Alternative Configurations of Conservation Reserves for Paraguayan Bats: Considerations of Spatial Scale

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Abstract: *The application of systematic and quantitative approaches to conservation planning is increasing, but the quality and quantity of data available to planners remains inadequate. We used two databases on bat species distributions at 25 sites in Paraguay to illustrate some of the effects of the spatial scale of sampling and data quality on decisions about reserve siting. We used a simulated annealing algorithm to identify alternative scenarios for comprehensive representation of the nation's bat fauna within a system of reserves and to evaluate the contribution of existing protected areas in Paraguay to this conservation goal. The location, efficiency, and level of protection (i.e., the number of populations of each species protected) were affected by both spatial scale and source of data. Our results suggest that systematic and intensive biodiversity surveys are an important element of efficient conservation planning for biodiversity conservation.*

Configuraciones Alternativas de Reservas de Conservación para Murciélagos del Paraguay: Consideraciones de Escala Espacial

Resumen: *La aplicación de estrategias sistemáticas y cuantitativas para la planeación de la conservación se está incrementando; sin embargo, la calidad y cantidad de datos disponibles para los planeadores es aún inadecuado. Usamos dos bases de datos de distribuciones de especies de murciélagos en 25 sitios en Paraguay para ilustrar algunas de las consecuencias de la escala espacial del muestreo y la calidad de los datos sobre las decisiones respecto a la ubicación de las reservas. Empleamos un algoritmo de templado simulado para identificar escenarios alternativos para la representación comprensiva de la fauna de murciélagos de la nación dentro de un sistema de reservas y evaluar la contribución de áreas protegidas existentes en el Paraguay para alcanzar esta meta. La ubicación, la eficiencia y el nivel de protección (por ejemplo, el número de poblaciones de cada una de las especies protegidas) fueron afectados tanto por la escala espacial como por la fuente de datos. Nuestros resultados sugieren que la sistemática y los monitoreos intensivos de la biodiversidad son elementos importantes de una planeación eficiente de la conservación para la conservación de la biodiversidad.*

Introduction

Many nations are now committed to implementing systems of nature reserves as a strategy for biodiversity conservation (e.g., McNeely et al. 1990; Myers et al. 2000). In this context, an important criterion for a reserve system is that it represents or comprises the full range of biodiversity within the region of interest (e.g., Pressey et al. 1993; Margules & Pressey 2000). By this criterion, a reserve system should contain, at a minimum, one example of every vegetation type and one population of every species present within the region of concern. Because social and economic factors constrain the amount of land that can be set aside for nature conservation, a set of identified sites should ideally achieve comprehensive representation of biodiversity at minimum cost (Pressey

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et al. 1993). Existing reserve systems throughout the world contain a biased sample of biodiversity (Margules & Pressey 2000) because reserve establishment has frequently been motivated by political agendas without explicit consideration of biodiversity representation goals. More systematic planning efforts are required to conserve the full complement of biodiversity, especially in developing nations where both human and conservation needs are pressing.

Operationalizing the representation principle in reserve-system design requires at least six steps: (1) identification of species, vegetation types, or other measures to use as surrogates for overall biodiversity; (2) quantification of representation goals for those features; (3) synthesis and analysis of suitable data on distribution and abundance patterns for the selected features of biodiversity; (4) assessment of the extent to which representation goals have already been met by existing reserves; (5) identification of additional sites to include in a reserve system to achieve unmet goals; and (6) consideration of important social, political, and economic constraints on placement of reserves (Margules & Pressey 2000).

Even when conservation planning efforts are systematic and quantitative, they often rely on whatever data are at hand, in part because conservation decisions seldom can be delayed until more data are gathered. But the extent to which reserve systems succeed at efficiently representing biodiversity can depend critically on the quantity and quality of data available for planning. Nonetheless, few empirical studies have explicitly evaluated the consequences of factors such as choice of database or the effect of the spatial scale of the database on the composition and efficiency of a national reserve system. Here we illustrate some of these potential consequences using two databases on bat species distributions at 25 sites in Paraguay (Willig et al. 2000).

Paraguay is a focus of increasing conservation concern because of its strategic position at the interface of several South American biomes and because it faces accelerating threats from anthropogenic activities (Redford et al. 1990; Keel et al. 1993; Yahnke et al. 1998; Willig et al. 2000). Moreover, mammalian diversity in the drylands of South America exceeds that of lowland Amazonian forests (Redford et al. 1990; Mares 1992). Historically, 85% of eastern Paraguay (138,000 km^2) was forested, but currently <22% of that original forest remains (Keel et al. 1993). Over the last 30 years, the federal government of Paraguay has identified land for inclusion within a system of parks (Yahnke et al. 1998; Owen 2000), and more than 1.5 million ha have been dedicated for conservation in national parks and private reserves (Willig et al. 2000). In Paraguay, though, as in most parts of the world, existing parks were not selected through a systematic effort of conservation planning based on representation principles. Consequently, more comprehensive inventories and analyses are required to evaluate the potential of the extant network of reserves to effectively conserve the country's biodiversity.

Yahnke et al. (1998) analyzed the effectiveness of national parks in Paraguay for conserving mammalian biodiversity, but their analysis was limited to only four sites. They relied solely on species-distribution maps (Redford & Eisenberg 1992) and museum records, rather than intensive systematic surveys, to determine species presence within particular parks. We have expanded on their study by using data from systematic field surveys and ad hoc museum collection records and range maps. Moreover, we analyzed data for eight protected areas and 17 additional sites throughout eastern and western Paraguay. We evaluated the extent to which decisions about reserve placement and assessments of the adequacy of biodiversity representation are likely to depend on the choice of a particular database (e.g., intensive, systematic surveys vs. museum specimens and range maps). We also considered how the scale of sampling used to determine species distributions may influence the efficiency of the resulting reserve system. Ecologists and biogeographers have become increasingly concerned about the effect of spatial scale on detection of patterns in nature, especially of patterns related to variation in diversity (e.g., Pastor et al. 1996; Lyons & Willig 1999, 2002; Waide et al. 1999; Gross et al. 2000; Scheiner et al. 2000; Willig 2000; Mittelbach et al. 2001). These concerns are relevant to the problem of selecting sites for incorporation into a reserve system because matching the spatial scale of the database to the spatial scale of the conservation decision may be particularly challenging when data are used opportunistically.

Methods

Databases

We used two databases containing presence and absence records of bat species at 25 sites throughout Paraguay. One set, hereafter referred to as the community database (data are available from M.R.W.), is the result of 2 years of systematic and intensive field surveys (Lopez-Gonzalez 1998; Lopez-Gonzalez et al. 1998; Owen 2000; Willig et al. 2000) and contains abundance data for 43 species of bats at all 25 sites. The other, called the faunal-pool database, contains records for 55 species and is derived from broad-scale distribution maps, as used in studies of macroecology and biogeography (Lyons & Willig 1997, 1999, 2002; Willig & Lyons 1998).

Records for the community database were obtained from surveys of bats conducted at 25 sites (Fig. 1), representing all major biomes, including many protected areas, and spanning salient gradients of moisture and temperature in Paraguay (Willig et al. 2000). The total number of sites was divided approximately equally be-

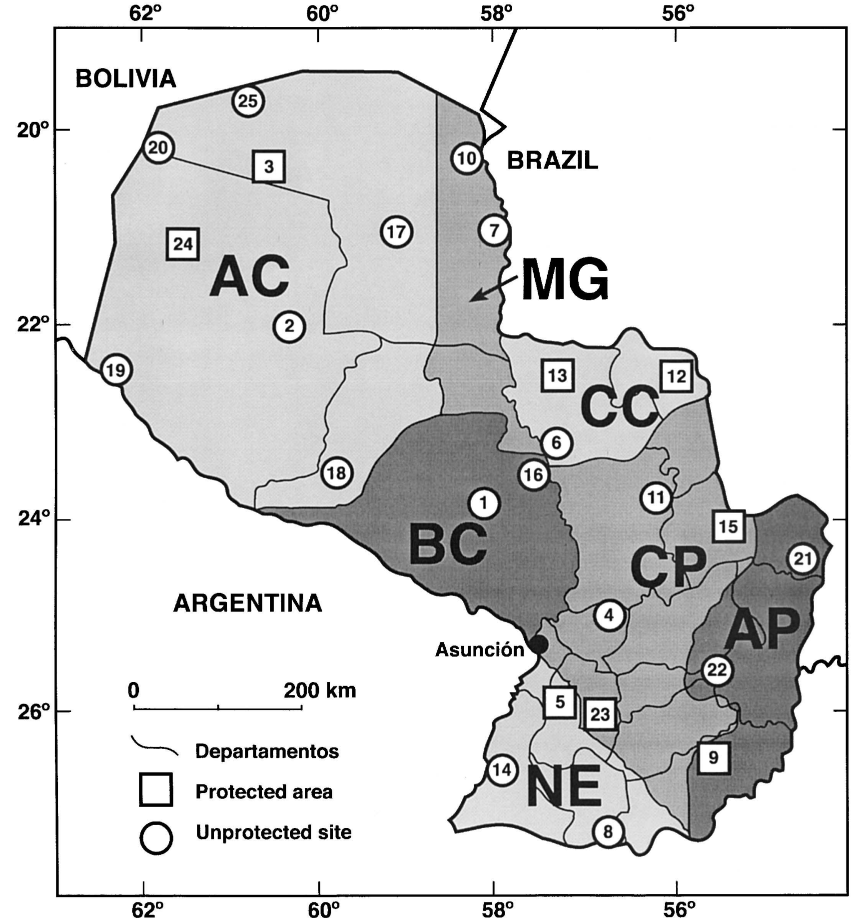

Figure 1. Map of Paraguay showing the location of 25 sites for which bat species composition was estimated based on a community database and a faunal-pool database. Shading identifies major biomes defined by phytogeographic considerations (Willig et al. 2000): AC, Alto Chaco; BC, Bajo Chaco; MG, Matogrosense; CC, Campos Cerrados; CP, Central Paraguay; AP, Alto Parana; NE, Neembucu. Protected areas are indicated by squares, and circles indicate unprotected sites. Numeric codes refer to site names as detailed in Table 1.

tween the eastern and western sides of the Río Paraguay because of the potential importance of the river as a biogeographic barrier (Myers 1982). To assess the efficacy of the current system of government reserves for the conservation of bats in Paraguay, seven federally protected sites (sites 3, 5, 9, 12, 13, 23, 24 in Fig. 1) and a site administered by the Moises Bertoni Foundation through government mandate (site 15 in Fig. 1) were included in the surveys. The primary goal of the surveys was to obtain a representative sample of the bats of Paraguay. Thus, measurements of the total area potentially suitable for conservation were not made, but the existing reserves that were surveyed ranged in size from approximately 5000 to over 61,000 ha. At each of the 25 sites, mist nets were erected within a circle with a 10-km radius, providing a minimum sampling area at each site of at least 314 km^2. Survey methods are described in detail by Willig et al. (2000).

The faunal pool of bat species for each of the 25 sites was obtained by locating each site on distribution maps constructed primarily from the work of Koopman (1982) and Redford and Eisenberg (1992). These distribution maps are based on museum records and expert knowledge of habitat requirements of bat species and were updated by recent systematics work in Paraguay (Lopez-Gonzalez 1998; Lopez-Gonzalez et al. 1998). If the mapped distribution of a particular taxon encompassed a site, that species was considered a member of the species pool.

Reserve-Selection Algorithm

We used a simulated annealing algorithm to identify representative and efficient reserve-system configurations. We applied the algorithm to the 25 sites where intensive sampling was performed, so it considered the maximum number of potential sites for the reserve network based on the data available. The algorithm is in the software program SITES (Andelman et al. 1999; Ball 2000) and is used by nongovernmental organizations and public agencies for conservation planning (e.g., Groves et al. 2000; Beck & Odaya 2001; Leslie et al. 2003). Simulated annealing is a minimization method based on the process of annealing metals and glass (Metropolis et al. 1953; Kirkpatrick et al. 1983; Possingham et al. 2000). The algorithm seeks to minimize the total cost of the reserve system by selecting the set of sites that comprises as many populations of species (or other specified biodiversity features) as possible, up to some specified representation goal, as inexpensively as possible. Site cost can be quantified in a variety of ways, such as acquisition cost, some combination of acquisition plus management cost, or opportunity cost. Because we lacked information to reasonably estimate site costs, however, we arbitrarily set all site costs to a value of one.

We specified that each reserve-system configuration generated by the algorithm must contain at least one population of each species. We considered two alternative approaches for identifying representative reserve systems. First, we identified the "best" potential reserve system as the one with the smallest number of sites that represented all species within a protected area at least once. We also identified the best reserve system under the assumption that a strong commitment exists for maintaining current sites as reserves. In this scenario, the objective was to add the minimum number of sites to the existing system to represent every species at least once.

Ideally, one would want a higher level of redundancy in representation, such as at least three populations of each species, to provide a buffer against catastrophes or local extinctions. We limited our representation goal to one population of each species because, for the community database, 15 of the 43 species occurred at only one or two sites, so higher representation goals were not feasible. We conducted analyses for four reserve-system scenarios based on a cross-classification of (1) the spatial scale of the database used to assess biodiversity (community vs. faunal pool) and (2) the extent to which the status of existing reserves was a constraint on selecting sites for the reserve system (i.e., a priori containing extant reserves vs. ignoring current reserve status when selecting sites). For each of the four reserve-system scenarios, we ran 200 simulations: we ran the algorithm 200 times and generated 200 potentially acceptable reserve systems for each scenario.

The algorithm begins by generating a completely random system of reserves consisting of a random number of sites. Thereafter, it iteratively compares potential reserve-system solutions by making sequential changes to the initial system. Either a site not yet incorporated in the system is added to the solution, or a site already in the system is deleted. Site additions and deletions at each step are random. In each iteration, the new system is compared with the previous system: if

$$e^{\left(\frac{-\text{change}}{\text{acceptance level}}\right)} < \text{random number},$$

then the change is accepted; otherwise it is rejected. The specified acceptance level determines what size change is accepted. Every 1000 iterations, the acceptance level is decreased. When the acceptance level approaches zero, then only changes that improve the solution are accepted. The use of the exponential term means the system spends relatively little time accepting undesirable changes and much more time resolving small differences. Each simulation ends after a specified number of annealing iterations. For each simulation, we specified a total of 10 million annealing iterations and 10,000 acceptance-level decreases. The algorithm is described in detail by Andelman et al. (1999), Ball (2000), and Possingham et al. (2000).

Site Conservation Value

We used the percentage of times a site was selected within a scenario (200 simulations per scenario) to represent the site conservation value, the contribution of the site to our specified biodiversity conservation goal. A site selected in all 200 simulations would have the highest value, 100%. A site with a conservation value of 100% is irreplaceable (Ferrier et al. 2000) in that the stated conservation goal cannot be met without including that site in the reserve system. In contrast, a site never selected by the algorithm would have low value (0%) and would likely be given low priority for incorporation into a reserve system.

Statistical Analyses

We quantified the extent to which conservation decisions may be predicated on the choice and spatial scale of a database by examining patterns in the conservation value of sites. More specifically, if the scale of the database has no effect on conservation decisions, then one would expect a significant positive correlation (one-tailed test) between site conservation values from the community database and site conservation values from the faunal-pool database. We conducted two correlation analyses. The first considered the conservation value of each site, regardless of its current reserve status (n = 25). The second considered only the conservation value of the sites unprotected by federal mandate (n = 17); however, the conservation value of these sites was determined with all current reserves a priori remaining in the reserve system. Using correlation analysis (two-tailed test) and the community database, we evaluated whether the conservation value of a site was related to the species richness or to the number of rare species at a site. We considered species rare if its cumulative abundance at all sites was $<1/S$ of the cumulative abundances of all species at all sites, where S is the number of species. In addition, we assessed the correlation between species richness and the number of rare species at a site. All correlations were nonparametric (Spearman rank) because no a priori linear associations were expected (Sokal & Rohlf 1995).

Effectiveness at conserving biodiversity is enhanced to the extent that a reserve configuration protects species at multiple sites, even though such a criterion was not specified when we ran the reserve-siting algorithm. Consequently, we categorized each species based on the number of sites at which it was protected in each of the four scenarios for reserve siting. Subsequently, we assessed the effectiveness of the reserve scenarios by constructing redundancy distributions, determining the proportion of species protected in 0 through *R* reserves, where *R* is the number of sites in the reserve-siting configuration for a particular scenario. We evaluated the consequences of using broad-scale data on species distributions, rather than intensive survey data, to determine reserve configuration by conducting contingency chi-square tests (Sokal & Rohlf 1995) for the pair of scenarios in which current protective status was ignored and for the pair of scenarios in which current reserves were forced into the reserve configuration.

Results

Adequacy of Representation and Site Conservation Value of Existing Reserves

Eight of the 25 sites are currently designated for nature conservation (Table 1; Fig. 1). Collectively, the existing reserve system in Paraguay conserves 74–96% of the nation's bat fauna, depending on which database is used to determine the species composition of sites. As measured by the community database ($n = 43$ species), 74% of the country's bats are protected in at least one existing site. Moreover, considerable redundancy in species composition characterized existing reserves. In fact, three existing reserves (sites 13, 15, and 24) comprised 65% of the species protected in the current system of reserves. When the reserve-selection algorithm was executed without consideration of current reserve status, five of the eight existing reserves were never selected as priority sites for conservation (Fig. 2). The sixth existing reserve, Reserva Natural del Bosque Mbaracayu (site 15), was of intermediate conservation value and was selected in 46% of the simulations. Only two existing reserves, Parque Nacional Serrania San Luis (site 13) and Parque Nacional Teniente Enciso (site 24), were irreplaceable and were selected in all the simulations (Fig. 2).

Analysis of the faunal-pool database ($n = 55$ species) indicated that 96% of Paraguay's bat fauna may be protected by existing reserves. There was considerable redundancy among bat species assemblages at existing reserves when the analysis was conducted on the faunal-pool database; consequently, four of the eight existing reserves were never selected as priority sites for conservation (Fig. 2).

Regardless of database, existing protected areas had relatively low conservation value for Paraguay's bat fauna, compared to other sites in our analyses. For both databases, the median conservation value of existing

Table 1. Description of each of 25 sites in Paraguay (Fig. 1) that were considered for incorporation into a reserve system based on the distribution of bat species.*

Site code	*Site name*	*Biome code*	*Departamento(s)*	*Latitude (S)*	*Longitude (W)*	*Elevation (m)*
1	Estancia La Victoria	BC	Presidente Hayes	23°39.03′	58°34.79′	120
2	Estancia San Jorge	AC	Boquerón	22°02.11′	60°19.93′	80
3	Cerro León	AC	Alto Paraguay	20°26.25′	60°19.19′	250
4	Estancia Sombrero	CP	Cordillera	25°04.26′	56°36.08′	100
5	Lago Ypoá	NE	Paraguari	25°56.71′	57°26.80′	120
6	Estancia Cerrito	CC	Concepción	23°15.14′	57°29.57′	120
7	Fuerte Olimpo	MG	Alto Paraguay	21°02.37′	57°52.29′	120
8	Ayolas	NE	Misiones	27°23.42′	56°50.15′	70
9	Parque Nacional San Rafael	AP	Itapúa	26°45.46′	55°51.67′	170
10	Bahía Negra	MG	Alto Paraguay	20°10.98′	58°09.42′	60
11	Yaguareté Forest	CP	San Pedro	23°48.50′	56°07.68′	200
12	Parque Nacional Cerro Corá	CC	Amambay	22°37.90′	56°01.43′	280
13	Parque Nacional Serranía San Luis	CC	Concepción	22°37.91′	57°21.35′	270
14	Estancia Yacaré	NE	Ñeembucú	26°37.94′	58°07.46′	60
15	Reserva Natural del Bosque Mbaracayú	CP	Canindeyú	24°07.69′	55°30.34′	200
16	Estancia Loma Porá	BC	Presidente Hayes	23°29.92′	57°32.92′	120
17	Estancia Tres Marias	AC	Alto Paraguay	21°16.72′	59°33.13′	70
18	Estancia Samaklay	AC	Presidente Hayes	23°28.81′	59°48.43′	120
19	Dr. Pedro P. Peña	AC	Boquerón	22°27.16′	62°20.65′	240
20	Destacamento Militar Gabino Mendoza	AC	Alto Paraguay/Boquerón	20°05.30′	61°47.22′	390
21	Estancia Rivas	AP	Canindeyú	24°30.43′	54°38.25′	300
22	Estancia Golondrina	AP	Caazapá	25°32.30′	55°29.02′	300
23	Parque Nacional Ybycuí	CP	Paraguari	26°04.64′	56°50.98′	100
24	Parque Nacional Teniente Enciso	AC	Boquerón	21°11.40′	61°41.81′	250
25	Palmar de las Islas	AC	Alto Paraguay	19°32.91′	60°31.64′	150

**Biome codes appear in Figure 1. Modified from Willig et al. (2000).*

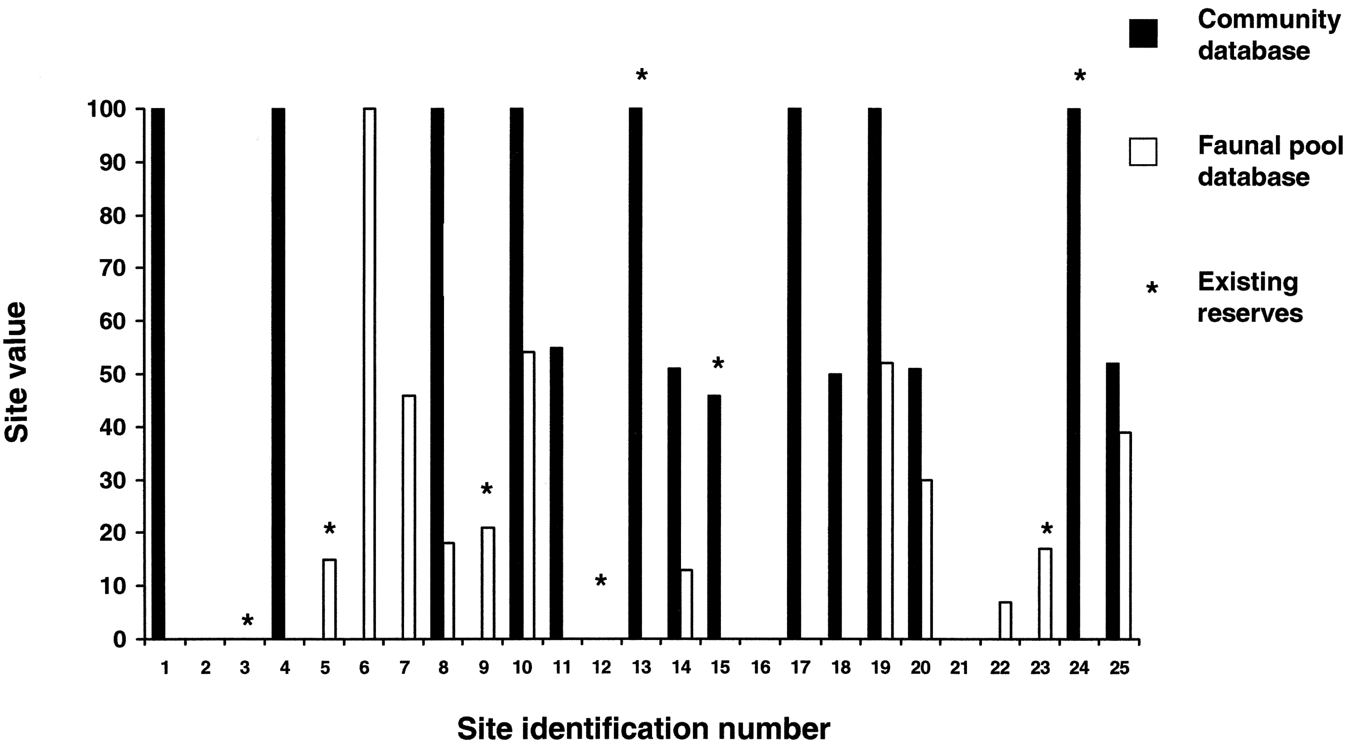

Figure 2. Conservation value of each of 25 sites based on community or faunal-pool databases. Conservation values of sites range from 0 to 100 and were estimated by running the reserve-selection algorithm 200 times and then calculating the percentage of times a particular site was included in an acceptable reserve system.

protected areas was 0%. However, conservation values ascribed to existing reserves based on analysis of the two databases were inversely but not significantly related (Spearman $r = -0.557, p > 0.05$, one-tailed test). For example, Parque Nacional Teniente Enciso (site 24) was selected in 100% of the 200 simulations when we used the community database but was never selected when the algorithm was run on the faunal-pool database. Similarly, Parque Nacional San Rafael (site 9) had the highest value based on analysis of the faunal-pool database (21%), but the same site had zero conservation value and was never selected based on the community database.

Determinants of Site Conservation Value

Conservation values of the 25 sites were variable and in some instances differed greatly between databases (Fig. 2). Estimation of site conservation value was sensitive to the choice and the spatial scale of the database used for analysis. When we ran the algorithm on all 25 sites without considering the status of existing reserves, the conservation values ascribed to particular sites based on analysis of the two databases were unrelated (Spearman $r = -0.056, p >> 0.05$, one-tailed test).

Estimates of species richness at particular sites were not related significantly between databases (Spearman $r = -0.016, p >> 0.05$). The association between measures of species richness and the richness of rare species for each site in the community database also was not significant (Spearman $r = 0.265, p > 0.05$). We completed this analysis only for the community database because little variation in species richness existed among sites in the faunal-pool database. For the community database, site conservation value was not related significantly to species richness (Spearman $r = 0.372, p > 0.05$). Instead, site conservation value was related significantly to the richness of rare species (Spearman $r = 0.842, p << 0.01$).

Efficiency of Representative Reserve Systems

Based on analysis of the community database, the most efficient reserve system consisted of 11 sites (Fig. 3a). Only 3 of the sites selected are protected currently. Six of the 11 sites are in western Paraguay, and 5 are in eastern Paraguay. When the objective was to add the minimum number of sites to the existing system to represent every species at least once, 16 sites were required (Fig. 3b), 5 in the west and 11 in the east.

When we used the faunal-pool database in a comparable process, the pattern was similar. A more efficient reserve system was identified when the status of existing reserves was ignored by the reserve-siting algorithm. In

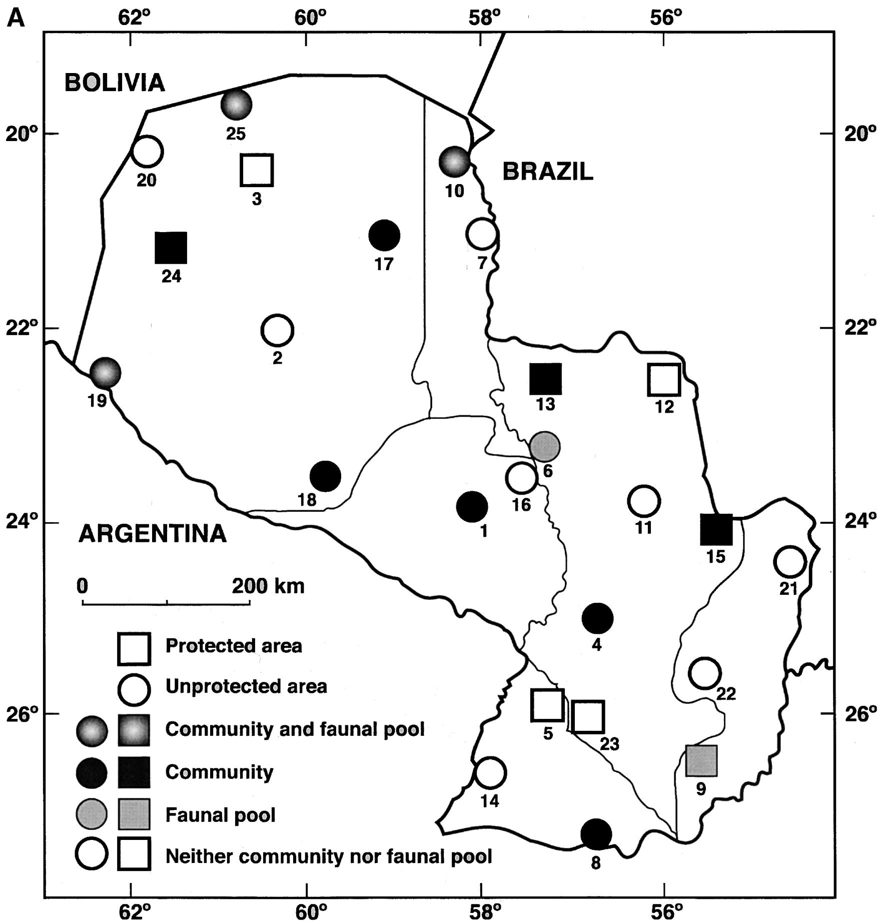

Figure 3. Map of Paraguay indicating the fate of each site based on the outcome from different parameterizations of the reserve-selection algorithms: (a) results when all 25 sites have equal a priori likelihood of incorporation into a system of reserves and (b) results when the 8 sites currently protected by federal mandate must remain in the reserve system.

this case, the best potential reserve system consisted of 5 sites (Fig. 3a). In contrast, the best potential reserve system built on existing protected areas consisted of 11 sites (Fig. 3b).

Measures of Reserve-System Adequacy and Scale of Database

Patterns of redundancy in species protection differed between scenarios constructed from the community and the faunal-pool databases when the status of current reserves was disregarded ($\chi^2 = 34.076$, df = 5, $p << 0.001$) (Fig. 4a) and when current reserves were retained in the reserve configuration ($\chi^2 = 15.161$, df = 5, $p = 0.010$) (Fig. 4b). In both analyses, statistical differences between scenarios were primarily a consequence of the proportion of species receiving no protection by the reserve configuration and the proportion of species protected at eight or more sites (Fig. 4). More specifically, when the siting algorithm ignored current reserve status, 21 species were not protected at any site based on the faunal-pool database, whereas all species were protected at one or more sites based on the community database. Similarly, 9 species were not protected at any site based on the faunal-pool database, whereas all species were protected at one or more sites based on the community database when current reserves were forced into the solution of the siting algorithm. No species was protected at eight or more sites when the faunal-pool database was used, whereas 3 species were protected at eight or more sites based on the community database when current protection status was ignored. Only 1 species was protected at eight or more sites based on the faunal-pool database, whereas 6 species were protected at eight or more sites based on the community database when current reserves were forced into the solution of the siting algorithm.

The number of sites at which a species was protected was reduced on average by 2.1 (median 2, SD = 1.8) when all reserves had an equal initial probability of inclusion in the system. Similarly, the average reduction in the number of sites at which a species was protected was reduced by 1.7 (median = 1, SD = 1.4) when the 8 currently protected sites were maintained in the reserve system. The extent to which species were unprotected was not appreciably related to taxonomy. About one-third of all Paraguayan species in the taxonomically rich families of New World bats (i.e., Phyllostomidae, Vespertilionidae, and Molossidae) were not included in the reserve system when sites had an equal initial likelihood of inclusion in the system. When the current eight reserves

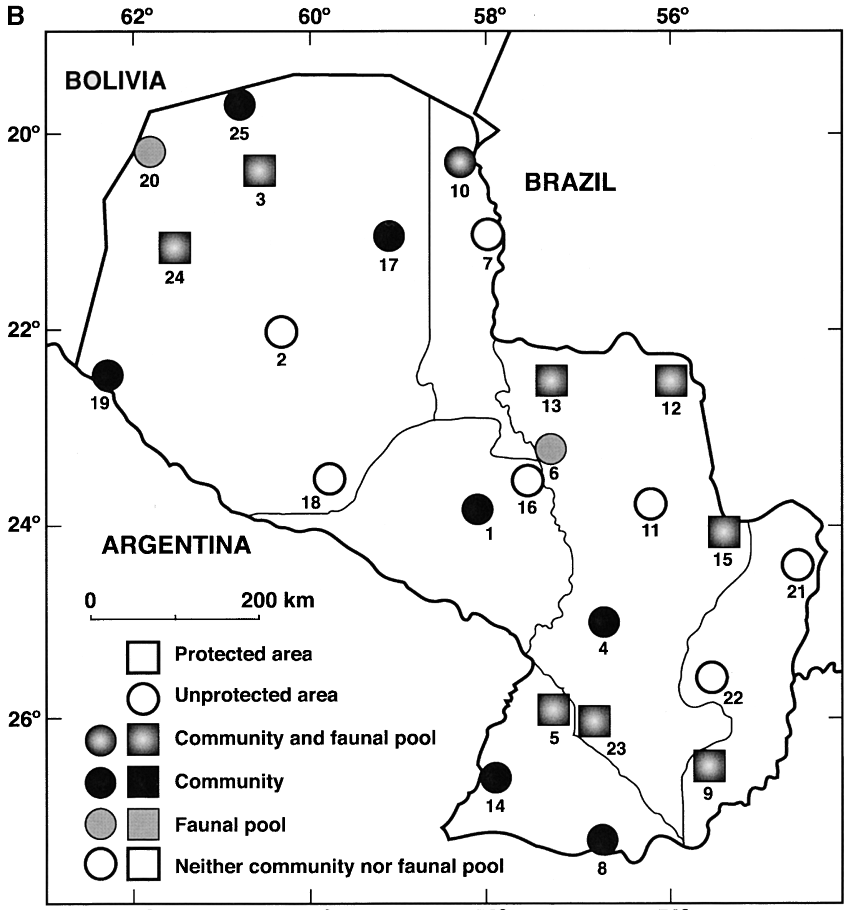

Figure 3. (continued)

were maintained in the reserve system, about one-sixth of all Paraguayan species in the taxonomically rich families were unprotected.

Discussion

Previous studies have raised concerns about the adequacy of existing reserves for conserving Paraguay's biodiversity (Rios & Zardini 1989; Redford et al. 1990; Yahnke et al. 1998; Willig et al. 2000). Our analyses of the adequacy of existing reserves for conserving Paraguay's bat fauna suggest that although 70–96% of the country's bat species may be protected in at least one reserve, 2–11 species are unprotected, depending on which database is used for analysis. Based on analysis of the community database, all 11 unprotected species are rare, occurring at only 1 or 2 of the 25 surveyed sites. This suggests that although the existing reserve system may be adequate for protecting common or abundant species, additional sites are required to protect rare species. Because rare species are typically most prone to extinction, securing additional sites to afford protection to these species should be a priority for conservation in Paraguay.

Our analyses considered representation of bat species only, not of other taxa or specific biomes or habitats. Although a single indicator group such as bats is insufficient for evaluating the effectiveness of a reserve system for all biodiversity (Andelman & Fagan 2000), evaluating the representation of bats is a reasonable first step in assessing an area's conservation value (Medellin et al. 2000). Bats are more numerous than all other mammal groups in the Neotropics and comprise over one-third of the 162 mammal species in Paraguay (Yahnke et al. 1998). Moreover, our findings that 70–96% of Paraguay's bat species are protected in at least one reserve are comparable to those of Yahnke et al. (1998), who found that 79% of Paraguay's mammal fauna is represented in at least one national park. Nonetheless, analyses of representation levels for other biodiversity features are needed to assess the extent to which the potential reserve-system scenarios we identified based on bat fauna would be effective for the full complement of Paraguay's biodiversity. The algorithm we used can accommodate both species- and habitat-based representation goals. Thus, our analysis was limited by data availability, not by our choice of model.

As is true elsewhere, most existing reserves in Para-

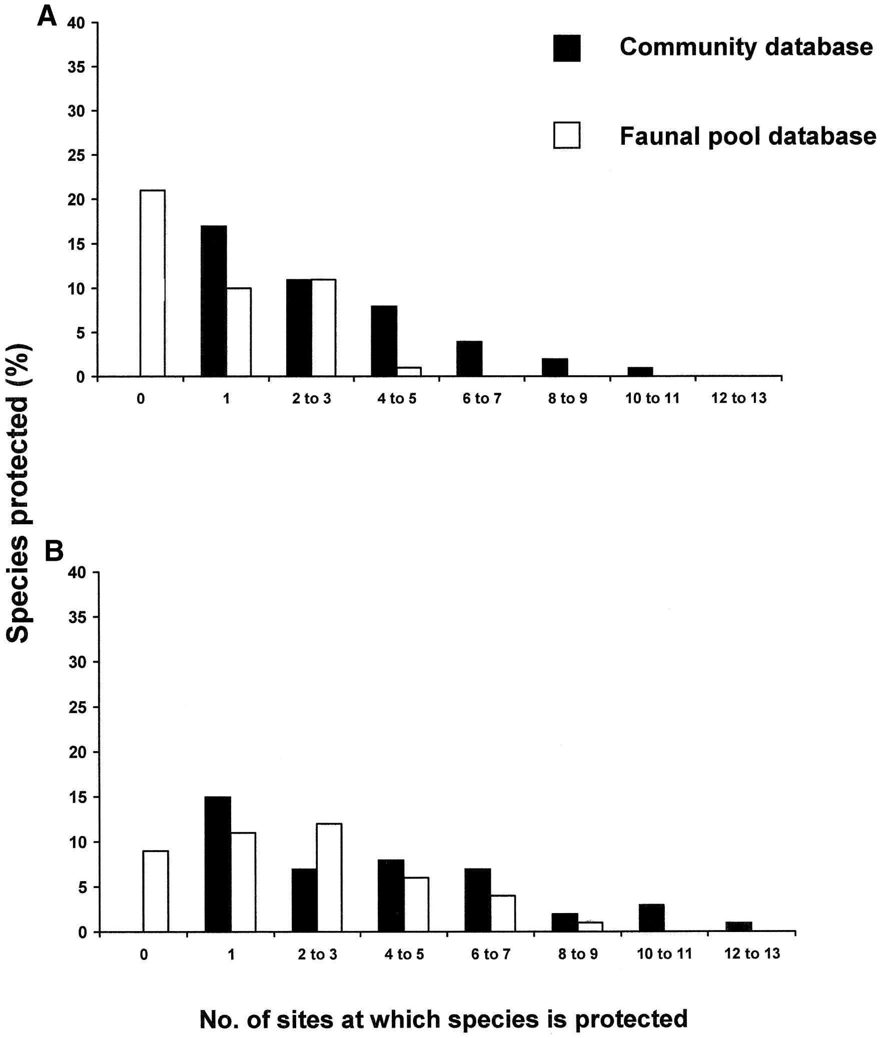

Figure 4. Level of taxonomic representation achieved by a particular solution to reserve-siting algorithms, illustrated by the percentage of species from the community database protected at a particular number of sites for each scenario. The results based on (a) community and faunal-pool databases for reserve-siting algorithms in which all sites have equal a priori likelihood of incorporation into a system of reserves can be compared with (b) the results in which the eight sites currently protected by federal mandate must remain in the reserve system.

guay were not established with the specific aim of protecting biodiversity (Merriam 1970; Yahnke et al. 1998), and existing reserves provide a biased representation of the country's biodiversity (Figs. 1 & 3). Seventy-five percent of existing protected areas in Paraguay are in the Chaco region (Fig. 1, biomes AC, BC) and 25% are in eastern Paraguay (Fig. 1, biomes CC, CP, AP, NE) (Yahnke et al. 1998). Even without explicit consideration of other elements or levels of biodiversity, identifying potential reserve systems based on representation of Paraguay's bat fauna resulted in improved representation of the country's biomes. When existing reserves were ignored, the most efficient potential reserve system provided for reserves in every biome except the Alto Parana (Fig. 3a). Retaining existing reserves resulted in a potential reserve system that included all seven of Paraguay's biomes (Fig. 3b).

Although systematic approaches to reserve-system design, such as mathematical algorithms, have become increasingly sophisticated in the last decade (Possingham et al. 2000), the data available for conservation planning have not improved similarly. Available data typically are limited, especially in developing nations. The convenience of readily available data, or the resources available for analysis, often determine the choice of data for a particular conservation planning exercise. The two databases we used are representative of those typically used to inform conservation decisions. Both systematic and intensive field surveys, which are time consuming and expensive, and museum collections and range maps have inherent biases. For example, the records of the community database were obtained from systematic and intensive field surveys, but these surveys were conducted for only 2 years. Species not found at particular sites may be truly absent or temporarily absent. Alternatively, they may be sufficiently rare that survey effort was inadequate to detect them. Although this may be a limitation of using intensive data for determining reserve-system configurations, it also may be reasonable from a conservation perspective. As habitat in areas adjacent to reserves is modified by or converted to human uses, reserves become increasingly isolated from one an-other and effectively smaller islands of high-quality habitat for constituent species. Reductions in effective area and increases in isolation enhance the likelihood that less common or rare species may become locally extinct. Consequently, surveys that fail to detect rare species at a site may provide a realistic projection of the species likely to be protected in a reserve during the decades following establishment.

Museum records are known to be spatially biased (Nelson et al. 1990; Margules & Austin 1994). They are likely to be most reliable for planning at relatively coarse scales (e.g., at the scale of grids 50 × 50 km or larger) and least reliable when used at the scale of individual reserves (Jennings 2000). It is significant that differences, such as those we found, in estimates of species richness or species composition at local sites determined from intensive sampling and those estimated for their corresponding species pools may be variable. For example, mean differences between the species richness of New World bat communities and their corresponding faunal pools increases toward the tropics, and the variation in richness and composition among local sites increases with decreasing latitude (Stevens & Willig 2002). Consequently, the utility of using species pools to determine the location of reserves may be variable at best and biased if beta diversity responds to salient gradients within a region targeted for conservation action. If intensive survey data at the site level provides a more accurate measure of the species composition of local sites, then the design of a reserve system based on a faunal-pool database leaves many species unprotected regardless of the status of the current eight reserves.

Nonetheless, museum records, in combination with expert opinion, including species distribution maps, are often used for conservation planning simply because they are readily available or even the only sources of information for some regions (Cato 1991; Biodiversity Support Program et al. 1995; Dinerstein et al. 1995; Yahnke et al. 1998; Airame et al. 2003). The results of our analyses, comparing the use of two types and scales of database for systematic conservation planning in Paraguay, suggest that the choice of database may be critical to the design of reserve systems. More specifically, the nature of the database may influence which sites are targeted for conservation, the efficiency of the reserve system, and the ability of the reserve system to meet biodiversity representation goals.

The species occurring at a site are not all equivalent in status; for example, they may differ in abundance, some may use the site only seasonally, or they may differ in degree of imperilment or legal status. Although species richness is both easily measured and easily understood, it treats all species as equivalent and thus may not be the most suitable metric for comparing potential sites for a reserve system. Notably, estimates of species richness are often scale-dependent (e.g., Lyons & Willig 1999, 2002; Gross et al. 2000; Scheiner et al. 2000; Mittelbach et al. 2001) and may be sensitive to the choice of database, as we found here. Moreover, conservation of biodiversity will not be achieved by simply maximizing species richness. To meet the biodiversity-representation goals of reserve systems, our analyses suggest that the richness of rare species may be a more important consideration than overall species richness for assessing the conservation value of individual sites.

Many bat species reach their southern or northern distributional limits in Paraguay (Koopman 1982). Although conservation biologists have tended to exclude species' range peripheries from conservation planning considerations (e.g., Wolf et al. 1996), recent work by Channel and Lomolino (2000) suggests that species' ranges tend to contract toward the periphery in response to anthropogenic forces. Thus, areas along the periphery of species' ranges may provide critical opportunities for species conservation. In Paraguay the combination of many species at the limits of their distributional ranges, the potential inadequacy of existing reserves to fully conserve the nation's bat fauna and other biodiversity features, and a shifting mosaic of habitat types subject to increasing fragmentation suggest that systematic conservation planning and implementation are urgently needed (Willig et al. 2000).

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