Birds as surrogates for biodiversity: an analysis of a data set from southern Québec

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Surrogacy analysis consists of determining a set of biotic or environmental parameters which can be rapidly assessed in the field and reliably used to prioritize places for biodiversity conservation. Whether adequate surrogate sets exist remains an open and relatively unexplored question though its solution is central to the aims of conservation biology. This paper analyses the surrogacy problem by prioritizing places using surrogate lists and comparing these results with those obtained by using more comprehensive species lists. More specifically, it explores (i) the possibility of using bird distributions, which are often easily available, as surrogates for species at risk (endangered and threatened species), which are presumed to be an important component of biodiversity; and (ii) the methodological question of how spatial scale influences surrogate success. The data set analysed, from southern Québec, is one of the most complete biotic data sets available at the regional scale. Contrary to some previous analyses, the results obtained suggest that the surrogacy problem is potentially solvable.

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1. Introduction

Since it is usually not economically and sociopolitically feasible to conserve every place that is of some biological interest, conserving biodiversity requires the prioritizing of places on the basis of their biodiversity value, selecting those places that have the highest priority, and devising adaptive management plans for them (Margules and Pressey 2000; Sarkar and Margules 2001). In order to carry out this process, the biodiversity value of sites have to be assessed. One major problem is that beyond a general consensus that "biodiversity" refers to the variety of life, there is little agreement about what constitutes biodiversity. Common candidates include the diversity of alleles, species, and communities, but there are many other alternatives (Sarkar and Margules 2001). As will be pointed out below, the choice of a measure of biodiversity will partly have to rely on conventions that capture deeply-held intuitions about what biodiversity is; empirical considerations alone will not suffice.

After such a measure of biodiversity is chosen, ideally, field surveys should be conducted to assess the distributions of the relevant biotic entities. However, in practice, this is unrealistic: at the relatively fine (local) scale that is relevant for selecting sites for conservation, surveys are expensive and time-consuming, though there is evidence to indicate that they are good value (Balmford and Gaston 2001). If we accept that biodiversity has to be assessed rapidly, and often [see e.g. Nix *et al* (2000)], then it has to be done indirectly through the use of estimators that have come to be called "surrogates" (Prendergast *et al* 1993; Colwell and Coddington 1994; Sarkar and Margules 2002). What is assessed in the field are these presumed surrogates for biodiversity such as sets of rare or endangered species or environmental parameter sets. However, the important question of the empirical adequacy of these surrogates as measures of biodiversity

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in the field has rarely been addressed (Landres *et al* 1988). On a continental scale that is unfortunately largely irrelevant for conservation decisions (each unit is a country), Balmford and Long (1995) analysed the use of birds with restricted ranges to predict bird endemism. At more relevant spatial scales, Ferrier and Watson (1997) have analysed faunal and floral distribution data from New South Wales; Howard *et al* (1998) have analysed similar data from Uganda; Andelman and Fagan (2000) have analysed US data at three different spatial scales (though not for the same data set); and Sarkar *et al* (2000) have analysed the Gap analysis environmental parameter and vertebrate species distribution data from Texas. By and large the generally negative results of these analyses have fueled the suspicion that the surrogacy problem is unsolvable, that is, adequate surrogate sets do not exist and, therefore, comprehensive and expensive biodiversity surveys are unavoidable.

The first problem that this paper explores is the potential for using the distributions of breeding bird species as surrogates. This is an interesting possibility because breeding bird records are among the easiest species distribution data sets to obtain, thanks to the presence of birding enthusiasts in most places. Moreover, since birders actively search for sightings, bird distribution data can be taken to be presence-absence data rather than presence-only data. This means that the absence of a data point of the former sort can be interpreted as an absence of the corresponding species whereas the absence of a data point of the latter sort can only be interpreted as, either the absence of that species, or the possibility that it was present but not noted since it was not actively searched for. However, there are at least two intuitive reasons to suspect that bird distributions may not be good surrogates for the distribution of other biota: (i) bird species are usually highly mobile and, therefore, not as sensitive to habitat modification as more sessile species; and (ii) birds are known to be adaptable to highly degraded habitats including garbage dumps and sewage treatment plants. There is also some evidence that birds in general may not be good surrogates (Lawton *et al* 1998) though birds with restricted ranges may be adequate on continental scales (Balmford and Long 1995).

The second problem explored in this paper is the role of spatial scale in the performance of surrogates. Intuitively, it is clear that too high a degree of resolution will make surrogates ineffective: biogeographical units will be so small that they will be unlikely to contain records both for a surrogate and its intended target. On the other hand, at too coarse a spatial scale, it is almost trivial that anything will be a perfect surrogate for everything because all entities will be present in every spatial unit. What is not clear is whether there is an optimal size for the success of surrogates (even within a particular region), one that is small enough for conservation to be feasible but large enough for identification using surrogates. A spatial scale analysis of this sort, using the same data set, does not seem to have been attempted before.

The analysis reported here uses a data set consisting of records on the distribution of species at risk and birds for southern Québec. This data set has been previously analysed by Sarakinos *et al* (2001) to suggest conservation priorities for Québec. It is particularly conducive to the analyses attempted here because it consists of data points at a very high degree of geographical precision, thus enabling the scale analysis mentioned in the last paragraph. This paper will not address policy issues in any detail. Its purpose is only to assess methodological questions about the choice and use of surrogates. The theoretical methods and the data set used in this analysis are described in § 2; § 3 presents the results that were obtained; § 4 provides a discussion.

2. Background and methods

During the last decade a significant consensus has emerged that biodiversity conservation planning requires the solution of four problems: (i) the place prioritization problem; (ii) the surrogacy problem; (iii) the viability problem; and (iv) the multiple constraint synchronization problem (Sarkar 2002; Sarkar and Margules 2002). The place prioritization problem consists of trying to prioritize places on the basis of their biodiversity content so that places can be sequentially targeted for conservation action starting at the top. The surrogacy problem consists of choosing and establishing a set of estimators for biodiversity that can be rapidly and accurately assessed in the field and reliably used to prioritize places. The viability problem consists of determining the prognosis with respect to persistence for biota of interest in places targeted for conservation. The multiple constraint synchronization problem is that of prioritizing places for biodiversity when other policy objectives must simultaneously be met: for instance, economic and social costs must be minimized, cultural priorities met, and so on. Of these four problems, the place prioritization and viability problems have been extensively studied. This paper studies the surrogacy problem which has been comparatively neglected; the multiple constraint synchronization problem has received even less attention but will not be broached in this paper.

2.1 *True and estimator-surrogates*

Surrogacy is a relation between an estimator variable and a target variable. Ultimately, the intended target of surrogacy determination is "general biodiversity" which, unfortunately is impossible to define fully precisely (Sarkar 2002; Sarkar and Margules 2002). No matter what definition is proposed (for instance, diversity of alleles, species, or communities), some type of biodiversity [for instance, endangered biological phenomena (Brower and Malcolm 1991)] will be left out. The “true surrogate” is what is taken to represent general biodiversity (its intended target). An element of convention necessarily enters into its choice because of the problem of defining general biodiversity that was noted above. In this analysis, species at risk will be used as true surrogates. The justification for this choice is that it should be uncontroversial that these species form a “component of biodiversity” (another vague term) that deserves special attention. In contrast to true surrogates, “estimator-surrogates” have true surrogates as their target. Given that a true surrogate set has been precisely delineated (even if only by convention), whether an estimator-surrogate set adequately represents the true surrogate set is an empirical question. (What “representation” means will be clarified in § 2·2.) In this analysis, breeding bird species distributions will be assessed for their adequacy as estimator-surrogates for species at risk.

2.2 *Place prioritization and surrogacy*

The relation of representation between estimator-surrogates and true surrogates (the former are supposed to represent the latter) has been interpreted in two ways: (i) the distribution of estimator-surrogates (or some other such pattern involving them) can be used to predict the distribution (or some other pattern) of true surrogates (Faith and Walker 1996; Ferrier and Watson 1997); or (ii) the places prioritized using estimator-surrogates capture what is desired of the true surrogate. The former problem is known to be difficult and, moreover, largely irrelevant if all that is to be accomplished using the estimator-surrogates is place prioritization. The latter option will, therefore, be followed here. This has become fairly routine in surrogacy analysis in recent years (Ferrier and Watson 1997; Howard *et al* 1998; Andelman and Fagan 2000; Sarkar *et al* 2000). Places will be prioritized using the estimator-surrogates. The question, then, is whether the results satisfy the conditions that would have been required, had they been prioritized using the true surrogates.

2.3 *Place prioritization schemes*

Explicit place prioritization schemes began to be formulated in the 1970s (Justus and Sarkar 2002). Since about 1980, three principles have come to be systematically used in these schemes.

(i) *Rarity*: First, surrogates are ordered inversely by the frequency of their appearance in the data set. Then, places are ordered according to whether they contain the rarest surrogate, the next rarest surrogate, and so on, iteratively.
(ii) *Complementarity*: Places are ordered on the basis of the number of surrogates they contain which have not met the targeted representation (which is set at the beginning of the process) that they contain (Margules *et al* 1988).
(iii) *Richness*: Places are ordered on the basis of the absolute number of surrogates present. Richness is not used in this analysis at all; this reflects the fact that the use of richness results in inefficient place selection (Williams *et al* 1996; Csuti *et al* 1997).

The analysis performed here used the ResNet software package (Aggarwal *et al* 2000). Places were prioritized by rarity (applied first) and, then, complementarity. Ties were broken randomly (by lexical order). The ResNet software package was developed at the University of Texas at Austin. Similar procedures have also been implemented elsewhere (Margules *et al* 1988; Vane-Wright *et al* 1991; Rebelo and Siegfried 1992).

2.4 *Spatial scale analysis*

At too fine a spatial scale, there will never be good surrogates. In the limit, a truly small cell may well be occupied by at most a single species (assuming, of course, we are not in the microbiological realm). At the other limit, if the entire region of interest is the spatial unit of analysis, any entity is a perfect surrogate for every other. What is not clear is exactly what happens when the spatial scale is increased (that is, the degree of resolution decreased) systematically within the spatial limits that are relevant for conservation policy decisions. The point made above shows that at least up to some scale, surrogates should systematically keep on performing better. There are two open questions: (i) is there a maximum scale beyond which surrogate performance does not get significantly better; and (ii) the rate at which the performance gets better as the spatial scale is increased. This is apparently the first paper that explores these problems. The data set used in this analysis records the presence of species at precise geographical locations (longitude and latitude at least to a resolution of 0·001°). Consequently, it was possible to divide southern Québec into data cells at resolutions of 0·1° × 0·1°, 0·2° × 0·2°, 0·33° × 0·33°, 0·5° × 0·5°, and 1·0° × 1·0°, of longitude and latitude and put data points in them.

2.5 *Southern Québec data set*

The data set used in this analysis is fully described by Sarakinos *et al* (2001) and that paper also explains the category "species at risk". The data on species at risk were obtained from the Québec Natural Heritage Data Center, a part of the former Québec Ministry of Environment and Wildlife. The data set consists of presence-only records for 346 plant and 56 animal species at risk in all of Québec. Data on 242 breeding bird species of Québec were obtained from the Canadian Wildlife Service, Environment Canada, Québec region. These data points are supposed to be presence-absence. In this analysis all data points will be regarded as presence-absence. Sarakinos *et al* (2001) made the same approximation which, without extensive new surveys, is unavoidable for southern Québec. Not using such data is tantamount to not using any of the information available for rational conservation decisions. It would continue the old practice of ad hoc conservation which is known to be inefficient in terms of the utilization of scarce resources (Margules and Pressey 2000; Pressey and Cowling 2001).

The area considered in this analysis is in southern Québec, south of 50° 30′ of latitude, and west of – 66° 05′ of longitude. The area east of this line in southern Québec was ignored because no breeding bird data were available. Islands in the Gulf of St. Lawrence which lie south of this region were also ignored for the same reason. Some inadequacies of the data set are noted in § 3.

3. Results

With a spatial resolution of 0·2° × 0·2° of longitude and latitude [the same scale that was used by Sarakinos *et al* (2001)]. Figure 1a shows the cells with records of species at risk and figure 1b shows the data points for birds; there are 51 cells with records of species at risk and no record for birds. Of the species at risk recorded in these cells, only 4 (or ≈ 1·2%) do not occur in any cell with records of birds. Consequently, these species will not be conserved even if every cell with bird records is targeted for protection. Therefore, the highest achievable degree of surrogacy is 98·8%. In this sense, birds can never be a perfect surrogate for species at risk, at least when used at this level of spatial resolution. However, an unexpectedly high number of cells have no records of breeding birds. Given the generally hospitable terrain for avifauna in southern Québec, it is unlikely that breeding birds are absent in these cells. It is much more likely that this shows an inadequacy of the data set. However, since only data sets with records are used for place prioritization, this inadequacy does not result in under-representation of either birds or species at risk in the selected cells. What it potentially does is make the selection process less optimal (that is, the selection process targets more cells) than what may have been possible with a fully adequate data set. Problems of this sort are ubiquitous in the context of biodiversity conservation. Perfect data sets are almost never available.

Using the same spatial resolution, figure 2a shows the percentage of species at risk that, at least once, fall within cells selected using bird data with representation targets of 1, 5, 10, and 20; figure 2b shows the cells selected. (Targets between 10 and 20 do not give unusual results; these data are not shown.) With 5 representations of birds, at most 76% of the species at risk are represented at least once; the area selected is 25,650 sq. km (or 5·3% of the total area of southern Québec). With 10 representations of birds, the maximum representation achieved for species at risk is 87%; with 20, it only goes up to 90%. Meanwhile the area selected goes up from 47,250 sq. km (or 9·8% of the total area) to 84,900 sq. km (or 17·7% of the total area); this would probably be deemed unacceptably inefficient in most policy-making situations. This suggests that an optimal conservation strategy for southern Québec should probably use a target of 10 and then devise individual plans for species at risk that remain underrepresented. What is interesting about figure 2b is that, at the target of 1 for species at risk, contrary to the results obtained by Sarakinos *et al* (2001) using species at risk directly, most of the selected cells are not clustered around the southern border, which is the most heavily populated area of Québec, thus making conservation action more difficult.

Figure 3 is the figure corresponding to figure 2a when it is required that species at risk are represented at least twice; figure 4 when those species are represented at least five times; and figure 5 when the required level of representation is at least 10. For figures 3–5, figure 2b continues to show the cells actually selected. Table 1 summarizes these data. As expected, the maximum achieved representation of species at risk declines as the target increases.

Figure 6 shows the percentages of species at risk selected at random, represented at least once. Results presented here are an average from 100 randomizations. The number of random cells selected is equal to those selected when figure 2b was generated. Thus the curves labelled "target = 1", "target = 5", etc. correspond to the random selection of the same number of cells as when the corresponding curves for figure 2a were generated by setting targets of 1, 5, etc. for birds. When figure 6 is compared to figure 2a, it becomes clear that there is a significant difference between selecting cells using birds as surrogates and selecting cells at random: the curves in figure 2a are consistently higher than the corresponding curves in figure 6. However, this difference decreases as higher targets for birds are set. It will be pointed out in the next section that this is an important (and desirable) result.

Figures 7–11 explore the dependence of surrogacy on spatial scale. Figure 7a shows the percentage of species at risk that fall at least once within cells selected using the bird data with targets 1, 5, 10 and 20; figure 7b shows the cells selected, but now with a resolution of 0·1° × 0·1° of longitude and latitude. Figure 8 shows the same data at a resolution of 0·33° × 0·33°; figure 9 at a resolution of 0·5° × 0·5°; figure 10 at a resolution of 1° × 1°. Figure 11 shows the percentage level of surrogacy achieved for at least one representation of species at risk when bird data with targets 1, 5, 10 and 20 are used as a function of spatial scale. It is clear that surrogacy improves monotonically with an increase of spatial scale. At a spatial resolution of 1° × 1°, the level of representation of spe-

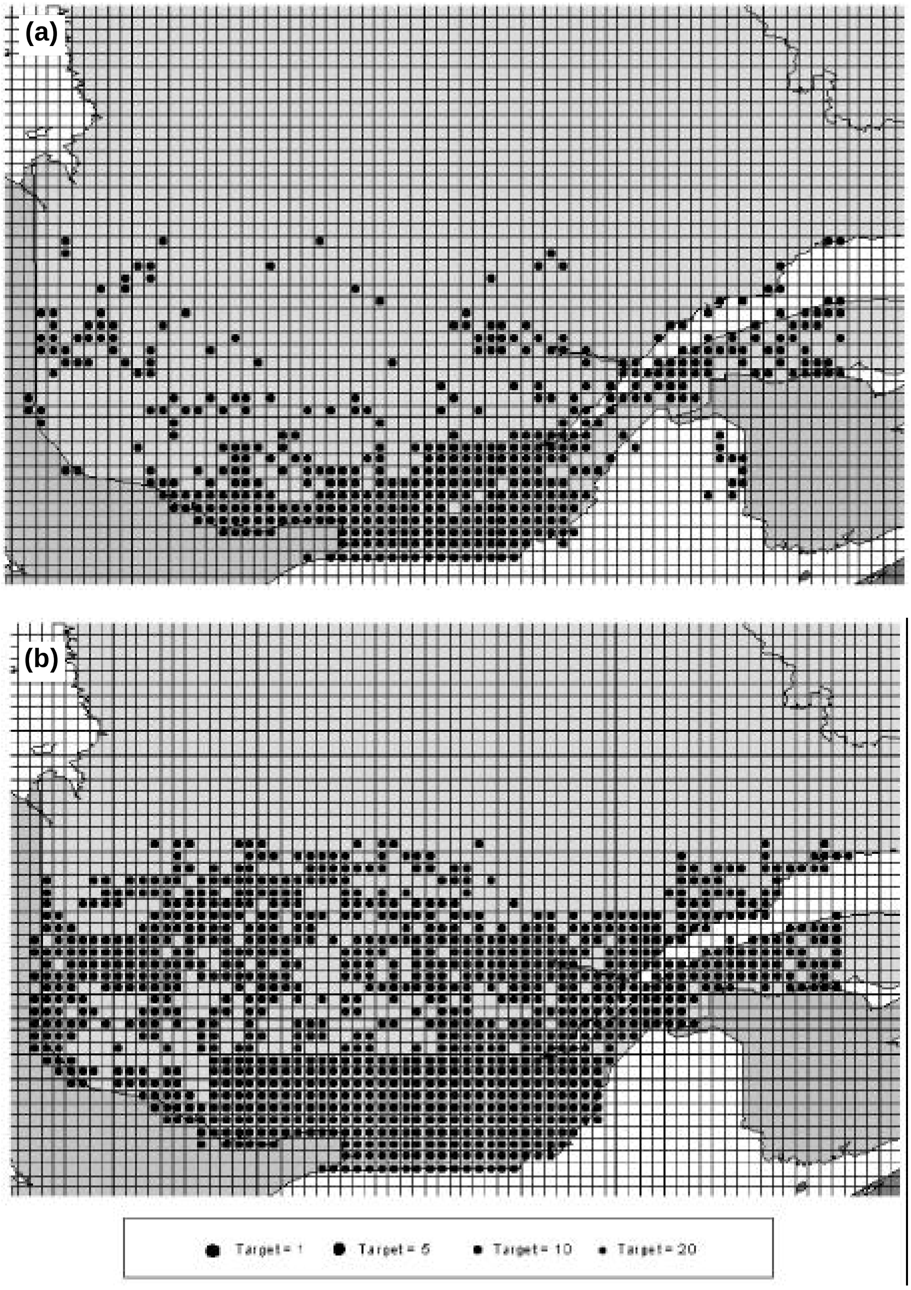

Figure 1. (**a**) Distribution of species at risk in southern Québec. (**b**) Distribution of birds in southern Québec. All cells with a record are marked with (•). The spatial resolution is 0·2° longitude × 0·2° latitude. The absence of bird records in so many cells almost certainly reflects inadequacy of the data set.

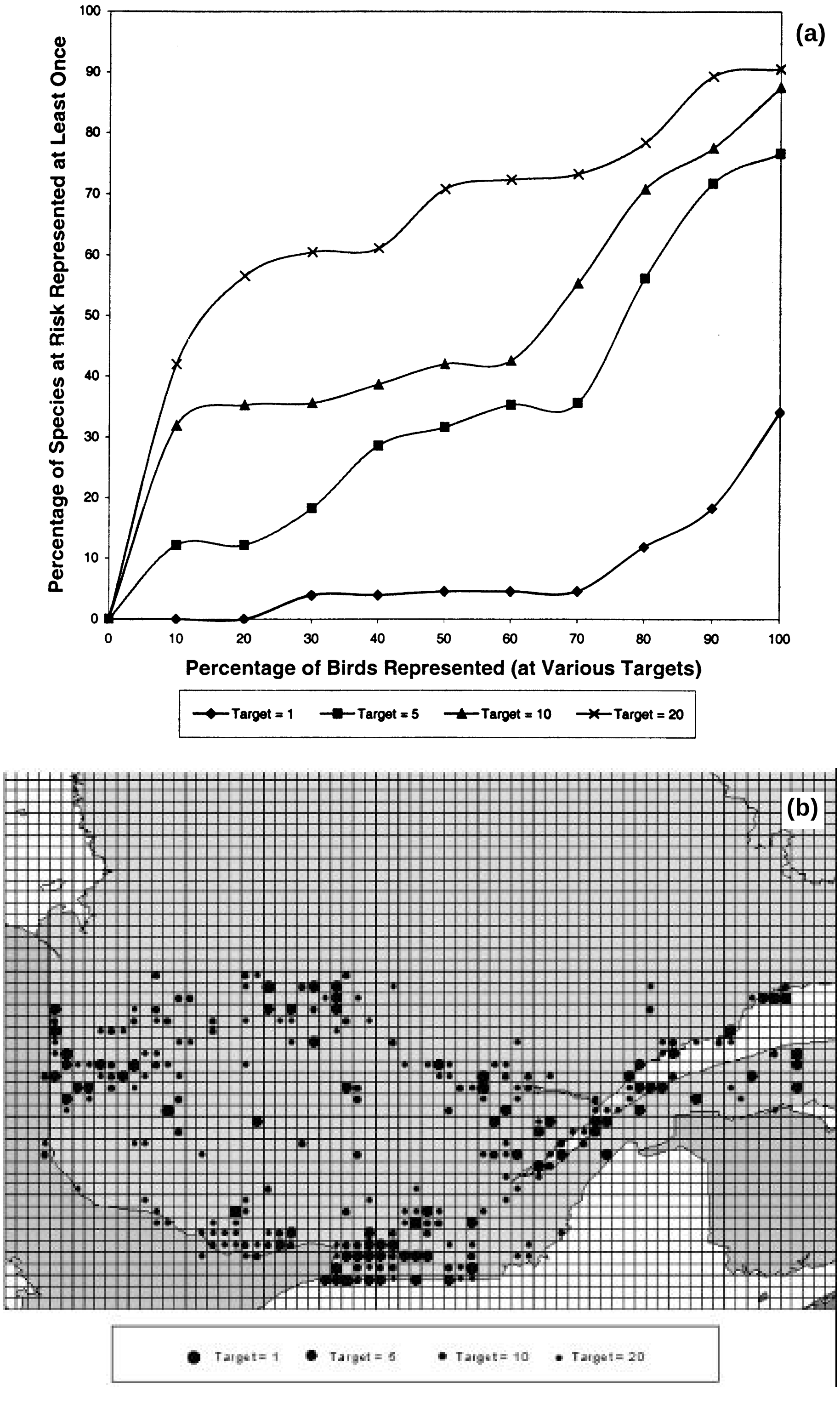

Figure 2. (**a**) Surrogacy graph with target of 1 for species at risk. These graphs show what percentage of species at risk get represented at least once when a certain percentage (along the x-axis) of birds get represented in cells selected by ResNet using birds as surrogates. The different graphs represent the number of representations of birds that are targeted by ResNet. (**b**) Cells selected in southern Québec using birds as surrogates. Note how the selected cells are not clustered along the southern border of the map. The relevance of this fact is discussed in the text.

cies at risk reaches 100%; at this scale, birds become a "perfect" surrogate provided that the target for bird representation is set at 20. However, beyond the 0·33° × 0·33° resolution it is unlikely that the gain in representation would outweigh the cost of selecting the much larger areas involved.

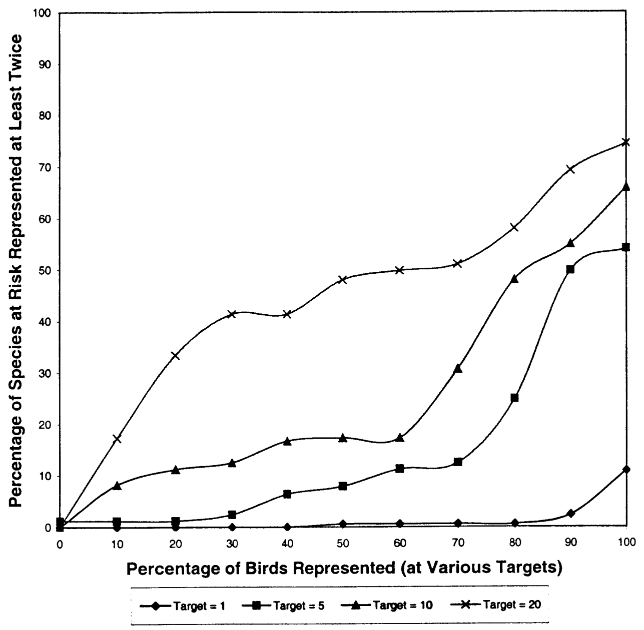

Figure 3. Surrogacy graph with target of 2 for species at risk. These graphs show what percentage of species at risk get represented at least twice; otherwise the interpretation of the figure is the same as for figure 2a.

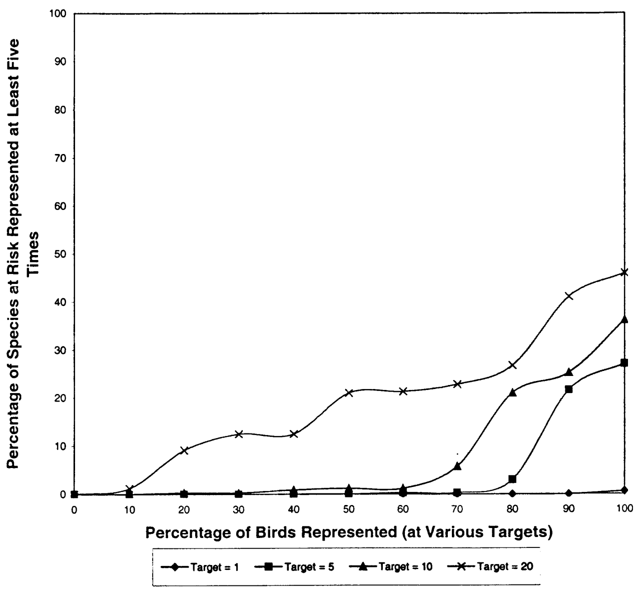

Figure 4. Surrogacy graph with target of 5 for species at risk. These graphs show what percentage of species at risk get represented at least five times; otherwise the interpretation of the figure is the same as for figure 2a.

4. Discussion

Explicit surrogacy analysis of the sort performed here is designed to replace the implicit use of untested surro-

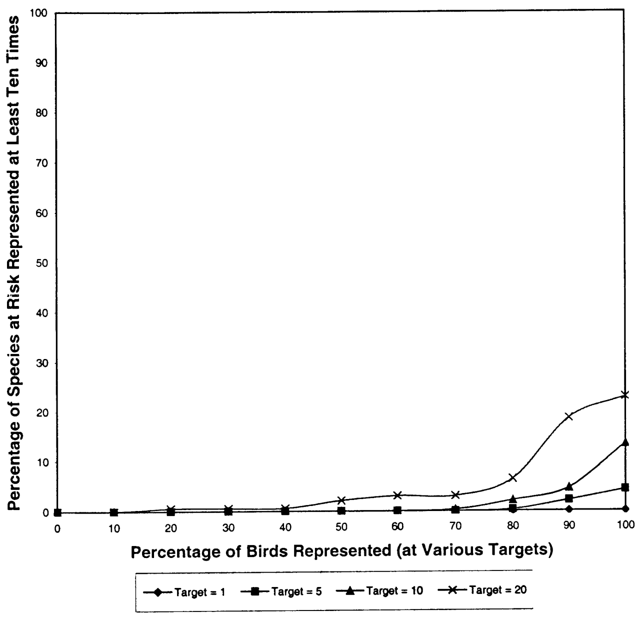

Figure 5. Surrogacy graph with target of 10 for species at risk. These graphs show what percentage of species at risk get represented at least ten times; otherwise the interpretation of the figure is the same as for figure 2a.

Table 1. Birds as surrogates for species at risk: best results.

Target set for birds	Maximum achieved percentage for species at risk at different targets of intended representation: 1	2	5	10
1	34	10	1	0
5	76	54	27	4
10	87	66	36	13
20	90	74	46	23

This table shows how the representation of species at risk changes with different targets set for birds at a spatial resolution is 0·2° longitude × 0·2° latitude. When more than one representation of species at risk is required, the results are not optimistic, with only a 74% success rate being achieved even when 20 representations of birds are achieved and only 2 representations of species at risk are required.

gates such as putative keystone, flagship, or umbrella species that was once *de rigeur* in conservation decision-making [see Simberloff (1998) for a discussion]. Also using threatened species as true surrogates, and umbrella, flagship and intuitive "biodiversity indicator" species as estimator-surrogates, Andelman and Fagan (2000) analysed three data sets at increasing spatial scales: (i) the southern California coastal sage scrub habitat; (ii) the Columbia Plateau in the northwest United States; (iii) the entire United States at a county-by-county resolution. Though different spatial scales were used, since no single database was analysed at different resolutions, these results cannot be compared to the spatial analysis presented here. In general, Andelman and Fagan (2000) found that their estimator-surrogates did not do significantly better than a random place selection procedure. The results presented here show that the use of birds as surrogates is better than random at least for southern Québec. However, for reasonable results, a target of at least 10 representations of birds must be set. This is not an unreasonable conservation demand for as widely dispersing a group as birds are: preserving 10 populations of each species of bird in a system of reserves should not constitute an undue burden for regional governments.

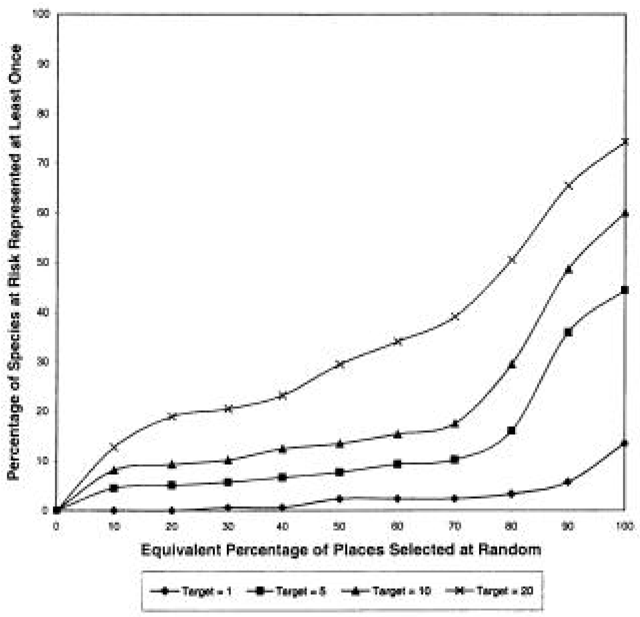

Figure 6. Representation of species at risk with random selection of cells. These graphs show what percentage of species at risk get represented at least once by random selection of cells. The graphs represent an average of 100 randomizations. "Target = 1" means that the same number of cells were selected as what resulted when ResNet was run on a 0·2° longitude × 0·2° latitude resolution with a target of 1 for birds, as in figure 2. The other "Targets" in this figure are analogous.

Analyses very similar to the one presented here were performed by Ferrier and Watson (1997) for the forested north-east of New South Wales, Howard *et al* (1998) for Uganda, and Sarkar *et al* (2001) for Texas. The first two of these studies selected sites with varying areas; with such a choice, spatial scale analysis becomes impossible. Ferrier and Watson used a wide variety of biological groups as true surrogates and both these groups, as well as environmental parameter sets, as estimator-surrogates. All estimator-surrogates performed particularly poorly for ground-dwelling invertebrates. Purely environmental surrogate sets fared the worst, Ferrier and Watson found that they could capture about 80% of the target variable at best, while selecting 20% of the land area using the surrogates in a complementarity-based algorithm. In an interesting result, Howard *et al* (1998) found that a wide variety of taxa (woody plants, large moths, butterflies, birds, small mammals, and all groups put together) did equally well when selecting areas, no matter what the target. However, a random selection procedure was just as good. As they point out, these results probably only reflect the fact that the different taxa have very similar biogeographic distributions with respect to diversity in Uganda. When they selected 20% of the total area using a complementarity-based algorithm, the maximum achieved representation of targets was less than 80%. Compared to both these studies, the results presented here are more optimistic about solving the surrogacy problem. Referring back to figure 2a, an 87% representation was achieved using birds while selecting only 9·8% of the total area and 90% was achieved while selecting only 17·7% of the total area. However, this optimism should be tempered by the possibility of slowing the surrogacy problem, and finalizing the best estimator-surrogate, both being heavily context-dependent. Results from one region may have no relevance for another. Many more analyses of this sort for a wide variety of habitats must be performed before an optimistic conclusion can be said to have been established.

Sarkar *et al* (2001) used environmental parameter sets as estimators to test for surrogacy on a hexagonal grid, created by the Environmental Protection Agency, and used in Texas by the GAP Analysis Program. Modeled distributions of all native vertebrates were used as true surrogates. The maximum level of representation achieved was about 86%; this required the use of all environmental parameters. Individual environmental classes (soil types, vegetation classes, etc.) achieved about 80%. The spatial scale of analysis would correspond to slightly more than the lowest scale (0·2° × 0·2° of longitude and latitude) used in this analysis. If, as has been the experience elsewhere, the use of biotic surrogates improves performance, the Texas case will be consistent with the positive results achieved here.

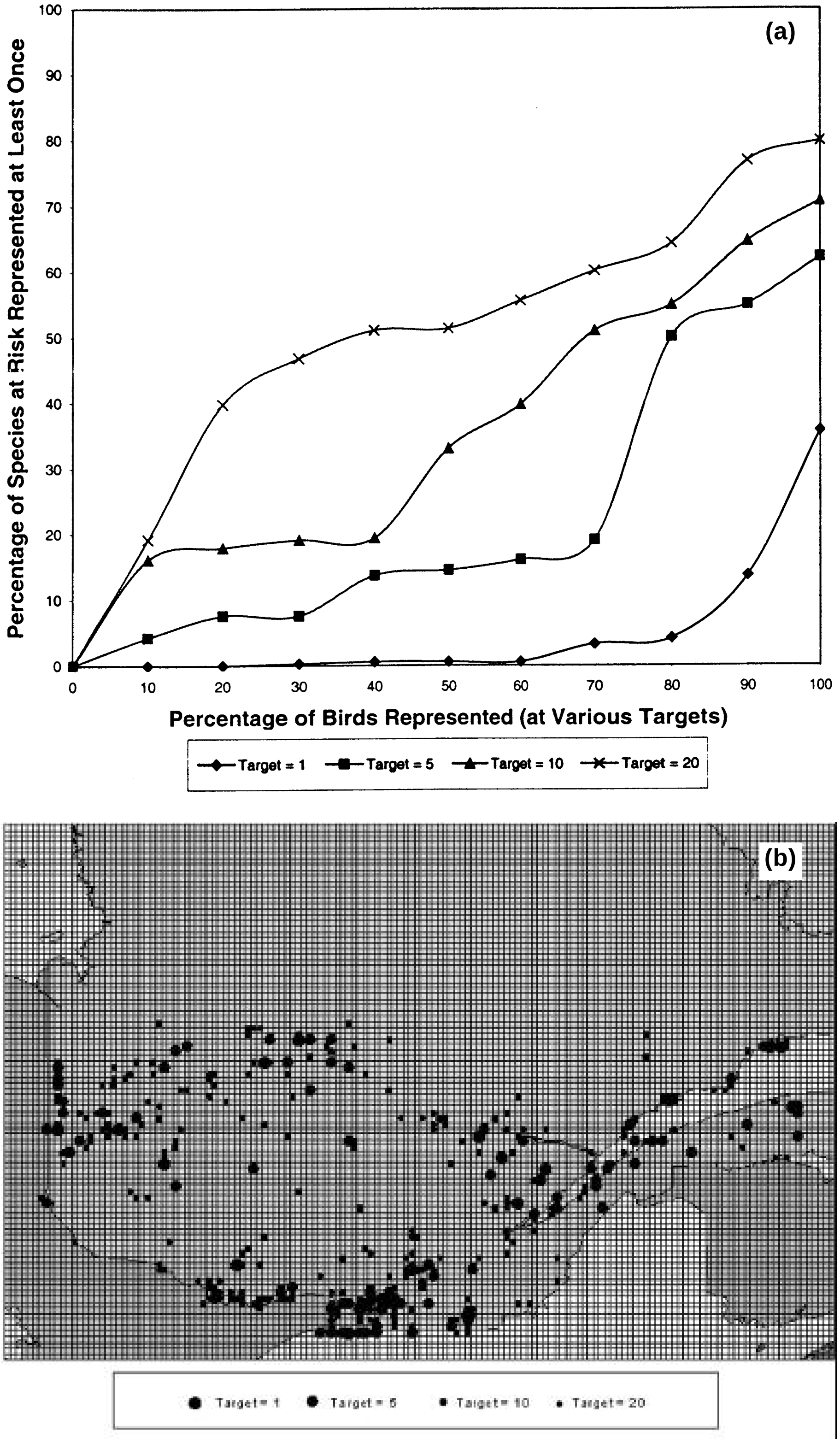

Figure 7. Surrogacy graph for species at risk with target of 1 at a spatial resolution of 0·1° longitude × 0·1° latitude. Except for the spatial resolution, the interpretation is the same as in figure 2.

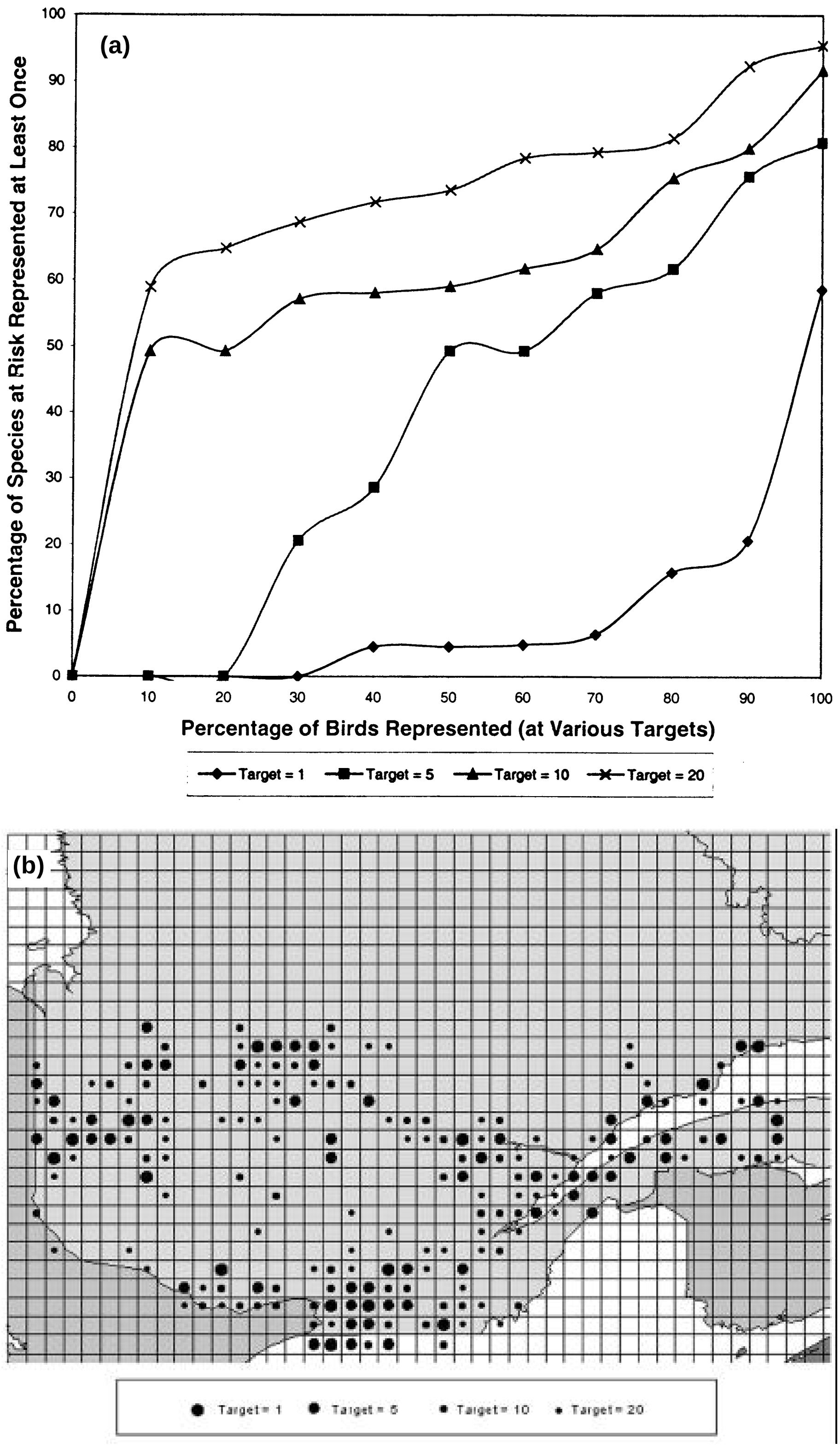

Figure 8. Surrogacy graph for species at risk with target of 1 at a spatial resolution of 0·33° longitude × 0·33° latitude. Except for the spatial resolution, the interpretation is the same as in figure 2.

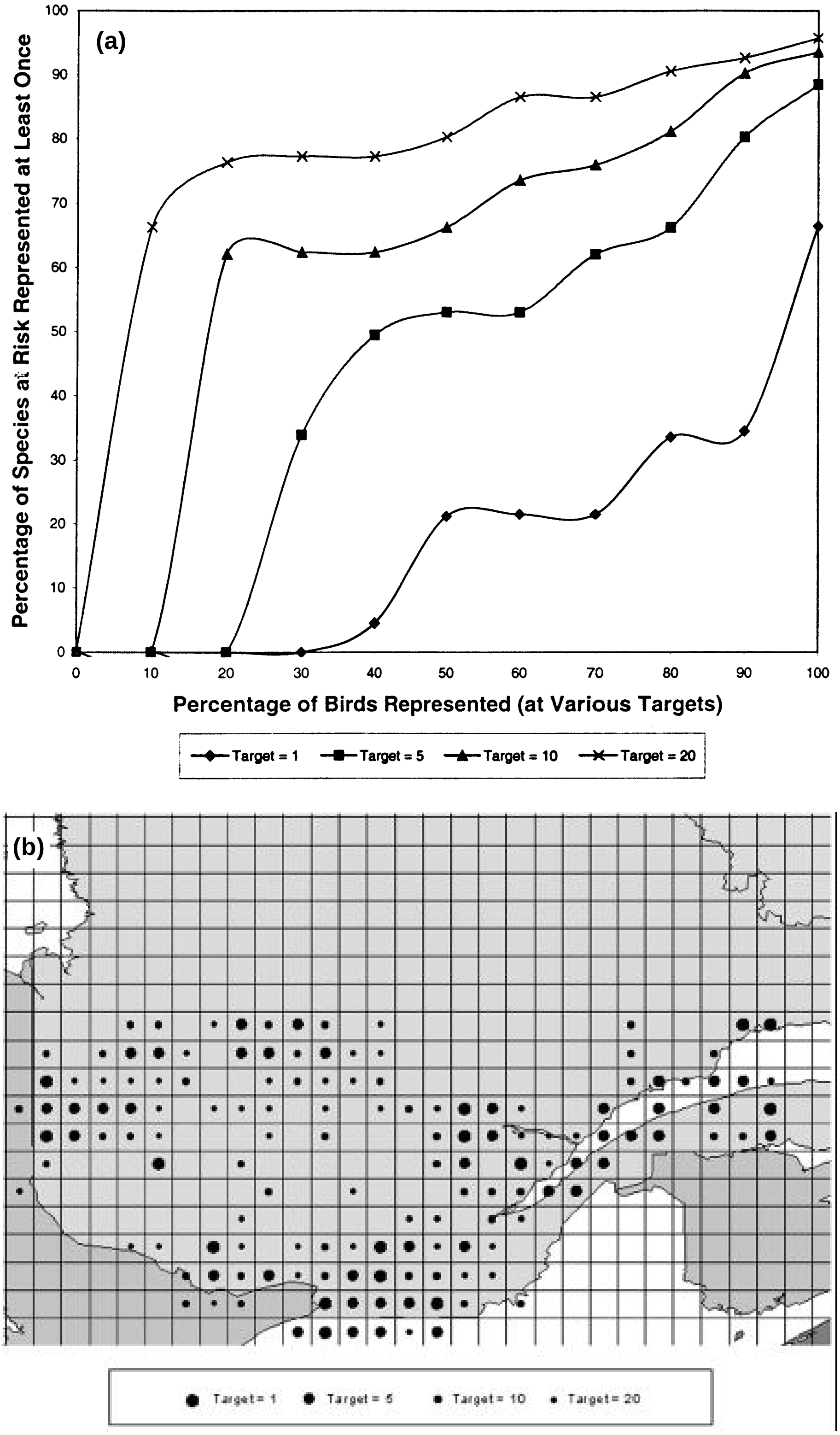

Figure 9. Surrogacy graph for species at risk with target of 1 at a spatial resolution of 0·5° longitude × 0·5° latitude. Except for the spatial resolution, the interpretation is the same as in figure 2.

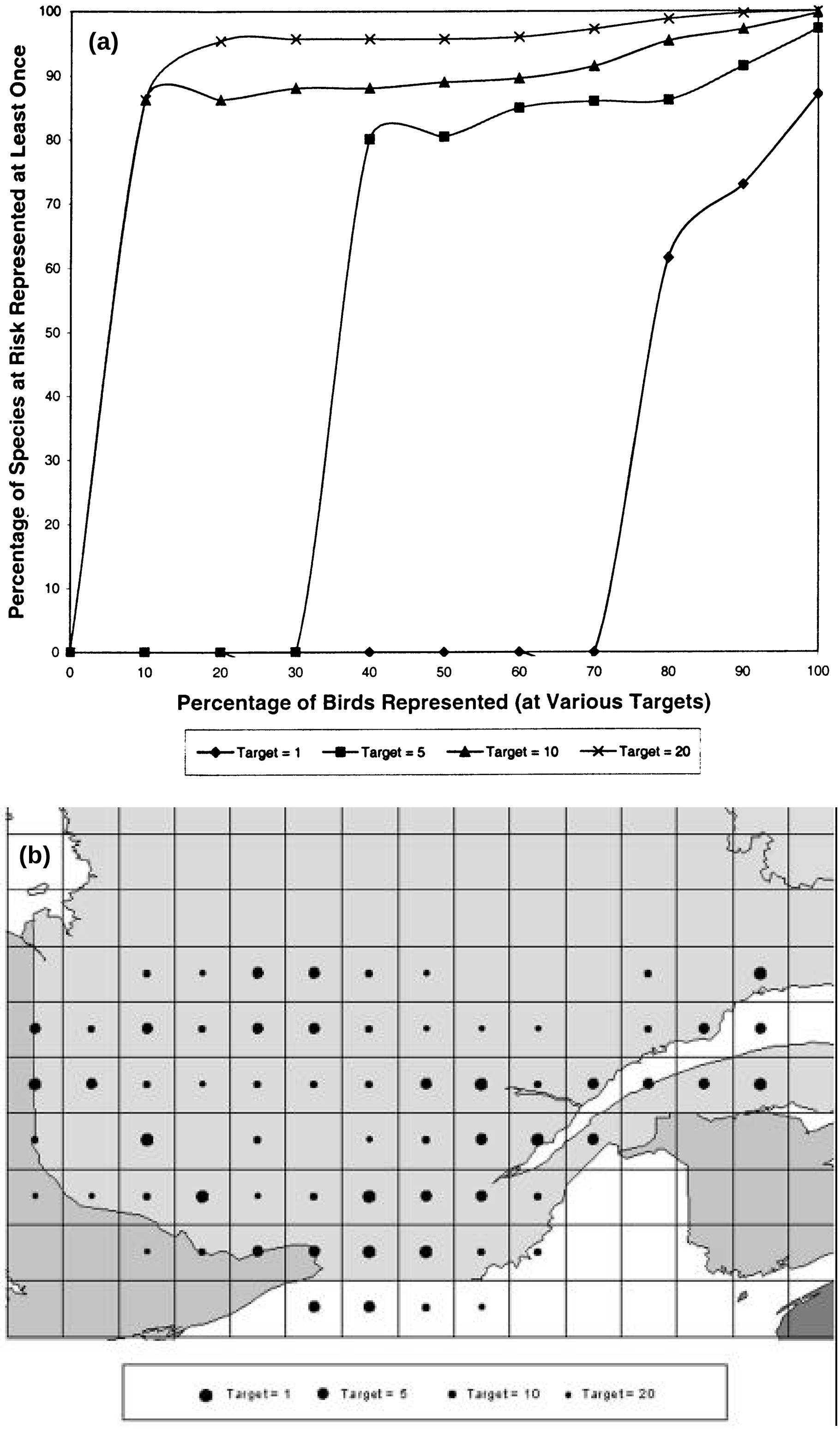

Figure 10. Surrogacy graph for species at risk with target of 1 at a spatial resolution of 1·0° longitude × 1·0° latitude. Except for the spatial resolution, the interpretation is the same as in figure 2.

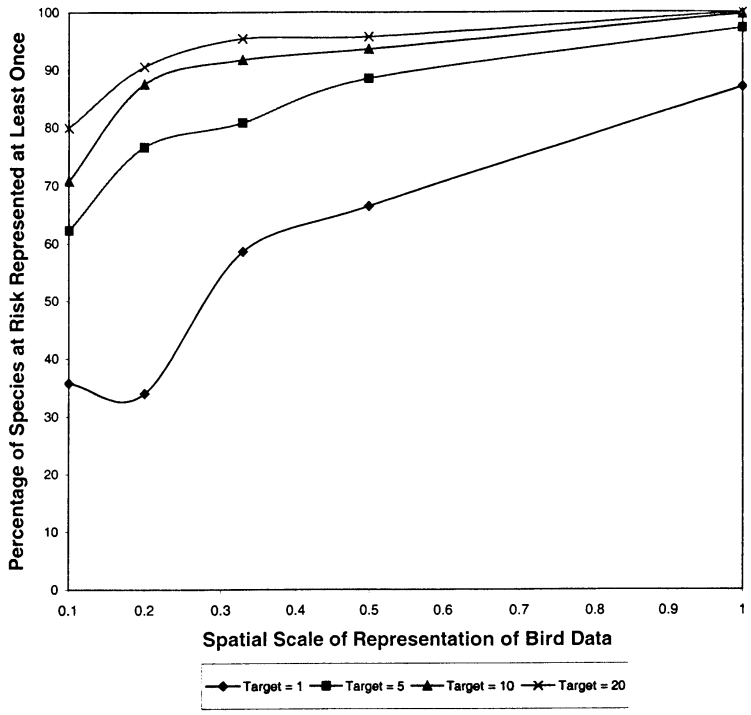

Figure 11. Success of surrogacy as a function of spatial scale. For different targets of bird representation, the graphs show the maximum success at representing species at risk (that is, the representation achieved when the bird target is fully met) as a function of the spatial scale of analysis.

The most interesting result obtained here is that, with a target of 10, there is some but not very significant, improvement in surrogacy on a spatial scale larger than 0·33° × 0·33° of longitude and latitude, and even a scale of 0·2° × 0·2° is fairly good: in figure 11, the slope of the curves become close to 0 at this spatial scale. At the lower scale, the average area of cells is 330 sq. km which is not unreasonable for individual members of a reserve network system. At the higher scale, that area is 917 sq. km which, in many contexts, may be too large. These are promising results for surrogacy analysis.

The main problem with this analysis is that the data set for species at risk is presence-only and there are some flaws with the bird data set. As pointed out in the last section, the latter problem does not vitiate the results that were obtained. However, the use of presence-only data must be recognized as problematic even while admitting that the requirements of rapid biodiversity assessment and place prioritization forces the use of such data in many policy contexts. Moreover, to establish the validity of a set of estimator-surrogates, presence-absence data for true surrogates must be collected for at least some representative regions. Thus, should the use of less than perfect data continue to suggest the effective use of birds as surrogates, before such a policy is even enshrined in everyday practice, proper surveys must be carried out for these regions. An alternative would be to devise place prioritization schemes that can take uncertainty of information into account. There have been some recent efforts in this direction (Polasky *et al* 2000; Sarkar S, unpublished results). This remains one of the major theoretical problems in conservation biology.

We will end with a note of caution. This is the only example of an investigation of the role of spatial scale in surrogacy analysis. Moreover, surrogacy analysis using place prioritization and complementarity-based algorithms has been attempted for only four data sets. The results of these analyses, positive or negative, should not remotely be regarded as definitive until many more data sets have been analysed.

References

Aggarwal A, Garson J, Margules C R, Nicholls A O and Sarkar S 2000 *ResNet Ver 1·1 Manual*, Report, Biodiversity and Biocultural Conservation Laboratory, University of Texas, Austin

Andelman S J and Fagan W F 2000 Umbrellas and flagships: efficient conservation surrogates, or expensive mistakes?; *Proc. Natl. Acad. Sci. USA* **97** 5954–5959

Balmford A and Gaston K J 2001 Why biodiversity surveys are good value; *Nature* (*London*) **398** 204–205

Balmford A and Long A 1995 Across-country analyses of biodiversity congruence and current conservation effort in the tropics; *Conserv. Biol.* **9** 1539–1547

Brower L P and Malcolm S B 1991 Animal migrations: endangered phenomena; *Am. Zool.* **31** 265–276

Colwell R K S and Coddington J A 1994 Estimating terrestrial biodiversity through extrapolation; *Philos. Trans. R. Soc. London* **B345** 101–108

Csuti B, Polasky S, Williams P H, Pressey R L, Camm J D, Kershaw M, Kiester A R, Downs B, Hamilton R, Huso M and Sahr K 1997 A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon; *Biol. Conserv.* **80** 83–97

Faith D P and Walker P A 1996 How do indicator groups provide information about the relative biodiversity of different sets of areas?: on hotspots, complementarity and pattern-based approaches; *Biodiver. Lett.* **3** 18–25

Ferrier S and Watson G 1997 *An evaluation of the effectiveness of environmental surrogates and modelling techniques in predicting the distribution of biological diversity. Consultancy report to the Biodiversity Convention and Strategy Section of the Biodiversity Group, Environment Australia* (New South Wales: Environment Australia)

Howard P C, Viskanic P, Davenport T, Kigenyi F, Baltzer M, Dickinson C, Lwanga J, Matthews R and Balmford A 1998 Complementarity and the use of indicator groups for reserve selection in Uganda; *Nature* (*London*) **394** 472–475

Justus J and Sarkar S 2002 The principle of complementarity in the design of reserve networks to conserve biodiversity; a preliminary history; *J. Biosci.* (*Suppl. 2*) **27** 421–435

Landres P B, Verner J and Thomas J W 1988 Ecological uses of vertebrate indicator species: a critique; *Conserv. Biol.* **2** 316–328

Lawton J H, Bignell D E, Boulton B, Bloemers G F, Eggleton P, Hammond P M, Hodda M, Holt R D, Larsen T B, Mawdsley N A, Stork N E, Srivastava D S and Watt A D 1998 Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest; *Nature* (*London*) **391** 72–76

Margules C R, Nicholls A O and Pressey R L 1988 Selecting networks of reserves to maximize biological diversity; *Biol. Conserv.* **43** 63–76

Margules C R and Pressey R L 2000 Systematic conservation planning; *Nature* (*London*) **405** 243–253

Nix H A, Faith D P, Hutchinson M F, Margules C R, West J, Allison A, Kesteven J L, Natera G, Slater W, Stein J L and Walker P 2000 *The BioRap toolbox: A national study of biodiversity assessment and planning for Papua New Guinea. Consultancy report to the World Bank* (Canberra: CSIRO Press)

Polasky S, Camm J D, Solow A R, Csuti B, White D and Ding R 2000 Choosing reserve networks with incomplete species information; *Biol. Conserv.* **94** 1–10

Prendergast J R, Quinn R M, Lawton J H, Eversham B C and Gibbons D W 1993 Rare species, the coincidence of diversity hotspots and conservation strategies; *Nature* (*London*) **365** 335–337

Pressey R L and Cowling R M 2001 Reserve selection algorithms and the real world; *Conserv. Biol.* **15** 275–277

Rebelo A G and Siegfried W R 1992 Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity; *Conserv. Biol.* **6** 243–252

Sarakinos H, Nicholls A O, Tubert A, Aggarwal A, Margules C R and Sarkar S 2001 Area prioritization for biodiversity conservation in Québec on the basis of species distributions: a preliminary analysis; *Biodiver. Conserv.* (in press)

Sarkar S 2001 Defining "biodiversity"; assessing biodiversity; *Monist* (in press)

Sarkar S and Margules C 2001 Operationalizing biodiversity for conservation planning; *J. Biosci.* (*Suppl. 2*) **27** 299–308

Sarkar S, Parker N, Garson J, Aggarwal A and Haskell S 2001 Place prioritization for Texas using GAP data: the use of biodiversity and environmental surrogates within socioeconomic constraints; *Gap Bull.* (in press)

Simberloff D 1998 Flagships, umbrellas, and keystones: is single species management passé in the landscape era?; *Biol. Conserv.* **83** 247–257

Williams P, Gibbons D, Margules C, Rebelo A, Humphries C and Pressey R 1996 A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds; *Conserv. Biol.* **10** 155–174

Vane-Wright R I, Humphries C J and Williams P H 1991 What to protect? Systematics and the agony of choice; *Biol. Conserv.* **55** 235–254