

How well do Important Bird Areas represent species and minimize conservation conflict in the tropical Andes?

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ABSTRACT

Where high species richness and high human population density coincide, potential exists for conflict between the imperatives of species conservation and human development. We examine the coincidence of at-risk bird species richness and human population in the countries of the tropical Andes. We then compare the performance of the expert-driven Important Bird Areas (IBA) scheme against a hypothetical protected-areas network identified with a systematic reserve selection algorithm seeking to maximize at-risk bird species representation. Our aim is to assess the degree to which: IBAs contain a higher richness of at-risk species than would be expected by chance, IBAs contain more people than would be expected by chance, and IBAs are congruent with complementary areas that maximize species representation with an equivalent number of sites. While the correlation of richness and population was low for the region as a whole, representation of all at-risk bird species required many sites to be located in areas of high human population density. IBA sites contained higher human population densities than expected by chance (P < 0.05) and were markedly less efficient in representing at-risk bird species of the region than sites selected using the reserve selection algorithm. Moreover, overlap between IBAs and these latter sites was very limited. Expert-driven selection procedures may better reflect existing sociopolitical forces, including land ownership and management regimes, but are limited in their ability to develop an efficient, integrated network of sites to represent priority species. Reserve selection algorithms may serve this end by optimizing complementarity in species representation among selected sites, whether these sites are adopted independently or as a supplement to the existing reserve network. As tools of site selection, they may be particularly useful in areas such as the tropical Andes where complex patterns of species disjunction and co-occurrence make the development of representative reserve networks particularly difficult. Furthermore, they facilitate making spatially explicit choices about how reserve sites are located in relation to human populations. We advocate their use not in replacement of approaches such as the IBA initiative but as an additional, complementary tool in ensuring that such reserve networks are developed as efficiently as practically possible.

Keywords

Conservation biogeography, conservation prioritization, human population density, protected areas, reserve selection algorithms, site-based conservation, species at risk, systematic conservation planning.

INTRODUCTION

Responsibility for habitat loss worldwide can largely be attributed to human activities (Soulé, 1991; Ehrlich, 1995; Bawa &

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Dayanandan, 1997; Chown *et al.*, 2003), and human population density is correlated with the extent of habitat modification (Thompson & Jones, 1999; Harcourt *et al.*, 2001). Potential conservation conflicts arise where species richness and human

population density are correlated because human development competes for the space that is most valuable to a diverse range of organisms. In the case of at-risk bird species, persisting only in small geographical areas or in low numbers, the concern is even greater (BirdLife International, 2004). In this paper we examine the coincidence of at-risk bird species richness and human population in the tropical Andes and compare the performance of the expert-driven Important Bird Areas (IBA) scheme against a systematic reserve selection procedure in maximizing at-risk bird species representation while minimizing conservation conflicts.

In the context of conservation planning, concern has been expressed about the pressures that humans may exert on existing and proposed reserve areas. Human population density is often used as a surrogate for human pressure as it is widely recorded in censuses and has been found to predict human impacts reliably (e.g. Kerr & Currie, 1995; Maurer, 1996; Thompson & Jones, 1999; Brashares et al., 2001; Harcourt & Parks, 2003). While some analyses have suggested that areas of high human population density and high biodiversity are separate (Huston, 1993), numerous other analyses have shown that they often coincide closely (reviewed in Gaston, 2005). Moreover, existing reserve networks have been shown often to coincide with populous areas as well (Chown et al., 2003; van Rensburg et al., 2004). The concern is that these conservation areas, protected or not, are less likely to persist in their current state in the face of human pressures than areas distant from human populations.

Reserves and site prioritization

Two important roles of reserves are to represent biodiversity and to separate biodiversity from the processes that threaten its persistence (Margules & Pressey, 2000). It is widely acknowledged that in the contemporary world many species are under threat from human activities, with human-induced habitat loss being among the principal drivers. In response to this threat to biodiversity, and recognizing that not all areas can be set aside from human use, a number of international organizations have proposed global schemes aimed at prioritizing and preserving a limited number of sites that are of greatest biodiversity value.

Increasingly, biogeographical knowledge and analysis have taken a central role in this endeavour, giving rise to the recently defined discipline of conservation biogeography (Whittaker et al., 2005). Under this rubric, conservation value is measured in various ways, but generally involves consideration of the species distributions of groups of organisms or more specifically of their at-risk members. Such conservation mapping and prioritization schemes have stimulated much debate in the literature as to whether they fulfil their own objectives or broader conservation imperatives (Cincotta et al., 2000; Brooks et al., 2001; Jepson & Canney, 2001). Whittaker et al. (2005) call for a programme of systematic testing and evaluation of all such schemes in order to strengthen and improve the effectiveness of conservation biogeography. Among the major schemes proposed, the IBA scheme developed by BirdLife International has received relatively little analytical consideration.

IBAs: rationale and selection procedure

The IBA programme, started in 1981, aims to develop a network of sites to protect the global avifauna. IBAs are designated using four criteria: the presence of (i) globally threatened species, (ii) restricted-range species, (iii) biome-restricted species, or (iv) significant single- or mixed-species congregations. They are selected 'so that when taken together they form a network throughout the species biogeographical distributions' and represent the 'minimum essential to ensure the survival of these species across their ranges should remaining habitat elsewhere be lost' (Grimmett & Jones, 1989). They represent areas whose loss would have disproportionately large consequences for the species concerned.

The selection of IBA sites has been expert driven. To identify IBAs for the tropical Andes, BirdLife first compiled an inventory of sites through a participatory process involving individual experts, government and non-governmental organizations (http://www.ibasandes.org/). Information on these sites was then compiled from existing sources and targeted fieldwork. The approach is intended to be pragmatic and therefore often takes the existing protected-area network as the backbone of the system, adding sites on the principle of additionality (i.e. priotizing species not already represented in existing reserves). A single site should be capable of supporting self-sustaining populations of the species for which it was identified. BirdLife recognizes that IBAs may not serve the needs of all species, particularly those that are widely dispersed at low densities and nomadic birds with large migration ranges. However, the strategy should be ideally suited to the countries under consideration as the majority of species, and more importantly, of at-risk species present, are resident year round and have relatively constrained geographical ranges.

Complementarity among sites is intended to be central to this endeavour, both to ensure full representation of at-risk and endemic species and to avoid redundancy in representation among selected sites (BirdLife International, 2004). This is particularly relevant in the Andean countries, where patterns of species distribution are highly complex.

IBAs in the tropical andes

Bolivia, Peru, Ecuador, Colombia, and Venezuela contain some of the most important areas for biodiversity conservation on Earth. Running along the spine of the Andes and incorporating a large portion of western Amazonia, as well as the Pacific lowlands of the Chocó, the Andean countries include some of Earth's largest remaining tracts of relatively untouched wilderness as well as many of its most threatened habitats. Indeed, BirdLife International recognizes these countries as among the highest priorities for the IBA programme. Moreover, in a recent coarsescaled global analysis of the existing protected-areas network, Rodrigues *et al.* (2004a,b) identified the tropical Andes as among the most poorly covered regions from the perspective of species representation across various taxa. These countries also represent an ideal test of site-based conservation prioritization, since the extent and overlap of Global 200 Ecoregions (Dinerstein & World Bank, 1995), Biodiversity Hotspots (Myers *et al.*, 2000) and Endemic Bird Areas (Stattersfield *et al.*, 1998) make prioritization based on these region-based schemes an impracticality.

BirdLife International has proposed 432 IBAs for the tropical Andes. Selection of a site as an IBA can be triggered by one or more of the four IBA criteria. The great majority of IBAs in the Andean countries qualify based on the presence of threatened species (93%), with a significant number qualifying based on the presence of restricted-range (63%) or biome-restricted (46%) species. Fewer (17%) qualify as significant congregatory sites. On the whole, IBAs cover more than 61 million ha, over 13% of the tropical Andes. They range in area from less than 6000 ha to in excess of 100,000 ha. Thirty-two percent are located in national parks. Peru contains the highest number of IBAs while Ecuador has the most per unit area.

Systematic conservation planning

While the expert-driven IBA selection process may be pragmatic (Prendergast et al., 1999), it is a qualitative process. It is hardly repeatable and, more importantly, does not include an assessment of the effectiveness of conservation decisions. By contrast, reserve selection algorithms offer an approach that ensures effectiveness and efficiency while preserving accountability. This is achieved by a process whereby conservation goals are explicitly expressed and then translated into objective functions that are implemented in computer algorithms. While these algorithms provide only tentative answers to complex decision processes, they allow us to assess the consequences of different starting assumptions on conservation outcomes (Pressey et al., 1993; Pressey, 1994; Araújo, 1999; Mace et al., 2000; Margules & Pressey, 2000). As such, these algorithms are capable of achieving greater efficiency in representing biodiversity and, when used as a tool in conservation planning, have been demonstrated to achieve lower cost hypothetical reserve networks (Pressey, 1994; Chown et al., 2001; Pressey & Cowling, 2001). Although often seen as limited in their ability to address the complex sociopolitical conflicts that are intrinsic to conservation planning, they can serve as invaluable decision-support systems - aids in the decision-making process (Williams et al., 2003). Despite the recognized advantages of such tools, their adoption by conservation managers and planners has been slow (Prendergast et al., 1999; Williams et al., 2004).

In this paper, we assess the performance of the IBA approach in achieving its own explicitly described objectives using quarter-degree grid cell resolution data on at-risk bird distributions and human population density, and by comparison with a systematic reserve selection approach. We assess the degree to which

1 IBAs contain a higher richness of at-risk species than would be expected by chance;

2 IBAs contain more people than would be expected by chance; and

3 IBAs are congruent with complementary areas that maximize species representation with an equivalent number of sites.

METHODS

Study area and IBA data

The analysis included the five Andean countries of South America, from North to South: Venezuela, Colombia, Ecuador, Peru, and Bolivia. These are the countries covered by the tropical Andes IBA programme of BirdLife International, which provided us with the data on the location, status, ownership, and management of each of the 432 IBAs designated for the region.

Bird distribution and human population data

The bird data used in the analysis were provided in WORLDMAP 4.19.25. They comprised distribution maps of 1284 at-risk bird species for Latin America (773 species for the Tropical Andes). Bird species included in the data set were those deemed to be at greatest risk of extinction based on analyses conducted by The Nature Conservancy, BirdLife International and Stotz et al. (1996) and represented over 25% of the birds known to exist in Latin America (http://nature.org/initiatives/programs/birds/ work/art8640.html). The data were adapted from the Digital Distribution Map of the Birds of the Western Hemisphere (Ridgely et al., 2003). This is the best publicly available data set for birds in this region and compiles extent of occurrence data from field guides. The data are recorded at quarter-degree grid cell resolution. At the equator, a quarter degree represents 769 km² or 76,900 ha. Bird data for each grid cell thus constitute the number of at-risk birds whose range overlaps that cell.

Use of range-filling maps results in an overestimate of the number of quadrats which a given species occupies; this has the potential to inflate error where a species is considered present in a reserve system when, in fact, it is not there (false presence). However, given that Latin America as a whole has received very little systematic survey effort for bird species, point locality data are almost certainly an unduly conservative representation of species distributions; moreover, they will inevitably be biased towards areas that have been more extensively surveyed. The analysis assumes that all at-risk bird species occur as viable populations in every grid cell within their range. This assumption will not necessarily be satisfied in all cases and must be considered when interpreting our results.

Human population density data for the tropical Andes were obtained from the Gridded Population of the World (GPW) Version 2 (CIESIN *et al.*, 2000). The data set comprised the most recent publicly available census data for the region, from 1993 for Colombia and Peru, and from 1995 for Bolivia, Ecuador and Venezuela. The data were reported at the municipality level, 1851 administrative units with an average resolution of 62 km². To ensure reliability, we used the data set adjusted to United Nations country population estimates; but in practice, the population difference from the unadjusted data set was only 0.3%. Human population density, in people/km², was calculated for the GPW by dividing the population of the administrative unit by the number of 2' grid cells required to fill that unit and then dividing this density figure by the area of the grid cell. For compatibility with the WORLDMAP at-risk bird species richness data, the population density data were reduced to quarter-degree resolution using ArcGIS 9.0.

Analysis

In the data provided by BirdLife International, locations of IBAs are given as central latitude–longitude coordinates (centroids). In WORLDMAP, each grid cell is reported by its centroid. Thus, for direct comparison with the avian richness and human population data, IBAs were assigned to their nearest corresponding WORLDMAP grid cell centroid using a nearest neighbour approach in ArcGIS 9.0. Two or more IBAs may occupy the same grid cell; the number of grid cells containing IBAs was 381. The tropical Andes IBAs varied greatly in area, but the great majority were smaller than the area of a single grid cell, often much smaller. As such, according to an IBA, the species complement of the grid cell it occurred in was, if anything, generous (Araújo, 2004), but was adopted here to allow like-for-like comparisons.

We restricted the at-risk bird species richness and human population data to the five Andean countries for which IBAs have been designated. To test whether IBAs contained higher richness of at-risk bird species than would be expected by chance, we first overlaid IBAs on the map of at-risk bird species richness and calculated the mean species richness for IBA grid cells. We then performed 1000 random selections of 381 sites and calculated the mean, 95% confidence interval and maximum mean species richness among these randomizations. Where the mean species richness of IBA grid cells exceeded the 95% confidence interval, the difference was significant at the 5% level; where it exceeded the maximum of all 1000 randomizations, the difference was significant at the 1% level. Using the human population density data, the same method was used to test whether IBAs contain higher human population density than would be expected by chance.

Correlation between at-risk bird species richness and human population density was quantified using Spearman's rank correlation coefficient, and patterns of covariation were assessed visually by overlaying richness and population maps in WORLDMAP (Williams & Gaston, 1998; Araújo, 2003). To test whether the 381 grid cells containing IBAs were congruent with areas selected to maximize at-risk bird species representation, we performed 20 free permutations of a near-maximum coverage solution that maximized representation of species for a given area (Church et al., 1996). The algorithm used to obtain this solution selected the 381 grid cells in which all species were represented in as many cells as possible (descriptions of the algorithm are provided in Williams et al., 2000 and; Araújo & Williams, 2001). Congruence was assessed using the Bray–Curtis dissimilarity statistic, calculated in spss 11.5. This statistic measures the degree of spatial overlap among grid cells selected with IBAs and with the reserve selection algorithm. Sites were considered as having higher degree of irreplaceability if they occurred in all 20maximum representation solutions (Pressey et al., 1993).

A number of alternative solutions could be selected to achieve this near-maximum coverage set. By breaking ties at random

among flexible grid cells, we were able to select 20 solutions that represented a range of alternative maximum-coverage solutions. To decide how many runs we would need to represent the range of variation in the spatial overlap between areas, we plotted cumulative standard deviations of the Bray-Curtis similarity statistic against the cumulative number of runs. The expectation was that the standard deviation between a small number of accumulated runs would vary considerably, but that this variability would stabilize as more runs were accumulated. It was further expected that the value at which the standard deviation stabilized would remain constant through further runs and as such, the number of runs at which this stabilization occurred would be sufficient to represent the variability among maximum representation solutions. Each of the 20 reserve selection runs was overlaid with the human population density surface and tested against 1000 randomized site draws to assess whether their human population was significantly higher than expected by chance.

We compared IBAs against near maximum coverage set reserve selections to assess their performance in representing at-risk birds within a given number of sites (effectively a given 'budget'). Additionally, 20 minimum-set reserve selections were performed in conjunction with the maximum coverage algorithm to assess how many would be required to represent each species in one grid cell (76,900 ha) and in five grid cells (384,500 ha).

RESULTS

For the Andean countries, at-risk bird species richness and human population density were weakly correlated overall (number of cells = 6573, $r_s = 0.178$, P < 0.001; Table 1). The pattern of covariation varied spatially. High levels of richness and population coincided on the north-western Andean flank. However, for most of the Amazon basin, species richness was proportionally higher than human population while the reverse was true in northern Venezuela and western Peru and Bolivia (Fig. 1).

IBA grid cells contained higher richness of at-risk bird species than expected by chance. The mean at-risk bird species richness of 1000 random selections of 381 grid cells was 22.7 species, with a minimum mean among randomizations of 20.3 and a maximum of 24.9 species. The mean richness of the 381 IBA grid cells was significantly higher at 34.2 species (P < 0.001).

Despite the low correlation between richness of at-risk bird species and human population, IBA grid cells contained more people than expected by chance. The mean human population density of 1000 random selections of 381 grid cells was 22 people per km² with a minimum mean among randomizations of 11 and a maximum of 49 people per km². By comparison, the mean human population density in the 381 IBA grid cells was significantly higher, at 70 people per km² (P < 0.001).

There was a significant difference between quadrat areas selected as IBAs and areas selected to represent maximally all atrisk bird species in the tropical Andes. The mean Bray–Curtis dissimilarity between 20 different maximum representation solutions was 26%, whereas the mean dissimilarity between

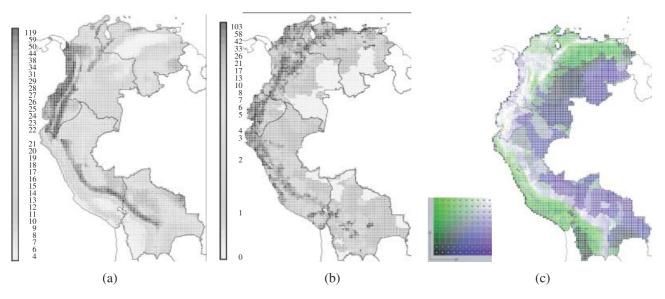


Figure 1 Quarter-degree resolution map of countries of the tropical Andes showing (a) distribution of at-risk bird species richness and (b) human population density, both on equal-interval scales. Panel c shows the covariation of at-risk bird species richness and human population density. Increasing intensities of blue represent increasing species richness relative to population density, whereas increasing intensities of green represent the converse. White grid cells represent high scores for both factors, while black cells represent low scores for both and shades of grey show linearly covarying scores for both.

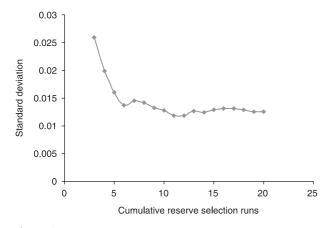


Figure 2 Standard deviation in Bray–Curtis dissimilarity measure over 20 cumulative runs of the maximum representation reserve selection algorithm.

maximum representation solutions and the IBA network was 83%. Among maximum representation solutions, 188 sites (49%) had a high degree of irreplaceability; only 38 of these sites were also IBAs. As such, the IBA network is in large part not congruent, with an equivalent number of areas selected using a reserve selection algorithm that maximizes species representation.

Variance in dissimilarity among maximum representation solutions stabilized at 1.3% within 13 accumulated runs, indicating that 20 runs were sufficient to capture potential variability among maximum representation solutions sets (Fig. 2). With a mean human population density of 49 people per km² and a standard deviation of 3, maximum representation solutions contained more people than expected by chance (P < 0.001).

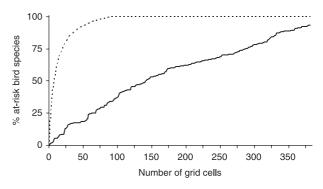


Figure 3 Comparing efficiency of IBAs against maximum representation solutions in representing at-risk bird species in the tropical Andes. Cumulative proportion of species represented at one or more sites as number of sites included in the network increases. Solid line, IBAs; dashed line, mean of 20 maximum representation solutions.

However, they contained significantly fewer people than did IBAs (P < 0.001), averaging 22 (31%) fewer people per km².

93.27% of the at-risk bird species of the Andean countries are represented within the 381 IBA grid cells. By contrast, maximum representation sets represent 100% of at-risk species in at least one grid cell with between 89 and 95 grid cells, and represent 93.27% of these species within 50 and 54 grid cells (Fig. 3). The 20 maximum representation sets of 381 grid cells also retained significantly higher mean species richness, at 39.7 species, than the 381 IBA grid cells, at 34.2 species (P < 0.001). A minimum coverage set to ensure the presence of 100% of species within at least 5 grid cells (covering 384,000 ha) would require 419 ± 1 grid cells based on 20 runs. If all such grid cells were preserved

Table 1 Summary of results

1. Correlation	r _s	Cells	
Richness and human population	0.178	6573	
2. Coincidence	Richness	People per km ²	
i) IBAs	34.2	70	
ii) Max Rep	39.7	49	
iii) Random	22.7 (max 24.9)	22 (max 49)	
3. Congruence	Bray–Curtis dissimilarity		
Among Max Rep solutions	26%		
Between IBAs and Max Rep	83%		
4. Irreplaceability			
Sites always selected in Max Rep	188 (49%)		
Overlap with IBAs	38 (10%)		
5. Representation		Cells for 1 rep	Cells for 5 reps
i) IBAs	93.27%	_	-
ii) Max Rep	100.00%	89–95	419 ± 1

(1) Spearman's rank correlation of at-risk bird species richness and human population density; (2) mean at-risk bird species richness and human population density in 381 grid cells representing (i) Important Bird Areas (IBAs), (ii) maximum representation solutions (Max Rep), and (iii) 1000 randomized site selections; (3) mean Bray–Curtis dissimilarity (i) among maximum representation solutions and (ii) between IBAs and maximum representation solutions; (4) irreplaceability (i) as measured by frequency of selection among maximum representation solutions and (ii) overlap between irreplaceable cells and IBAs; (5) Percentage of at-risk bird species represented in (i) IBAs and (ii) maximum representation solutions along with number of cells required to represent each species in one cell and five cells.

in their entirety they would cover 32 million ha (6.8% of the tropical Andes).

DISCUSSION

The IBA scheme is undoubtedly stronger than our analysis can possibly show. It has built-in knowledge of great practical relevance to the problems of conservation that is absent from our approach. As an individual example, with a mere 6000 ha, the Maquipucuna Reserve in north-west Ecuador protects some 347 bird species, among which 27 are endemic and a further 11 are considered vulnerable or near-threatened by the IUCN (Prieto, 2003). Moreover, their conservation efforts are achieved in consort with a variety of ecotourism and sustainable development activities that provide economic benefit to and foster good relations with local residents.

Insofar as our assumptions have not been met, our analyses may also give undue value to specific grid cells or grid cell networks chosen to maximally represent at-risk bird species. Our approach assumes that designating a grid cell as a priority could be followed by effective conservation of all at-risk bird species in that cell. While caution in interpretation is therefore necessary, the results presented here offer valuable insights into the performance of the IBA scheme and suggest modifications that could improve its effectiveness, and that of other site-based conservation, when applied in the future.

Human population and at-risk bird species richness

The overall correlation of human population density and at-risk bird species richness in the Andean countries was very weak.

While in certain areas — particularly the western flank of the Andes in Ecuador and Colombia - the covariation was consistently high, throughout the rest of the region either one factor or the other was present in excess. On the presupposition that human population density is a correlate of conservation threat for the Andean countries, it would make sense to choose conservation sites where the ratio of at-risk bird species richness to human population density was highest. However, choosing sites based purely on species richness can blind us to the more important issue, for both biodiversity and individual species conservation, of species representation (Araújo, 1999; Williams et al., 2000; Jetz & Rahbek, 2002; Lennon et al., 2004; Vazquez & Gaston, 2004). Large portions of the Amazon basin, with a high ratio of species richness per unit area to human population density, would appear to be the best investments for conservation, but individual species in the Amazon tend to have larger ranges than in the Andes and on the Pacific coast, producing a high degree of redundancy in species representation among cells. Ensuring adequate representation of all species requires that some priority sites be located in more populous areas, meaning that some coincidence of human population and species conservation needs may be inevitable (and for practical reasons may also be desirable: see below). Representation is a priority of the IBA scheme (BirdLife International, 2004) and is also the target driving the maximum coverage algorithm used.

IBA grid cells contain significantly higher richness of at-risk bird species than would be expected by chance, despite the fact that IBA selection is not based on species richness. Since 93% of the IBAs were selected in part for harbouring substantial populations of at-risk birds, this is unsurprising and reassuring. Perhaps less predictably, however, IBA grid cells also contained significantly more people than would be expected by chance. In fact, the mean population density of IBA grid cells was more than triple the mean population density among 1000 randomized site selection trials.

Considering the low correlation of human population density and at-risk bird species richness for the region as a whole, we hypothesized that higher than expected human population density in IBAs was a result of constraints imposed in the location of IBAs by the requirement of species representation (Fjeldså et al., 1999). We tested this hypothesis by comparing the distribution of IBAs with that of an equivalent number of sites explicitly selected to maximize species representation. While grid cells selected to maximize species representation were highly similar among the 20 runs of the algorithm, they overlapped very little with IBA grid cells. This did not in itself demonstrate that the siting of IBAs in areas of high human population density was unrelated to the constraints of species representation. Indeed, maximum representation site networks also had significantly more people than would be expected by chance (for similar results in Europe see Araújo et al., 2002b). However, they did contain significantly fewer people than IBA grid cells. As such, on its own, the constraint of species representation does not explain the distribution and consequent high human population density of IBAs.

Should humans be avoided?

The question of whether reserves should be located near or far from areas of high human population is hotly contested. Proximity to human populations may offer benefits. For instance, ecotourism, if pursued sustainably, can help to fund the reserve network by raising money through both foreign and local visitors. It may also serve to raise awareness among local communities of the values, economic and otherwise, of biodiversity, particularly for vulnerable flagship species. This is critical, since conservation, as a social movement, ultimately relies on popular support (Jepson & Canney, 2003). The involvement of local people in conservation management has recently emerged as an important theme in the IBA programme (BirdLife International, 2004). However, the success of such a strategy will depend on a variety of factors, from the size of protected area to the cohesiveness of local communities. Terborgh (1999) cautions, moreover, that only a limited number of sites worldwide can be supported by ecotourism and related activities that directly benefit local populations.

The more immediate question arising in the present context is 'what are IBAs intended to do?' The IBA program is a site-based conservation strategy with the objective of ensuring the survival of the global avifauna. Various authors have found human population density to be highly correlated with threats to wildlife posed by humans (reviewed in Gaston, 2005). On this understanding, the IBA objective might best be achieved by selecting reserve sites where conflicts with human populations are minimal, i.e. with low human population densities in and near reserve areas (Araújo & Williams, 2000). This might mitigate threats to wildlife posed by humans, while also reducing opportunity costs local communities incur as a result of conservation efforts (Faith & Walker, 1996).

Even if viewed as desirable, in practice, human populations will be difficult to avoid entirely in choosing reserve sites. In the Andean countries, IBAs and maximum representation networks both contained significantly more people than would be expected by chance. By contrast, in Europe, human population density was correlated with overall species richness, but not with species richness for birds or for endemic species (Araújo, 2003). Stable high density European populations have been present in fixed and expanding locations for a much longer period of time than in the tropical Andes (Denevan, 1992). As such, an area like the north-western flank of the Andes, where high human population density and bird species richness coincide, may represent an 'extinction debt' not yet called in (Tilman et al., 1994; Hanski & Ovaskainen, 2002; Lindborg & Eriksson, 2004). Andean countries also have among the highest population growth rates in the world, in excess of 2% a year (UNDP, 2004). As a consequence, we can only anticipate that conflicts for available land will become even more intense in the future. Consequently, securing the integrity of any reserve network aimed at protecting the avifauna of the tropical Andes will require mediating between and aligning where possible the needs of people and the fragility of the natural environment.

Should reserve network design be expert driven?

The expert-driven IBA approach offers many benefits. It is participatory, engaging with conservation managers and scientists with direct and detailed knowledge of the regional avifauna. Sites selected by these experts may also better reflect practicalities of land ownership as well as other social and political realities (Loiselle et al., 2003). What is more difficult for experts to develop is a systematic and comprehensive picture of how the network as a whole should be designed (Williams et al., 2003). For southern Africa, Cowling et al. (2003) found that sites selected by experts - primarily conservation managers tended to be biased, particularly in excluding large lowland areas underrepresented in the existing reserve network. Areas selected outside reserves may not represent the best options for supplementing, or filling species representation gaps in, the existing reserve network. This runs counter to the IBA scheme's aim of ensuring complementarity among sites.

The underlying concern is that a purely expert-driven scheme may lead to misallocation, or suboptimal allocation, of limited resources for conservation (Pressey et al., 1993). The IBA network represented virtually all at-risk species in the Andean countries within 381 grid cells. However, by comparison, maximum representation reserve networks represented the same proportion of species in one-eighth and represented 100% of these species in one-quarter the number of sites. In fact, sites considered irreplaceable for representing at-risk bird species - selected in all 20 maximum representation networks - were largely not included in the IBA network, indicating that in the absence of other considerations, at-risk species could be represented more effectively than they are in the IBA network. Thus, as far as representing each species in this many sites is sufficient, the maximum representation solutions are considerably more efficient. Furthermore, these methods can also accommodate

criteria for persistence (Araújo *et al.*, 2002a, 2004) as well as complex sociopolitical factors (Finkel, 1998a,b; Pressey, 1998; Williams *et al.*, 2003). Clearly, species representation is not the sole aim of IBA scheme. It is, however, a central one, and our results indicate its limitation in this respect.

Should we use the existing reserve network?

In most cases, it is not practical or sensible to ignore or revoke an existing reserve network (Pressey & Cowling, 2001), and BirdLife International explicitly sets out to incorporate existing protected areas as IBAs wherever possible. Existing reserves may have existing infrastructure and management as well as legal protected status. They also may be recognized and respected by local people with whom relationships have been established (Perreault, 1996), particularly where they are directly engaged in management. It is, however, important to recognize that this view of the status of reserves, particularly in the South American context, may be overly optimistic. While 62% of sites in the tropical Andean IBA database are categorized as 'nature conservation and research', only 32% are in national protected areas and only 17% have existing management plans. Many reserves will have legal status but, without enforcement, will have little or no capacity to protect the species that inhabit them. It is also debatable to assume that existing reserve networks are always in areas of particular value for biodiversity (Pressey, 1994; Terborgh, 1999); in South America they have generally been established on an ad hoc basis, to support indigenous people, or protect cultural or scenic landscapes (Fjeldsa & Rahbek, 1997). Furthermore, the findings of a coarse-scale analysis by Rodrigues et al. (2004a,b) indicate that there are substantial gaps in species representation for various taxa in the existing reserve network of the tropical Andes. We argue that, where representation is the goal, identifying and securing the most critical supplementary areas needed to fill these gaps should be a priority, and that such analyses as provided herein can make a contribution to this process.

Pressey (1994) argues that, worldwide, inclusion of existing reserves as part of a site-based species conservation network has generally resulted in a lower effectiveness in representing species of concern. To the extent that the maximum representation reserve networks were more effective in representing at-risk bird species than the IBA scheme, our results support this conclusion. However, systematic conservation planning need not be at odds with pragmatism. On the contrary, it provides the flexibility in decision-making that is central to pragmatism by offering a variety of alternate solutions for representing species of concern, both within the existing reserve network and outside it (Hopkinson *et al.*, 2001; Pressey & Cowling, 2001; Araújo *et al.*, 2002b; van Rensburg *et al.*, 2004). In this paper, our intention has been to provide some new observations and some alternative scenarios for conservation planners working in the region.

CONCLUSION

The IBA scheme is a well-established and important approach to identifying areas for conservation. Its particular strength has

been in identifying individual sites for conservation; as such, it has formed the basis for the recently developed key biodiversity areas initiative (Eken *et al.*, 2004). Our aim in this paper is not to undermine such efforts, but rather to demonstrate how widely available information and analytical tools can be used to improve or quality-check the basis on which such conservation decisions are made (Whittaker *et al.*, 2005).

IBAs in the tropical Andes harbour a high proportion of the region's at-risk bird species richness. However, IBAs represented at-risk bird species less effectively and with significantly higher human population densities than an equal number of sites selected purely to maximize species representation. Where desirable, complementarity methods that explicitly seek to minimize human population within selected areas offer the possibility of reducing this level of coincidence even further (Araújo et al., 2002b). Whether it is a matter of supplementing the existing protected-areas network, or establishing priority areas completely independent of that network and identifying areas of overlap, a systematic reserve selection procedure can provide an important aid to the process. By providing a variety of options to satisfy the same need for representation, it also provides the flexibility that planners and managers need to generate a protected-areas network that satisfies a broad range of conservation objectives.

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