ENERGY, SPECIES RICHNESS, AND HUMAN POPULATION SIZE: CONSERVATION IMPLICATIONS AT A NATIONAL SCALE

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Abstract. The maintenance of biodiversity rests on understanding and resolving conflict between patterns of species occurrence and human activity. Recent debate has centered on the relationship between species richness and human population density. However, conclusions have been limited by the lack of investigations of these relationships for individual countries, at which level most practical conservation actions are determined, and for a spatial resolution at which practical conservation planning takes place. Here, we report the results of the first such analysis, for birds in South Africa. Species richness and human density are positively correlated, apparently because both respond positively to increasing levels of primary productivity. High species richness is maintained by currently designated reserves, but the areas surrounding these have higher human population densities than expected by chance, placing the reserves under increasing external pressure. Not all species lie within protected areas, but the options are limited for building on the present network to generate a more comprehensive one, which protects all species and significantly reduces the conflict with human activities by designating new reserves in areas with lower human populations. Ultimately, the only solution to the conflict between biodiversity and people is likely to be individual-based regulation of human population size.

Key words: area selection; avian species richness; conservation conflicts; human population size; primary productivity; reserves; scale.

INTRODUCTION

It is widely accepted that habitat destruction is a key component of species extinction (Bibby 1995, Brooks et al. 1997, 1999*a*), that human activities are responsible for the vast majority of current habitat loss (Soulé 1991, Ehrlich 1995, Bawa and Dayanandan 1997), and that human population density is correlated with habitat modification (Thompson and Jones 1999, Harcourt et al. 2001). What is much less clear is whether areas of high human activity and high species richness are spatially congruent. If, on the one hand, the two are inversely related, areas rich in species might not be severely compromised by the ongoing development required to sustain growth in human numbers and expectations. On the other hand, if the relationship between species richness and human impact is positive, conservation conflicts can be expected to increase, because increasing human resource demands will pose ever greater threats to biodiversity. Under the latter scenario, considerably larger efforts will have to be made to set aside and protect conservation areas in

species rich regions (Soulé and Sanjayan 1998), and to integrate more carefully conservation requirements into land use planning, than is currently the case.

Despite the existence of several studies that have examined these issues (e.g., Kerr and Currie 1995, Thompson and Jones 1999, Cincotta et al. 2000, Rivard et al. 2000), debate (Margules and Gaston 1994, Redford and Dinerstein 1994, Faith 2001, Balmford et al. 2001*a*, Huston 2001, Hansen and Rotella 2002) has been polarized around two recent studies. In the first, Huston (1993) concluded that because agricultural productivity is low and plant species richness generally high in low productivity areas (and vice versa), conflicts between conservation and other human land uses (especially agriculture) can be avoided. In contrast, Balmford et al. (2001*b*) showed that, at the one-degree resolution across Africa, the relationship between primary productivity and species richness of vertebrates, and primary productivity and human population density, were both unimodal, resulting in a positive relationship between species richness and human population density. They concluded that future conflicts between conservation and development cannot readily be avoided, and that maintaining reserves in high human population density areas would become increasingly difficult.

Given that increasing human demand for resources, and especially for agricultural resources, is likely to

mean significant future environmental change (Tilman et al. 2001), understanding the relationship between human activity and biodiversity is critical for reducing the rate at which species continue to be lost. This is particularly true for the scale at which conservation is likely to be implemented. That is, within countries, and using data that are at the finest resolution available for the region (e.g., Lombard 1995a, b, van Jaarsveld et al. 1998). The form of the relationship between productivity and species richness might change significantly at smaller spatial extents, thus providing different outcomes to those of studies undertaken over larger areas (Margules and Gaston 1994, Redford and Dinerstein 1994). If, at a finer spatial scale (both extent and resolution), the relationships between productivity, human activity, and biodiversity are positive, then efforts to integrate land use planning at the national level clearly need to be stepped up in synchrony with broader scale, often global, initiatives (Mace et al. 2000, Myers et al. 2000). Likewise, if finer resolution information is available, local heterogeneity might mean that in at least some areas conservation and human development needs can be integrated with less compromise (Balmford et al. 2001b).

Investigations of the relationships between human activity, species richness, and conservation requirements have, to date, not been undertaken at the within-country scale, and using the data resolution employed for local conservation. Thus, it is not clear what the sign or form of the relationships are, a significant gap in the knowledge required to undertake rational conservation planning within a framework of ongoing human need (see Faith 2001). Here, we address this lacuna by examining relationships between bird species richness, human population density, landscape transformation, and conservation areas in South Africa at three spatial resolutions (quarter, half, and one degree). Following Harcourt et al. (2001) and Parks and Harcourt (2002), we also determine whether existing conservation areas are located in areas of unusually high population density, whether small reserves are particularly prone to this effect, and whether conservation agencies are proclaiming increasingly smaller protected areas in regions of high population density. If fine-scale heterogeneity in species distributions and human land use can potentially be used to minimize conflict between conservation and development, but conservation agencies are not making use of this opportunity, then longer-term maintenance of biodiversity could be under greater risk than is presently thought to be the case (see, e.g., Woodroffe and Ginsberg 1998, Inamdar et al. 1999, Liu et al. 2001).

We chose South Africa and data on birds for several reasons. First, although South Africa is considered a developing country (O'Riordan 1998), it has a well-developed, mechanized, agricultural infrastructure, which means both local food security and substantial export-based agricultural contributions to its GDP

(World Development Report 2000/2001). Huston (2001) argued that such an infrastructure is likely to reduce the correlation between human population density and net primary productivity that is apparently a characteristic of developing nations. That is, people can occupy areas for reasons other than those associated with the exploitation of local resources for subsistence agriculture.

Second, species richness data (here considered a reasonable surrogate for biodiversity, see Gaston 2000) at a quarter-degree resolution are generally used for conservation planning in South Africa (Lombard 1995b, Anonymous 1997). Although reserves are often smaller in area than an entire quarter-degree grid cell, this resolution is regularly used to identify areas in need of conservation attention (e.g., Lombard et al. 1995). Third, the most comprehensively surveyed taxon at the quarter degree resolution is the birds (Harrison et al. 1997). Fourth, there are modern data available on human population density (Statistics South Africa 1996) and landscape transformation (Fairbanks et al. 2000), as well as for the relationships between net primary productivity (NPP), rainfall (a major correlate of NPP) and species richness (van Rensburg et al. 2002), thus making it possible to explore explicitly the interrelationships between these variables.

METHODS

Avian species richness data for South Africa (including Lesotho) were obtained from the Southern African Bird Atlas Project (SABAP; Harrison et al. 1997), which compiled data on species occurrences on a quarter-degree grid ($15' \times 15' \approx 676$ km^2) (Fig. 1). In a previous study, van Rensburg et al. (2002) investigated relationships between avian species richness and several environmental variables at three spatial resolutions: quarter degree (1858 grid cells of approximately equal area, but varying from 635 km^2 in the north to 712 km^2 in the south), half degree (458 cells), and one degree (102 cells of $\sim100 \times 100$ km). They showed that net primary productivity (NPP) (at the half-degree and one-degree resolutions) and precipitation (PPT) were strongly correlated, and were significant, strong positive, linear correlates of avian species richness at all spatial scales (Table 1). For this analysis, we use the same species richness data, precipitation, and NPP data, but now include additional data on human population density, land transformation, and the position, extent, and date of declaration of conservation areas. We also examine four species richness categories, based on Balmford et al.'s (2001b) finding that the relationships between human population density and species richness differ between groups with different range sizes. The four avian species richness categories calculated for each quarter-degree cell were (1) all 651 species, (2) the 25% most widespread species (163 of 651 species), (3) the 25% most range restricted species (163 species), and (4) only those 152 species classified

a

Avian species richness
- 15–98
- 98–152
- 152–209
- 209–277
- 277–405

b

Human population density
- 0–6684
- 6684–18 831
- 18 831–36 108
- 36 108–57 903
- 57 903–89 755
- 89 755–136 793
- 136 793–231 172
- 231 172–400 196
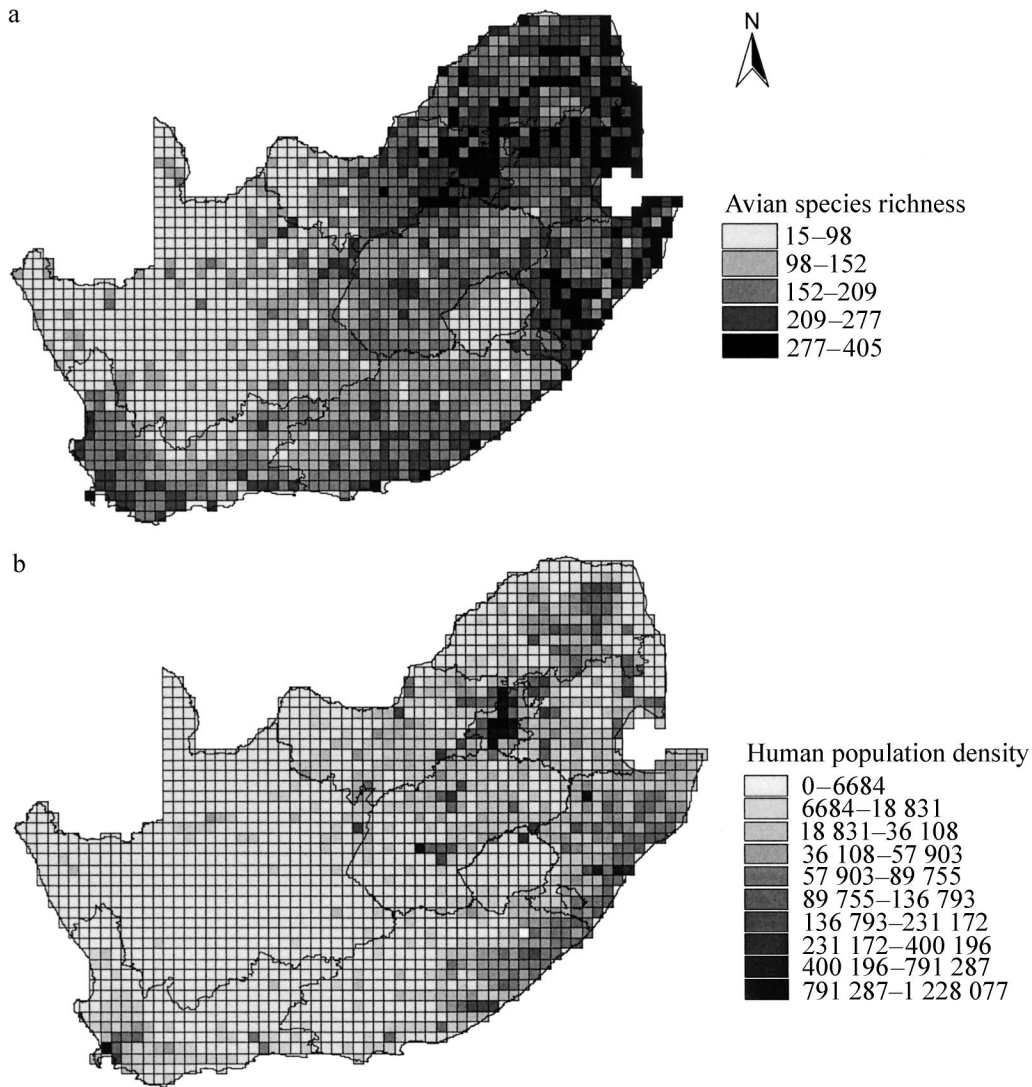- 400 196–791 287
- 791 287–1 228 077

FIG. 1. (a) Avian species richness and (b) human population density variation across South Africa.

as red data species based on Baillie and Groombridge (1996) and Barnes (2000) red list categories.

Data on land transformation in the study area were obtained by calculating the percentage of each land-cover class in each quarter-degree cell, based on six transformed land-cover classes provided by Thompson (1996) and Fairbanks et al. (2000). These percentage land-cover values were then summed in each grid cell.

TABLE 1. Pearson correlation coefficients between mean annual net primary productivity (NPP, g C·m^{-2}·yr^{-1}), mean annual precipitation (PPT, mm/yr), avian species richness, and human population density at the quarter-, half- and one-degree resolutions before taking spatial autocorrelation into account.

Variables	Quarter degree	Half degree	One degree
NPP vs. PPT	⋯	0.90***	0.80***
Avian richness vs. PPT	0.65***	0.77***	0.82***
Avian richness vs. NPP	⋯	0.79***	0.71***
Human population density vs. PPT	0.71***	0.76**	0.80***
Human population density vs. NPP	⋯	0.78**	0.73***

Note: Significance was calculated after a sequential Bonferroni correction was applied (df at quarter degree = 1, 1856; half degree = 1, 456; one degree = 1, 100).
** $P < 0.01$; *** $P < 0.001$.

These classes were based on seasonally standardized Landsat satellite imagery captured primarily during 1994–1995 and included cultivated lands, forest plantations, urban/built-up lands, mines and quarries, degraded lands, and water bodies. As was the case with the avian richness data, percentage land cover was rescaled for grid cell sizes of one-half degree and one degree. The most recent South African population census data (1996) were supplied as numbers of humans per quarter-degree grid cell by Statistics South Africa (1996) (Fig. 1), and were appropriately rescaled for the half-degree and one-degree analyses. Finally, based on the 1997 United Nations list of protected areas for South Africa (World Conservation Union [IUCN] 1998), information on the size and year of proclamation for 264 protected areas were obtained, and these areas were mapped using ArcView GIS (Environmental Systems Research Institute [ESRI], Redlands, California, USA). While acknowledging that there are other areas utilized for conservation on a less formal basis, and a small turnover of formal reserve designations, this list covers the large majority of the established conservation network in South Africa.

For each resolution, Pearson product-moment correlation coefficients were used to investigate relationships between human population density and NPP/PPT, human population density and each of the avian species richness categories, and human population density and the percentage of land transformation. Tabulated results were subject to sequential Bonferroni corrections (Rice 1989). Spatial structure in the data was examined using partial regression analyses to partition variation in the dependent variable of interest into its nonenvironmental spatial, spatially structured environmental, nonspatial environmental, and residual variation (see Legendre and Legendre 1998).

Gaston et al. (2001) identified 30 optimal solutions, each one requiring 19 quarter-degree cells, to represent each avian species in at least one grid cell across South Africa and Lesotho (overlapped, these 30 solutions occupy 53 cells). To determine whether these minimum complementary cells represent areas with larger human population densities than expected by chance, the total human population size for each of the 30 optimal solutions (consisting of 19 cells each) was calculated. This value was then compared with the mean total human population found for 10 000 sets of 19 randomly selected grid cells. To determine whether human population density in the cells bordering protected areas tends to be higher than expected by chance, the total population of the 588 cells which are neighbors (i.e., one of the eight bordering cells) of a cell containing a protected area (but excluding those that include a protected area themselves), was calculated. This value was then compared to the mean population size found in 10 000 random draws of 588 cells.

RESULTS AND DISCUSSION

Avian species richness, primary productivity, and mean annual precipitation showed strong, significant positive correlations at all spatial scales (Table 1), with no strong nonlinear or asymptotic effects (checked using a quadratic term, see also van Rensburg et al. [2002]). In this respect, the southern African avifauna shows patterns similar to those of species richness at larger scales, although habitat heterogeneity was generally less important than has been found at larger spatial extents (compare van Rensburg et al. [2002] with Rahbek and Graves [2001], and with Jetz and Rahbek [2002]). Much of this covariation between richness and the environmental variables in southern Africa was a consequence of spatially structured environmental variation (Table 2), largely the result of a strong east–west moisture gradient in southern Africa (O'Brien 1993, van Rensburg et al. 2002). Human population density was likewise significantly correlated with both precipitation and primary productivity at all of the scales examined and here too the covariation was largely a consequence of spatially structured environmental variation (Tables 1 and 2). Thus, at all three spatial resolutions, human population density and bird species richness respond positively to increases in net primary productivity and rainfall (a strong surrogate for NPP). Consequently, it is not surprising that at all spatial scales strong correlations between human population density and avian species richness were found (for all species as well as common and range-restricted species) (Table 3). The large contribution of the spatially structured environmental variation component in the partial regression analyses of avian richness and human population density (Table 2) indicates that the covariation is probably a result of similar responses by both humans and birds to the aridity gradient in southern Africa.

Irrespective of the underlying cause, it is clear that at the extent and resolution at which conservation is usually undertaken there are strong relationships between NPP, human population density, and avian species richness. These results provide considerable support for Balmford et al.'s (2001a, b) conclusions, and cast some doubt on Huston's (2001) suggestion that a well-developed agricultural infrastructure, such as that characteristic of South Africa, is likely to obscure these relationships. Furthermore, the magnitude of the relationships found at the one-degree resolution were quite similar to those of Balmford et al. (2001b), suggesting that, in other regions, investigations at finer resolutions are likely to reveal qualitatively similar results. This means that both species rich areas, and areas containing range-restricted taxa are likely to contain high numbers of humans. Indeed, in a similar analysis at the country scale, but under rather different climatic conditions (those of Canada), Rivard et al. (2000) found that energy availability, vertebrate species richness, and human activity were positively related.

TABLE 2. Results from partial regression analyses indicating the extent to which, at each spatial resolution, variation in the relationships between the two variables of interest is partitioned into a, nonenvironmental spatial component; b, spatially structured environmental variation component; and c, nonspatial environmental component. The unexplained component d, is not provided here.

Variables and resolution	Coefficients of determination				
	$a + b + c$	a	b	c	$a + b$
Species richness and PPT					
Quarter degree	0.618***	0.199	0.415	0.003	0.614***
Half degree	0.822***	0.229	0.532	0.061	0.761***
One degree	0.805***	0.131	0.672	0.002	0.803***
Population density and PPT					
Quarter degree	0.568***	0.051	0.503	0.014	0.554***
Half degree	0.628***	0.051	0.403	0.174	0.454***
One degree	0.721***	0.051	0.652	0.018	0.703***
Species richness and population density					
Quarter degree	0.659***	0.167	0.447	0.045	0.614***
Half degree	0.855***	0.168	0.593	0.094	0.761***
One degree	0.906***	0.024	0.779	0.103	0.803***

Notes: The total variation, excluding the residual component, is given by $a + b + c$, while the variation accounted for by the spatially structured components in combination is given by $a + b$ (see Legendre and Legendre 1998). The spatial component of the dependent variable was modeled using a third-order polynomial of the form: $f(x,y) = b_0 + b_1 x + b_2 y + b_3 x^2 + b_4 xy + b_5 y^2 + b_6 x^3 + b_7 x^2 y + b_8 xy^2 + b_9 y^3$, where x and y represent longitude and latitude, respectively. The coefficient of determination (r^2) for this relationship was used as a measure of that component of the variation in the dependent variable that is explained by a combination of components $a + b$. The variation in the dependent variable explained by components $b + c$ was determined from a model only incorporating the independent variable. The variation in the dependent variable explained by components $a + b + c$ was determined from a model incorporating both the independent and spatial variables. All partial regression values remained significant after a sequential Bonferroni correction was applied.

*** $P < 0.001$.

In southern Africa, high population densities clearly translate into considerable landscape transformation (Table 3), as has previously been suggested for Africa and other regions (Ehrlich 1995, Bawa and Dayanandan 1997, McKinney 2001, 2002, Parks and Harcourt 2002). In consequence, it is not clear why the relationship between avian species richness and human population density has persisted. If landscapes were massively transformed, it might be expected that the relationship between human population density and avian species richness would be considerably weakened. There are several reasons why this might not be the case: (1) African birds might be capable of withstanding considerable habitat modification and disturbance (the resilience of the African fauna to human activities has repeatedly been discussed in the context of the low levels of recorded Quaternary extinctions; see MacPhee [1999] and references therein); (2) there is sufficient habitat heterogeneity at the quarter-degree level to allow persistence of birds despite apparently high human population densities (Redford and Dinerstein 1994); (3) landscape transformation is too recent for there to have been any effect (Brooks et al. 1999*b*), and therefore there is a pending extinction crisis as the debt run up by habitat transformation is collected (Brooks et al. 1999*b*, Baillie et al. 2001); (4) some combination of these factors. Whatever the reason, it seems likely that over time the relationships between species richness, NPP, and human population density should change substantially as populations in the region continue to increase (estimated population growth rate in South Africa between 1996 and 2001 is 2.2% per year; Statistics South Africa [1996]). Conservation agencies will increasingly have to consider these changes when assessing both future policies and the likely success of their current actions (see also discussion in Scholtz and Chown 1993, McKinney 2001, Nizeyimana et al. 2001, Hansen and Rotella 2002, Parks and Harcourt 2002).

The relationships between avian species richness and human population size raise the question of whether

TABLE 3. Pearson correlation coefficients between human population density and four avian species richness categories, and percentage land transformation at each resolution before taking spatial autocorrelation into account.

Variable	Quarter degree	Half degree	One degree
All species	0.67***	0.79***	0.90***
Widely distributed species	0.56***	0.60***	0.69***
Narrowly distributed species	0.35**	0.45***	0.59***
Red data species	0.52**	0.69**	0.88**
Land transformation (%)	0.58**	0.63**	0.57**

Note: Significance was calculated after a sequential Bonferroni correction was applied (df at quarter degree = 1, 1856; half degree = 1, 456; one degree = 1, 100).

** $P < 0.01$; *** $P < 0.001$.

cells containing currently designated reserves are likely to be characterized by higher numbers of humans, and whether such a problem might be avoided during designation of new potential conservation areas. Quarter-degree grid cells bordering on currently designated conservation areas have significantly greater human population densities than expected by chance ($P <$ 0.025, 10 000 permutations). In addition, this effect is stronger for smaller conservation areas because there is a significant negative relationship between human population density and protected area size ($r = -0.3$, $P < 0.0001$, df $= 1, 263$). These relationships, and the significant decline in size of newly proclaimed conservation areas ($r = -0.2$, $P < 0.05$, df $= 1, 263$), suggest that, in future, currently designated conservation areas are going to face increasing human pressure. This situation is not unique to South Africa (Newmark 1996, Harcourt et al. 2001, Hansen and Rotella 2002, Parks and Harcourt 2002, Sinclair et al. 2002). It also suggests that, unless conservation authorities resist external demands on the resources they are protecting, or seek alternative and additional means to protect both plants and animals (McNeely 1994), species face an increasingly uncertain future (Thompson and Jones 1999, Terborgh 1999, Liu et al. 2001).

One form that such action could take is the selection of additional areas for species conservation. Balmford et al. (2001*b*) suggested that at fine scales this option does appear to be promising, though actual designation of such sites will still depend on integration of competing land uses (Vane-Wright 1996). Here, total human population size in the 30 minimum representation complementary sets of 19 quarter-degree cells (Gaston et al. 2001) was either slightly higher than or not different from that of randomly drawn cells (in 18 out of 30 cases, the mean human population size of the minimum complementary sets was significantly higher than expected for a random selection of sites). However, there is a diversity of equally optimal complementary networks (representing all species in 19 cells), which are distinct in terms of the spatial location of particular sites (Rodrigues and Gaston 2002*a*). This may provide some flexibility for minimizing the human population in reserve networks while still representing all species efficiently. To explore this flexibility (see Rodrigues et al. 2000*a*), we determined the maximum and minimum human population size contained within optimal reserve networks representing all species. This was done by solving the integer linear problems that maximize or minimize (respectively) the total human population in the cells selected, subject to all species being represented in 19 cells. We found that for optimal complementary sets representing all species, the total human population can vary between 360 733 and 947 142. When compared with the limits of the 95% confidence intervals for 10 000 random draws of 19 cells (390 183–401 630), these values indicate a wide variation in the total population of optimal complementary sets. Al-

though the maximum possible total population in these sets is much larger (more than twice) that of randomly selected cells, the minimum possible population is only slightly smaller. This indicates that there is some, but not much, flexibility in optimal complementary sets for the selection of reserve networks that minimize conservation conflict by minimizing the total human population contained in them.

Further flexibility may be achieved by relaxing the restriction that 19 cells are selected, that is, by searching for the set of cells with minimum human population that represents all species at least once without restricting the number of cells selected. This results in a set of 23 cells with a total population of 287 271, indicating that it is possible to obtain a reserve network representing all species while having a smaller total human population (79.6% of the best possible option for sets of 19 cells), at the expense of selecting additional sites. Unfortunately, this flexibility does not include much of the currently designated reserve network, because only six of these 23 cells have a considerable fraction of their area (>25%) currently reserved. Forcing the inclusion of other reserved cells raises substantially the human population included in the network: a set of 22 cells also representing all species but now maximizing the overlap with cells having more than 25% of their area reserved (without any restriction on the total human population) includes 13 of these cells but has a total population of 441 929. Thus, not only is the current reserve network subject to the threat of land use conflict because of pressure from high population density areas surrounding reserves, but there may also be little room left for minimizing potential land use conflicts by selecting new reserve areas in the context of the current reserve network (Lombard 1995*b*, Freitag et al. 1998). Given the considerable significance of undisturbed areas for the conservation of intact ecosystems (Redford 1992), other ways must be sought to minimize conflicts while retaining the currently designated network of reserves.

One way in which the potential for such conflicts could be minimized, and the problem of high human population densities surrounding reserve areas could be addressed, might be to relax the requirement that all species are represented. While such a compromise might be unappealing from a conservation perspective, and philosophically problematic (see Morowitz 1991), it is a question that should be addressed given that land use (and consequently species survival) trade-offs are likely to be made because of competing demands for the same areas. This procedure can be implemented by solving two coupled optimization problems. The first obtains a set of cells that minimizes the total human population subject to representing a given number of species. If more than one solution exists, a second problem is solved which finds the smallest number of cells while keeping the total human population equal to the minimum value found in the first problem (see Ro-

FIG. 2. Trade-off between species represented and total human population included in complementary reserve networks. Circles represent the minimum total population (as a percentage of the population in the set of 23 cells representing all 651 species) that is represented in selected sites (cells) while representing at least a given percentage of species. Triangles represent the variation in the number of sites selected in each case.
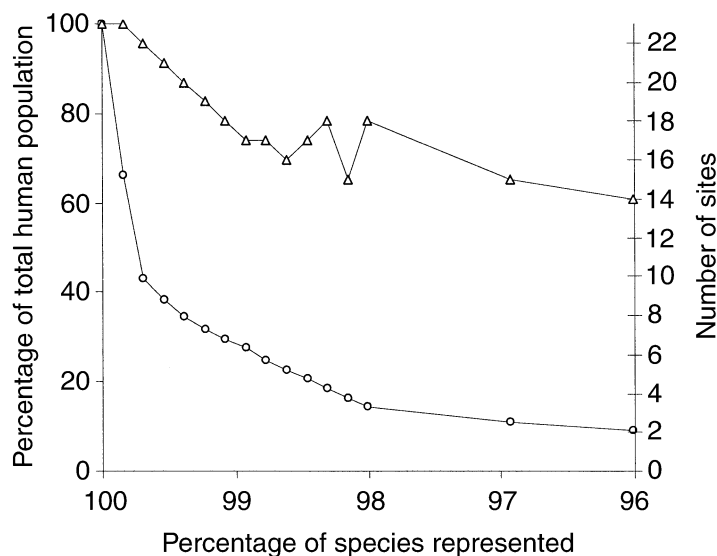
drigues et al. 2000a, Chown et al. 2001). When this is done, it becomes clear that as the requirement for species inclusiveness is relaxed, so the total population included in the minimum representation complementary set declines (Fig. 2). Because total human population decreases very rapidly as fewer species are selected, 96% of the bird species can be represented in cells with a total human population of 9.1% of that where all species are required. This result is not simply a consequence of a reduction in the total number of sites selected (Fig. 2). In other words, most avian species can be represented in cells with low human population density. It is just a few, often rare species (such as Green Barbet [*Stactolaema olivacea*]) that can only be represented in a single or just a few cells (see Rodrigues and Gaston 2002b) characterized by high human population density. This result echoes Balmford et al.'s (2001b) statement that conservation conflicts cannot be totally avoided because some species are found in densely populated areas and nowhere else. Nonetheless, if these species are disregarded then it is possible to select sites that can represent the majority of species in areas where human population density and thus the likelihood of land transformation is low.

Unfortunately, these sites include only a small proportion (~10) of the 264 currently protected areas in South Africa. It is therefore clear that areas immediately adjacent to currently protected areas have much higher human population densities, and consequently a higher risk of habitat modification (see Terborgh 1999, Liu et al. 2001, Harcourt et al. 2001, Hansen and Rotella 2002, Parks and Harcourt 2002, Sinclair et al. 2002), than areas selected to reduce these risks. Although we are not suggesting that the currently protected areas be relinquished, we are of the opinion that programs of new protected area acquisitions should be done in a way to minimize conflict. Furthermore, if

areas with low human population density are selected, then the opportunity cost (see Vane-Wright 1996, Faith 2001) of establishing the protected area might also be lower. In short, it appears that there may be ways of addressing conservation conflicts at fine spatial scales (Balmford et al. 2001b).

However, such optimism (if acceptance of species losses could be called optimism) is based on the assumption that the physical and biotic landscape is static, and that a single representation is sufficient to conserve a species. It is widely appreciated that using single representations represents only a starting point for conservation planning (Cabeza and Moilanen 2001). Here, a requirement for several representations is likely to mean even fewer opportunities to minimize land use conflicts. Moreover, several studies have shown that for the long-term survival of species, reserve networks must be selected in ways that not only ensure species representation, but also their long-term persistence (Rodrigues et al. 2000b, c), and this is likely to be particularly true under scenarios of climate change (see Erasmus et al. 2002). Likewise, protected areas might act as attractors for humans, so changing the population density in the surrounding area and thus compromising conservation (Oates 1999, Terborgh 1999, Hansen and Rotella 2002).

Conservation solutions could explicitly incorporate changing landscapes and the need for multiple representation in one, or a combination, of three ways. First, larger areas could be set aside for conservation (see Soulé and Sanjayan 1998). Despite arguments to the effect that the economic difficulties of doing so are insurmountable (Musters et al. 2000), in relative terms the cost of conservation is low (Balmford and Gaston 1999, James et al. 2001, Pimm et al. 2001). Second, conservation (biodiversity remediation) in as much of the landscape outside conservation areas as is possible

could be undertaken (McNeely 1994, James et al. 2001). Unfortunately, even in countries where this requirement has long been recognized, once common species are now in decline (Baillie et al. 2001). Moreover, reversing the effects of urbanization is likely to be particularly difficult, if not impossible (Scholtz and Chown 1993, Thompson and Jones 1999). Finally, the conservation conflicts associated with human expectations and the changing landscapes they bring could be ameliorated by altering the variable that is rarely considered: human population size. Individual-based regulation of human population size to a point that ensures both species survival and the satisfaction of human expectations appears to us to be one of the most effective means of ensuring a reduction in the rates of species loss over the longer term. Such regulation amounts to prevention of a problem that is unlikely to be solved by tinkering with alternative cures.

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