Bird diversity and selection of protected areas in a large neotropical forest tract

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Abstract. The unbroken primary rain forest currently covering the interior of French Guiana still offers a unique opportunity to establish a network of large protected areas. Bird species richness was surveyed within 20 study areas spread over the country to assess the relative abundance and frequency of occurrence of forest interior and natural gap taxa (391 species, excluding raptors and non-resident birds). Richness, rarity, restricted range, hot spot and conservation value algorithms were used to rank sites in decreasing orders of importance and draw sets of survey sites likely to maximize bird diversity. In most sets from different methodological approaches, the southern region consistently emerged as a priority area for conservation, with the central mountain range contributing some specialized taxa and the northern region incorporating additional species, mostly from marginal habitats and more typical of the nearby coastal zone. Estimates of areas likely to preserve an almost complete sample of the regional biodiversity amounted to about 1–2 million hectares, either in one large area (national park) or divided into 2–3 reserves overlapping regional hot spots. However, representation of all species and habitats in a protected area system is not an assurance of long-term viability when minimum viable population sizes and demographic patterns are little known, and when the risks and impacts of persistent human disturbances such as mining, logging and hunting are growing.

Introduction

Designing networks of protected areas for the conservation of species assemblages is a frequent concern, and a way to minimize the mounting loss of natural habitats and biodiversity. Although it is recognized that most species cannot be conserved only within a few restricted areas, focusing conservation efforts on a selection of priority sites with limited human pressure is still a widely used approach because of its efficiency and ease of implementation. It must also be a critical element of any large-scale policy of land use planning, even in the few countries where it is not yet an urgent need.

Such an opportunity is available in French Guiana, whose interior is largely free of human settlements and covered with a continuous primary rain forest. In that case, the question is where to establish protected areas, and how large they should be, in a seemingly uniform and unbroken forest blanket. This is a different question than in the usual situation where representative areas have to be chosen among distinct forest patches resulting from the previous fragmentation of the original forest cover (Kirkpatrick 1983; Bedward et al. 1992; Pressey et al. 1993). The

challenge is to identify the most critical areas and to define the most appropriate number and sizes of reserves to maintain viable populations of every species (Diamond 1978; Shaffer 1990; Schwartz 1999). This selection must ideally include all habitat types and can be either a network of several reserves or a single large national park encompassing a number of complementary sites. Both strategies were already pledged in French Guiana by the establishment of two forest natural reserves and a large national park project. With those ends in view, systematic local inventories were conducted throughout the country to obtain representative samples of biodiversity in the main sectors of Guiana and use them to support the designation of the most suitable areas for long-term conservation.

The theoretical basis and usual approach to design such conservation schemes are founded on the pattern of species turnover across landscapes or along environmental gradients. The mosaic of different natural habitats, specific communities and patch sizes results in variable population sizes, dynamics and viabilities. Hot spots of species richness, rarity or endemism may be identified and used to define priority areas (Curnutt et al. 1994; Lombard 1995; Balmford 1998; Reid 1998). Complementary measures can be applied to include additional sites and to have most species represented in the network design (Williams et al. 1996; Howard et al. 1998; Reyers et al. 1999). Since global biodiversity is almost impossible to fully assess, a substitute must be used that can be surveyed within a reasonable time and cost (Noss 1990; Belbin 1993; Williams and Gaston 1994, 1998; Faith and Walker 1996), although the choice of a particular surrogate of biodiversity may influence the site selection (Ryti 1992; Prendergast and Eversham 1997). Birds are often used as indicator taxa because they are well known, easy to census, charismatic and they have been found to be among the best surrogate taxa for biodiversity in conservation area planning (Saethersdal et al. 1993; Gaston 1996; Reyers et al. 1999). A gap analysis may also ensure a better representativity and viability of the taxon studied within the selected areas (Scott et al. 1993; Kiester et al. 1996; Flather et al. 1997).

Large-scale predictive geographical models are used to simulate the spatial distribution of species along environmental gradients and to draw the potentially richest areas (Guissan and Zimmermann 2000). This was not feasible at the scale of this study because too few relevant environmental information was stored in Geographical Information Systems at the required spatial resolution, and little came from the actual study sites which were often in previously unexplored areas. Predictions of species abundances from a mapping of natural habitats were unlikely to be reliable because boundaries between vegetation types were rarely sharp or even visible on aerial photographs and no consistent gradient could be documented among heteregeneous local habitat mosaics.

Reserve selection principles

The guiding principles in nature reserve selection have been defined by Margules and Usher (1981) and Pressey et al. (1993). A set of reserves must be comprehensive (i.e. sample the full range of biodiversity), adequate (i.e. include enough individuals and area to ensure population viability) and representative (i.e. include

all the regional species pool). Objectives involve methodological principles: *complementarity* (i.e. an additional area should contribute the most previously unrepresented taxa), *efficiency* (i.e. minimize duplication of species in reserve selection), *flexibility* (i.e. allow alternative areas to be substituted in a system if they are equivalent) and *irreplaceability* (i.e. the degree to which a site makes a unique contribution). The complementarity approach may be applied to maximize species number (richness), rarity (extinction risk) or frequency of occurrence (distribution or endemism). Rodrigues et al. (2000) gave specific meanings to flexibility, i.e. representing each species ≥ 1 time(s) in the minimum number of sites or in the minimum area, and including a given percentage of the range, or of the population, of each species in the minimum area. Also, efficiency involves optimal and heuristic solutions that can be applicable to many situations. Finally, solutions should be accountable, i.e. explicit, to be easily explained and defended.

I shall use the context of a huge tract of Amazonian rain forest, sampled across a substantial number of widespread survey sites. Only birds will be considered, although plants, amphibians and large mammals were also surveyed, but not as extensively as birds. There will be no considerations of constraints to the design of reserves (location, size) other than ecological guidelines, since most survey areas were uninhabited and marginally threatened in the long term, if at all, by hunting, logging or mining.

A first analysis (Thiollay 2002) had shown that the overall bird species richness (442 resident species) was high and not significantly different between the three main regions of French Guiana, from north to south. There was, however, a relatively high turnover rate in species composition among the 20 survey areas and a low level of nestedness between poor and richer samples. This was probably related to the large proportion of rare species and the low detectability of many of them. Moreover, no general correlate of rarity could be found across species or guilds. I used a smaller subset of species from comparable transect counts on 20 sites to define a conservation strategy of the bird community in the forested interior of French Guiana.

Methods

Study area

The interior of French Guiana (about 90% of the country, i.e. >80000 km^2) is covered with a continuous rain forest, sparsely inhabited, almost only along its borders. The main relief is a succession of hills and streams between 50 and 300 m, with a few bare granitic outcrops (inselbergs) 200–600 m high, and still fewer 'mountains' topped with forested lateritic plateaus, all ≤ 850 m. Mean temperatures are lowest during the January–June rainy season (21–22 °C) and highest during the August–November drier season (29–30 °C). Along a NE–SW axis, the annual rainfall decreases from 3500–4000 to ≤ 2000 mm (CNRS-ORSTOM 1979). This is the only known gradient, although it is generated by the spatial interpolation of data

from very few stations and it is not reflected by an obvious change in forest structure and composition from north to south.

The forest zone (2°30–5° N) was divided into three regions (Figure 1) on the basis of general geographical features. They were, respectively, about 120-, 90- and 130-km-wide belts and included 8, 6 and 6 sample sites.

- The most accessible northern region has high rainfall (3–4 m/year), medium elevation (100–300 m), some prominent isolated inselbergs, the only logged forest tracts, local agricultural developments and associated roads, limited gold
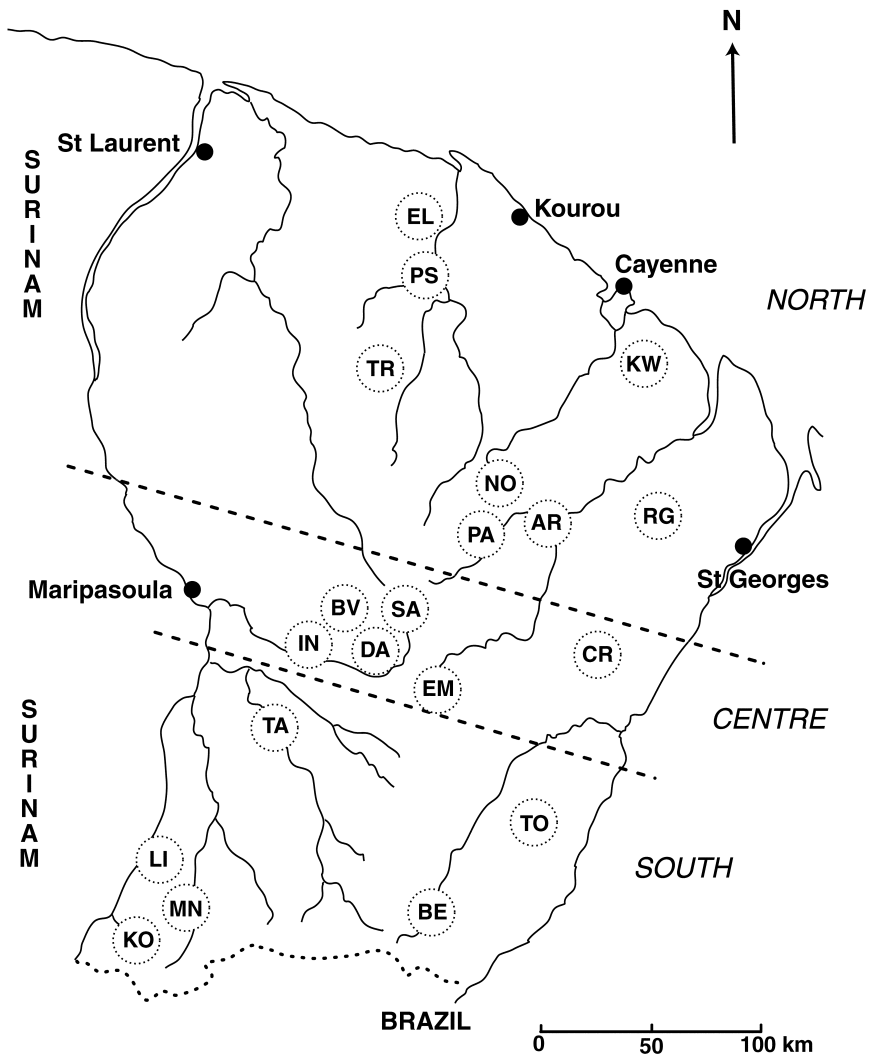

Figure 1. Study sites in French Guiana. The dotted lines divide the central from the northern and southern regions.

mining, but the highest overall hunting pressure. The survey sites (see Figure 1) were: NO – Nouragues field station; PA – Saut Pararé; AR – Camp Arataye; EL – Piste de Saint-Elie; PS – Petit Saut (Camp Saint-Eugène); TR – Montagne de la Trinité; KW – Montagne de Kaw; RG – Régina–Saint-Georges road.

- The central range, called Inini-Camopi, has the highest mean elevation, including all Guianan summits between 650 and 850 m, and the highest proportion of upper altitude vegetation (Table 1). It also harbours most gold mining areas and three settlements. Survey sites: CR – Pic du Grand Croissant; SA – Saül; EM – Massif des Emerillons; DA – Dachine; IN – Grand Inini river; BV – Montagne Bellevue.

- The most inaccessible southern part, used by Indians, has no commercially exploitable resources, and is earmarked for ecotourism and conservation. It has the lowest average rainfall (≤2.5 m), elevation (≤250 m) and hunting pressure, but includes 67% of all the Guianan inselbergs (>80, several of them between 500 and 700 m) and the largest floodplains. Survey sites: TO – Roche Touatou; BE – Mont Belvédère; TA – Saut Tampok; MN – Upper Marouini river; LI – Upper Litani river; KO – Koulé-koulé.

Two broad habitat categories were considered, between which bird species were partitioned: forest and natural openings, also called clearings or forest gaps. The continuous lowland primary evergreen rainforest (described in de Granville 1979; Blancanaux 1981; Hoff 1991) was the dominant habitat of every survey area (>95%). At a finer scale, it was a mosaic of different forest types, but all of them were usually well represented in each area, although in unequal proportions. The widespread 40–50-m-high orderly mature stands, on well-drained slopes and plateaus, frequently merged into a more disturbed forest with an increasingly lower, vine-loaded canopy and denser understorey, or even local patches of bamboo thickets. Palm swamp (*Euterpe*) forest occupied most valley bottoms, and wet stunted mossy forest occurred on lateritic shields on few isolated summits. Small watercourses of variable size were frequent everywhere.

Table 1. Regional pattern of large-scale habitat diversity and environmental variables in the forested interior of French Guiana.

	North	Centre	South
% Area of low dry forest on rocks	0.38	1.74	0.16
% Area of wet submontane forest	0.12	1.64	0.37
% Area palm swamp or seasonally flooded forest	5.40	3.57	3.11
% Area between 300 and 850 m	1.8	19.3	0.4
Number of granitic inselbergs/100 km^2	0.83	1.24	3.36
Number of rivers[a] across an east-west transect (per 100 km)	10.3	7.9	9.5
Mean (extremes) annual rainfall (mm)	3100 (2000–4000)	2500 (2000–2800)	2100 (1950–2500)

[a] >25 m wide. Only large, well contrasted patches of distinctive woodland types in the matrix of taller upland forest are cited here, but not the numerous and loosely limited stands of bamboos, vine tangles, or small swamps.

Within this forest matrix, each survey site also included one or more types of large natural openings. They were usually successions of lower and more open vegetation belts, associated either with granitic inselbergs or rivers, i.e. respectively dry, low forest stands (*Clusia, Myrtaceae*) on rocky outcrops and patches of grass or spiny bromeliads at the top of inselbergs, or riverine forest and, less often, lower marshy vegetation along streams. In the three outer northern sites, they were replaced by artificial gaps, i.e. forest roads, logging gaps and small clearings, and their associated secondary growths. Aerial photographs and ground surveys in other areas confirmed that the sample sites were representative of the regional forest types and that all natural habitats were represented two or more times in the study areas selected in each region.

Site selection

The distribution of the 20 survey sites was equivalent to a random sampling design aimed at covering the main sectors of the interior of Guiana. Most areas were previously unknown and had to be selected on the basis of logistical constraints, i.e. accessibility by helicopter or boat. Except for the initial landing site (inselberg or river), there was anywhere an equal probability to find any forest type, bird community or particular species in every site. The sampling procedure was stratified as much as possible, i.e. to survey as many sites and similar numbers in each region, including either an inselberg or a river. Sites were distributed in such a way that in a 20×20 km (400 km^2) grid cell superimposed on the country map, there was never more than one sample plot per cell. Overall, $20/190$ of these arbitrary squares were thus sampled, i.e. 11% of the forest interior of French Guiana.

All but four sites were in virgin forest far from any trail or clearing and were visited only once during the main breeding seasons (September–December and March–April), for 14–23 full days each, between 1983 and 1998. Additional species records from longer field studies at some sites were not taken into account to allow meaningful comparisons between sites. The convex polygon defined by outermost sites encompassed half of the Guianan forest area (320 km from north to south between extreme sites), of which 1% was actually surveyed. Botanists, participating in all surveys, confirmed that there were no consistent and critical differences in average forest structure and overall tree species composition among regions of French Guiana, even if many individual plant species were found in only one or few sites. Therefore, I assumed that neither habitat features nor the relatively narrow range of elevation (700 m), latitude (2°5) and annual rainfall (<1.5 m) were likely to explain differences in bird communities among sites, although none of these variables could be accurately measured across all sites. Terborgh and Andresen (1998) also did not find significant forest composition changes within such small regions in Amazonia.

Census technique

At each locality, a single campsite was established, around which daily surveys were conducted in every direction along random line transects, as straight as possible

through the understorey, mainly within a 3-km radius, i.e. dawn to dusk return walks. The total area actually covered at each site was at least 2000 ha, including all locally existing forest types, as well as clearings associated with rivers and/or inselbergs, according to the locality.

Extensive transect-counts were preferred to point-counts because the aim was to record as many birds and species as possible over the largest possible area. Along the unlimited-length transects, 1–2 observers walked very slowly (<1 km/h), with frequent stops, recording every bird, seen or heard, that was perched within 25 m of the walking line at any height. Each morning transect was different and walked back in the afternoon. Only species records were used, the number of individuals involved at each record being sometimes difficult to assess. Successive records were spaced to rule out double counts. Only the highest number of contacts per species during one of the two daily passages was kept. The goal was to assess the relative frequency of species, not a density estimate, and the narrow strip minimized biases against the least detectable species. After summing the daily totals, I used the number of sightings/1000 species-records at each site to allow for differences in sample sizes between sites. Any index related to distance or time would have been more dependent on bird detectability, which was affected by speed, weather, hour and vegetation. Though dependent on the frequency of other species, this index usually proved to be correlated with apparent abundances. The underestimated abundance of the few species living in flocks (a flock or a solitary bird were both a single record) was compensated for by the higher conspicuousness and mobility of flocking birds.

Forest opening species could not be recorded along similarly extensive transects because of the limited extent of open patches. Therefore, I searched all accessible clearings, and within each patch, I attributed to each species a frequency score from 1 (rare) to 4 (abundant) and I averaged the daily values over all patches of a given type.

A number of species were excluded from the data set:

- all diurnal (Falconiforms) and nocturnal (Strigiforms) raptors, i.e. 39 species, because they were censused using different methodologies and they will be analysed elsewhere over more sampling sites;
- all migrants, occasional, vagrant or marginal species in the forest zone of French Guiana, as well as some species whose identification could not be confirmed;
- nine resident species were removed because they were only seen outside census periods, on sites repeatedly visited.

I used only the actual number of species recorded within the restricted area and period of each site survey, because correcting for sampling biases by computing an estimated species richness was only possible on understorey transects, and not in the more opportunistically surveyed clearings.

Species distribution and abundance

Detection probabilities, diversity indices, turnover rates and levels of nestedness

between sites were computed elsewhere for a detailed community analysis (Thiollay 2002). I focused here on the main components of species distribution, i.e. their local and regional occurrence and relative abundance.

On the basis of previous experience and lists of species encountered in different habitats, species were classified as *forest species*, i.e. mostly, if not only, recorded on understorey line transects, or *open habitat* or *edge species*, i.e. almost only recorded in or along forest clearings (inselbergs, watercourses, roads), and associated dense second growths, wetlands or rocky areas. Some forest canopy species were also found along edges or even in clearings. At each site, an abundance index was attributed to forest species (number of sightings/1000 species records) and an abundance score to open habitat species (1–4). The percentage of sites where the species were recorded, irrespective of abundance, was used as an occurrence index. For species of clearings, restricted to a single habitat type (e.g. rivers or rocky inselbergs), this occurrence was calculated on the number of sites where their specific habitat actually occurred. This further reduces the number of rare species. However, because even in most intensive, but relatively short, rain forest surveys, some species may be missed, or their abundance underestimated, I used a conservative definition of rarity.

Rare species were those that had both a low mean abundance index over the sites where they occurred (<3/1000 records or the lowest score) and a low rate of occurrence (in <50% of all sites, or in ≤4 suitable sites for species associated with rivers or inselbergs). According to this definition, rare species did not necessarily exhibit all classical components of rarity (Rabinowitz et al. 1986), e.g. many of them did not have a narrow habitat distribution, nor a restricted geographic range, and their low local density was probably among the highest possible in a natural habitat.

Endemic species were species whose world distribution range was limited to the Guianas or at most to the Guianan Shield, i.e. the northeastern corner of the large Amazonian region (Meyer de Schauensee and Phelps 1978; Ridgely and Tudor 1989–1994). Almost all species had a comparatively wide distribution over French Guiana and could theorically occur in any patch of suitable habitat. Therefore, I did not consider low occurrence species as restricted-range species, unless all records were concentrated in a particular area. I also did not compute restricted-range scores for whole communities or regions (Kershaw et al. 1994).

Restricted-range species were those absent from at least one of the three regions dividing the interior of Guiana. Again, a conservative definition excluded from this category the marginal species restricted by habitat availability or observed in additional regions outside census periods, or inconspicuous and too likely to be missed. Many of the local species, not considered to have a restricted range in Guiana's interior, in fact mainly occurred in coastal wetlands or savannas, and marginally entered the forest zone (mostly the northern part) in suitable habitats.

Reserve selection procedure

I used four different approaches according to different conservation objectives and leading to different sets of priority sites.

(1) The most classical aim is to select the minimum number of sites necessary to include every species of the full regional set at least once. This does not rank the sites in a priority sequence, but follows the principle of complementarity (Vane-Wright et al. 1991) that seeks to minimize the number of reserves. It is the most widely used (Margules et al. 1988; Pressey et al. 1993; Howard et al. 2000), though it was criticized on mathematical grounds because of suboptimal algorithms that do not allow sites to be dropped from the priority set once they have been selected at an earlier iteration (Underhill 1994). Two complementarity iterative algorithms were used. The richness-based procedure first selected the most species-rich site, and then sequentially included sites that added the most unrepresented new species at each step (Kirkpatrick 1983; Saethersdal et al. 1993; Howard et al. 1998). The rarity-based algorithm also proceeded in a stepwise fashion, starting with sites containing species represented only once in the whole set, i.e. irreplaceable sites. Then it progressively added sites which contained the rarest unrepresented species (Margules et al. 1988; Nicholls and Margules 1993). At each new step, I selected from all sites where the rarest unrepresented species occurred, the site contributing the maximum number of additional unrepresented species, and, where two or more sites contributed an equal number of additional species, I selected the most species-rich.

The same heuristic stepwise algorithm using the mere presence/absence in the sample sites was run to select a network where all species were represented two or more times, thus excluding the rarest ones. It began by the rarest species represented only twice in the data matrix, then it selected remaining sites containing still unrepresented species on the same basis. The frequency of occurrence has a high conservation value, since it is an insurance of long-term persistence in a network of areas.

(2) Another goal was to get the highest biodiversity (greatest number of species) within the smallest area (fewest possible sites). I applied this 'hot spot' strategy to each of the three subregions where I selected a set of three sites, together including the highest number of species. Such hot spots could suggest suitable areas for reserves. Identifying hot spots of species richness which contain the highest number of species records per grid cell is a first straightforward approach to define suitable reserves, i.e. the most effective at representing the largest number of species within the fewest grid cells (Lombard 1995; Williams et al. 1996; Reyers et al. 1999).

(3) Although more sophisticated assessments may be used (Williams and Araujo 2000), the abundance index alone may be a reliable indicator of a species persistence probability or population viability. As a result, a site where a species is more abundant than in another site has presumably a higher conservation value, and the higher the number of species at their top abundance it contains, the higher the conservation value of a site. In such an algorithm, the first site to be entered in the selection process is the one where most species reach their highest abundance score. I selected for each species the two sites with the highest abundance score and I ordered the sites in order of decreasing total species abundance.

(4) Habitat representativeness (Margules et al. 1988) and occurrence of species in each vegetation type (Margules and Nicholls 1987) are other criteria used in reserve selection. They were not appropriate here because all sites were covered with forest, including most forest types that were not clearly separated along the transects where

birds were continuously recorded. Only main open habitat types were differentiated, with their specific set of specialized taxa. Instead, I used an iterative selection approach based on site scoring derived from criteria relevant to conservation areas, independent of the species represented (Kershaw et al. 1994; Howard et al. 2000). The sites were ranked using broad attributes: total species richness, number of restricted habitat types, and disturbances from logging, gold mining or hunting. The existence of uncommon habitats was an indicator of the potential presence of habitat specialists, and disturbance criteria were likely threats to vulnerable or sensitive species. I began to select sites that were both richest, with highest habitat score and no disturbance. Then I added species and habitat-richest sites with increasing disturbance, then repeating the process with successively lower habitat scores and finally the lowest richness score. Thus, in this decreasing order of prioritization, sites were ranked according not only to their species richness and habitat diversity, but also to present or future threats to at least some sensitive components of their bird communities. This procedure allowed either to identify the subregion where top sites occurred, or to search for a small set of neighbouring sites with the highest cumulative score that should be included in a protected area.

A coefficient of site similarity was calculated over the five sets of sites derived from different approaches, as $5C/(\Sigma N_i) \times 100$, where C was the number of sites common to the five sets and N_i the first 10 sites of each set (Able and Noon 1976).

Results

Species richness algorithms

The conservative data set used here (resident, non-raptor species on 20 sample sites surveyed during limited periods) included 391 species, i.e. 267 forest taxa and 124 edge species, whereas 442 species were recorded in these sites (Thiollay 2002). The high taxonomic diversity (1.9 species/genus, 8.5 species/family) emphasized the conservation value of this bird community.

Average sites (11) had 230–259 species (Table 2). The positive correlation between sample size and observed richness ($r = 0.607$, $P = 0.004$) partly explained the four lower (165–206) and five higher counts (269–293 species). The mean species richness of a single site was 242 ± 32 species, i.e. 62% of the whole regional set (extremes $= 42$–75%). Compared with this pool, fewer species (26) were missing from the southern region than from the central (43) and northern (35) regions. Thus, the 6–8 sites of each region contributed 89–93% (348–365 species) of the whole species set. Every site had 7–47 species unrepresented in the richest site (SA). Each region had one of the most species-rich sites (NO, SA, MN, 283–293 species) and the mean numbers of species of the three richest sites of each region were not significantly different between regions (North $= 267$, Centre $= 255$, South $= 272$, Mann–Whitney U test, $P = 0.513$).

Using a species–area relationship approach, I reckoned the species recorded at least once in five sites randomly drawn from the whole set of 20 sites, repeating the

Table 2. Site scoring for conservation value.

| Study sites | Forest | | Gap species (b) | Scores | | | | | Total (h) |
	Sample	Species (a)		Richness (c)	Habitat (d)	Logging (e)	Mining (f)	Hunting (g)	
NO	3	245	40	2	I	2	2	2	9
PA	3	221	47	2	R	2	2	2	9
AR	2	200	42	2	R	2	2	2	9
EL	3	193	54	2		1	1	1	5
PS	1	181	52	2	R	2	1	1	7
TR	1	178	28	1	I, M	2	2	2	9
KW	2	183	52	2		1	1	1	5
RG	2	207	39	2		1	2	1	6
CR	2	195	43	2	I	2	2	2	9
SA	3	228	65	2	M	2	1	1	7
EM	1	164	25	1	I	2	2	2	8
DA	2	195	38	2	I	2	1	2	8
IN	1	188	42	2	R	2	1	1	7
BV	1	154	11	1	M	2	2	2	8
TO	1	168	31	1	I	2	2	2	8
BE	2	217	57	2	I, R	2	2	2	10
TA	1	191	58	2	R	2	1	1	7
MN	2	212	71	2	I, R	2	2	2	10
LI	1	193	52	2	R	2	2	1	8
KO	2	199	60	2	R	2	2	2	9

Site initials: see text and map. Sample size: 1 = small (1000–1264 forest species records); 2 = medium (1403–1704 records); 3 = large (3259–6264 records). (c) = observed number of species on forest strip transects (a) + gap habitats (b) 1 = 165–206 species; 2 = 230–295 species. (d) restricted open habitat types within the study area: I = inselberg, M = submontane forest, R = large river; score 0–2 (number of types). (e) 1 = forest logged or planned as production forest; 2 = undisturbed primary forest. (f) 1 = recent or current gold mining activity; 2 = no mining. (g) 1 = frequent hunting; 2 = rare or no hunting. (h) = sum of five scores.

process 10 times. Totals of 348–379 species were recorded per set of five random sites, i.e. 89–97% of all the species. The same procedure was repeated with randomly selected sets of 10 sites producing 91–99% of all species.

When using a richness algorithm, starting from the richest site and listing sites that successively added the highest number of previously unrepresented taxa, a minimum of five sites were necessary to include 95% of the regional pool at least once: SA (293 species), MN (+47), TA (+13), PA (+9), KW (+9). The next sites were BE (+5), NO (+3), AR (+3), CR (+2), DA (+2), IN (+2), PS (+1), EM (+1). Again, sites of all three regions were equally represented in this top selection.

Instead of mixing sites over a very large area, a more realistic way to locate reserves is to identify actual hot spots of species richness. Therefore, I selected in each region the three closest sites including the richest one. Thus, three regional hot spots emerged: NO + AR + PA in the north, including together 319 species (they were all within the main current forest reserve), SA + DA + IN in the centre (336 species) and LI + MN + KO in the south (333 species). However, each set only comprised 89.6, 96.5 and 91.2% of their respective regional bird populations. To

improve the regional representativeness of such hot spots, at least five sites (randomly selected) were necessary to include ≥99% of all species known from that region (10 simulations run in each region).

Rarity-based algorithms

According to criteria defined above (see 'Methods' section), one-third of all species (127) were rare, including 69 forest species (26%) and 58 open habitat species (47%). Among them were 13 species recorded only once, from nine different sites. Both these unique species and their sites were equally distributed in all three regions. A network that would contain every species at least once should include first the sites harbouring two of the unique species, then the sites with one such species, ranking the sites at each step in decreasing order of their total richness. The resulting list was as follows: 1/BE, AR CR; 2/SA, NO, MN, DA, PS, IN. Together, these nine sites included only 97% of all the species of the data set. It would be necessary to add 10 other sites to have all the species represented at least once. Ironically, the only site not appearing in this selection process (TR) was in one of the two current reserves!

However, unique species may be too rare to be representative or to have viable populations within a reserve. So, setting them aside, we can search for a network where all species could be represented at least twice. Starting with the 17 species occurring in only two sites, a first set of seven sites was necessary to include all of them at least once (MN, SA, KW, TA, NO, KO, EM) and nine additional sites to have them represented twice (BV, LI, CR, TO, EL, RG, AR, DA, IN). Two more sites (BE, PA) allowed to include two additional species not yet represented twice in the above sites. The only two still unselected localities (PS, TR) were again in the northern region, one of which in a reserve!

Abundance algorithms

Assuming that a site is all the more valuable for a species as the density of this species is higher, one may order the sites according to a cumulative abundance index. For each species, I recorded the two sites where its abundance was highest (up to four sites in case of *ex aequo*). Then I summed the number of records for each site. The 10 top sites (63%) included five southern, four central and only one northern site (SA, LI, MN, EL, BE, TA, CR, BV, KO, IN). The last five sites (PA, AR, TO, PS, TR) comprised only 14% of the highest abundance records and were mostly northern sites (4/5), the lowest one being TR, already cited at the last rank in previous algorithms.

Restricted range and endemic species

Few species had really restricted ranges in the forest zone of Guiana. I excluded those mostly, if not only, found in the northern part into which they just marginally extended their range, from the non-forest habitats of the coastal zone where they had

their core distribution. Only five rare species were restricted to the northern and central regions (*Iodopleura fusca, Euphonia cyanocephala, Eucometis pennicillata*) or to the central and southern regions (*Forpus sclateri, Neopelma chrysocephalum*). Four, at least locally abundant species, were also found almost exclusively in the southern half of the country (*Ara severa, Myrmoborus leucophrys, Henicorhina leucosticta, Zonotrichia capensis*), while two others were restricted, at least for breeding, to the forests at the highest elevations (*Piranga flava, Procnias alba*). Some taxa, typical of the coastal marshes and palm forests, are currently localized in the forest zone to remote southern areas where their habitat is well represented, and where hunting pressure is minimal (*Ardea cocoi, Cairina moschata, A. ararauna, Tyranopsis sulphurea*).

Of the 18 so-called endemic species, whose global distribution is restricted to the Guianas, 10 were classified as rare, and eight were widespread and at least locally common (*Phaethornis malaris, Sakesphorus melanothorax, Herpsilochmus stictocephalus, Myrmerciza ferruginea, Pipra serena, Corapipo gutturalis, Tyranneutes virescens, Contopus albobularis*).

No species in our study set is globally threatened and only one (*Amazona dufresniana*) is near-threatened (Birdlife International 2000).

Ranking sites by conservation value

Species occurrence or abundance are not the only criteria for the design of nature reserves. Habitat diversity and human disturbances are potential determinants of species richness and population viability. The habitat diversity was measured by the number of open habitat types included in the matrix of lowland forest of each site. Then, I listed the occurrence of three main categories of anthropogenic disturbances (past, current or future threats) without assessing their relative importance or influence. These variables were scored, then summed, although their respective scores do not have an equivalent meaning or value (Table 2).

The mean total scores of sites increased, though not significantly (Mann–Whitney U test, $P = 0.207$) from the northern (7.37 ± 1.72) to the southern region (8.67 ± 1.10), suggesting that the average species and habitat diversity increased slightly, and that the human pressure tended to decrease, from north to south.

Representing all species in at least one site, or above a given level of abundance or occurrence led to different sets of sites. The coefficient of similarity was low (20%) between the sets of 10 sites selected by each procedure (Table 3). Only two sites were common to all sets (MN, CR), two sites never appeared in this top selection (RG, TO) and four sites were mentioned only once (EL, PS, TR, EM). The low priority sites were mostly from the northern region (4/6), whereas the highest priority sites (listed 4–5 times in Table 3) were all in the South (MN, BE, KO) and Centre (SA, CR). The mean number of times a site from the northern, central or southern regions appeared in the five sets was, respectively, 1.7, 2.1 and 3.2. Again, this suggested that the mean conservation value of an average area tended to be higher in the south than in the north of Guiana. Moreover, the rank of sites in each selection should be taken into account. If a value of 10 is given to the first site of

Table 3. First 10 most valuable forest sites for conservation in Guiana according to different criteria.

Ranking base	Sites in decreasing order of conservation value									
Site richness	SA	MN	TA	PA	KW	BE	NO	AR	CR	DA
Species rarity	BE	AR	CR	SA	NO	MN	DA	PS	IN	KO
Species double occurrence	MN	SA	KW	TA	NO	KO	EM	BV	LI	CR
Specific abundance	SA	LI	MN	EL	BE	TA	CR	BV	KO	IN
Conservation score	MN	BE	NO	PA	KO	AR	CR	TR	LI	DA

each set, down to one for the last one, the cumulative scores of each site ranged from 3 to 42 and the top five sites were MN (42), SA (36), BE (30), NO (24) and TA (20). Besides the two sites most intensively studied (SA, NO), three southern sites stood out again.

Estimating reserve size

To estimate the minimum size of a single reserve where the largest possible proportion of the regional species pool would be represented, I measured the total area of the convex polygon defined by the outermost 20×20 km^2-grid cells containing a study site, i.e. 44 000 km^2. If one assumed that study sites were randomly selected, as far as their species richness was concerned, then each of the 20 sites was equivalent to an equal share of the whole study area. If 5–10 such sites were necessary to include most species (see Results), then a conservative estimate of the area likely to include a full bird community representative of the Guianan forest zone studied should be 44 000 km^2 $\times$ 5 (or 10)/20, i.e. 11 000–22 000 km^2, according to the proportion of species required.

An alternative approach would be to select a representative area within each of the three main regions since their bird communities have been shown to differ slightly. The areas (A) of the convex polygons defined by the grid cells containing the outermost study sites were respectively 19 000, 8000 and 16 800 km^2 in the northern, central and southern regions. Using a random selection of three or five sites per region to allow for the representation of ≤95% or ≥99% of the local species pools, the estimated size of a protected area would be $A \times 3$ (or 5)/6 (centre, south) or >8 (north), i.e. 7200–12 000 (north), 4000–6600 (centre) and 8400–14 000 km^2 (south). However, there is still no evidence that every species would have viable populations in the long term within even such large areas.

Discussion

Species attributes

Because of a high species diversity, patchy distribution and variability of abundances, all complementarity approaches led to the selection of a relatively large number of sites, although there was little similarity in their order of priority between

different algorithms. The conservation value of species, more than their mere number, should be the main criterion for the selection of a protected area. Rarity was used as an indicator of conservation value. Abundance and frequency of occurrence, which were both involved in the definition of rarity, are often correlated (Gaston et al. 2000), but this positive relationship did not hold for every species in our data set. These two components may have different implications for the long-term persistence of a species (local abundance vs. wide distribution). Probably many cases of apparent absences in individual localities were actually due to limited sample sizes, and to the very low density or patchy distribution of the unrecorded species. However, such undetected taxa, whose inclusion would have altered the results, were unlikely to be of major conservation value since they were presumably those with the lowest, and hence the least viable, populations. Yet, rare species are also likely to be the most vulnerable taxa, and they are often indicators of rare habitat types of special conservation concern. Therefore, protected areas designed to accommodate them are likely to be large enough to include also larger, and hence more secure, populations of common species.

The critical goal of a reserve is to harbour viable populations of most species. The dispersion and demographic parameters on which population viability is estimated are virtually unknown for the species involved here. Nevertheless, many of them may be naturally rare, i.e. may well persist for long periods at low densities or with patchy distributions. A minimum viable population size was originally estimated by the 50/500 rule (Franklin 1980). The 50 individuals refer to the effective population needed to prevent serious inbreeding depression and to ensure high levels of genetic diversity. The 500 individual mark was required for long-term maintenance of additive genetic variation as a balance between drift and mutation. Although this is now considered too crude (Templeton 1995), there is still no generally applicable rule. Assessing population size requires an estimate of specific average densities. From data obtained for 248 species on a 1-km^2 plot of unbroken primary forest at the Nouragues site (Thiollay 1994), I computed a local density value for all forest species. In short, 59% of them had an average density <1 pair/km^2. This suggested that an area of primary forest, taken at random, and likely to harbour at least 100 pairs of any of these species, should be well over 100 km^2.

Forest-dependent species are those which are targeted when designing forest reserves. Yet, 32% of species in our data set were made up of edge species that included a high proportion of rare taxa, mostly because of their low frequency of occurrence due to the patchy distribution of their habitats. Some of these open habitats and their associated species were found only in the forest zone (e.g. inselbergs), but a majority of them had a higher frequency and extent in the coastal area (e.g. palm swamps, marshes, edges, secondary growth, . . .). Not only open habitat species may be more numerous outside the study area, but even within the forest zone, they would be better protected by a network of small reserves matching the distribution of their limited habitats, provided they move readily between suitable patches to maintain their metapopulations.

Attributes other than the conservation status, geographic distribution, rarity or habitats specialization have been applied to assess the value of taxa in a bird

community and to rank different protected areas, e.g the taxonomic distinctness of the species involved (Daniels et al. 1991). The game status is particularly relevant in Guiana where heavily hunted species may become locally extinct (Thiollay 1985). Their presence in a protected area is more significant than that of naturally rare species not otherwise threatened. Thus curassows (*Crax alector*), trumpeters (*Psophia crepitans*) and macaws (3 *Ara* spp.) are still common in most study sites, but are now rare or absent in the northern-most sites.

Land use planning and the design of protected areas

The first goal of this study was to identify the most suitable area(s) to set up one or more reserves, or a national park, within a huge, continuous forest zone, little disturbed for the time being. For land use planners, the question was also to use such a protected area for the development of ecotourism. Most areas far from the coast are not readily accessible, but the southern (most inaccessible) region is claimed by indians as traditional land.

Most analyses indicated that the southern region was the potentially richest area, or at least likely to include species-rich spots more often, and also species of conservation concern. Even though the difference with the other regions was not large, the trend was consistent among various algorithms used, and the lower sampling pressure in the south (no intensively surveyed site) made the results all the more significant. This region also had the highest frequency of both inselbergs and flood plains, and consequently the highest diversity of open habitat species (on average 55/site vs. 37/44 elsewhere, Table 2). The lower overall hunting pressure and gold mining potential, and the low risk of large-scale logging in the future due to its remoteness are additional factors increasing the long-term conservation value of the southern third of the country, compared with the northern parts.

A majority of birds have low densities, further reduced by variable abundances, uneven distributions and habitat patchiness. In the largest current reserve (Nouragues, 100 000 ha), intensively surveyed (three study sites, including all habitat types from rivers and swamps to inselbergs), 72 species (i.e. 18.4% of the sample bird community) were never recorded on the transect counts.

The species–area relationship has a major relevance to conservation practice and reserve size (Williamson 1988) when it is coupled with minimum viable population size, persistence time and autoecological requirements (Shaffer 1990). However, measuring the determinants of population viability, from genetic and demographic parameters to catastrophic events and human interferences, has rarely been done (Shaffer 1987). Gap analysis, used with species assemblage data at different spatial scales, selects a reserve system, maximizing the representation of a set of species (Scott et al. 1993; Kiester et al. 1996).

A country wide conservation goal should be to preserve long-term viable populations of every species and complete bird communities in a full set of natural habitat types, preferably with replicates to allow for recolonization after stochastic extinctions. This also implies the maintenance of natural disturbance regimes at all scales and minimizing human impacts. The representation of all habitat types would

also buffer climate changes, especially a projected increased frequency of severe droughts.

Various estimates of the area necessary to include a full complement of the regional bird diversity consistently reached an order of magnitude of about 1–2 million hectares, either in a single reserve or divided into 2–3 patches. Any such large area, even if it was randomly selected, could include almost every habitat types, except submontane forests that are mostly found in the central range. Up to now, only two nature reserves have been established: the 1000-km^2 Nouragues Reserve (including NO, PA and AR sites) and the 760-km^2 Trinité Reserve (around TR). This study strongly suggests that, for a long-term conservation of every forest bird species, a protected area network in French Guiana not only should be based on a large national park across the southern and central parts of the country, but also should be complemented by additional reserves in the northern region.

Acknowledgements

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