wooded areas are almost restricted to the coastal zone. They include marshes, savanna grasslands, improved pastures, cultivated fields, plantations, and suburban areas. Mangrove swamps, found all along the 350-km coastline, may be >2 km wide. Large palm swamps occur in the eastern coastal lowlands, and in the southwestern interior along major rivers. Naturally isolated woodlots and low dense forest on sand are confined to the northeastern coastal plain.

Raptors using rainforest may be best observed from disturbed or open patches within the seemingly continuous primary forest. Tree-fall gaps of various sizes and frequencies were by far the most common form of disturbance, followed by streams, from small to large, some of them with wide, seasonally flooded flat lowland areas. The next most frequent large openings were the rocky inselbergs (i.e., granite outcrops) sometimes with cliffs, from almost bare to partly forested. Hill slopes were more frequently disturbed than plateaus or lowlands, and contained dense, vine-laden, but discontinuous forests. Palm swamps of various sizes occurred in valley bottoms. Rare natural gaps included patches of dense bamboos, oxbow lakes, or marshes and sand banks along rivers.

Site Survey and Census Technique. The 32 study sites were surveyed over 23 yr and most months, except January–February. Most surveys were conducted during the driest months (August to December and March) and only three of them were made in the rainy season (April–June), but during periods with little rain. The schedule of surveys was highly dependent on expensive logistics, and therefore had to be shared with other programs.

The total time spent effectively surveying raptors (daylight, full hours without rain) was 5472 hr spread over >600 d: 70–100 hr at 11 sites, 120–280 hr at 20 sites, and 899 hr at one site (Appendix). The 13 most remote forest sites were studied only once (15–23 d each), the six coastal sites, accessible by car, were visited 4–5 times for 1–3 d each and the remaining sites were surveyed 2–3 times. This does not include subsequent visits for other ornithological studies, in which raptor records were not taken into account (no additional species were then ever detected). Such differences in the time spent at each site does not compromise the comparison between them because in nearly every case no new species were recorded after the first 50 hr in the forest understory. Also, no new species were recorded from open lookouts after the first 20 survey hr including 10 hr in the late morning (see Thiollay 1989a). At almost all survey sites, these limits were exceeded, often by far. All sites were surveyed for much longer periods (Appendix). The maximum number of pairs (or groups, or individuals, according to species) was also reached always well before the end of the survey. Therefore, the time spent in most sites was considered reasonably sufficient to sample the raptor community, as much longer periods would have been needed to add very few birds, an unrealistic endeavor given the logistical difficulties of staying in remote areas.

At each site, a central campsite was established around which full-day surveys were conducted on foot (rarely by boat) along line transects, as straight as possible, radiating in at least six directions from the campsite, through the forest (or along existing trails, if any), at random in relation to the vegetation type encountered. The transect length was that which could be covered from early morning to early afternoon and which would allow me to return by nightfall. Thus, most of the surveys were within a straight-line radius of 3 km from the campsite (confirmed by using a GPS receiver at transect ends in the later survey years) and, in all, an estimated ≥2000 ha were actually covered. Each line transect was covered twice the same day at different times, and two or more times on different days. Additional shorter circuits were made to reach the most suitable lookouts, selected from the map or found along line transects. The resulting network of foot circuits was dense enough to sample every distinctive vegetation cover type within the survey area, and the time spent in each vegetation type was roughly proportional to the relative area of that type because the average walking speed was similar among habitats. This ≥2000 ha area was the largest area that a single observer could reasonably cover within the above time constraints such that few pairs or species present would be be missed, given the field conditions and observer experience. It was also the minimum area likely to include at least part of one home range of most species of a local rainforest raptor community.

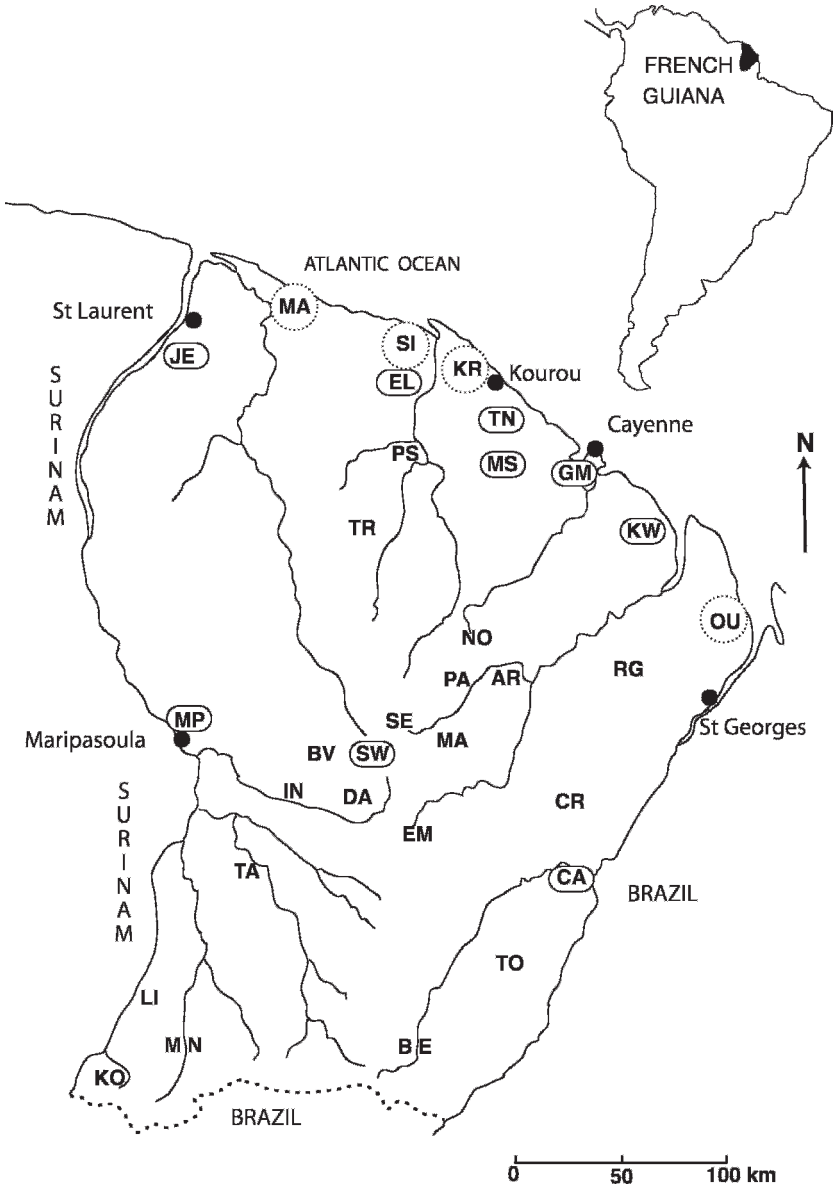

Figure 1. Distribution of 32 survey areas in French Guiana. The four dotted circles are coastal sites with swamps, savannas, and mangroves. The nine plain circles are disturbed and hunted forest sites. The other 19 sites (not circled) are continuous, undisturbed primary forest (see Table 1).

These surveys were a combination of several methods that could be used within a limited time in such a pristine environment (Fuller and Mosher 1987, Thiollay 1989a, Bibby et al. 2000). Techniques had to be adapted to different species behaviors, topography and weather conditions. My objective was to detect all territorial, potentially breeding pairs, groups or individuals, taking into account the social behavior of species involved.

Line transect. This was the basic technique used on most days: very slow walking through the understory with frequent stops to aid in the detection of perched, flying, or calling birds. As much as possible, I recorded the gender, age class, behavior, and position of each individual to help assign individuals as members of established pairs. I also recorded the perpendicular distance from the transect to the point at which a raptor was first detected.

Table 1. Study sites and habitat features in French Guiana. The first four localities (*a*) are mostly open habitat, coastal sites; the next nine localities (*b*) are outer, disturbed forest sites; and the last 19 localities (*c*) are primary forest sites in the interior. In each category, they are listed from north to south.

CODE	LOCALITY	FOREST[a]	GAPS[b]	DISTURBANCE[c]
MA (*a*)	Mana	mangrove	swamp, ricefields	hunting
SI (*a*)	Sinnamary	fragmented, flooded	grassland, marsh	hunting
KR (*a*)	Kourou	fragmented	grassland	hunting
OU (*a*)	Ouanary	partly flooded	marsh, river, clearing	hunting
JE (*b*)	Saint-Jean	fragmented	clearing, grassland	logging, hunting
EL (*b*)	Piste Saint-Elie	continuous	road	logging, hunting
TN (*b*)	Tonate	fragmented	grassland	logging, hunting
MS (*b*)	Montsinéry	continuous	road	logging, hunting
GM (*b*)	Grand Matoury	fragmented	clearing	logging, hunting
KW (*b*)	Montagne Kaw	continuous	road	logging, hunting, mining
SW (*b*)	Saül-Galbao	continuous	clearing	hunting, mining
CA (*b*)	Camopi	continuous	clearing, river	hunting
MP (*b*)	Maripasoula	continuous	clearing, river	hunting
PS (*c*)	Petit Saut	continuous	river	hunting
RG (*c*)	East Regina	continuous	road	hunting
TR (*c*)	Mont. Trinité	continuous	inselberg	
AR (*c*)	Camp Arataye	continuous	river	
NO (*c*)	Nouragues	continuous	inselberg	
PA (*c*)	Saut Pararé	continuous	river	
CR (*c*)	Grand Croissant	continuous	inselberg	
MO (*c*)	Pic Matécho	continuous	inselberg	
SE (*c*)	Saül-Est	continuous	clearing	hunting
DA (*c*)	Mont Dachine	continuous	inselberg	
EM (*c*)	Emerillons	continuous	inselberg	
BV (*c*)	Mont Bellevue	continuous	small mountain top	
IN (*c*)	Grand Inini	continuous	river	
TA (*c*)	Saut Tampok	continuous	river	hunting
TO (*c*)	Roche Touatou	continuous	inselberg	
BE (*c*)	Mont Belvédère	continuous	river, inselberg	
LI (*c*)	Litani	continuous	river	
MN (*c*)	Haut Marouini	continuous	river, inselberg	
KO (*c*)	Koulé-Koulé	continuous	river	

[a] Forest type: *continuous*, except small gaps; *fragmented*, but most patches still linked to each other; and *flooded* = mangroves and *Mauritia* or *Euterpe* palm swamps.

[b] Largest gaps in forest cover: *inselberg* = granitic hilltop with bare rocky areas; *river* = stream with open canopy above, all along; *clearings* = small fields and associated roads or settlements; *road*, and cutover verges; *grasslands* = cattle pastures and/or savannas; and *marshes* = grassy or partly wooded swamps.

[c] Selective *logging*, current or past; small scale *mining*; and variable *hunting* pressure.

Search for flying birds. Soaring, displaying, hunting, or flying birds were surveyed from stationary vantage points above the canopy (especially from inselbergs) or from large openings (rivers, roads, clearings), with a focus on late morning (0900–1300 H) during which many species perform display flights, indicators of territorial pairs. Perched birds otherwise difficult to detect (*Harpia*, *Falco*), were also detected from such lookouts.

Detection of vocalizations. Some species, which never soar above the forest, occasionally (*Leucopternis melanops*) or often (*Daptrius/Ibycter*) call. Their location, number of individuals involved, and movements were recorded. Listening sessions early in the morning, and to a lesser extent in the late afternoon, were the best ways to detect forest-falcons (*Micrastur*) which are secretive, never soaring, but highly vocal at dawn.

Trapping. Some birds were detected by using specific live-baited snares, or occasional captures in mistnets, sometimes enhanced by audio-luring (i.e., broadcasting specific calls or distressed prey vocalizations) when particular species were suspected, but not yet confirmed. Such methods were too time-consuming for general surveys.

The estimated minimum number of territorial pairs included within the approximate 2000-ha survey area, was

used as an abundance index. For social and wide-ranging aerial species (*Cathartes*, *Elanoides*, *Ictinia*), I recorded the minimum number of different birds seen daily, later using a rough conversion equivalent of three individuals for one pair to compare with other species. For forest Caracaras (*Daptrius*), the number of flocks was used, whatever the flock size, as they are stable, social, and territorial units in which a single pair is breeding (Thiollay 1991). The identity of pairs was derived from the location of and distance between observations, associated with behavior (e.g., display flight or territorial call), and independently estimated home-range sizes (Thiollay 1989b). All data were based on birds actually recorded, with no estimates or extrapolations made. Therefore, estimates were conservative, particularly for the secretive species. Most information on behavior and ecology came from years of fieldwork in French Guiana, confirmed or supplemented by appropriate references (e.g., del Hoyo et al. 1994).

The time spent searching for raptors was also used for a general survey of the whole bird community, supplemented by data obtained during additional visits or time spent, not included in the Appendix, and by other observers. As a result, the total bird species richness was reasonably well assessed in 20 of the 32 survey sites and could be compared among these sites.

Statistical Analysis. Assumptions of the DISTANCE sampling program (Buckland et al. 1993) to estimate densities were rarely met (e.g., too few records of perched birds). Therefore no estimated densities calculated from line transect data were used. Rarefaction curves, or accumulation rates of daily records using a jacknife procedure or the Chao (1989) estimator, provided species richness estimates close to actual counts. As a result, they are not included here. Diversity indices were not employed because abundance data were not always comparable among species.

The significance of comparisons of mean abundances or species richness between areas or habitats was tested by ANOVAs on log-transformed data. Chi-square tests were used to compare the frequency of occurrence of some species among sites, and Spearman rank correlation coefficients were employed to correlate raptor species richness to overall bird diversity independently assessed through additional fieldwork. Significance levels were set at $P < 0.05$.

RESULTS

Species Status, Distribution, and Habitat Use. All 27 forest species ranged, at least potentially, over the whole forest area (i.e., >95% of the country), whereas most of the 16 coastal species and four migrants were usually restricted to a part of the narrow coastal strip (Table 2). Therefore, most species distribution maps would appear similar and are not given. Specific characteristics are critical to explain species range and abundance within French Guiana. More details may be found in Tostain et al. (1992) and Jullien and Thiollay (1995).

Black Vulture (Coragyps atratus). Numbers are recovering from past persecution. Now common in northern coastal areas (savannas, mangroves, beaches, farms, and towns), where all observations were recorded (155 individuals from eight sites). Still absent from forested interior, even in large, but isolated clearings (Saül, Maripasoula; Table 1).

Turkey Vulture (Cathartes aura). Same habitat and distribution as the Black Vulture (68 individuals from seven coastal sites), but much less partial to seaside, estuaries, and settlements. Forage solitarily more often in fragmented coastal forests. Never seen in the interior, whereas elsewhere in Latin America, it forages over forests where the Greater Yellow-headed Vulture is absent (pers. obs.).

Lesser Yellow-headed Vulture (Cathartes burrovianus). Local and uncommon in coastal areas (54 individuals from six sites). Forages low over humid grasslands and marshes.

Greater Yellow-headed Vulture (Cathartes melambrotus). Common throughout the forest zone (143 individuals at 30 sites), including near the coast, but with little overlap with the Turkey Vulture. Mean abundance of this vulture (4–6 individuals/site) tends to decrease in some disturbed forests, but the maximum number was recorded in a large coastal palm swamp (Ouanary; 16 individuals). Seen eating any mammal or bird, including a conspecific.

King Vulture (Sarcoramphus papa). Territorial pairs ranging over wide areas throughout the country, sometimes over coastal grasslands (35 pairs from 30 sites). Associated with the Greater Yellow-headed Vulture, which it follows and dominates on carcasses.

Osprey (Pandion haliaetus). Wintering migrant common along the coast, but also regularly found on large rivers, even far into the forest zone (17 individuals at 16 sites).

Gray-headed Kite (Leptodon cayanensis). Mainly associated with riparian or partly flooded forest, even old mangroves, throughout the country (22 pairs at 17 sites).

Hook-billed Kite (Chondrohierax uncinatus). Little known and inconspicuous, but probably rare (or possibly hard to detect) over most of the country (12 pairs at 12 sites), in various forest types (including palm swamps and mangroves). Suspected nomadic movements and irregular at repeatedly surveyed sites.

Swallow-tailed Kite (Elanoides forficatus) and Plumbeous Kite (Ictinia plumbea). Small flocks of 2–10 birds usually foraged over any forest type at most survey areas (131 individuals at 29 sites and 128 individuals at 26 sites, respectively), catching prey in flight

Table 2. Distribution and habitat associations of raptor species in French Guiana. Percent of survey sites (*N*) where the species was recorded. The mean abundance per occupied site is given in parentheses. Abundance is the minimum number of documented pairs, or the mean daily number of individuals observed (*Coragyps*, *Cathartes*, *Ictinia*, *Elanoides*, and migrants), or the number of social groups (*Daptrius*) per site.

SPECIES	PRIMARY FOREST SITES (*N* = 19)	DISTURBED AND EDGE SITES (*N* = 9)	OPEN COASTAL SITES (*N* = 4)	SPECIFIC HABITAT AFFINITIES
Black Vulture, *Coragyps atratus*		44% (11.3)	100% (29.8)	farmlands, mangroves
Turkey Vulture, *Cathartes aura*		33% (3.5)	100% (15.0)	grasslands
Lesser Yellow-headed Vulture, *Cathartes burrovianus*		22% (1.5)[a]	100% (12.8)	marshes, pastures
Greater Yellow-headed Vulture, *Cathartes melambrotus*	100% (4.7)	100% (3.8)	50% (5.0)	all forests
King Vulture, *Sarcoramphus papa*	100% (1.2)	89% (1.5)	75% (1.5)	all forests
Osprey, *Pandion haliaetus*[b]	47% (1.0)	33% (1.0)	100% (1.5)	coast, rivers
Gray-headed Kite, *Leptodon cayanensis*	53% (1.2)	67% (1.5)	25% (1.0)	riparian forest
Hook-billed Kite, *Chondrohierax uncinatus*	37% (1.0)	33% (1.0)	50% (1.0)	some forests
Swallow-tailed Kite, *Elanoides forficatus*	95% (5.6)	78% (3.7)	100% (2.3)	all forests
Snail Kite, *Rostrhamus sociabilis*			50% (1.0)	open marshes
Slender-billed Kite, *Rostrhamus hamatus*			50% (1.0)	wooded marshes
Double-toothed Kite, *Harpagus bidentatus*	100% (3.0)	100% (2.3)	75% (2.0)	all forests
Rufous-thighed Kite, *Harpagus diodon*	68% (1.0)	56% (1.0)	50% (1.5)	most forests
Plumbeous Kite, *Ictinia plumbea*	84% (5.1)	89% (4.1)	50% (6.5)	all forests
Long-winged Harrier, *Circus buffoni*			75% (3.0)	wet grasslands, marshes
Gray-bellied Goshawk, *Accipiter poliogaster*	5% (1.0)	11% (1.0)		primary forest
Tiny Hawk, *Accipiter superciliosus*	32% (1.0)	44% (1.3)	25% (1.0)	most forests
Bicolored Hawk, *Accipiter bicolor*	47% (1.0)	22% (1.0)		some forests
Crane Hawk, *Geranospiza caerulescens*	5% (1.0)[a]	44% (1.0)		forest edges, swamp forests, woodlands
Slate-colored Hawk, *Leucopternis schistacea*			25% (1.0)	Eastern mangroves
Black-faced Hawk, *Leucopternis melanops*	63% (1.2)	44% (1.0)		primary forest
White Hawk, *Leucopternis albicollis*	100% (1.7)	89% (21.9)	50% (1.0)	forest gaps and edges
Gray Hawk*, *Asturina nitida*	16% (1.0)[a]	100% (1.9)	75% (2.3)	forest edges, woodlands
Rufous Crab-Hawk, *Buteogallus aequinoctialis*			100% (6.5)	mangrove
Great Black-Hawk, *Buteogallus urubitinga*	95% (1.4)	78% (1.3)	100% (1.8)	forests with gaps
Savanna Hawk, *Buteogallus meridionalis*		22% (1.0)[a]	75% (2.7)	grasslands
Black-collared Hawk, *Busarellus nigricollis*		11% (1.0)[a]	100% (2.3)	marshes
Roadside Hawk, *Buteo magnirostris*	5% (1.0)[a]	67% (2.5)	100% (4.5)	farmlands, swamp forests, settlements
Broad-winged Hawk, *Buteo platypterus*[b]	11% (1.0)	56% (1.2)		forest edges
Short-tailed Hawk, *Buteo brachyurus*	5% (1.0)[a]	33% (1.7)	75% (1.3)	secondary coastal forests
White-tailed Hawk, *Buteo albicaudatus*	5% (1.0)[a]	33% (1.0)	75% (1.5)	grasslands
Zone-tailed Hawk, *Buteo albonotatus*			50% (2.0)	wet grasslands
Crested Eagle, *Morphnus guianensis*	74% (1.0)	44% (1.0)	25% (1.0)	primary and logged forests
Harpy Eagle, *Harpia harpyja*	63% (1.0)	22% (1.0)		primary forest
Black-and-white Hawk-Eagle, *Spizastur melanoleucus*	89% (1.0)	78% (1.4)	25% (2.0)	most high forests
Ornate Hawk-Eagle, *Spizaetus ornatus*	100% (1.5)	56% (1.0)	25% (1.0)	mostly primary forest
Black Hawk-Eagle, *Spizaetus tyrannus*	63% (1.1)	100% (1.6)	75% (1.3)	disturbed forest
Black Caracara, *Daptrius ater*	21% (1.0)[a]	11% (1.0)[a]		riparian forest
Red-throated Caracara, *Ibycter americanus*	100% (2.2)	56% (1.8)	50% (1.0)	undisturbed forests
Yellow-headed Caracara, *Milvago chimachima*		22% (2.0)[a]	75% (5.0)	grasslands
Laughing Falcon, *Herpetotheres cachinnans*		33% (1.0)	100% (1.5)	forest edges, woodlands

Table 2. Continued.

SPECIES	PRIMARY FOREST SITES (N = 19)	DISTURBED AND EDGE SITES (N = 9)	OPEN COASTAL SITES (N = 4)	SPECIFIC HABITAT AFFINITIES
Barred Forest-Falcon, *Micrastur ruficollis*	58% (1.3)	56% (1.2)	25% (1.0)	forests (often secondary)
Lined Forest-Falcon, *Micrastur gilvicollis*	100% (3.4)	100% (2.3)	25% (1.0)	forests (preferably undisturbed)
Slaty-backed Forest-Falcon, *Micrastur mirandollei*	95% (1.4)	67% (1.0)	25% (1.0)	forests (mostly primary)
Collared Forest-Falcon, *Micrastur semitorquatus*	79% (1.6)	89% (1.5)	100% (1.0)	forests (often secondary)
Bat Falcon, *Falco rufigularis*	42% (1.6)[a]	100% (1.4)	100% (2.5)	forest rivers, clearings
Merlin, *Falco columbarius*[b]			25% (1.0)	grasslands
Peregrine Falcon, *Falco peregrinus*[b]		11% (1.0)	75% (2.5)	open coastal habitats
Orange-breasted Falcon, *Falco deiroleucus*	32% (1.0)[a]	22% (1.0)	75% (1.0)[c]	inselbergs

[a] Isolated pairs associated with an open habitat patch (large river, inselberg, marsh).
[b] Nearctic wintering migrants.
[c] Probably nonbreeding vagrants only?
[*] Reclassified as *Buteo nitidus* by A.O.U. 2006.

above and around upper canopy. Their numbers seemed to fluctuate daily and seasonally involving movements of possibly both resident birds and migrants of northern or southern origin.

Double-toothed Kite (Harpagus bidentatus). One of the most frequent raptors recorded at all forest sites surveyed (84 pairs from 31 sites), detected mainly when displaying high over the forest every morning. Kite abundance tended to decrease from primary to disturbed and coastal forests (Table 2). This kite is a regular monkey follower (mostly *Cebus* sp.; pers. obs.).

Rufous-thighed Kite (Harpagus diodon). Much rarer and less regular than the above species, but also found in several forest types, including coastal palm swamps (21 pairs at 20 sites). Never seen displaying over the forest nor following monkeys.

Long-winged Harrier (Circus buffoni) and Zone-tailed Hawk (Buteo albonotatus). Both species are confined to savannas and rice fields of the central and western coastal area where they may be locally frequent (7 pairs at 3 sites and 4 pairs at 2 sites, respectively). Hunt in flight low over the ground.

Gray-bellied Goshawk (Accipiter poliogaster), Bicolored Hawk (Accipiter bicolor), and Tiny Hawk (Accipiter superciliosus). Accipiters were exceedingly secretive, but they seemed also to be very uncommon forest hawks in this country. This rarity is perhaps related to competition with the much more numerous forest-falcons (*Micrastur* spp.). Even if some accipiters went undetected, none of them seemed to occur in more than half of the suitable survey sites. The Tiny Hawk (12 pairs at 11 sites), the smallest species, was the most frequent and was seen foraging and building nests only in the canopy of primary and secondary forests (including coastal). The medium-size Bicolored Hawk (11 pairs at 11 sites) was surprisingly rare, compared to other countries of Latin America (pers. obs.) and has beeen recorded only in the undergrowth of dense mature or disturbed forests. The larger Gray-bellied Goshawk was identified at only two sites in the lower canopy of primary (Nouragues) and recently logged (Montagne Kaw) forests.

Crane Hawk (Geranospiza caerulescens). Uncommon forest-edge species (12 pairs at 9 sites) associated with fragmented, secondary or swamp forests in the coastal area and locally with large clearings in the interior (Saül and along the Maroni and Litani rivers).

Slate-colored Hawk (Leucopternis schistacea). Local in mangroves and palm swamp forests near the coast, only east of Cayenne (Ouanary).

Black-faced Hawk (Leucopternis melanops). Secretive understory primary forest species (18 pairs at 16 sites), never seen in the open or soaring over the canopy. At some study sites, it was detected only by vocalizations and its actual occurrence may be underestimated.

White Hawk (Leucopternis albicollis). Widespread (49 pairs from 29 sites) and conspicuous species found in almost every wooded locality surveyed (ex-

cept mangroves and swamps), even in continuous primary forest, although it needs some forest openings or edges (tree-fall gaps, inselbergs, roads, clearings), where it prefers to hunt.

Gray Hawk (Asturina nitida) and Roadside Hawk (Buteo magnirostris). Both are typical of forest edges, open woodlands, and farmlands (26 pairs at 15 sites, and 34 pairs from 11 sites, respectively), mostly in the coastal zone, but locally in large clearings of the interior. They do not enter dense or continuous forest. The Gray Hawk tends to use more forested habitats than the more widespread Roadside Hawk, which occurs even in urban areas and edges of mangroves.

Rufous Crab-Hawk (Buteogallus aequinoctialis). Quite common along the coast (mangroves and beaches) and in major estuaries and coastal marshes, where it forages for crabs mostly at low tide (13 pairs at 4 sites).

Great Black-Hawk (Buteogallus urubitinga). Occurs in almost any large extent of primary or secondary forest though it requires gaps and water (43 pairs at 29 sites). Often seen hunting along small forest streams, on edges of inselbergs, or in highly-disturbed forest patches. Easily detected by its conspicuous and vocal display flight. Also found in old mangroves and palm swamps.

Savanna Hawk (Buteogallus meridionalis). Regular and widespread in coastal savannas and pastures, even closely surrounded with forest (10 pairs at 5 sites). Avoids marshes, but uses rice fields.

Black-collared Hawk (Busarellus nigricollis). Small numbers on large coastal marshes with areas of open water (10 pairs at 5 sites). Not found in mangroves or palm swamps.

Broad-winged Hawk (Buteo platypterus). A few isolated individuals winter along the coastal zone (forest edges, forest roads, and clearings) and rarely in large openings of the interior (8 individuals at 7 sites).

Short-tailed Hawk (Buteo brachyurus). Curiously restricted to forest along a narrow coastal belt, usually logged or secondary, sometimes undisturbed, though not far from savannas or marshes (10 pairs at 7 sites). Occasional in mangroves or in the interior. Hunts mostly in flight over the canopy.

White-tailed Hawk (Buteo albicaudatus). Frequent in savannas and pastures of the coastal zone from Mana to Cayenne (7 pairs at 6 sites). Vagrants on large inselbergs of the interior (Roche Touatou).

Crested Eagle (Morphnus guianensis) and Harpy Eagle (Harpia harpyja). The two largest eagles are widespread throughout the forest zone. The Crested Eagle is significantly more frequent than the Harpy Eagle in logged or otherwise disturbed forests (Table 2) and is even found in extensive palm swamps. In primary forest, the Crested Eagle is more frequent (recorded in 19 sites) than the Harpy (14 sites), but not significantly ($\chi^2 = 1.68$, 1 df, $P > 0.1$) and the two species are found less frequently together than alone, but again not significantly so ($\chi^2 = 2.68$–4.46, 3 df, $P > 0.2$). When both were seen at the same survey area, they tended to be in separate zones, suggesting interspecific avoidance.

Black-and-white Hawk-Eagle (Spizastur melanoleucus). An aerial hunting specialist of the upper canopy, this small eagle was recorded in most forest areas (29 pairs at 25 sites), even in the disturbed northern forests and in a large palm swamp. It regularly attacks birds in fruiting trees.

Ornate Hawk-Eagle (Spizaetus ornatus) and Black Hawk-Eagle (Spizaetus tyrannus). Though common and widespread, and often recorded in the same study areas (11 of 19 primary forest sites), these two species are clearly segregated. The Ornate Hawk-Eagle (33 pairs at 25 sites) is typical of primary undisturbed forests. Its frequency of occurrence decreases in logged forests, but it reaches the northernmost forest areas. Conversely, the Black Hawk-Eagle (31 pairs at 24 sites) is associated with disturbed (lower, denser) patches within mature stands, and with natural (inselbergs, rivers) or artificial edges (clearings, roads, logging), secondary and fragmented forests. Both species are easy to detect when they perform daily, in fair weather, their vocal display flight.

Black Caracara (Daptrius ater). Rare or local bird in French Guiana (5 groups at 5 sites), found in riverine forest along some large rivers from the far south (Litani, Mana), to estuaries (Oyapock, Kaw). Group size is often 2–4 individuals and human hunting pressure may play a role in the patchy distribution of this species (all large species are scarce along rivers where indiscriminate hunting often takes place).

Red-throated Caracara (Ibycter americanus). This unusual (Thiollay 1991) and social raptor has a typical group size of 4–8, and can be heard everywhere in the primary forest (52 flocks at 26 sites), but declines markedly in logged, secondary, and hunted forests.

Yellow-headed Caracara (Milvago chimachima). A common bird of open coastal grasslands (18 pairs at 5 sites), more abundant in improved pastures

with cattle than in natural savannas or cultivated fields. Usually in pairs.

Laughing Falcon (Herpetotheres cachinnans). Never seen or heard in primary forest. Only in the coastal zone (9 pairs at 7 sites), where it is more common in open cultivated woodlands and pastures than in its original habitat (edges of fragmented forest and old mangroves).

Barred Forest-Falcon (Micrastur ruficollis), Lined Forest-Falcon (Micrastur gilvicollis), Slaty-backed Forest-Falcon (Micrastur mirandollei), and Collared Forest-Falcon (Micrastur semitorquatus). Because of their relatively high density, the forest-falcons are the dominant raptors in every forest types. The Lined (86 pairs at 29 sites) far outnumbers the Barred Forest-Falcon (21 pairs at 17 sites) in primary and even secondary forests, although the latter often maintains high abundances in disturbed forest, where the former seems to decrease. The two less abundant, larger taxa also exhibit a marked segregation. The Slaty-backed Forest-Falcon (32 pairs at 25 sites) is dominant in primary mature forest, but is also found in some coastal forest patches, whereas the Collared Forest-Falcon (40 pairs at 27 sites) has its highest abundance in disturbed and fragmented forests, and occurs even in mangroves and swamp forests. When encountered at random (calling, hunting, or resting), >90% of the two smaller species were perched between 3–16 m ($N = 262$ individuals), compared to 15–35 m for the two larger species ($N = 110$). There was no significant difference between perch height of the two smaller species, nor between the two larger species (ANOVAs, $P > 0.09$), but a significant difference between small and large species ($P < 0.004$). This suggests a segregation between understory and canopy species.

Bat Falcon (Falco rufigularis). In continuous primary forest areas, the Bat Falcon has been seen exclusively along large rivers, where pairs are well spaced. It becomes common in large clearings, savannas, and even mangroves, often on top of isolated trees (36 pairs at 21 sites).

Merlin (Falco columbarius) and Peregrine Falcon (Falco peregrinus). Nearctic wintering migrants restricted to the coastal zone. The Merlin is quite rare and found mostly in pastures, rarely mudflats. The peregrine is frequent in every open habitat, rich in medium-sized birds along the coast, mainly mudflats, towns, marshes, grasslands, and rice fields. Solitary peregrines tend to be territorial and faithful to particular perch sites.

Orange-breasted Falcon (Falco deiroleucus). Breeding pairs have been found only on small cliffs of large inselbergs from where they hunt birds and bats over the primary forest (at least four sites, probably six). However, solitary adults are also encountered in the coastal area far from rocks (five sites), suggesting that some pairs may breed in tree cavities (provisionally listed as nonbreeding vagrants in Table 2).

Occasional and Unconfirmed Species. Pearl Kite (*Gampsonyx swainsonii*), Crested Caracara (*Caracara cheriway*), and American Kestrel (*Falco sparverius*) are vagrants, and the White-tailed Kite (*Elanus leucurus*) is regular, but probably not breeding in the coastal grasslands.

Three species have been repeatedly reported (Tostain et al. 1992, Ingels et al. 2003), but they are unknown from Surinam (Haverschmidt and Mees 1994), and would be well outside their known range (Ferguson-Lees and Christie 2001). Therefore, in spite of careful descriptions, they should be supported by a specimen. These are: the Common Black-Hawk (*Buteogallus anthracinus*), restricted to the mangrove of the Kourou-Sinnamary area, where it coexists on two survey sites with three other *Buteogallus*; the Solitary Eagle (*Harpyhaliaetus solitarius*) reported to occur at two survey sites, and possibly more; and a small forest *Accipiter* with pure white underparts, seen well by several people (including myself) in the understory of three survey sites (PS, NO, SW; Table 1) and identified by some as the Plain-breasted Hawk (*Accipiter ventralis*), an unlikely Andean montane taxon. This may well be a new, undescribed species.

Raptor Community Composition. Each study site was a habitat mosaic and many raptor species were dependent on a combination of two or more vegetation types (e.g., forest and a type of gap), or on subtle habitat characteristics (e.g., forest height, density, wetness, or disturbance). Many of the raptors recorded occupied an array of habitats at different abundances, or used differently distinct patches of their heterogeneous large home ranges. The 49 species detected (Table 2) may be divided into five groups: (1) Primary forest and natural gap species, including *Cathartes melambrotus*, *Sarcoramphus*, *Leptodon*, *Chondrohierax*, *Elanoides*, 2 *Harpagus*, *Ictinia*, 3 *Accipiter*, 2 *Leucopternis*, *Buteogallus urubitinga*, *Morphnus*, *Harpia*, *Spizastur*, 2 *Spizaetus*, *Daptrius*, *Ibycter*, 4 *Micrastur*, and 2 *Falco*; (2) Secondary forest and edge or clearing specialists, mostly in the coastal zone, including *Geranospiza*, *Asturina*, *Buteo magnirostris*, *B. brachyurus*, and *Herpetotheres*; (3)

Table 3. Species richness, distribution patterns, and abundance indices of raptors in French Guiana.

	CONTINUOUS, UPLAND PRIMARY FOREST	FRAGMENTED OR LOGGED FOREST AND EDGES	COASTAL GRASSLANDS, WETLANDS AND MANGROVES
Number of sites surveyed	19	9	4
Number of resident species	32	39	40
Nearctic wintering migrants	2	3	3
Resident species recorded in ≥50% of sites	20	20	27
Number of species per site[a]	19.63 (±2.97)	21.55 (±4.74)	26.25 (±2.58)
Total abundance index of raptors[a]	29.89 (±6.68)	31.11 (±7.01)	63.50 (±11.62)

[a] $\bar{X}$ (±SD) with migrants excluded.

Coastal wetland and mangrove species, including 2 *Rostrhamus*, *Leucopternis schistacea*, *Busarellus*, and *Buteogallus aequinoctialis*; (4) Coastal, open grassland, and wetland species, including *Coragyps*, 2 *Cathartes*, *Circus*, *Buteogallus meridionalis*, *Buteo albicaudatus*, *B. albonotatus*, and *Milvago*; and (5) Nearctic wintering migrants, including *Pandion*, *Buteo platypterus*, and 2 *Falco*.

The primary forest raptor community was highly diversified. Species sizes ranged from 80–116 g (male and female Tiny Hawk; Dunning 1993) to 4800–7600 g (Harpy Eagle). All habitats were used, from upper slopes and rocky inselbergs, to swamps and rivers, as well as all strata from low understory (forest-falcons) to high above the canopy (kites). Diets also included everything from fruits and wasp nests (caracaras; Thiollay 1991) to aerial, foliage or ground insects, to large mammals and birds (eagles). Among continuous primary forest sites, disturbed forest and more open coastal sites, neither the mean number of species per site nor the mean abundance index of all raptors differed significantly (ANOVAs, $P > 0.05$), except the abundance in coastal sites because of higher densities of non-forest vultures (Table 3).

In the 19 primary forest sites, the two caracara species made up 7% ($N = 39$) of the birds observed; the two vulture species, 9.5% ($N = 53$); the five eagle species, 15% ($N = 84$); the four aerial hunters (*Elanoides*, *Ictinia*, *Falco*), 14.1% ($N = 79$); the five breeding hawks (mostly *Leucopternis* and *Buteogallus*), 16.4% ($N = 92$); nine smaller species (*Harpagus*, *Accipiter*, *Micrastur*), 38% ($N = 213$; all proportions determined using numbers of pairs or flocks, as described in Methods). The last category may be underestimated, especially when compared to the more conspicuous or larger species whose home ranges were more likely to extend outside the limits of the study areas.

In primary forest, the forest-falcons were the most numerous species and 51% of them on average were Lined Forest-Falcons. The mean number of forest-falcon species per site decreased, although nonsignificantly, from primary (range = 2–4, $\bar{x} = 3.3$) to disturbed forests (range = 2–4, $\bar{x} = 3.1$), but sharply in coastal woodlands and mangroves (range = 1–2, $\bar{x} = 1.8$). Their mean abundance decreased more markedly from 6.63 to 5.00 and 1.75 pairs per site, respectively (ANOVA, $P < 0.001$).

Other pairs of congeneric species often coexisted within the same forest area. Either each member used habitats different from the other (*Daptrius/Ibycter*, *Falco*, *Spizaetus*), or one of them was much rarer than the other (*Harpagus*, small *Micrastur*), or they had different body sizes and used different forest strata (*Accipiter*), or they had mostly nonoverlapping territories (*Harpia*, *Morphnus*), or they were nomadic, flocking species occurring together only on temporary insect swarms (*Elanoides*, *Ictinia*).

A striking feature was the relative rarity of widespread neotropical forest species that occur alone in a large part of their range (e.g., *Micrastur ruficollis*, *M. semitorquatus*, and *Accipiter bicolor* in Central America) and are outnumbered in the French Guianan forests by Amazonian counterparts (*Micrastur gilvicollis*, *M. mirandollei*, *Accipiter poliogaster*, and *A. superciliosus*) or are probably socially excluded from the forest (*Cathartes aura* by *C. melambrotus*). However, other such widespread species remain common everywhere (2 *Spizaetus*, *Buteogallus urubitinga*) even in the presence of an Amazonian competitor (*Harpagus bidentatus*, *Leucopternis albicollis*).

The overall bird species richness including owls, but not Falconiforms (see Methods, and data in

Thiollay 2002a) was correlated to the raptor species richness at a sample of 20 study areas (Spearman rank correlation coefficient $r_s = 0.838$, $P = 0.0003$). Raptors alone, may thus be considered as representative, or used as indicators of bird diversity.

Effects of Hunting and Forest Disturbance. Whether every species recorded or only the regular breeding species were included (Table 3), all primary forest areas together had a lower total species richness (34 species including every species recorded, 27 species including only the regular breeders) than all outer disturbed forests (42 and 34, respectively) and coastal landscapes (43 and 40, respectively) because the last two groups of areas included more habitat types than the continuous primary-forest sites, while they still retained some tall dense forest.

Among primary-forest areas, six were both hunted and partly logged, seven were only hunted, and seven were undisturbed (neither logging nor hunting). The mean raptor species richness was similar between all three groups of sites (21.2, 19.3, and 20.3, respectively, $P = 0.780$), but the mean abundance increased (from 30.8 to 35.2), though not significantly ($P = 0.334$). The abundance of vultures (mean/site = 2.4, 2.7, and 3.6 respectively) and all eagles (3.3, 4.0, and 4.6) increased more markedly, but still not signifcantly ($P = 0.157$ and 0.250, respectively), as did the Harpy Eagle (0.0, 0.3 and 0.6/site respectively).

Each species had its own pattern of habitat affinity along gradients of forest structure, maturity or level of disturbance (Jullien and Thiollay 1995) and subtle degrees of association with forest landscape components (gaps, edges, rocks, rivers, slopes, wetlands).

Distribution Patterns. The frequency of occurence of resident species among survey sites were quite similar among the three major landscape areas surveyed (Table 2): 10–15% of them were rare (found in only 5–11% of the localities); 22–38% were common, but patchily distributed (found in 16–47% of sites); 31–40% could be considered as very common species, but still present in no more than 50–90% of sites; and the last 15–30% were abundant and occurred almost everywhere (91–100% of sites). Within the matrix of 23 forest species (excluding those associated with large gaps) by 19 primary forest sites, there was 11% occurrences of species with 3–6 pairs, 64% of 1–2 pairs, and 25% with no birds. Overall species abundance was positively correlated with the number of sites occupied ($r_s = 0.925$, $P < 0.0001$).

Across all study sites, 18 species inhabited almost only open and edge habitats of the coastal zone, whereas the 27 forest species were widespread and only four of them were absent from the coastal sites. Among primary forest sites, all 27 forest species have been recorded from north to south, and the apparent increase of the mean number of species per site from the three northernmost areas (16.6 species) to the nine central areas (18.4), and seven southern areas (19.7) was not significant ($P = 0.222$). There was no apparent clustering of species among plots, nor any concentration of rare species that could suggest a distinct biodiversity ''hot spot.''

Population Estimates. Over the 80 000 km^2 of forest, the largest species, the Harpy Eagle, was recorded at 50% of 28 20-km^2 interior forest sites. Using for each pair recorded an average conservative home range of 100 km^2 (Thiollay 1989b), coupled with the fact that 50% of the survey sites were not occupied by Harpy Eagles, we calculated an estimate of 14 pairs/2800 km^2 or 400 estimated pairs for all French Guiana. With such a conservative density estimate, the Crested Eagle population, recorded at 64% of the same sample sites, had an estimated population of around 500 pairs.

The two rarest species, the Orange-breasted Falcon and the Black Caracara, closely associated with inselbergs and large rivers, respectively, have been recorded at 18 and 29%, respectively, of the 28 interior forest sites, but only 32% of these sites included an inselberg and 39% a large river. Yet the overall occurrence of these two habitats, selectively chosen as study sites because of their accessibility, is probably less than the proportion within the sample areas. Therefore, I suggest that these two species have a total population in French Guiana probably well below 100 pairs each.

At the other extreme, at least 2–6 pairs of the most abundant species, the Lined Forest-Falcon occurred in all sites (≥3.1/site). This translates into a mean of 2–6 pairs/20 km^2, i.e. 8000–24 000 pairs throughout the country.

DISCUSSION

Census Biases. The species most visible (*Cathartes*, *Elanoides*, *Ictinia*) were also wide ranging and gregarious so that it was difficult to distinguish breeding pairs. Species easy to census were territorial, vocal, or performed regular display flights (e.g., *Spizaetus*, *Harpagus*, *Daptrius/Ibycter*). Forest-falcons were less thoroughly censused far from, relative to near the campsites because effective surveys required me to

reach distant listening plots before dawn in trackless understories. Forest interior species that rarely called and irregularly or never soared (e.g., *Accipiter* spp.) were the most likely to be missed.

These surveys were not devised to measure accurate densities, but to provide an estimate of the minimum number of resident pairs recorded within, but not necessarily restricted to, a sample area. Two or more pairs were recorded only when their territorial behaviors were seen simultaneously, an infrequent occurrence. Therefore, the abundances of at least the smaller common species (*Micrastur*, *Harpagus*) at many sites were almost certainly underestimated. In contrast, *Spizaetus* or *Buteogallus* displaying over the survey area seemed to temporarily attract a more distant pair showing territorial defense behaviors at what was probably a common boundary.

Large species may have had only a part of their home range overlapping the study area, and thus, a corresponding low probability of being detected. Few nests were found or other evidence of breeding obtained, and it is possible that a few species at some sites had no breeding territory. Given these uncertainties, the number of pairs estimated per site must be considered an abundance index, not an accurate density estimate.

Species Richness and Abundance. Differences in species richness or turnover between sites may be explained by landscape structure (composition of local vegetation type mosaic), time surveying, and chance (e.g., when a rare and secretive species happened to be in the survey areas). There was no significant geographical trend in any species distribution, nor apparent hot spot of diversity and most, if not all, species seemed likely to occur everywhere in the country in their suitable habitats.

Using all resident birds other than raptors and ranking sites by species richness, rarity, or restricted range algorithms, the southern region was consistently richer (Thiollay 2002a, 2002b). The same trend was apparent for raptors, but not significant. This pattern may be related to greater habitat diversity (inselbergs, rivers, flood plains) and lack of hunting pressure in the remote southern part of the country.

Very few studies have measured the density of neotropical rainforest raptors. Thorstrom (2001) in a relatively species-poor community in Guatemala found on average one pair of *Micrastur ruficollis* per 100 ha and one pair of *M. semitorquatus* per 1000 ha. On intensive study plots of 97 to 104 ha, designed to investigate mainly smaller bird density, 1 to 2 pairs of the commonest small raptors were consistently found: *Harpagus bidentatus*, *Micrastur gilvicollis*, and *M. ruficollis* in Peru (Terborgh et al. 1990), *M. gilvicollis* in French Guiana (Thiollay 1994), *H. bidentatus*, *M. ruficollis*, *M. semitorquatus*, and *Accipiter superciliosus* in Panama (Robinson et al. 2000). This would suggest that some of these species may reach up to 10–20 pairs in a study site the size of those surveyed in French Guiana.

Rarity Patterns and Consequences. Most raptor species of French Guiana have wide distribution ranges in Amazonia, if not in the Neotropics. Their abundance should be determined by habitat appropriateness. Some of them, however, reach their northern limit in French Guiana (e.g., *Accipiter poliogaster*, *Leucopternis schistacea*), which may explain their rarity and local occurence.

In the primary forest, the most continuous and widespread habitat, only eight of the 27 forest species occurred in every locality and 15 were recorded at fewer than half the sample sites. The rarest taxa (or least detected) were among those with the lowest local densities and they included more small (*Accipiter*, *Falco*) than large (*Harpia*) species. However, even locally abundant and conspicuous species were not present in every forest locality (e.g., *Elanoides* and *Ictinia*), at least at the time of the survey. This suggests that there may be several forms of rarity (Rabinowitz et al. 1986) among rain-forest raptors and that complex habitat mosaics of the rain forest may obscure abundance-occupancy relationships and interspecifc interactions.

Patchy distribution of tropical forest birds has long been emphasized (Willson and Moriarty 1976, Diamond 1980). Here also, unexpected local absences resulted in no clear nested-subset pattern between richer and poorer plots. The occurrence of some rare species was obviously dependent on the presence of their specific habitat (e.g., river for the Bat Falcon and inselberg for the Orange-breasted Falcon within the continuous primary forest), but for many taxa, there was no apparent cause for local absence. At the most intensively studied site (NO), many unoccupied gaps were found between the territorial boundaries of several species, without detectable habitat differences between occupied territories and outside areas (Thiollay 1989b). Large home ranges, that may only partly overlap with a study area, may also account for some absences, as well as variable detectability due to time of year, breeding stage, suitability of lookouts, and use of specific methods.

Natural and Human Disturbances. Roads, logged areas, and clearings for shifting cultivation or gold mining are larger and leave more permanent scars in the forest cover than natural tree-fall gaps and may not match the species diversity of successional habitats associated with rivers, swamps, or inselbergs. In French Guiana, selective logging (Thiollay 1992, 1997, Mason and Thiollay 2001) and road building (Thiollay 1999) were found to impoverish and change the composition of forest bird communities, and raptor populations.

Earlier surveys (Thiollay 1985b) suggested that the occurence of at least some eagles and vultures might be limited by human hunting pressure. Raptors are shot only occasionally, except for the forest caracaras whose loud and persistent alarm calls disturb the hunters. Currently, there is still no regulation of hunting in French Guiana, and hunting has a negative impact on large game birds (*Crax*, *Psophia*) as elsewhere in Amazonia (Peres 2000, Thiollay 2005).

Eagles and vultures were found to be the raptors most sensitive to hunting pressure, even though their decrease over all hunted areas was not significant. The Red-throated Cacacaras disappeared almost completely from heavily-hunted areas, and elsewhere their mean group size decreased significantly with hunting pressure (from 6.3 to 4.1, $P < 0.001$).

Large natural gaps and lasting human-made clearings thoughout the forest are critical for the maintenance of patchy populations of raptors associated with open woodlands and forest edges (*Geranospiza*, *Asturina*, *Buteo*, *Falco*). Some isolated pairs of such species were found further than 100 km from their nearest known neighbor.

Population Viability and Conservation. When the largest eagles have populations of perhaps several hundred pairs, and smaller species have estimated populations of at least several thousand pairs, one may assume that they are viable, as long as their forest habitat is not degraded or fragmented. No Guianan raptor species is Globally Threatened (BirdLife International 2000) and only the Harpy Eagle and Crested Eagle are considered Near-Threatened.

A few naturally rare forest species, with highly patchy distributions (e.g., *Accipiter poliogaster*, *Daptrius ater*, *Falco deiroleucus*) may have very small populations in Guiana (<50 pairs?), but human pressure is probably not the cause of these limited populations. The Guianan forest is still continuous and is adjacent to larger expanses of undisturbed forest in neighboring Brazil and Surinam.

Some species associated with coastal grasslands or mangroves may also have small populations in French Guiana because of the limited area of their suitable habitats or because they are near the northern extent of their range in French Guiana (e.g., *Leucopternis schistacea*). These species have larger populations elsewhere in northern South America.

No evidence currently suggests that any raptor species is markedly declining in French Guiana, although selected areas may have lost their most sensitive species, as a result of disturbances related to hunting and logging. However, the pristine conditions that prevailed during my study period have been recently degraded because of a gold rush. The invasion into several areas by thousands of goldminers has resulted in local forest clearing, river pollution, and hunting. In the long term, if the development of new roads, increased cultivation, and logging continues, the maintenance of complete natural communities of raptors may depend on the newly created two million-ha national park in the southern part of the country, contiguous with the larger Tumucumaque National Park in Brazil, together with the two 100 000-ha nature reserves in the northern forest zone (Trinité and Nouragues) and two others in the coastal marshes (Amana and Kaw). An improved enforcement of the protected status of raptors would also help conserve the raptor community, as would more sustainable forest management and conversion to low-impact logging operations. The maintenance of sizeable populations of game species may be critical for the long-term conservation of large eagles, and therefore, preservation of natural animal communities and rainforest ecosystems.

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Appendix. Site survey period and effort. Only the sampling time for raptors is reported. Additional, later visits, if any, are not included (no additional species recorded). Time mostly devoted to other activities (e.g., banding or nonraptor studies), as well as rainy periods (even if raptor searching was not fully discontinued) are not included.

			HOURS	
LOCALITY CODE[a]	YEARS[b]	MONTHS[c]	FOREST[d]	OPEN[e]
MA	1981–2003	March, July, December	2	89
SI	1981–89	July to November	12	74
KR	1981–88	July to December	16	82
OU	1989	August	8	56
JE	1985–2003	March, July, September	77	19
EL	1981–89	July to November	208	24
TN	1988–2001	August, October, November	118	32
MS	1986–2001	September, October, November	101	31
GM	1981–98	July to December	106	47
KW	1985–97	July to December	169	34
SW	1983–84	November, December	178	47
CA	1984–94	October, November	50	27
MP	1985–94	July, August, September	57	35
PS[f]	1994–95	September, October	72	14
RG	1998	June	91	23
TR	1997	March	93	26
AR	1986, 1997	March, September	115	45
NO	1986–87	September to December	732	167
PA	1987–92	August to December	81	10
CR	1984	October, November	134	70
MO	2000	December	198	18
SE	1983–84	November, December	198	43
DA	1997	April	122	17
EM	1983	December	119	35
BV	1985	August	70	11
IN	1985	August	167	16
TA	1998	November	79	17
TO	1995	May	131	23
BE	1984	November, December	202	79
LI	1985–94	July, September	163	15
MN	1998	December	147	24
KO	1985–94	July, September	180	26

[a] See Table 1.

[b] For sites with repeated visits, only the first and most-intensive surveys, focused on raptor searching, were included (one visit/site/yr).

[c] Periods when surveys were conducted. On average, August to November, and March, are the dry season, while December–February and April–July are the rainiest months.

[d] Slow walking and associated stops in any type of forest understory.

[e] Still scanning or slow moving (by foot or boat) in large forest gaps (river, inselberg, road, clearing).

[f] Additional data for 1993–96 from O. Claessens (pers. comm.).