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# Structure, density and rarity in an Amazonian rainforest bird community

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**ABSTRACT.** A 100-ha quadrat of primary rainforest in French Guiana was censused over two consecutive years by the mapping method, and a 24-ha core area was intensively mistnetted at the same time. More extensive surveys were conducted in successively larger areas including up to a large part of the forested interior of the country. From a total of 441 resident species found in the rainforest zone, 248 were regularly recorded within the 100-ha plot, 157 of which had mean densities of more than 1 pair  $\text{km}^{-2}$ . The total estimated density of birds was at least 829 pairs  $\text{km}^{-2}$ . Only two dominant species exceeded 20 pairs  $\text{km}^{-2}$ , while 52% of all the species were represented by less than 2 pairs  $\text{km}^{-2}$ . The distribution of body masses and niche characteristics among the bird community is given as well as the sample bias of the mistnet captures.

Rare species were a key component of this primary rainforest community. Several patterns of rarity were described and no marked and constant relationships were found between rarity and body size, habitat, diet, foraging behaviour or social system. Among a wide set of environmental constraints, the population of each species may be limited by a different combination of factors. Habitat heterogeneity, low, irregular and seasonal food availability, interspecific competition or heavy predation pressure were prominent and likely causes of the low density of most species which in turn facilitated the high species richness.

**KEY WORDS:** Amazonia, birds, community structure, density, French Guiana, rainforest, rarity, species richness.

## INTRODUCTION

The high diversity of tropical forest communities has long been recognized as well as their peculiar structure involving many rare species (Richards 1952). The explanation of such patterns has given rise to a wide range of theories (see Ashton 1989) and is still debated (Thiollay 1991a). In spite of general interest in the fate of rainforests and in contrast with the wealth of information on temperate forests, there are still very few accurate data on the density and structure of the whole bird communities in primary tropical rainforests. Most studies give the species composition and, at best, the relative abundance of birds from restricted areas of forest, that are sometimes disturbed, in Australasia (Driscoll & Kikkawa 1989, Fogden 1972), Africa (Colston & Curry-Lindahl 1986, Elgood 1977, Mann 1985), South America (Greenberg 1981, Lovejoy 1974, Thiollay 1986, 1990, Willis 1979) or over several continents (Erard 1989,

Pearson 1977). Few studies also provide information on actual densities and they usually involve incomplete bird communities or unsuitably small plots (Bell 1982, Fogden 1976, McClure 1969 in Asia; Brosset 1990 in Gabon; Karr 1971, 1977, Kikkawa *et al.* 1980, Robinson *et al.* 1990, Silva & Constantino 1988, Thiollay 1989a in tropical America). Only Terborgh *et al.* (1990) presented a detailed analysis of a complete bird community, on a sample plot of adequate size, in a really virgin rainforest of western Amazonia, including density estimates for most species. Comparative data are presented here for a similar site on the opposite side of Amazonia.

Most former studies used mistnet sampling to census tropical forest birds because this technique was considered to give more unbiased results than visual and auditory censuses. An intensive mistnetting programme was carried out on the study plot to compare the relative efficiency of the two methods and to assess their limits. Another objective of the study was to examine the patterns of rarity among this rainforest bird community using data on the ecology of most species accumulated over 12 years in Guiana. This empirical approach may provide a preliminary insight into how such a species-rich community is structured.

#### STUDY AREA AND METHODS

##### *Study site*

The Nouragues field station (4° 05' N, 52° 41' W) 100 km south of Cayenne is located inside the vast unbroken primary lowland rainforest that still covers the interior of French Guiana in north-eastern Amazonia. This area is hilly (altitude: 40–400 m), and dissected by numerous small streams (Figure 1). The mean annual rainfall is 3500 mm, mostly from December to July, with a long rainy season barely interrupted by a lower rainfall period around March. The dry season is well marked between August and November. The mean annual temperature is around 26°C and the monthly humidity between 80 and 90%. There are 2000–2500 sunny hours per year.

Several hundred species of tree over 10 cm dbh are known or likely to occur within the 100-ha quadrat studied intensively (J. J. de Granville and D. Sabatier, pers. comm.), most of them belonging to the Sapotaceae, Lecythidaceae, Caesalpiniaceae and Chrysobalanaceae in the canopy and to the Annonaceae, Euphorbiaceae and Myristicaceae in the undergrowth. Palms are usually abundant in the understorey (*Astrocaryum*, *Attalea*, *Bactris*, *Geonoma*) and scattered at canopy level (*Jessenia*, *Oenocarpus*). The primary forest cover was divided into four main habitat types:

FOR 1 = High mature stands with open understorey and closed canopy about 40 m high with occasional emergent trees  $\geq 50$  m. This dominant forest type usually occurs on well-drained slopes or plateaux.

FOR 2 = More irregular, less stable and lower forest type than above with a denser understorey and a 5–35 m high, more vine-loaded, canopy.

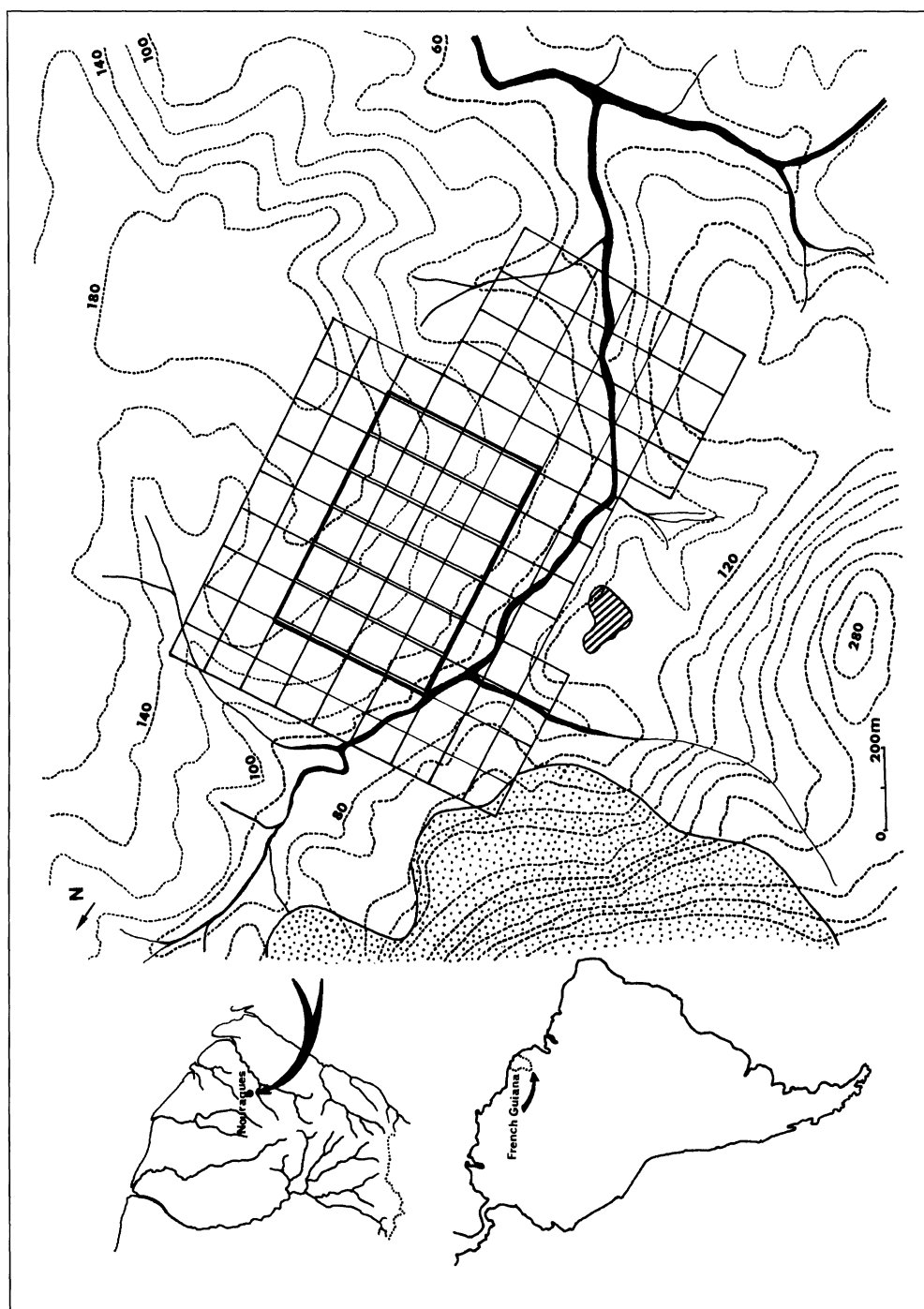


Figure 1. Map of the study area. The 100-ha and the central 24-ha plots are outlined by heavy lines. The contour lines (with altitudes in metres asl) are marked by dashed lines and the trails by thin lines, doubled for those where mistnets were set. The small striped area is the artificial clearing of the camp site. The large dotted area is a little wooded rocky inselberg.

FOR 3 = Low, heavily disturbed areas where the dense undergrowth is overshadowed by a 5–20 m subcanopy of thick vine tangles, dominated by isolated emergent trees. Another low, dry and dense forest type on rocky outcrop, rich in Myrtaceae and Clusiaceae, was found on the slope of a granitic inselberg at the edge of the study area and was combined with FOR 3.

FOR 4 = Wet or swampy forest types (often pure stands of 15–25 m *Euterpe oleracea* palms) or seasonally flooded areas along small streams. The medium height canopy is little broken.

Treefall gaps are an important component of the spatial heterogeneity and they occur in every forest type. They were ranked in two classes according to the area opened at subcanopy level (10–20 m): small gaps (50–250 m<sup>2</sup>) resulting from the fall of a single tree or part of it, and large gaps (300–800 m<sup>2</sup>) usually from the fall of two or more trees. On the 100-ha plot in 1990, the total percentage coverage was: FOR 1 = 55.1; FOR 2 = 25.4; FOR 3 = 8.9; FOR 4 = 4.1; 146 small gaps = 1.72; 59 large gaps = 2.98. In 1991, on the 24-ha core study area (Figure 2), the 78 most recent gaps covered 3.7% of the plot.

### *Census technique*

Tropical forest birds are notoriously difficult to census and several different methods must be used in conjunction to obtain density estimates of all the species at a time (Karr 1981, Terborgh *et al.* 1990) or even within a single guild (Thiollay 1989b). Gaining sufficient experience of the behaviour, vocalizations and identification of most species requires several years. This experience has been gained throughout French Guiana since 1980, with the invaluable help of J. L. Dujardin and O. Tostain. From 1986 onwards, when the Nouragues field station was established, the 100-ha quadrat on which this paper is based was the area most intensively surveyed by every researcher, although without standardized method until 1990. During this first 4-year period, at least one ornithologist was working during a total of more than 21 months. All the species were identified visually, many of them were tape-recorded, mistnetted and their nidification documented (see Appendix 1). Then an 8-month census took place, during the major breeding periods, from February 1990 to November 1992, with the participation of J. L. Dujardin and M. Jullien. Density estimates come only from this period. Data from all 3 years were pooled because no significant year to year differences were detected in the distribution or abundance of most species. Data from previous years were used only for occurrence of species outside the 100-ha plot, as well as for mass, habitat, foraging and breeding parameters.

The classical spot-mapping method was used on the 100-ha sample quadrat, designed to include the most widespread undisturbed forest types in Guiana without edge effects (Figure 1). The plot had the minimum size required to include a significant proportion of the species in a rich bird community of tropical forest (Terborgh *et al.* 1990). It covered a gentle slope from a plateau up to 180 m down to a small stream 60 m in elevation.

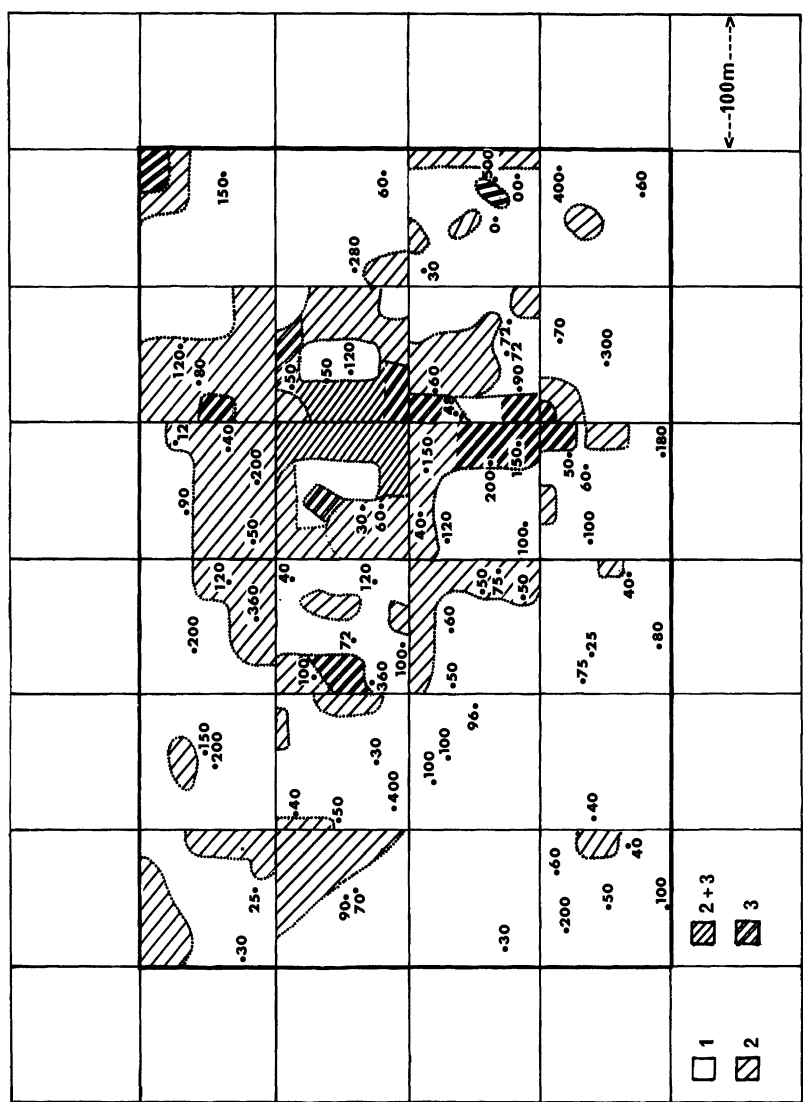


Figure 2. Distribution of the main forest types (FOR 1 to 3, see text for description) on the 24-ha intensive study plot, and location of every treefall gap in September 1991 (dots, with their area in m<sup>2</sup>).

Birds were searched for systematically from dawn to dusk along a regular network of straight perpendicular foot trails, evenly spaced 100 m apart, that divided the entire study area into 1-ha quadrats (Figure 1). Each quadrat was also crossed several times to help detect the most secretive species. All individuals, when first seen or heard, were located on a grid map, using numbered colour marks along trails and subdividing each 1-ha plot into nine 33 m  $\times$  33 m subsquares. Each record was used as one location irrespective of the number of individuals and their subsequent movements. The sex, age, behaviour and grouping of birds were recorded, especially pairs, families, number of individuals in monospecific groups, mixed flocks or leks and the position of two males singing simultaneously. Birds just crossing the area were not considered. Random searching was occasionally supplemented by playbacks of vocalizations, nest location, observation from gaps or tree tops, listening sessions in the first half of the night and tracking of radio-tagged birds. Visual checking of colour-banded individuals and following the daily movements of mixed flocks provided critical information to assess home range sizes.

Visual and auditory detections may underestimate the abundance of dense forest birds and must be supplemented by a less biased technique (Rappole *et al.* 1993). From November 1986 to October 1988, unstandardized mistnetting operations took place in several areas of the whole 100-ha plot over a total of 104 days where 659 individual birds were caught. Intensive mistnetting sessions were undertaken in September 1991 and March and October 1992 within the 24-ha core quadrat (Figure 1). Twenty 12-m long mistnets were set for two consecutive days successively along all the seven 400-m parallel trails. During the three operations (5880 net-hours), 694 individuals were marked. Bird nomenclature follows Meyer de Schauensee & Phelps (1978).

### *Density estimates*

All 6658 records (Appendix 1) were mapped with a special emphasis on singing males, pairs and families. Successive locations of a given species obtained on the same day were considered as coming from different individuals when they were  $\geq 200$  m apart and when the behaviour and flight range of birds made it very likely or when separate birds were heard simultaneously. The mapping method is based on the interpretation of clusters of locations supposed to represent distinct territories or home ranges. This interpretation is partly subjective and has some serious limitations (Oelke 1981), especially in tropical forests (Karr 1981) where the birds have very different social structures, breeding periods, singing behaviours and degrees of detectability.

The discrimination between separate pairs was always conservative and took into account the existence of a floating population or excess individuals suggested by field observations and banding results. Singers were carefully identified to dismiss the cases of females singing together with, or separately from, the male, or duetting within social groups. Individual singers were followed in



order to map movements and temporary gatherings (e.g. trogons) to avoid an overestimate of their numbers. During the last month of the field survey, no new species, or surely ascertained new pair of any species, were recorded. This suggested that at least the majority, if not all, of the resident, permanently settled, adult birds had been detected.

For the sake of a global analysis, the density of every species was expressed in number of pairs. Adult males were considered as representatives of breeding units, including birds with uncertain mating systems (e.g. Tinamous) and lekking species (*Phaethornis*, Cotingidae, Pipridae). The following equivalences were used when it was not possible to single out a conventional pair:

- group living species (e.g. *Daptrius*, *Psophia*, *Querula*): 1 pair = a group of up to 6 individuals (2 pairs if >6 birds).
- colonial icterids: 1 pair = each simultaneously occupied nest.
- canopy mixed species flocks (e.g. Thraupidae), wide-ranging ant followers (*Pithys*, *Gymnopithys*) and monospecific flocks of Psittacidae (unless identifiable pairs or occupied nestholes were found): 1 pair = 3 adult-plumaged birds. This conservative treatment tried to reduce the potentially overestimated abundance of this last group because of the frequent and wide-ranging movements of the species involved.

When the distribution of a pair overlapped the quadrat's limits, the proportion of the home range included inside the 100-ha plot was estimated from the relative number of records within the quadrat and rounded to the nearest 0.25 ha. Home range areas were drawn conservatively according to Samuel & Garton (1985) when the sample size was small. The density estimate within the 100-ha plot formed the basis for the ranking of species occurrence in successively larger nested areas ( $\log_{10}$  scores in Appendices), from data accumulated previously (Thiollay 1986, 1988a, 1989a, Tostain *et al.* 1992).

### *Niche characteristics*

*Body mass* is the most widely used measure of size in birds. A rounded mean weight was computed from birds caught in French Guiana, sometimes supplemented by data from Surinam (Haverschmidt 1968) or Amazonia (Bierregaard 1988, Dunning 1993). Because many sample sizes were too small, only broad classes of body mass are given and the densities are not converted into biomass.

*Social behaviour* here includes the mating system and the foraging association: 1 = lekking, polygynous or polyandrous species where males and females mostly breed and forage separately; 2 = monogamous and territorial species most often foraging in pairs; 3 = monogamous species, breeding in isolated pairs, but regularly foraging in monospecific or mixed species flocks; 4 = species living in small monospecific flocks, presumably extended family units.

*Habitat*. Only the most widespread habitat types were considered. The high mature primary forest was divided into three layers: L = low understorey and ground (0–3 m); M = mid-understorey to lower canopy (3–25 m); C = upper



canopy and tall emergent trees. Upper canopy species also often occur lower in gaps or along edges.

In habitats other than primary forest, the levels were not distinguished:

D = moderately to highly disturbed forest with a lower and denser canopy than in the mature forest, often heavily loaded with vine tangles dominated by isolated emergent trees; G = treefall gaps; I = bare rocky slopes, stands of Bromeliaceae (*Pitcairnia*), dense woodlots of *Clusia* or Myrtaceae on the granitic inselberg; O = large openings in heavily disturbed areas (floods, landslides, rocky outcrops), covered with low dense second growth or bamboo-like stands; S = *Euterpe oleracea* palm swamps, as well as small streams and their banks under closed canopy; R = species associated with rivers, their forested banks or seasonally flooded flats.

*Foraging* methods, substrates and heights were grouped: Aer = hunting insects above the canopy; Per = hunting aerial or terrestrial prey from trees only used as perches; Arb = arboreal foraging in foliage and branches; Bar = searching the bark, dead wood and epiphytes of trunks and branches; Low = inhabiting the low dense vegetation of gaps, edges and secondary growth; Gro = foraging on or near the ground; Wat = restricted to palm swamps, streams or their immediate vicinity.

*Diet*: C = carnivores (vertebrates, carrion and some arthropods); F = frugivores, including pulp, fruit seeds, buds or young leaves; G = granivores, including fallen fruits; I = insectivores; N = nectarivores (some species partly insectivorous); O = omnivores (regularly both fruits and insects); P = piscivores (all aquatic prey).

## RESULTS

### *Species richness*

A total of 248 species have been found resident on the 100-ha study plot, i.e. have at least part of one home range regularly overlapping this area. Breeding has been actually proved for 115 of them at least once within the 100-ha limits between 1986 and 1992. Twenty additional species were occasionally recorded but may be only visitors from surrounding areas. No wintering migrant was recorded inside the primary forest, or at least no species known to be a true migrant in Guiana and regularly absent during a given season. Evidence of some local movements is not taken into account since the abundance of each species is considered during the less rainy months where the survey took place (August–December and February–March). Among the 248 regular species, 220 had a density of  $\geq 0.50$  pair  $(100 \text{ ha})^{-1}$  and 157 of 1 pair  $(100 \text{ ha})^{-1}$ . The study plot covered by the most widespread primary forest types in Guiana included only 56% of the 441 resident species found in the forested interior of the country (Figure 3) and

77% (234/305) of the most strictly forest species (habitats I, O, S and R excluded).

The territory limits of many species were not sufficiently known to map the exact distribution of alpha diversity. Instead, I summed the number of regular species recorded on each 1-ha square of the 24-ha core area (Figure 4). This point diversity did not exceed 33% of that found on the 100 times larger study

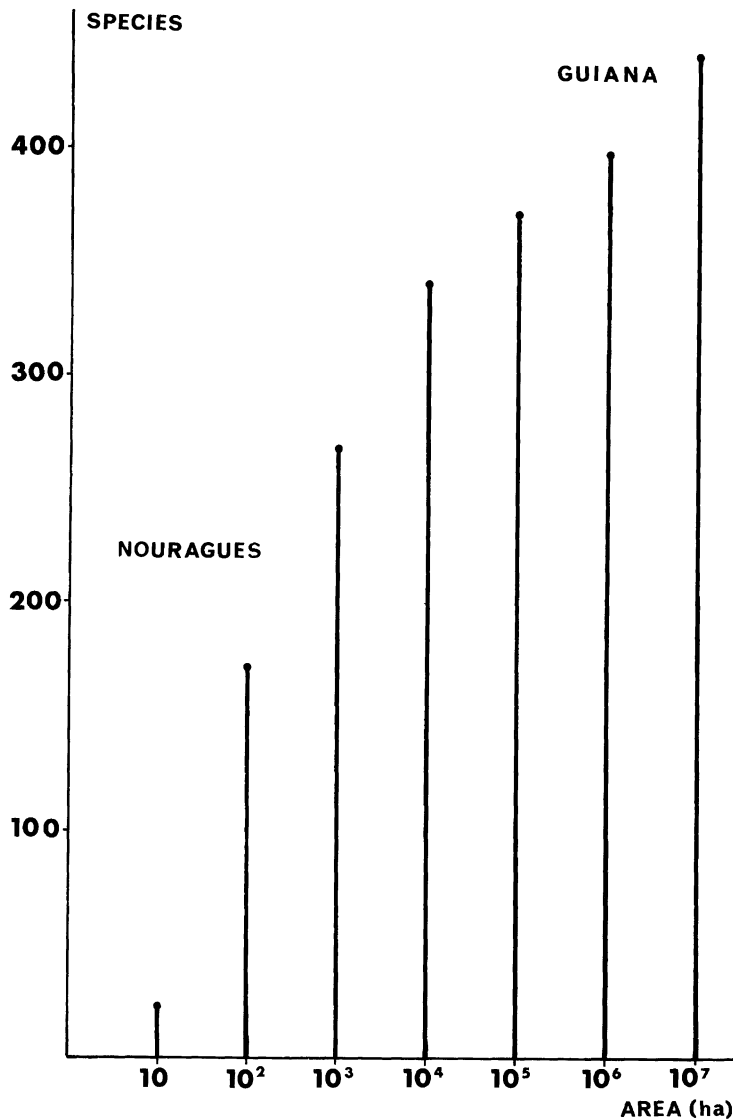


Figure 3. Number of species recorded in each successively larger area of primary rainforest in the interior of French Guiana. At least, one resident pair and its home range must have been recorded in the area for a species to be included in a class.

51	54	72	63	81	70
48	61	68	78	82	62
55	53	74	80	71	66
60	59	63	74	60	72

Figure 4. Number of resident species (pairs, groups or singing males) recorded in each 1-ha square of the 24-ha core study area (compare to Figure 2).

plot, but it was likely to be underestimated because secretive species were rarely contacted in every part of their range. Comparison with Figure 2 shows that substantially more species were associated with the disturbed, structurally more varied, patches.

*Density patterns and population structure*

The overall estimated density was 829 pairs (100 ha)<sup>-1</sup>. If the abundance of the species most common in the 24-ha core area was multiplied by four the total, and probably overestimated, density would be 1280 pairs (100 ha)<sup>-1</sup>. The Shannon's diversity index is relatively high ( $H' = 4.957$ ), as expected in such a rich community, but the equitability of species abundances is also high ( $J' = H'/\ln S = 0.899$ ).

On a log<sub>2</sub> scale, the distribution of abundances among the species displays a remarkable evenness (Figure 5). Over 83% of the species are distributed in four distinct classes:

- 1) Two numerically dominant species are far more abundant than any other, i.e. the Wedge-billed Woodcreeper, *Glyphorhynchus spirurus* and the Grey Antbird, *Cercomacra cinerascens*, 28 to 38 pairs (100 ha)<sup>-1</sup>.
- 2) Ten subdominant species (14–18 pairs (100 ha)<sup>-1</sup>). They include a variety of small omnivores (*Tyranneutes*, *Turdus*, *Coereba*) or understorey insectivores (5 Thamnophilidae and 2 Tyrannidae).
- 3) Fifty-eight widespread species with a moderate density (4–8 pairs (100 ha)<sup>-1</sup>). A large number of them are permanently associated with mixed species flocks, in which membership is usually restricted to a single pair per species. These flocks have relatively large home ranges and this may explain why their obligate members maintain rather low and similar abundances.
- 4) One hundred and thirty-seven species (or 52% of the community) that can be called rare (<2 pairs (100 ha)<sup>-1</sup>). Every guild, family and ecological adaptation is represented in this category which is important in primary tropical forests.

This species abundance distribution fits more a 'broken-stick' type than a classical log-normal distribution. In number of individuals, the two dominant

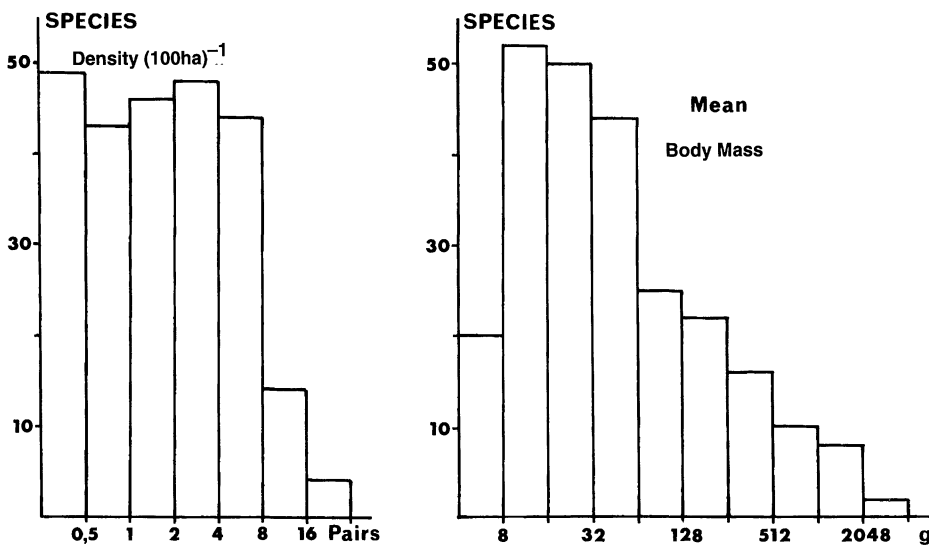


Figure 5. Density and body mass distributions among the 248 species of the 100-ha study plot (log<sub>2</sub> scale).

species make up 8% of the population, against 23% for the 10 subdominant species and 3.4% for the 64 rarest species ( $<1$  pair  $(100 \text{ ha})^{-1}$ ). Over the 80,000 km<sup>2</sup> of primary forest in the interior of Guiana, 58% of the 441 forest species have an average density of under 1 pair  $(100 \text{ ha})^{-1}$ . Indeed, some of them may be locally more abundant but they have a patchy distribution.

The distribution of body masses (Figure 5) is similar among the species pool of the study plot and all over Guiana: 7% of them are very small ( $<8$  g), 59% are small to medium-sized (8–64 g), 25% are larger (65–510 g) and 9% are in the highest class (0.5–5 kg). This distribution is somewhat different within particular guilds. Nectarivores are all small species and carnivores are mostly of the largest size classes. The granivores + frugivores + omnivores are all over 8 g, 51% of them are under 64 g and 11% over 500 g. Insectivores have no species over 500 g, 78% in the 8–64 g class and 6% under 8 g.

The relationship between size and abundance in many animals, including birds, has been typically found to take the form  $A = W^{-0.75}$ , where  $A$  is the species abundance and  $W$  the body weight (Damuth 1991 and references therein). However, this negative relationship is often very weak when whole communities are sampled, probably because many rare species are limited by factors other than food availability (Lawton 1989). When the two highest densities are selected in each size class (as suggested by Blackburn *et al.* 1992) and a least square regression line is plotted through them, this upper bound slope is still not approaching  $-0.75$  ( $A = 21.23 - 2.16 W$ ,  $R^2 = 0.42$ ).

Some general features emerge from the broad ecological categorization of the species found in the main study plot (Appendix 1). As expected, most species (79%) are associated with the mature forest, but their number increases from

the lowest level ( $L = 12.9\%$ ), to mid-understorey ( $M = 23.8\%$ ) and canopy ( $42.3\%$ ). This may be partly related to the increased volume and structural complexity of the vegetation. A much smaller proportion of species is strictly associated with marginal but yet significant habitat:  $9.2\%$  in highly disturbed forest,  $6.0\%$  in gaps and  $3.2\%$  in swamps and along stream banks. This distribution is strikingly similar to the area covered by each habitat type on the plot (respectively  $8.9$ ,  $6.5$  and  $4.1\%$  of the total area).

The foraging substrates exploited by the highest proportion of species are the tree crowns and foliage ( $59.7\%$ ), the bark, dead wood or epiphytes ( $12.5\%$ ) and the litter ( $14.1\%$ ). Most species are monogamous with exclusive territory ( $61.7\%$ ),  $25\%$  are regular members of mixed foraging flocks and the remaining  $13.3\%$  have various other social systems. The insectivores alone ( $52.8\%$ ) are almost twice as abundant as all vegetarians. The largest family (Thamnophilidae) includes here 30 species, but the flycatchers (26 Tyrannidae) and even the raptors (27 species from 4 families) are surprisingly diversified for such a small area. Over all the Guianan forest bird community, these three groups include, respectively, 42, 55 and 40 species, i.e. almost one-third of all the species.

#### *Comparative efficiency of mistnets*

On the 24-ha plot intensively netted, 214 resident species were found. Even when the captures of three netting sessions over 2 years are summed, nearly two-thirds of the species were never caught, 30 species ( $14\%$ ) were taken in markedly lower numbers than their estimated density and 51 species (245) were captured in equal or higher numbers than their known adult population on the plot. Among the 248 species occurring on the 100-ha quadrat, only 99 ( $40\%$ ) were mistnetted at least once during the 5-year period (1353 individuals banded).

Obviously, mistnetting alone gives a strongly biased composition of the whole bird community in this primary forest when contrasted with direct counts. Respectively, 78, 66 and  $12\%$  of the species of the low undergrowth, mid-understorey and canopy were caught in mistnets, but for only 53, 44 and  $2\%$  of them was the number of individuals caught at least equal to half the known resident population.

#### *Patterns of rarity*

Terborgh *et al.* (1990) called a species 'rare' if it had a mean population density  $\leq 1$  pair  $(100 \text{ ha})^{-1}$ . According to this arbitrary limit,  $37\%$  of the 248 species in the main study plot and all the species of Appendix 2 are rare. Two basically different situations are involved. Many large species are intrinsically rare because they have large home ranges. They may be overlooked when the size of the sample plot is inadequate and when they are shy or secretive, such as many raptors. The second category includes species that do not fully occupy the apparently suitable habitat. Pairs are unaccountably isolated and far from

each other. This patchy distribution is found in different situations (see Appendices 1 and 2 for specific names; data in Thiollay 1986, 1988a, 1989a and Tostain *et al.* 1992).

1) Species widespread in primary forest: (*Chondrohierax*, *Accipiter bicolor*, *Discosura*, *Bucco*, *Nasica*, *Automolus ochrolaemus*, *Philydor pyrrhodes*, *Pygiptila*, *Conopophaga*, *Leptopogon*, *Tyrannus algobularis*, *Xenopipo*, *Neopipo*, *Neopelma*, *Cyanocorax*, *Parula*, *Eucometis*, *Cyanicterus*) or locally frequent, but rare or absent in other localities: *Geotrygon*, *Lepidocolaptes*, *Frederickena*, *Iodopleura*, *Piprites*, *Laniocera*, *Lamprospiza*) or coexisting with a much more abundant congeneric species (*Harpagus diodon*, *Micarastur ruficollis*, *Piculus chrysochloros*, *Picumnus spilogaster*, *Philydor ruficaudatus*, the 3 *Xenops* of Appendix 2, *Cercomacra tyrannina*, *Mionectes oleagineus*).

2) Habitat specialists in localized habitats: 3 *Pachyramphus*, 2 *Lophotriccus*, *Onychorhynchus*, *Contopus*, *Cyclarhis* and *Granatellus* of Appendix 2.

3) Apparent rarity: the density of some rainforest species is probably underestimated because of their low detectability, unknown vocalizations or an inadequate timing of the census. Some species exhibit seasonal or irregular movements (*Ara*, *Amazona*, *Crax*, *Ramphastos*) or temporary habitat shifts (*Mionectes*, *Topaza*, *Phaethornis malaris*).

4) Checkerboard distribution: several species have large distributional gaps in Guiana leading to unaccountably local absences (*Aburria*, *Touit*, *Amazona*, *Haematoderus*, *Procnias*, *Henicorhina*, *Cyanocorax*, *Periporphyrus*) without any apparent lack of suitable habitat or food resource. They are globally rare but they may be locally quite common (*Myrmoborus*) or strikingly absent from just one well-studied locality (*Hylophylax naevia*).

4) Social systems: species associated with mixed flocks of foliage insectivores, obligate followers of army ants and group-living species (Psittacids, *Daptrius*, *Querula*) may appear patchily distributed although their home ranges are more or less contiguous.

#### *Some correlates of rarity*

*Body size.* There is an inverse relationship between body size and density ( $r = -0.28$ ,  $P < 0.001$ , Appendix 1) because the quantitative food requirements of larger species can only be met on average in home ranges larger than those of smaller species. This relationship holds for insectivores ( $r = -0.27$ ,  $P < 0.001$ ,  $N = 131$ ) as well as for frugivores and granivores ( $r = -0.31$ ,  $P < 0.05$ ,  $N = 46$ ) but frugivores span a broader spectrum of sizes (10–3000 g) than insectivores (7–120 g) and carnivores (200–>2000 g). Only 20% of the smaller species (mass index 1–2) are rare against 32% for species of mass index 3–4, 50% in the mass index 5–7 and 70% for species over 1 kg.

*Distribution.* Patchy distribution patterns are found among every guild or family. For instance, within the Formicariidae (ground insectivores in mature forest), *Formicarius colma* is much rarer than the widespread *F. analis* with which it coexists; *Hylopezus macularius* leaves unoccupied areas between groups of 2–4

contiguous territories; *Grallaria varia* has large and isolated home ranges; *Myrmothera campanisona* is associated with dense regrowth in old gaps. Many raptor species also leave 10–50% of the forest area seemingly not included in a territory (Thiollay 1989a).

A positive relationship has been found in both North (Bock & Ricklefs 1983, Brown 1983) and South America (Kattan 1992) between the size of the geographical distribution and the level of abundance (width of habitat specificity and population density). Conversely, one may hypothesize that birds originating from, and still restricted to, the Guianan Shield, one of the recognized Pleistocene refuges (Cracraft 1985, Haffer 1974), may be better adapted to local conditions and thus competitively superior to alien species and more abundant. A previous analysis of foliage insectivores has shown that both Guianan endemics and widespread species include common and rare species and either group on average is not significantly more abundant than the other. Because of the geographic position of Guiana, it is also possible that species with a wide Neotropical distribution are on the margin of their distribution, a fact that could negatively affect their local density.

There are some striking examples where species with wide geographical distribution and broad habitat niche elsewhere (*Micrastur ruficollis*, *Sittasomus griseicapillus*, *Platyrinchus mystaceus*) are much rarer here and more habitat-restricted than their local Amazonian counterpart (*M. gilvicollis*, *Glyphorhynchus*, *P. coronatus*).

*Social behaviour.* No mating system or flocking behaviour results in significantly different proportions of rare species (23–45%) than the proportion in the overall community (37%) used as the null hypothesis in two-tailed binomial tests with  $\alpha = 0.05$ . Only the first category (Soc. 1 in Appendix 1) has a lower proportion of rare species (2/24) but it contains rare species at the regional level (Appendix 2). Regular members of mixed flocks (Thamnophilidae, Dendrocolaptidae, Thraupinae) as well as lekking species (*Phaethornis*, *Pipra*, *Lipaugus*) are among the most common species, although the localization of leks or the foraging range of flocks should limit their populations.

Interspecific relationships may also involve competitive exclusion of similar species. There are striking examples where two or more congeneric species occupy the same habitat but where one species seems to displace the other since they are rarely, if ever, found side by side (*Veniliornis*, *Dendrocolaptes*, *Xiphorhynchus*, *Polioptila*). However, there are even more similar species pairs which closely coexist without obvious indication of significant competition (*Columba*, *Pionus*, *Amazona*, *Trogon*, *Sclerurus*, *Dendrocincla*, *Thamnomanes*, *Myrmotherula*, *Hylophylax*, *Pipra*, *Cyanerpes*, *Tangara*).

*Diet.* The proportions of rare species are not significantly different between the main guilds and between each of them and the whole community (binomial tests): 34% in the frugivores + granivores, 30% in the insectivores and 28% in the nectarivores + omnivores. Only the carnivores and piscivores are almost all rare (24/25) because they are large and top predators.



Diet specificity is sometimes considered a likely predictor of abundance. The diet of local species has not been studied in detail but even strictly insectivorous or frugivorous species seem to consume a variety of insects or fruits, presumably because of the high biodiversity of the rainforest and the low availability of most species. Highly specialized birds may be abundant. A specialist of wasp nests (*Daptrius*, Thiollay 1991b), of arthropods around army ants (*Pithys*), in dead branchlets (*Xenops*) or fallen dead logs (*Microcerculus*) are common. The guan *Penelope marail*, has a higher density than other more food generalist game birds such as *Tinamus*, *Crax* and *Psophia* (Erard *et al.* 1991, Théry *et al.* 1992).

*Habitat.* Many species have macro- or microhabitat specializations and patchily distributed breeding sites (see Thiollay 1986, 1988a, 1990). On the study plot, 5.6% of the species are associated with large gaps, watercourses, edges, highly disturbed, swampy or rocky areas, against 30.8% in the Guianan community (Table 1). All are rare except four small species found near small forest streams. Nevertheless, many of these globally rare species may locally reach fairly high densities in their preferred habitat. In mature forest alone, the lowest proportion of rare species is found at ground or near-ground levels (Table 1). This proportion increases to about one-third of all the species at higher levels and in disturbed areas. When species are classified according to their foraging sites, aerial and semiaquatic birds have a significantly higher proportion of rare species (89%), terrestrial or low-level foragers have a lower proportion (19%) and arboreal species a similar proportion (38%) to that of the overall community (binomial tests,  $P < 0.05$ , Appendix 1).

Table 1. Habitat distribution of birds and proportion of rare species ( $\leq 1$  pair (100 ha) $^{-1}$ ) in the 100-ha plot and over all the primary forest zone of Guiana. Species from large openings (last column) are grouped because none are associated with truly forest habitats (see Appendix 1 and text for definitions).

Habitat types	L	M	C	G	D	S	O + I + R
In study plot:							
number of species	32	59	105	15	23	8	6
% rare species	12.5	32.2	43.8	33.3	34.8	50.0	100
Number of species among 193 additional species	3	10	30	6	22	17	105
% rare species among all 441 species	20.0	42.0	50.7	52.4	66.7	84.0	100.0

## DISCUSSION

### *Community structure*

Brosset (1990) in a review of the relevant literature showed that the species richness of 2–3 km<sup>2</sup> plots of primary rainforest was consistently 170–176 species in Asia and Africa and 224–254 in South America. The best documented, and maybe the richest area, is the 97-ha plot of lowland primary forest in the Manu National Park, Peru, censused by Terborgh *et al.* (1990), where 245 resident

(density  $\geq 0.5$  pair (100 ha) $^{-1}$ ) and 74 other occasional species were recorded, with a point diversity of up to 160 species (v. 221, 47 and  $>80$ , respectively, in Guiana). The study plots of Robinson *et al.* (1990) in six mature forest types in Peru also contained 200–260 species (200 ha) $^{-1}$ .

Our area is within this upper range of bird species richness in any terrestrial system. The magnitude of overall bird density is also consistent with the western Amazonian study (at least 829 pairs (100 ha) $^{-1}$  v. 1910 individuals in Peru) as are the density and the proportion of the dominant species (19 species with  $\geq 10$  pairs (100 ha) $^{-1}$  in Peru v. 15 in Guiana) as well as those of the rarest, but still regular species (75 species in Peru v. 85 in Guiana with density = 0.25–1.00 pair (100 ha) $^{-1}$ ) and the additional species recorded at least once on the plot (72 in Peru, 27 in Guiana). Several other tropical studies (Bell 1982, Brosset 1990) gave higher density estimates, or sometimes smaller ones (McClure 1969) but they were based on small sample plots or inadequate census methods. Because of the steep slope of the species–area curve and the very low or irregular density of many species, the size of the study plot and its habitat diversity are of the utmost importance in evaluating species richness or density in tropical forests. There may be also differences in home range size between sex or seasons and the floating or non-breeding population may be high, as exemplified in the manakins (Théry 1990).

Although the species richness is about five times lower in temperate than in tropical forests (Ferry & Frochot 1968, Holmes *et al.* 1986, Karr 1971, Tomialojc *et al.* 1984), the overall bird density remains roughly similar. Whereas the 1–2 most abundant species barely reach 20–40 pairs (100 ha) $^{-1}$  in Peru and Guiana, the numerically dominant species commonly reach 120–200 pairs (100 ha) $^{-1}$  in any temperate forest. The proportion of rare species, whose upper limit is set at 2 pairs (100 ha) $^{-1}$  by temperate standards, is 21–58% of the 29–58 species recorded in temperate forests and 59–60% of the 268–319 species recorded on the Amazonian plots (references above). A majority of rare species and a few moderately dominant species is a typical structure of most primary tropical forest communities (Driscoll & Kikkawa 1989, Erard 1989, Gentry 1990, Hubbell & Foster 1987, Lawton 1990). However, in Guiana, the ranking of species abundance is highly variable from one locality to another (Thiollay 1986, 1988a) and this may involve different combinations of competitive interactions and dominance.

Most species exhibited here an apparent stability in both abundance and distribution (as was also found in small insectivores by Greenberg & Gradwohl (1986)). At least 232 species were recorded on the study plot in each of the three study years, usually in the same areas, and 229 each year from 1986 to 1992. All irregular species were among the rarest ones. The leks of some conspicuous species (*Phaethornis*, *Lipaugus*, *Perissocephalus*, *Rupicola*, *Pipra*) were checked every year and found to be remarkably stable in both number of singing males and localization. Some interannual or seasonal fluctuations, however, were noticed, especially among probably nomadic frugivores (*Amazona*, *Ara*,

*Crax*) or aerial insectivores (*Ictinia*, *Elanoides*). The supposed movements of the former species may be associated with variations in local food supplies, whereas those of the latter raptors may have been caused by more extensive and regular migrations. Some seasonal habitat shifts were also documented (*Phaethornis malaris*, *Topaza pella*, *Mionectes macconnellii*).

The distribution of species among foraging guilds is not significantly different from that found in Peru (Terborgh *et al.* 1990) and is roughly proportional to the volume of vegetation available at different levels. The species diversity is high at every level from the ground to the emergent trees and on every type of substrate. The dominance of insectivores in the understorey and that of frugivores and omnivores in the canopy probably reflects the relative availability of the different food resources.

A number of species have evolved striking specializations, but almost as many species tend to be generalists. The two opposite trends seem to be equally successful in overcoming the constraints of rainforest environment such as heterogeneity, seasonality and low availability of most resources (Karr 1976, Karr *et al.* 1983, Schemske & Brokaw 1981, Thiollay 1991a). Generalism may be a strategy adapted to species-rich communities where the identity of competitors and predators is unpredictable and where different species may replace each other in time or space (Buckley 1983, Hubbell & Foster 1987). This may explain the coexistence within most guilds of species pairs with high niche similarity. Some of them may exclude each other (observed interspecific territoriality or no recorded territorial overlap), for instance *Harpia-Morphnus*, *Sclerurus*, or they coexist but one is markedly less abundant than the other (*Ramphastos*, *Philydor*, *Formicarius*) or their respective densities are variable but globally similar (*Columba*, *Amazona*, *Trogon*) or they are regular members of mixed species flocks where they occur in almost equal numbers (*Thamnomanes*, *Myrmotherula*, *Cyanerpes*) or there is a trend for their respective abundances to co-vary negatively (several foliage gleaners, Thiollay (1988a)). Numerous examples of habitat shifts or changes in relative abundance among similar species between different localities (Thiollay 1986) are additional clues to the possible importance of interspecific competition, at least under certain circumstances, as suggested by Karr (1977).

#### *Patterns and correlates of rarity*

Species densities here are almost an order of magnitude lower than those found in managed temperate forest. However, the difference is smaller with a virgin temperate forest (Tomialojc *et al.* 1984) and at least some species in secondary forests of Guiana have higher densities than in the undisturbed study site (Thiollay, unpubl.).

Many species are rare because they are associated with habitat types little represented in the study area or because they have widely differing levels of abundances between different localities (diffusive rarity of Schoener (1987)).

However, interlocality abundance fluctuations are markedly higher for rarer species than for common ones (Thiollay 1986, 1988a).

Species that are consistently rare have either large home ranges rather evenly spaced or they are patchily distributed and, as yet, no obvious factor can explain their localization. Individual pairs are sometimes so far apart from each other that the maintenance of such dispersed populations may look problematical. These rare species are often the largest of their guild, but over the whole bird community, the relationship between rarity and body size is not constant. Similarly, there is no clear relationship between rarity and habitat, diet specialization, niche breadth, foraging behaviour or social system. In other words, there are many forms of rarity (see Rabinowitz *et al.* 1986) and rare species have no common characteristics and no constant differences from more abundant species.

#### *Causes and consequences of rarity*

Most rarity patterns may result from environmental constraints reviewed in Thiollay (1991a). All of them are apparent in the study area but their respective and species-specific importance cannot be assessed. Habitat heterogeneity, together with bird species response by habitat specialization, is a cause of population fragmentation and hence overall population limitation (Thiollay 1990). Natural disturbance regimes, such as treefall gaps, floods or even predation by army ants (Franks & Bossert 1983), at different spatial scales, are a major source of heterogeneity and patchy distribution of both food resources, breeding sites, foraging substrates and dependent species. A generally low availability of food resources (compared with peak spring season in temperate areas), illustrated by low foraging success (Thiollay 1988b), comes from a high diversity of tree and prey species, low density and irregular distribution of most of them (Karr & Brawn 1990), seasonal and interannual fluctuations or multiple and highly evolved antipredator defences. Interspecific competition, so often indirectly suggested by distributional gaps (Diamond 1980), niche shifts, inverse correlation of abundance (Thiollay 1988a) or interspecific aggressivity (Pierpont 1986) cannot be dismissed and may only be exacerbated by the high species richness. The heavy predation pressure suggested by the diversity of predators (from mammals to ants), and documented at least on broods (Skutch 1985), may be another powerful limiting factor. Other likely consequences of constraints that may increase the trend towards rarity include niche specializations, strikingly low clutch sizes and breeding success (Tostain *et al.* 1992), permanent membership in mixed species flocks (Munn & Terborgh 1979, Powell 1989) and the persistence of subordinate species maintained in marginal habitats or at the periphery of food sources by more aggressive dominant species (Willis 1981).

Patchy habitat uses and distribution patterns are central to understanding species richness and rarity in tropical forests (Karr & Freemark 1983). They have no single explanation and may be due to undetected subtleties of specific

habitat selection, or interspecific competitive exclusions, or chance establishment of widely dispersing individuals. This increases the vulnerability of populations through a colonization–extinction process.

For a species, to be rare implies behavioural, dispersal and demographic adaptations to maintain a widely scattered population. These mechanisms are still little understood. The ecological role played by some rare species in the community structure or ecosystem equilibrium may be out of proportion to their actual abundance. The role of frugivores as seed dispersers or top predators checking the abundance of smaller, bird nest predators has been emphasized (Karr 1982, Oniki 1979, Terborgh 1988). A fundamental consequence of the low and irregular density of most species is to allow the coexistence of more species where the total amount of resources is limited. This may increase potential interspecific competition, hence species rarity and in turn species richness. Moreover, there may also be an advantage to be rare in such a competitive environment (Janzen 1970).

Finally, rarity has important conservation implications. If a substantial proportion of the species (here 56%) can be seen within a single square km, a much larger area is necessary to include viable populations of most species of the regional assemblage (here maybe more than  $10^4$  km<sup>2</sup> Thioallay 1989a) and this becomes a real challenge to set aside such areas of primary forest.

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#### APPENDIX 1

Bird population of the 100-ha study plot in the Nouragues area. Families and species are listed in systematic order. An asterisk means that at least one definite breeding record was obtained within the 100-ha plot from 1986 to 1992 (active nest or adult carrying food or nest material). Bird nomenclature follows Meyer de Schauensee & Phelps (1978).

**Capt** = Number of individual birds caught on the 100-ha plot in 1986–1988 and on the 24-ha core quadrat in 1991–1992.

**Rec** = Total number of accurately mapped, visual or acoustic records within the 100-ha quadrat. A record was the first location of a species (isolated birds or groups). No more than one contact per site per day was used.

**Dens** = Estimated number of pairs or singing resident adult males or small social groups ( $\leq 6$  individuals) from the mapping results in the 100-ha plot (see Methods). The number of pairs on the more intensively surveyed 24-ha core area is given in parentheses, multiplied by 4 and rounded to the nearest unit, when this value is higher than the 100-ha estimate.

**Log D** = Density index in nested areas from the Nouragues study plot to the whole Guiana rainforest zone. Species are ranked according to their recorded occurrence in quadrats successively larger by an order of magnitude from 0.1 km<sup>2</sup> (i.e.  $\geq 10$  pairs km<sup>-2</sup> = index 7) to 1 km<sup>2</sup> (i.e. 1–9 pairs km<sup>-2</sup> = index 6), 10 km<sup>2</sup> ( $\geq 1$  pair 10 km<sup>-2</sup>, but not found in the previous smaller plot = 5), 100 km<sup>2</sup> (= 4, Nouragues–Arataye area), 1000 km<sup>2</sup> (3), 10,000 km<sup>2</sup> (2) and 80,000 km<sup>2</sup> (1) progressively including more distant localities surveyed outside the coastal zone.

**Mass** = Log<sub>2</sub> classes of mean body weight (grams) from 1 (<8 g), to 2 (8–16 g), 3 (16–32 g), . . . 9 (1024–2048 g) and 10 (>2048 g).

**Soc** = Social behaviour or mating systems.

1 = <2 adults per breeding unit = lekking, polygynous or polyandrous species. This includes species with little known and unclear mating systems.

2 = Monogamous, territorial pairs.

3 = Monogamous breeders but regularly foraging in monospecific or mixed species flocks.

4 = Permanent monospecific groups or family units, or species breeding in small colonies and foraging communally.

**Hab** = Species' natural habitat most often recorded in the forest interior of Guiana.

In mature primary forests: L = low understorey and ground; M = mid-understorey to lower canopy; C = upper canopy and high emergent trees.

In other habitats all strata are pooled: D = disturbed natural or secondary forest, with lower and denser canopy than in primary forest. Also dense, low and drier stands on rocky outcrops; G = treefall gaps, in any of the above forest types; I = granitic inselbergs with bare rocks and clumps of shrubs or small trees; O = other large openings and forest edges; S = small forest streams under closed canopy and palm swamps; R = larger rivers and their forested banks.

**For** = Level and substrate where the species usually forages:

Aer = Aerial hunting above the canopy (in parentheses when searching for terrestrial prey).

Per = Only perch hunting from trees (flycatching or pouncing).

Gleaning, probing or snatching prey on foliage and branches (Arb = arboreal), bark, epiphytes and trunks (Bar), low dense growth (Low), ground and the lowest vegetation (Gro) or watercourses, banks and forest swamps (Wat).

**Diet** = Main characteristics of the diet. Does not include occasional prey items or categories including less than 10% of the diet. C = carnivores; F = frugivores; G = granivores; I = insectivores; N = nectarivores; O = omnivores. P = piscivores.

	Capt	Rec	Dens	Log D	Mass	Soc	Hab	For	Diet
<b>TINAMIDAE</b>									
<i>Tinamus major</i> *		20	1.25 (2)	6	9	1	L	Gro	G
<i>Crypturellus soui</i>		15	3.00 (4)	6	6	1	L	Gro	G
<i>Crypturellus variegatus</i> *		48	7.50 (11)	6	7	1	L	Gro	G
<b>ARDEIDAE</b>									
<i>Tigrisoma lineatum</i> *		6	0.75	5	8	2	S	Wat	P
<b>CATHARTIDAE</b>									
<i>Cathartes melambrotus</i>		20	0.25	5	9	2	C	(Aer)	C
<i>Sarcorampus papa</i>		4	+	4	10	2	C	(Aer)	C

	Capt	Rec	Dens	Log D	Mass	Soc	Hab	For	Diet
ACCIPITRIDAE									
<i>Leptodon cayanensis</i>		2	0.25	4	7	2	C	Arb	C
<i>Chondrohierax uncinatus*</i>		5	0.25	4	7	2	C	Arb	C
<i>Elanoides forficatus</i>		11	0.25	5	7	3	C	Aer	I
<i>Harpagus bidentatus</i>		11	0.50	5	6	2	C	Arb	C
<i>Harpagus diodon</i>		3	0.25	4	6	2	M	Arb	C
<i>Ictinia plumbea*</i>		27	0.75	5	6	2	C	Aer	I
<i>Accipiter superciliosus*</i>		9	0.75	5	6	2	G	Arb	C
<i>Accipiter bicolor</i>		5	0.50	5	7	2	M	Arb	C
<i>Leucopternis melanops</i>		4	0.25	5	7	2	M	Per	C
<i>Leucopternis albigollis*</i>		19	0.25	5	8	2	O	Per	C
<i>Buteogallus urubitinga</i>		12	0.25	5	9	2	S	Per	C
<i>Morphnus guianensis</i>		5	+	4	9	2	C	Arb	C
<i>Spizastur melanoleucus</i>		10	0.25	5	8	2	C	Arb	C
<i>Spizaetus ornatus</i>		8	+	4	9	2	C	Arb	C
FALCONIDAE									
<i>Daptrius americanus*</i>		148	0.50	5	8	4	C	Arb	O
<i>Micrastur ruficollis</i>		14	0.50	5	6	2	M	Per	C
<i>Micrastur gilvicollis*</i>	7	38	1.75	(2) 6	6	2	M	Per	C
<i>Micrastur mirandollei</i>	1	8	0.25	5	8	2	C	Arb	C
<i>Micrastur semitorquatus</i>		13	0.50	5	8	2	C	Arb	C
CRACIDAE									
<i>Penelope marail*</i>		30	3.00	(5) 6	9	2	C	Arb	F
<i>Crax alector*</i>		18	1.00	5	10	2	L	Gro	F
PHASIANIDAE									
<i>Odontophorus gujanensis*</i>		11	2.25	6	7	4	L	Gro	G
PSOPHIIDAE									
<i>Psophia crepitans*</i>	1	58	1.00	(2) 6	9	4	L	Gro	O
COLUMBIDAE									
<i>Columba subvinacea</i>		41	3.50	(7) 6	6	2	C	Arb	F
<i>Columba plumbea*</i>		83	6.00	(8) 6	6	2	C	Arb	F
<i>Leptotila rufaxilla*</i>		17	2.25	(4) 6	6	2	D	Gro	G
<i>Geotrygon montana*</i>	2	8	1.00	(2) 6	5	2	L	Gro	G
PSITTACIDAE									
<i>Ara chloroptera</i>		48	0.50	5	9	3	C	Arb	F
<i>Pyrrhura picta*</i>		15	0.50	5	5	3	C	Arb	F
<i>Brotoperys chrysopterus*</i>		44	6.00	(7) 6	4	4	C	Arb	F
<i>Touit purpurata*</i>		7	0.50	5	4	3	C	Arb	F
<i>Pionites melanocephala</i>		18	1.50	6	6	3	C	Arb	F
<i>Pionopsitta caica</i>		9	0.50	5	6	3	C	Arb	F
<i>Pionus menstruus*</i>		22	1.25	(3) 6	7	3	C	Arb	F
<i>Pionus fuscus</i>		25	1.00	5	7	2	C	Arb	F
<i>Amazona amazonica</i>		52	1.50	(2) 6	7	3	C	Arb	F
<i>Amazona farinosa</i>		49	1.50	(2) 6	8	3	C	Arb	F
<i>Deroptyx accipitrinus</i>		37	1.00	(2) 6	6	3	C	Arb	F
CUCULIDAE									
<i>Piaya cayana</i>		7	0.75	(1) 5	5	2	D	Arb	I
<i>Piaya melanogaster</i>		20	1.50	(2) 6	5	2	C	Arb	I
STRIGIDAE									
<i>Otus watsonii</i>	1	15	1.75	(2) 6	6	2	D	Arb	I
<i>Lophotrix cristata</i>		4	0.25	5	8	2	M	Per	C
<i>Pulsatrix perspicillata</i>		6	0.50	5	8	2	C	Arb	C
<i>Strix virgata</i>		8	0.75	5	7	2	M	Arb	C
<i>Strix nigrolineata</i>		3	0.50	5	7	2	M	Arb	C
<i>Glaucidium hardyi</i>		16	1.50	(2) 6	5	2	M	Arb	I
APODIDAE									
<i>Chaetura spinicauda*</i>		10	0.50	5	3	3	C	Aer	I

	Capt	Rec	Dens	Log D	Mass	Soc	Hab	For	Diet
<b>TROCHILIDAE</b>									
<i>Glaucis hirsuta</i>	2	6	1.00	6	1	2	O	Arb	N
<i>Phaethornis superciliosus</i> *	27	55	7.50 (14)	7	1	1	L	Arb	N
<i>Phaethornis malaris</i> *	8	20	2.75	6	2	1	C	Arb	N
<i>Phaethornis bourcieri</i> *	19	18	3.00	6	1	1	L	Arb	N
<i>Phaethornis ruber</i> *		14	2.50 (4)	6	1	1	G	Low	N
<i>Phaethornis longuemareus</i> *		9	1.50	6	1	1	G	Arb	N
<i>Camptyllopterus largipennis</i> *	23	38	6.00 (11)	6	2	2	M	Arb	N
<i>Florisuga mellivora</i> *	4	16	4.00 (6)	6	1	2	C	Arb	N
<i>Discosura longicauda</i>		3	0.50	5	1	2	C	Arb	N
<i>Thalurania furcata</i> *	38	50	7.50 (12)	7	1	2	M	Arb	N
<i>Hylocharis sapphirina</i>	5	2	+	4	1	2	O	Low	N
<i>Hylocharis cyanus</i>		4	0.50	5	1	2	C	Arb	N
<i>Topaza pella</i> *	2	19	2.00	6	2	2	S	Arb	N
<i>Heliothryx aurita</i>	1	8	1.25	6	1	2	C	Arb	N
<i>Helimaster longirostris</i>		3	0.50	6	1	2	C	Arb	N
<b>TROGONIDAE</b>									
<i>Trogon melanurus</i>		38	4.75 (10)	6	5	2	C	Arb	O
<i>Trogon viridis</i>		37	4.50 (9)	6	5	2	C	Arb	O
<i>Trogon collaris</i> *		33	4.00 (10)	6	4	2	C	Arb	O
<i>Trogon rufus</i> *	1	15	2.75 (3)	6	4	2	M	Arb	O
<i>Trogon violaceus</i>		4	0.25	5	4	2	D	Arb	O
<b>ALCEDINIDAE</b>									
<i>Chloroceryle inda</i> *	1	4	0.25	5	4	2	S	Wat	P
<i>Chloroceryle aenea</i> *		2	+	5	2	2	S	Wat	P
<b>MOMOTIDAE</b>									
<i>Momotus momota</i> *	4	76	5.00 (7)	6	6	2	M	Per	I
<b>GALBULIDAE</b>									
<i>Galbula albirostris</i> *	2	14	3.00	6	3	2	G	Per	I
<i>Galbula dea</i>		12	1.50	6	3	2	C	Per	I
<i>Jacamerops aurea</i>		8	0.75	5	5	2	M	Per	I
<b>BUCCONIDAE</b>									
<i>Notharchus macrorhynchus</i>		10	1.00 (2)	6	5	2	C	Per	I
<i>Notharchus tectus</i>		4	0.75	5	4	2	O	Per	I
<i>Bucco capensis</i>		5	0.50	5	4	2	M	Per	I
<i>Malacoptila fusca</i>	1	12	1.50 (2)	6	4	2	M	Per	I
<i>Monasa atra</i> *	1	43	5.50 (8)	6	4	3	C	Arb	I
<b>CAPITONIDAE</b>									
<i>Capito niger</i> *		7	1.00	6	4	2	D	Arb	F
<b>RAMPHASTIDAE</b>									
<i>Pteroglossus aracari</i>		10	1.00	6	6	3	C	Arb	F
<i>Pteroglossus viridis</i>		6	0.75 (1)	5	6	3	C	Arb	F
<i>Selenidera culik</i> *		18	1.75 (3)	6	6	2	C	Arb	F
<i>Ramphastos vitellinus</i>		21	1.00 (2)	6	7	2	C	Arb	F
<i>Ramphastos tucanus</i> *		74	3.50 (6)	6	8	2	C	Arb	F
<b>PICIDAE</b>									
<i>Picumnus exilis</i> *		8	1.00	6	2	2	D	Bar	I
<i>Veniliornis passerinus</i>		6	0.25	5	4	2	D	Bar	I
<i>Veniliornis cassini</i>		12	1.50	6	4	2	C	Bar	I
<i>Piculus flavigula</i>		13	1.75 (2)	6	4	3	M	Bar	I
<i>Piculus chrysocloros</i>		5	0.50	5	5	2	C	Bar	I
<i>Piculus rubiginosus</i>		10	1.25	6	5	2	M	Bar	I
<i>Celeus undatus</i>		11	1.50 (2)	6	5	2	C	Bar	I
<i>Celeus elegans</i>	2	18	3.25 (4)	6	6	2	M	Bar	I
<i>Celeus torquatus</i>		3	0.25	5	5	2	C	Bar	I
<i>Dryocopus lineatus</i>		3	0.25	5	6	2	G	Bar	I
<i>Campephilus rubricollis</i> *	1	60	3.50 (4)	6	6	2	C	Bar	I

	Capt	Rec	Dens		Log D	Mass	Soc	Hab	For	Diet
FURNARIIDAE										
<i>Philydor erythrocercus</i> *	17	87	5.25	(8)	6	3	3	M	Bar	I
<i>Philydor pyrrhodes</i>	4	8	1.50	(2)	6	3	2	M	Bar	I
<i>Philydor ruficaudatus</i>	3	10	0.75	(1)	5	3	3	M	Bar	I
<i>Automolus infuscatus</i> *	19	68	4.75	(6)	6	4	3	M	Bar	I
<i>Automolus rubiginosus</i> *	3	14	2.75	(3)	6	4	2	L	Gro	I
<i>Automolus ochrolaemus</i>		4	1.00		5	4	2	M	Bar	I
<i>Sclerurus mexicanus</i>	4	15	2.75	(3)	6	4	2	L	Gro	I
<i>Sclerurus rufigularis</i>	5	18	2.00		6	4	2	L	Gro	I
<i>Sclerurus caudacutus</i> *	16	44	7.00	(4)	6	4	2	L	Gro	I
<i>Xenops minutus</i>	8	28	6.50	(9)	6	2	3	M	Arb	I
DENDROCOLAPTIDAE										
<i>Dendrocincla fuliginosa</i> *	2	18	1.50	(3)	6	4	3	M	Bar	I
<i>Dendrocincla merula</i>	4	19	2.00	(3)	6	4	3	M	Bar	I
<i>Deconychura longicauda</i> *	5	11	1.50	(2)	6	3	3	M	Bar	I
<i>Deconychura stictolaema</i>	4	7	1.00		6	3	2	M	Bar	I
<i>Sittasomus griseicapillus</i>		4	0.75		5	3	3	C	Bar	I
<i>Sittasomus</i> sp. nov.	2	2	1.00		5	3	2	M	Bar	I
<i>Glyphorhynchus spirurus</i> *	160	218	28.00	(36)	7	2	3	M	Bar	I
<i>Dendrexetastes rufigula</i> *	2	5	0.50		5	5	2	C	Bar	I
<i>Hylexetastes perrotii</i>		4	0.25		5	5	2	C	Bar	I
<i>Dendrocolaptes certhia</i>	1	8	1.50		6	5	3	M	Bar	I
<i>Dendrocolaptes picumius</i>		2	0.25		5	5	2	M	Bar	I
<i>Xiphorhynchus obsoletus</i>		2	0.25		5	4	2	M	Bar	I
<i>Xiphorhynchus pardalotus</i> *	29	109	7.00	(12)	6	4	3	M	Bar	I
<i>Lepidocolaptes albolineatus</i>		3	0.50		5	4	2	M	Bar	I
<i>Camptylorhamphus procurviroides</i> *	1	18	1.25	(2)	6	4	3	M	Bar	I
THAMNOPHILIDAE										
<i>Cymbilaimus lineatus</i> *	1	22	3.50	(5)	6	4	2	D	Arb	I
<i>Federickena viridis</i> *		3	+		4	5	2	G	Gro	I
<i>Sakesphorus melanothorax</i>	1	6	1.25	(4)	6	3	2	D	Gro	I
<i>Thamnophilus murinus</i> *	4	88	7.75	(12)	6	3	2	M	Arb	I
<i>Thamnophilus amazonicus</i>		12	4.00	(8)	6	3	3	D	Arb	I
<i>Thamnophilus punctatus</i>		2	0.25		5	3	2	I	Arb	I
<i>Pygiptila stellaris</i>		2	+		4	3	2	M	Arb	I
<i>Thamnomanes ardesiacus</i> *	46	98	6.00	(10)	6	3	3	M	Arb	I
<i>Thamnomanes caesius</i> *	28	107	6.25	(10)	6	3	3	M	Arb	I
<i>Myrmotherula brachyura</i> *		48	11.25	(22)	7	1	3	C	Arb	I
<i>Myrmotherula guttata</i> *	17	39	8.25	(12)	7	2	2	L	Gro	I
<i>Myrmotherula gutturalis</i> *	20	82	6.25	(10)	6	2	3	M	Arb	I
<i>Myrmotherula axillaris</i> *	13	46	7.00	(10)	6	1	3	D	Arb	I
<i>Myrmotherula longipennis</i> *	28	92	7.00	(12)	6	2	3	M	Arb	I
<i>Myrmotherula menetriesii</i> *	14	78	6.00	(9)	6	2	3	M	Arb	I
<i>Herpsilochmus sticturus</i> *		4	1.00	(3)	6	2	2	M	Arb	I
<i>Herpsilochmus stictocephalus</i>		9	2.50	(5)	6	2	3	C	Arb	I
<i>Microrhopias quixensis</i>		10	3.00	(8)	6	2	2	D	Arb	I
<i>Terenura spodioptila</i>		5	1.75	(4)	6	1	2	C	Arb	I
<i>Cercomacra cinerascens</i> *		196	38.00	(68)	7	3	2	D	Arb	I
<i>Cercomacra tyrannina</i>		3	1.00		5	2	2	D	Low	I
<i>Hypocnemis cantator</i> *	9	115	14.00	(19)	7	2	2	G	Low	I
<i>Percnostola rufifrons</i> *	6	36	5.50	(9)	6	3	2	D	Gro	I
<i>Percnostola leucostigma</i> *	2	19	4.00		6	3	2	S	Gro	I
<i>Myrmeciza ferruginea</i> *	4	76	17.00	(19)	7	3	2	G	Gro	I
<i>Pithys albifrons</i> *	113	151	15.00	(20)	7	3	3	L	Gro	I
<i>Gymnopathys rufigula</i>	28	43	3.00	(4)	6	3	3	L	Gro	I
<i>Hylophylax naevia</i> *	23	38	14.00	(22)	7	2	2	G	Gro	I
<i>Hylophylax poecilonota</i> *	49	59	15.00	(31)	7	3	2	L	Gro	I
<i>Myrmornis torquata</i> *	11	28	4.00	(8)	6	4	2	L	Gro	I

	Capt	Rec	Dens		Log D	Mass	Soc	Hab	For	Diet
<b>FORMICARIIDAE</b>										
<i>Formicarius colma</i> *	5	9	2.00	(5)	6	4	2	L	Gro	I
<i>Formicarius analis</i> *	1	67	7.75	(14)	7	4	2	L	Gro	I
<i>Grallaria varia</i> *		8	1.50		6	5	2	L	Gro	I
<i>Hylopezus macularius</i> *	2	36	6.00	(7)	6	4	2	L	Gro	I
<i>Myrmothera campanisona</i>		30	5.75	(8)	6	4	2	G	Gro	I
<b>CONOPOPHAGIDAE</b>										
<i>Conopophaga aurita</i> *	2	5	1.00	(3)	6	3	2	L	Gro	I
<b>TITYRIDAE</b>										
<i>Tityra cayana</i> *		8	1.50	(3)	6	5	2	C	Arb	O
<i>Tityra inquisitor</i>		4	0.75		6	4	2	C	Arb	O
<i>Pachyramphus minor</i> *	1	11	2.50	(4)	6	4	3	C	Arb	I
<b>COTINGIDAE</b>										
<i>Phoenicircus carnifex</i>	1	22	3.00	(4)	6	5	1	M	Arb	F
<i>Iodopleura fusca</i>		4	1.00		5	2	2	C	Arb	F
<i>Cotinga cotinga</i>		5	1.00		5	4	1	C	Arb	F
<i>Cotinga cayana</i> *		20	2.25	(4)	6	5	1	C	Arb	F
<i>Xipholena punicea</i> *		34	4.50	(6)	6	5	1	C	Arb	F
<i>Lipaugus vociferans</i> *	1	158	11.00		7	5	1	M	Arb	F
<i>Querula purpurata</i>		51	1.00		6	5	4	C	Arb	F
<i>Perissocephalus tricolor</i> *	1	55	5.00		6	7	1	C	Arb	F
<i>Rupicola rupicola</i> *		68	4.00		6	7	1	M	Arb	F
<i>Oxyruncus cristatus</i>		5	0.75	(1)	5	3	2	C	Arb	O
<b>PIPRIDAE</b>										
<i>Manacus manacus</i>	3	4	0.25		5	3	1	O	Low	F
<i>Corapipo gutturalis</i> *	10	14	2.50	(6)	6	2	1	L	Arb	F
<i>Pipra erythrocephala</i> *	34	40	7.00	(16)	6	2	1	M	Arb	F
<i>Pipra pipra</i> *	86	67	7.00	(13)	6	2	1	M	Arb	F
<i>Pipra serena</i> *	55	92	8.00	(20)	7	2	1	L	Arb	F
<i>Piprites chloris</i>		5	1.00	(2)	6	3	2	D	Arb	I
<i>Tyrannuleutes virescens</i>		65	18.00	(28)	7	2	1	D	Arb	F
<i>Schiffornis turdinus</i> *	4	7	1.50	(4)	6	3	1	L	Arb	F
<b>TYRANNIDAE</b>										
<i>Zimmerius gracilepes</i>		6	1.50	(2)	6	2	2	C	Arb	O
<i>Mionectes macconnelli</i> *	57	38	6.50	(10)	6	2	2	M	Arb	O
<i>Leptopogon amaurocephalus</i>	1	3	1.00	(2)	6	2	2	M	Arb	I
<i>Corythopsis torquata</i>	14	16	3.75		6	3	2	L	Gro	I
<i>Myiopagis gaimardii</i>		15	3.25	(6)	6	2	3	C	Arb	I
<i>Rhynchocyclus olivaceus</i> *	1	7	2.00		6	3	2	C	Arb	I
<i>Tolmomyias assimilis</i>		11	2.00	(4)	6	2	2	C	Arb	I
<i>Tolmomyias flaviventris</i>		3	0.75		5	2	2	C	Arb	I
<i>Platyrinchus mystaceus</i>	1	16	4.00	(7)	6	2	1	M	Arb	I
<i>Platyrinchus coronatus</i> *	26	88	15.00	(30)	7	2	1	M	Arb	I
<i>Platyrinchus saturatus</i> *	6	10	3.00	(6)	6	2	2	S	Arb	I
<i>Todirostrum pictum</i>		12	3.50	(4)	6	1	2	C	Arb	I
<i>Hemitriccus ecaudatus</i> *		14	4.00	(6)	6	1	2	C	Arb	I
<i>Hemitriccus zosterops</i> *	3	81	16.00	(38)	7	2	2	M	Arb	I
<i>Hemitriccus minor</i>		18	6.00	(10)	6	2	2	D	Arb	I
<i>Hemitriccus josephinae</i>		9	2.00	(4)	6	2	2	D	Arb	I
<i>Contopus albogularis</i>		6	1.00		5	3	2	G	Per	I
<i>Myiobius erythrurus</i>	8	21	6.00	(13)	6	1	2	D	Arb	I
<i>Myiobius barbatus</i> *	30	49	6.50	(10)	6	2	3	M	Arb	I
<i>Attila spadiceus</i>	3	27	4.50	(8)	6	4	2	C	Arb	I
<i>Laniocera hypopyrrha</i>		6	1.00		5	4	2	C	Arb	O
<i>Ramphotrigon ruficauda</i> *		7	1.75		6	3	2	G	Arb	I
<i>Rhytipterna simplex</i> *	1	19	3.75		6	4	2	D	Arb	I
<i>Sirystes sibilator</i>		10	1.50	(2)	6	4	2	C	Per	I
<i>Tyrannus albogularis</i>		5	1.00		5	4	2	C	Per	I
<i>Conopias albobittata</i>		32	4.50	(6)	6	3	2	C	Per	I

	Capt	Rec	Dens	Log D	Mass	Soc	Hab	For	Diet
TROGLODYTIDAE									
<i>Thryothorus coraya*</i>	2	33	6.00 (11)	6	3	2	D	Low	I
<i>Microcerculus bambla*</i>	7	39	10.00 (12)	7	2	2	L	Gro	I
<i>Cyphorhinus arada*</i>	10	34	4.00 (8)	6	3	4	L	Gro	O
TURDIDAE									
<i>Turdus albicollis*</i>	61	162	14.00 (20)	7	4	2	L	Gro	O
SYLVIIDAE									
<i>Polioptila plumbea</i>		16	2.50 (4)	6	1	3	C	Arb	I
<i>Piliptila guianensis</i>		4	0.75	5	1	3	C	Arb	I
<i>Microbates collaris*</i>	7	23	7.00 (9)	6	2	2	G	Gro	I
<i>Ramphocaenus melanurus</i>		11	1.00	6	2	2	G	Arb	I
VIREONIDAE									
<i>Vireolanius leucotis</i>		6	1.50 (2)	6	3	3	C	Arb	I
<i>Vireo olivaceus</i>		43	10.50	7	2	2	C	Arb	I
<i>Hylophilus semicinereus</i>		3	1.00	5	2	2	C	Arb	I
<i>Hylophilus muscicapinus</i>		12	2.50 (4)	6	2	2	C	Arb	I
<i>Hylophilus ochraceiceps</i>	10	13	4.00 (8)	6	2	2	M	Arb	I
PARULIDAE									
<i>Basileuterus rivularis*</i>	3	20	4.00	6	2	2	S	Wat	I
ICTERIDAE									
<i>Psarocolius viridis*</i>		65	5.00 (8)	6	7	4	C	Arb	O
THRAUPINAE									
<i>Coereba flaveola*</i>	2	48	14.00 (18)	7	2	3	G	Arb	O
<i>Dacnis cayana</i>	2	17	3.75 (6)	6	2	3	C	Arb	O
<i>Dacnis lineata</i>		4	1.50	6	2	3	C	Arb	O
<i>Cyanerpes caeruleus*</i>		24	4.50 (8)	6	2	3	C	Arb	O
<i>Cyanerpes cyaneus</i>		32	6.50 (12)	6	2	3	C	Arb	O
<i>Chlorophanes spiza*</i>		16	3.50 (6)	6	3	3	C	Arb	O
<i>Hemithraupis guira</i>		9	1.25 (2)	6	2	3	C	Arb	I
<i>Hemithraupis flavicollis</i>		4	0.75 (1)	5	3	3	C	Arb	I
<i>Tangara gyrola</i>		10	2.00 (3)	6	3	3	C	Arb	O
<i>Tangara punctata</i>		8	1.25 (2)	6	3	3	C	Arb	O
<i>Tangara velia*</i>		14	2.75 (4)	6	3	3	C	Arb	O
<i>Tangara chilensis*</i>		59	10.00 (14)	7	3	3	C	Arb	O
<i>Euphonia cayennensis</i>		16	2.50 (4)	6	2	3	C	Arb	F
<i>Euphonia chrysopasta</i>		5	1.25	6	2	3	C	Arb	F
<i>Eucometis penicillata</i>		5	0.50	5	3	3	C	Arb	I
<i>Lanio fulvus*</i>	3	37	4.00 (7)	6	3	3	C	Arb	I
<i>Tachyphonus luctuosus</i>		4	0.75 (1)	5	3	3	D	Arb	I
<i>Tachyphonus cristatus*</i>		10	1.50 (3)	6	3	3	C	Arb	I
<i>Tachyphonus surinamus*</i>	17	28	6.00 (8)	6	3	2	M	Arb	I
<i>Lamprospiza melanoleuca</i>		3	0.50	5	4	4	C	Arb	O
CARDINALINAE									
<i>Pitylus grossus</i>		40	7.50 (12)	6	4	2	M	Arb	O
<i>Caryothraustes canadensis*</i>		51	3.00 (6)	6	4	4	C	Arb	O
<i>Cyanocompsa cyanoides</i>	5	10	2.00 (4)	6	3	2	L	Low	G
EMBERIZINAE									
<i>Arremon taciturnus</i>		13	4.50	6	3	2	L	Gro	G



## APPENDIX 2

Proved or presumed breeding species (migrants excluded) from the primary forest and associated habitats of the interior of French Guiana (outside coastal zone), not recorded within the 100-ha Nouragues study plot, or only as vagrants (see Thiollay 1986, 1989a, Tostain *et al.* 1992). See Appendix 1 for definitions.

	Log D	Mass	Soc	For	Diet	Hab
<b>TINAMIDAE</b>						
<i>Crypturellus cinereus</i>	4	7	1	Gro	G	O
<i>Crypturellus undulatus</i>	1	8	1	Gro	G	D
<i>Crypturellus brevirostris</i>	1	7	1	Gro	G	L
<i>Crypturellus erythropus</i>	5	7	1	Gro	G	D
<b>PHALACROCORACIDAE</b>						
<i>Phalacrocorax olivaceus</i>	1	9	4	Wat	P	R
<b>ANHINGIDAE</b>						
<i>Anhinga anhinga</i>	3	9	2	Wat	P	R
<b>ARDEIDAE</b>						
<i>Ardea cocoi</i>	1	9	2	Wat	P	R
<i>Egretta alba</i>	1	8	4	Wat	P	R
<i>Butorides striatus</i>	3	6	2	Wat	P	R
<i>Agamia agami</i>	4	8	2	Wat	P	R
<i>Pilherodius pileatus</i>	2	8	2	Wat	P	R
<i>Zebilus undulatus</i>	1	6	2	Wat	P	R
<b>THRESKIORNITHIDAE</b>						
<i>Mesembrinibis cayennensis</i>	3	8	3	Wat	P	R
<b>CATHARTIDAE</b>						
<i>Coragyps atratus</i>	2	9	3	(Aer)	C	O
<b>ANATIDAE</b>						
<i>Cairina moschata</i>	2	10	2	Wat	G	R
<i>Oxyura dominica</i>	1	7	2	Wat	G	R
<b>ACCIPITRIDAE</b>						
<i>Accipiter poliogaster</i>	4	8	2	Arb	C	M
<i>Buteo magnirostris</i>	1	7	2	Per	C	O
<i>Buteo brachyurus</i>	2	7	2	Arb	C	O
<i>Asturina nitida</i>	2	7	2	Per	C	O
<i>Leucopternis schistacea</i>	3	8	2	Per	C	S
<i>Harpia harpyja</i>	3	10	2	Arb	C	C
<i>Spizaetus tyrannus</i>	4	9	2	Arb	C	D
<i>Geranospiza caerulescens</i>	2	7	2	Arb	C	D
<b>FALCONIDAE</b>						
<i>Herpetotheres cachinnans</i>	1	8	2	Per	C	O
<i>Daptrius ater</i>	3	7	4	Arb	O	R
<i>Falco deiroleucus</i>	4	7	2	Aer	C	I
<i>Falco ruficularis</i>	3	6	2	Aer	C	R
<b>CRACIDAE</b>						
<i>Ortalis motmot</i>	5	7	4	Arb	F	D
<i>Aburria pipile</i>		9	2	Arb	F	M
<b>OPISTHOCOMIDAE</b>						
<i>Opisthocomus hoazin</i>	1	8	4	Wat	F	R
<b>RALLIDAE</b>						
<i>Aramides cajanea</i>	4	7	2	Wat	I	S
<i>Anurolimnas viridis</i>	1	7	2	Wat	I	S
<b>HELIORNITHIDAE</b>						
<i>Heliornis fulica</i>	1	6	2	Wat	P	R

	Log D	Mass	Soc	For	Diet	Hab
EURYPYGIDAE						
<i>Eurypyga helias</i>	2	6	2	Wat	P	S
COLUMBIDAE						
<i>Columba speciosa</i>	5	7	2	Arb	F	D
<i>Columba cayennensis</i>	4	7	2	Arb	F	D
<i>Columbina minuta</i>	3	3	2	Gro	G	I
<i>Columbina talpacoti</i>	1	4	2	Gro	G	O
<i>Leptotila verreauxi</i>	4	6	2	Gro	G	I
PSITTACIDAE						
<i>Ara ararauna</i>	3	9	3	Arb	G	S
<i>Ara macao</i>	4	9	3	Arb	G	C
<i>Ara severa</i>	4	7	3	Arb	G	C
<i>Aratinga leucophthalmus</i>	4	6	3	Arb	G	D
<i>Forpus sclateri</i>	2	3	3	Low	G	O
<i>Touit batavica</i>	4	4	3	Arb	G	C
<i>Amazona dufresniana</i>	4	7	3	Arb	G	C
<i>Amazona ochrocephala</i>	4	7	3	Arb	G	C
CUCULIDAE						
<i>Piaya minuta</i>	4	4	2	Arb	I	O
<i>Taera naevia</i>	1	4	2	Low	I	O
<i>Crotophaga ani</i>	1	5	4	Low	I	O
NYCTIBIIDAE						
<i>Nyctibius grandis</i>	5	8	2	Per	I	C
<i>Nyctibius griseus</i>	4	6	2	Per	I	O
CAPRIMULGIDAE						
<i>Lurocalis semitorquatus</i>	3	5	2	Aer	I	O
<i>Podager nacunda</i>	1	5	2	Aer	I	O
<i>Nyctidromus albicollis</i>	4	5	2	Aer	I	O
<i>Chordeiles acutipennis</i>	4	4	2	Aer	I	O
<i>Caprimulgus rufus</i>	3	4	2	Aer	I	I
<i>Caprimulgus nigrescens</i>	5	4	2	Aer	I	I
<i>Hydropsalis climacocerca</i>	4	4	2	Aer	I	R
APODIDAE						
<i>Streptoprocne zonaris</i>	4	5	3	Aer	I	C
<i>Chaetura chamani</i>	4	3	3	Aer	I	C
<i>Panyptila cayennensis</i>	4	3	3	Aer	I	O
TROCHILIDAE						
<i>Threnetes niger</i>	4	1	2	Arb	N	S
<i>Threnetes leucurus</i>	1	1	2	Arb	N	R
<i>Eupetomena macroura</i>	5	1	2	Arb	N	S
<i>Anthracothonax nigricollis</i>	1	2	2	Arb	N	O
<i>Avocettula recurvirostris</i>	5	1	2	Arb	N	C
<i>Lophornis ornatus</i>	2	1	2	Arb	N	O
<i>Chlorestes notatus</i>	5	1	2	Arb	N	O
<i>Chlorostilbon mellisugus</i>	4	1	2	Arb	N	O
ALCEDINIDAE						
<i>Megaceryle torquata</i>	4	7	2	Wat	P	R
<i>Chloroceryle amazona</i>	4	5	2	Wat	P	R
<i>Chloroceryle americana</i>	4	3	2	Wat	P	R
GALBULIDAE						
<i>Brachygalba lugubris</i>	4	3	2	Per	I	O
<i>Galbula leucogastra</i>	4	3	2	Per	I	R

	Log D	Mass	Soc	For	Diet	Hab
<b>BUCCONIDAE</b>						
<i>Bucco tamatia</i>	5	4	2	Per	I	D
<i>Nonnula rubecula</i>	1	3	2	Per	I	M
<i>Chelidoptera tenebrosa</i>	3	4	2	Per	I	O
<b>PICIDAE</b>						
<i>Picumnus spilogaster</i>	3	3	2	Bar	I	M
<i>Picumnus minutissimus</i>	1	2	2	Bar	I	D
<i>Melanerpes cruentatus</i>	5	4	4	Bar	I	O
<i>Celeus grammicus</i>	5	5	2	Bar	I	M
<i>Campephilus melanoleucos</i>	4	6	2	Bar	I	R
<b>FURNARIIDAE</b>						
<i>Synallaxis macconnelli</i>	5	3	2	Low	I	D
<i>Synallaxis gujanensis</i>	2	3	2	Low	I	O
<i>Certhiaxis gutturata</i>	4	3	2	Low	I	D
<i>Automolus rufipileatus</i>	4	4	2	Wat	I	S
<i>Xenops milleri</i>	4	2	3	Arb	I	C
<i>Xenops tenuirostris</i>	2	2	2	Arb	I	C
<i>Xenops rutilans</i>	2	2	2	Arb	I	C
<b>DENDROCOLAPTIDAE</b>						
<i>Nasica longirostris</i>	4	5	2	Bar	I	S
<i>Xiphocolaptes promeropirhynchus</i>	4	6	2	Bar	I	C
<i>Xiphorhynchus guttatus</i>	3	5	3	Bar	I	S
<i>Campyloramphus trochilirostris</i>	4	4	3	bar	I	M
<b>THAMNOPHILIDAE</b>						
<i>Taraba major</i>	3	4	2	Low	I	O
<i>Thamnophilus doliatus</i>	4	3	2	Low	I	O
<i>Myrmotherula surinamensis</i>	4	2	2	Wat	I	R
<i>Myrmotherula behni</i>	3	2	3	Arb	I	M
<i>Herpsilochmus dorsimaculatus</i>	1	2	2	Arb	I	M
<i>Cercomacra nigrescens</i>	4	3	2	Low	I	D
<i>Myrmoborus leucophrys</i>	1	3	2	Arb	I	D
<i>Hypocnemoides melanopogon</i>	4	2	2	Wat	I	R
<i>Sclatera naevia</i>	4	3	2	Wat	I	R
<i>Myrmeciza longipes</i>	4	3	2	Low	I	G
<i>Myrmeciza atrothorax</i>	5	3	2	Low	I	O
<i>Hylophylax punctulata</i>	1	2	2	Gro	I	S
<b>TITYRIDAE</b>						
<i>Tityra semifasciata</i>	2	5	2	Arb	O	G
<i>Pachyramphus rufus</i>	4	3	2	Arb	I	O
<i>Pachyramphus marginatus</i>	4	3	2	Arb	I	D
<i>Pachyramphus surinamus</i>	4	3	2	Arb	I	D
<b>COTINGIDAE</b>						
<i>Gymnoderus foetidus</i>	3	7	1	Arb	F	S
<i>Haematoderus militaris</i>	3	7	1	Arb	F	C
<i>Procnias alba</i>	2	5	1	Arb	F	C
<b>PIPRIDAE</b>						
<i>Chiroxiphia pareola</i>	1	2	1	Arb	F	D
<i>Xenopipo atronitens</i>	1	2	2	Arb	F	D
<i>Neopipo cinnamomea</i>	2	2	2	Arb	I	D
<i>Neopelma chryscephalum</i>	1	3	2	Arb	I	L
<b>TYRANNIDAE</b>						
<i>Ornithion inerne</i>	1	1	2	Arb	I	S
<i>Phaeomyias murina</i>	1	2	2	Arb	I	O
<i>Myiopagis caniceps</i>	2	2	2	Arb	I	C

	Log D	Mass	Soc	For	Diet	Hab
<i>Myiopais flavivertex</i>	3	2	2	Arb	I	S
<i>Elaenia flavogaster</i>	1	3	2	Per	I	O
<i>Mionectes oleagineus</i>	3	2	2	Arb	O	S
<i>Lophotriccus vitiensis</i>	3	2	2	Arb	I	D
<i>Lophotriccus galeatus</i>	4	2	2	Low	I	G
<i>Todirostrum sylvia</i>	3	2	2	Low	I	O
<i>Todirostrum maculatum</i>	1	1	2	Low	I	O
<i>Todirostrum cinereum</i>	5	1	2	Low	I	O
<i>Tolmomyias poliocephalus</i>	5	2	2	Arb	I	C
<i>Platyrhynchus platyrhynchus</i>	4	2	2	Arb	I	M
<i>Onychorhynchus coronatus</i>	4	2	2	Wat	I	S
<i>Myiophobus fasciatus</i>	4	2	2	Arb	I	I
<i>Contopus cinereus</i>	2	3	2	Arb	I	C
<i>Colonia colonus</i>	3	3	2	Per	I	C
<i>Hirundinea ferruginea</i>	5	3	2	Gro	I	I
<i>Attila cinnamomeus</i>	4	3	2	Arb	I	S
<i>Myiarchus swainsoni</i>	1	3	2	Per	I	O
<i>Myiarchus ferox</i>	2	3	2	Per	I	I
<i>Pitangus lictor</i>	2	4	2	Wat	I	R
<i>Pitangus sulphuratus</i>	1	4	2	Per	I	O
<i>Megarynchus pitangua</i>	1	4	2	Per	I	O
<i>Myiozetetes cayanensis</i>	1	3	2	Per	I	O
<i>Myiozetetes similis</i>	2	3	2	Per	I	O
<i>Myiozetetes luteiventris</i>	3	3	2	Per	I	O
<i>Legatus leucophaeus</i>	4	3	2	Per	O	R
<i>Tyrannus melancholicus</i>	5	4	2	Per	I	O
HIRUNDINIDAE						
<i>Tachycineta albiventer</i>	2	2	2	Aer	I	R
<i>Phaeoprogne tapera</i>	2	3	3	Aer	I	R
<i>Progne chalybeata</i>	1	4	3	Aer	I	O
<i>Atticora fasciata</i>	4	2	3	Aer	I	R
<i>Atticora melanoleuca</i>	2	2	3	Aer	I	R
<i>Neochelidon tibialis</i>	4	2	2	Aer	I	O
<i>Stelgidopteryx ruficollis</i>	4	2	3	Aer	I	O
CORVIDAE						
<i>Cyanocorax cayanus</i>	4	6	4	Arb	O	C
TROGLODYTIDAE						
<i>Thryothorus leucotis</i>	4	3	2	Low	I	R
<i>Henicorhina leucosticta</i>	1	3	2	Gro	I	L
TURDIDAE						
<i>Turdus fumigatus</i>	3	4	2	Gro	O	O
VIREONIDAE						
<i>Cyclarhis guyanensis</i>	4	3	2	Arb	I	O
<i>Hylophilus thoracicus</i>	4	2	2	Arb	I	O
<i>Hylophilus pectoralis</i>	5	2	2	Arb	I	C
PARULIDAE						
<i>Parula pitiayumi</i>	3	2	2	Arb	I	C
<i>Gratanellus pelzelni</i>	3	2	3	Arb	I	D
ICTERIDAE						
<i>Scaphidura oryzivora</i>	2	6	4	Arb	O	O
<i>Psarocolius decumanus</i>	4	7	4	Arb	O	O
<i>Cacicus cela</i>	4	5	4	Arb	O	R
<i>Cacicus haemorrhous</i>	5	5	4	Arb	O	G
<i>Icterus cayanensis</i>	5	4	2	Arb	O	G

	Log D	Mass	Soc	For	Diet	Hab
THRAUPINAE						
<i>Conirostrum speciosum</i>	5	2	2	Arb	O	C
<i>Tersina viridis</i>	5	3	2	Arb	I	G
<i>Tangara mexicana</i>	1	3	3	Arb	O	O
<i>Euphonia aureata</i>	1	2	2	Arb	F	C
<i>Euphonia minuta</i>	2	2	2	Arb	F	D
<i>Euphonia chlorotica</i>	1	2	2	Arb	F	C
<i>Euphonia violacea</i>	4	2	2	Arb	F	O
<i>Euphonia plumbea</i>	1	2	2	Arb	F	C
<i>Thraupis episcopus</i>	5	4	2	Arb	O	O
<i>Thraupis palmarum</i>	5	4	2	Low	O	O
<i>Ramphocelus carbo</i>	5	3	2	Arb	O	O
<i>Piranga flava</i>	1	3	2	Arb	O	C
<i>Cyanicterus cyanicterus</i>	5	4	2	Arb	O	C
<i>Tachyphonus phoenicius</i>	5	3	3	Arb	I	I
<i>Nemosia pileata</i>	2	3	2	Arb	I	C
CARDINALINAE						
<i>Saltator maximus</i>	5	4	2	Arb	O	O
<i>Saltator coerulescens</i>	4	4	2	Arb	O	O
<i>Periporphyrus erythromelas</i>	2	4	2	Arb	F	M
EMBERIZINAE						
<i>Oryzoborus angolensis</i>	4	2	2	Gro	G	O
<i>Oryzoborus crassirostris</i>	3	2	2	Gro	G	I
<i>Sporophila americana</i>	1	2	3	Gro	G	O
<i>Sporophila lineola</i>	2	2	3	Gro	G	O
<i>Sporophila castaneiventris</i>	4	2	3	Gro	G	O
<i>Volatinia jacarina</i>	1	2	3	Gro	G	O
<i>Zonotrichia capensis</i>	2	3	2	Gro	G	I