Sensitivity of Systematic Reserve Selection to Decisions about Scale, Biological Data, and Targets: Case Study from Southern British Columbia

LEANNA D. WARMAN,*§ A. R. E. SINCLAIR,* G. G. E. SCUDDER,* BRIAN KLINKENBERG,†
AND ROBERT L. PRESSEY‡

*Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada
†Department of Geography, University of British Columbia, 1984 West Mall, Vancouver, BC V6T 1Z2, Canada
‡New South Wales National Parks and Wildlife Service, P.O. Box 402, Armidale, NSW, 2350, Australia

Abstract: *The identification of conservation areas based on systematic reserve-selection algorithms requires decisions related to both spatial and ecological scale. These decisions may affect the distribution and number of sites considered priorities for conservation within a region. We explored the sensitivity of systematic reserve selection by altering values of three essential variables. We used a 1:20,000-scale terrestrial ecosystem map and habitat suitability data for 29 threatened vertebrate species in the Okanagan region of British Columbia, Canada. To these data we applied a reserve-selection algorithm to select conservation sites while altering selection unit size and shape, features of biodiversity (i.e., vertebrate species), and area conservation targets for each biodiversity feature. The spatial similarity, or percentage overlap, of selected sets of conservation sites identified (1) with different selection units was* $\leq$*40%, (2) with different biodiversity features was 59%, and (3) with different conservation targets was* $\geq$*94%. Because any selected set of sites is only one of many possible sets, we also compared the conservation value (irreplaceability) of all sites in the region for each variation of the data. The correlations of irreplaceability were weak for different selection units (*$0.23 \leq r \leq 0.67$*), strong for different biodiversity features (*$r = 0.84$*), and mixed for different conservation targets (*$r = 0.16; 0.16; 1.00$*). Because of the low congruence of selected sites and weak correlations of irreplaceability for different selection units, recommendations from studies that have been applied at only one spatial scale must be considered cautiously.*

Key Words: biodiversity, conservation targets, irreplaceability, minimum sets, reserve selection, spatial scale, surrogates

Sensibilidad de la Selección Sistemática de Reservas a Decisiones sobre Escala, Datos Biológicos y Objetivos: Estudio de Caso del Sur de Columbia Británica

Resumen: *La identificación de áreas de conservación basada en algoritmos de selección sistemática de reservas requiere decisiones relacionadas tanto con la escala espacial como la ecológica. Estas decisiones pueden afectar la distribución y el número de sitios considerados prioridades de conservación en una región. Exploramos la sensibilidad de la selección sistemática de reservas alterando los valores de tres variables esenciales. Utilizamos un mapa de ecosistema terrestre a escala 1:20,000 y datos de aptitud de hábitat para 29 especies amenazadas de vertebrados en la región de Okanagan en Columbia Británica, Canadá. Aplicamos un algoritmo de selección sistemática de reservas a estos datos para seleccionar sitios de conservación mientras se alteraba el tamaño y la forma de la unidad seleccionada, las características de la biodiversidad (es decir, especies de vertebrados) y los objetivos de conservación para cada característica de biodiversidad del paisaje. La similitud espacial, o porcentaje de traslapamiento, de conjuntos de sitios de conservación selectos identificada*

---

§*email warman@zoology.ubc.ca*

Paper submitted December 9, 2002; revised manuscript accepted October 14, 2003.

Conservation Biology, Pages 655–666
Volume 18, No. 3, June 2004

con (1) diferentes unidades de selección fue ≤40%, (2) diferentes características de biodiversidad fue 59% y (3) diferentes objetivos de conservación fue ≥94%. Debido a que cualquier conjunto de sitios seleccionado es solo uno de muchos conjuntos posibles, también comparamos el valor de conservación (irreemplazabilidad) de todos los sitios en la región para cada variación de los datos. Las correlaciones de irremplazabilidad fueron débiles para diferentes unidades de selección ($0.23 \le r \le 0.67$), fuerte para diferentes características de biodiversidad ($r = 0.84$), y variable para diferentes objetivos de conservación ($r = 0.16; 0.16; 1.00$). Debido a la baja congruencia de sitios seleccionados y las correlaciones débiles de irremplazabilidad para diferentes unidades de selección, las recomendaciones de estudios que se han aplicado en solo una escala espacial deben tomarse con cautela.

Palabras Clave: biodiversidad, conjuntos mínimos, escala espacial, irremplazabilidad, objetivos de conservación, reemplazo, selección de reserva

Introduction

Systematic reserve-selection procedures have been developed as a tool to aid in identifying priority conservation areas in light of limited knowledge and understanding of ecological systems (Pressey et al. 1993; Margules & Pressey 2000). The advantage of systematic reserve-selection procedures is that conservation goals and rules are explicit and the selection process is repeatable (Bedward et al. 1992). However, there are uncertainties associated with the criteria used to select sites (individual areas) for conservation. Systematic techniques of reserve selection require decisions related to both spatial and ecological scale. These decisions set the values for algorithm variables in systematic reserve selection, which in turn influence the spatial analysis of ecological data (Stoms 1994). Therefore, we must determine the sensitivity of systematic reserve selection to variation in these values.

There are three variables that potentially have a large influence on site selection: (1) selection units, delineating the sites available for selection, (2) features of biodiversity (e.g., species) included in the algorithm, and (3) conservation targets or goals for biodiversity features within a region. Selection units provide the framework for compiling data on the occurrence and distribution of biodiversity features within a region. Determining the size and shape of selection units appropriate for conservation within a region is problematic because there is no strong theoretical basis for using a specific selection unit (Stoms 1994; Pressey & Logan 1998). Small selection units achieve conservation targets for biodiversity features within a region more efficiently (i.e., in less area) than larger units (Pressey & Logan 1995). However, small isolated units may not be large enough for species and natural processes to persist within them. Because there are no strict guidelines for choosing a selection unit, justification in published studies for using a particular unit varies considerably.

In some studies, selection-unit size has been decided arbitrarily (Nicholls & Margules 1993; Lombard et al. 1995; Freemark et al. 2000; Williams et al. 2000; Brooks et al. 2001). In others it has varied with administrative or ownership boundaries (Strittholt & Boerner 1995; Pressey et al. 1997; Ando et al. 1998), with biology (Price et al. 1995), or as a compromise between management and viability (Kiester et al. 1996; Lombard et al. 1997). The problem is that different selection units alter the pattern of biodiversity occurrence within a region, thereby affecting the selection of sites for conservation. However, none of these studies examined the consequences of their choice of selection unit on site selection.

A second issue with systematic reserve selection is data quality. Often, detailed information on location and life-history requirements is known only for a subset of species because comprehensive surveys of biodiversity require expertise and large amounts of money and time (Ricketts et al. 1999). It is often assumed that subsets of regional biodiversity, such as endangered species and more easily studied species, can be used to identify areas that also provide habitat for other taxa (Scott et al. 1993; Ricketts et al. 1999; Margules & Pressey 2000; Brooks et al. 2001). The success of such surrogates at identifying habitat is variable, however, and likely depends on the assessment techniques, spatial scale, geographic location, and biodiversity features used for the analysis (Saetersdal et al. 1993; Vanderklift et al. 1998; Reyers & van Jaarsveld 2000; Klinkenberg 2002; Rouget 2003). Therefore, it cannot be assumed that surrogates can successfully identify conservation areas for biodiversity, and they should be examined on a regional basis.

The identification of appropriate conservation targets is also affected by the lack of species data. The goal of most conservation programs is to conserve viable populations of species for a specified period of time into the future (Soulé 1987). Unfortunately, it is difficult to identify appropriate conservation targets for most species because the data required for identifying viable populations of species are limited. Consequently, many reserve-selection studies are essentially theoretical exercises with arbitrary targets, such as representing species in one or more sites, that do not account for the amount of habitat available in each site (e.g., Freemark et al. 2000; Brooks et al. 2001). Although different conservation targets likely affect the total area required to maintain biodiversity, it is unknown how conservation priorities within a region will change as targets are varied.

Many reserve-selection studies have used spatial scales, species, or conservation targets that are not practical for conservation within their respective study regions. In our study we included data that could be used to apply solutions to the conservation issues facing the South Okanagan. The South Okanagan is a small region with a large number of endangered and vulnerable species (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2002), which are threatened by a high rate of habitat loss from human impacts. This region is the northern extent of the Columbia Basin grasslands and shrub-steppe habitats found in the northwestern United States and has been identified as a priority for conservation within Canada (Freemark et al. 2000).

We examined the variation in conservation sites selected by a heuristic reserve-selection algorithm by altering values for three algorithm variables. We measured the congruence of the sites selected by a reserve-selection algorithm when different selection units, biodiversity features, and conservation targets are used. By altering the species included as biodiversity features, we evaluated whether a subset of the vertebrate species, based on their national at-risk status, are surrogates for other vertebrates in the region. Because the reserve-selection algorithm identifies only one of many possible solutions, we also use the irreplaceability (Pressey et al. 1994; Ferrier et al. 2000) of sites to measure sensitivity. The use of alternative measures to minimum-set overlap has not been widely demonstrated in the literature, so we compared the two methods for measuring similarity to determine whether the same trends emerge.

Methods

Data

The South Okanagan region encompasses an 1800-km^2 area consisting of two valleys located in the southern interior of British Columbia (BC), Canada. A 1:20,000–scale terrestrial ecosystem map (TEM), developed by the Ministry of Environment, Lands and Parks (MELP) in 1989, classifies the regional landscape into 111 vegetation types based on climate, physiography, surficial material, soil, and vegetation. The map is comprised of 10,125 irregular polygons, each of which can consist of up to three different vegetation types. Large lake and completely urban polygons were excluded from the analyses because these areas were not considered available for conservation. We used the irregular TEM polygons and three regular hexagonal grids for our analyses (White et al. 1992). Although regular grids decrease the accuracy of ecological data because of the arbitrary boundary imposed on the landscape (Fotheringham 1989; Stoms 1994), they provide a simple method for mapping data and evaluating the effects of selection-unit variation on reserve selection.

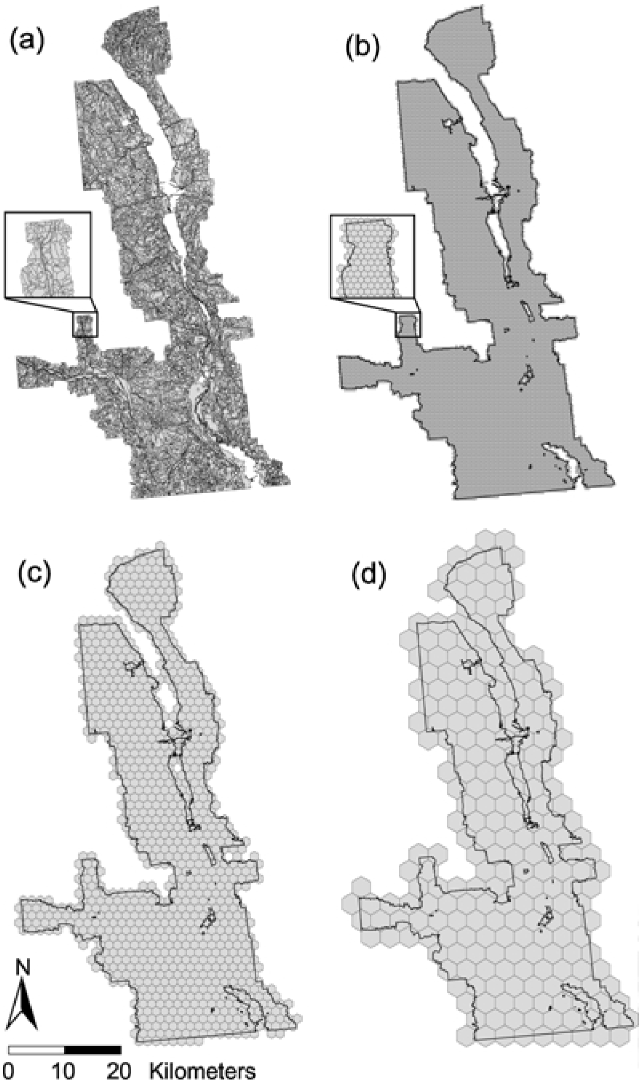

Figure 1. Selection units used to identify minimum sets of sites and irreplaceability of sites: (a) terrestrial ecosystem map polygons, (b) 0.16-km^2 hexagons, (c) 2-km^2 hexagons, and (d) 10-km^2 hexagons.

The mean area of the polygons in the terrestrial ecosystem map is 0.16 km^2 (SD = 0.23; Fig. 1a). We used this value to create the smallest hexagon size for our analyses, which resulted in 10,935 selection units for the region (Fig. 1b). The intermediate hexagon size was 2 km^2, resulting in 963 selection units for the region (Fig. 1c). The 2-km^2 hexagon represents the mean size of existing areas that are either provincial parks or managed for conservation by private organizations (October 2000). The largest hexagon size was 10 km^2, which resulted in 233 selection units (Fig. 1d). The 10-km^2 hexagon size was chosen because Ferruginous Hawks (*Buteo regalis*) occur at an average density of 0.1/km^2 (e.g., Schmutz 1984; Canadian Ferruginous Hawk Recovery Team 1994), the lowest density of the 29 vertebrate species included in our analyses. Because Ferruginous Hawks are wide-ranging and not known to be territorial, we assumed that an array of 10-km^2 sites (even if individual sites were not adjacent) would provide enough habitat to maintain breeding pairs.

We used 29 wildlife habitat relationship models (MELP 1999) for red-listed (potentially endangered or threatened within British Columbia) or blue-listed (vulnerable and at risk of becoming endangered or threatened within British Columbia) vertebrate species (Vennesland et al. 2002). The provincial status in British Columbia and national status in Canada of the 29 vertebrate species is available from L.D.W. The models identify the suitability of each vegetation type for each species based on the probability of current habitat use. Although they are qualitative, habitat-suitability ratings were determined from species' distribution and habitat preferences from published and unpublished reports, local knowledge of biologists and naturalists, and expert review (Warman et al. 1998). We calculated the area of habitat available in a polygon for a given species with a conversion factor based on the suitability rating associated with each vegetation type (Warman 2001). The calculated area for each vegetation type was summed to determine the total amount of habitat area in a polygon for each species (Table 1). Although this calculation may not determine the exact amount of habitat area available per polygon, it provides a conservative estimate. The wildlife habitat models were verified based on known occurrences of each species (Warman 2001). Because the species occurrence data were not collected systematically for the entire region and are biased to roads (Warman 2001) we did not use them for reserve selection. Although the wildlife habitat model data may be limited for systematic reserve selection (Araújo & Williams 2000), species may be lost from the region if conservation priorities are not assessed with existing data and implemented.

Conservation Targets

Systematic reserve selection requires a conservation target to be identified for each biodiversity feature. We used three different sets of conservation targets for site selection. The targets represent habitat area for (1) general estimates of minimum viable populations (MVP), (2) current populations, and (3) an arbitrary target set at half of the current populations of the red- or blue- listed vertebrates. The arbitrary target was included in the analyses because the minimum set that represented the current population of each species required 37.2% of the area within the region, which was too large for effective comparison of variation in minimum sets. This target is referred to as "half populations." The conservation targets used in the analyses for minimum viable populations, current populations, and half populations of the 29 vertebrate species are available from L.D.W.

Table 1. Example calculation for determining the amount of available habitat in a polygon for a given species.*

Habitat type	*Habitat suitability rating*	*Conversion factor*	*Total area (km^2)*	*Calculated area (km^2)*
X	high	0.875	6.0	5.250
Y	moderate	0.500	1.0	0.500
Z	low	0.125	3.0	0.375

**Calculations are for species A in a 10-km^2 polygon composed of 60% habitat type X, 10% habitat type Y, and 30% habitat type Z. Total calculated habitat area in polygon for species A = 6.125 km^2.*

We obtained current population sizes from status reports or other local government documents on individual species within the study area. Although these estimates provide the most reasonable population targets for the endangered and vulnerable species within the South Okanagan, many of these species are already at population sizes lower than what could potentially be maintained within the region. Therefore, we included general MVP estimates in our analyses. The general MVP targets were based on estimates that ranged from 50 to a few thousand individuals (Franklin 1980; Soulé 1987). Whether such estimates actually represent true viable populations remains problematic. However, the data required to perform population viability analyses for the species considered in this study do not exist. The MVP conservation targets for resident species with localized ranges (i.e., amphibians and reptiles) were set at 1000 individuals. Because the study area is not large enough to maintain populations in the low thousands of migratory red- or blue-listed birds and mammals, MVP conservation targets for these species represent habitat for 500 individuals. This assumes that the South Okanagan could make a substantial contribution to the persistence of these species over geographic areas that extend beyond the study area. We chose the general MVP estimates only to illustrate how conservation targets affect selection of conservation sites, so they should not be cited as true viable population estimates for these species. Similarly, because many of the current population sizes of the threatened species are likely not viable, empirical evidence is necessary to refine the conservation targets for these species before a reserve network is implemented based on our results.

We calculated the amount of habitat required to maintain populations of species based on known densities of each species in suitable habitat. Known densities were obtained from the literature, with preference given to studies located close to the South Okanagan (Warman 2001). Because densities varied between these studies, we averaged reported densities for each species (Warman 2001). The average density was used to determine both the number of individuals that could potentially occur in each site based on the calculated habitat area in each selection unit and the total area required to maintain each species at their population target.

Reserve-Selection Algorithm

We used a stepwise selection procedure (greedy heuristic algorithm) in the C-Plan conservation planning package (Pressey 1998; National Parks and Wildlife Service [NPWS] 1999) to identify conservation sites. The algorithm identifies a minimum or near-minimum set of sites that satisfies conservation targets for biodiversity features in a region, referred to here as the "minimum set" of sites, using a measure termed irreplaceability. Irreplaceability is derived multiplicatively across all features in a site to give a value ranging from zero to one that indicates the likelihood that a site will need to be protected to satisfy the conservation targets (Pressey et al. 1994; NPWS 1999; Ferrier et al. 2000).

The first rule in the algorithm was to select the site with the highest irreplaceability. If there were two or more sites with the same irreplaceability value, the site with the highest "summed irreplaceability" was selected; summed irreplaceability is the sum of the irreplaceability values for each biodiversity feature found in a site (Ferrier et al. 2000). In the event of a further tie, the site with the highest proportion of total area contributing to conservation targets was selected (NPWS 1999). After each site was selected, all measures were recalculated for the unrepresented biodiversity features in the remaining unselected sites. The process continued iteratively until all biodiversity features were represented at their target. Because we used a heuristic algorithm, solutions may contain redundant sites. Therefore, we included a check to determine whether any initially selected sites had become redundant. If a site was considered redundant, it was deselected but remained available for selection at later stages in the algorithm. Although there are some existing reserves in the region, they were ignored for the purposes of this exercise.

Sensitivity of Systematic Reserve Selection

We based our calculations for systematic reserve selection on three variables: (1) the matrix of selection units, (2) biodiversity features in each selection unit, and (3) conservation targets for each biodiversity feature. We examined the effect of these variables on minimum set selection and initial irreplaceability values of each site (i.e., before any sites were selected) within the region. To determine the effect of the altered variable on the solution, the values for the other two variables were fixed.

VARIABLE 1: SELECTION UNITS

We examined four selection units: TEM polygons, 0.16-km^2 hexagons, 2-km^2 hexagons, and 10-km^2 hexagons. For each variation in selection unit, all 29 vertebrate species were included (variable 2) and the conservation targets identified habitat to maintain these species at half population sizes (variable 3).

VARIABLE 2: BIODIVERSITY FEATURES

The Canadian Species at Risk Act focuses primarily on endangered species identified by COSEWIC, which include six of the red-listed species. Therefore, in addition to examining the effect of using different biodiversity features on site selection, we identified conservation sites and irreplaceability values for the 11 red-listed species to determine whether this subset of species could adequately represent the habitat area requirements of the 18 blue-listed species. We used all 29 red- or blue-listed species as one of the biodiversity feature data sets and 11 red-listed species as the other. For the two variations in biodiversity features, we used the 10-km^2 hexagonal grid (variable 1), and the conservation targets identified habitat to maintain half populations of the species being considered (variable 3).

VARIABLE 3: CONSERVATION TARGETS

The conservation targets represented habitat area for (1) general estimates of minimum viable populations, (2) current populations, and (3) half populations of the red- or blue-listed vertebrates. For each variation in conservation targets, the 10-km^2 hexagonal grid was used (variable 1) and all 29 vertebrate species were included (variable 2).

Minimum Set Comparisons

We calculated the following measures for each minimum set: total area of the minimum set; number of selection units in the minimum set; number of isolated, contiguous groups of sites; mean and median area of contiguous sites; and mean perimeter-to-area ratio of contiguous sites in the minimum set.

We measured the similarity of minimum sets of sites using Jaccard's similarity coefficient (van Jaarsveld et al. 1998; Krebs 1999). The coefficient was calculated as $A/(A+B+C)$, where A represents sites present in two minimum sets of sites, and B and C represent sites present in only one of the minimum sets and absent in the other. We calculated coefficients of similarity between minimum sets with different selection units using total area of overlap to represent joint occurrences (A) and total area without overlap to represent differences ($B+C$). The number or total area of sites considered for both B and C was limited by the smaller minimum set in each comparison (van Jaarsveld et al. 1998).

To determine the significance of minimum set similarity, we compared the observed values with randomly generated Jaccard values. For each pairwise comparison, we noted the number (or area for TEM polygons) of selected sites in each of the two minimum sets. We then randomly selected (1000 times) the same number or area of sites from each of the respective data sets, giving two large collections of random sets, one corresponding to each of the two minimum sets being compared. We generated Jaccard values for 1000 pairs of these two randomly selected sets. We compared the observed Jaccard value to the distribution of randomly derived values and identified the probability of obtaining the observed value by chance.

Irreplaceability Comparisons

Irreplaceability calculations in C-Plan are influenced by both the conservation targets and combination size (Ferrier et al. 2000). Combination size refers to the number of sites that will, in combination, satisfy the conservation targets at each iteration of the selection algorithm. Irreplaceability varies depending on the number of sites included in a reserve system and is therefore estimated and interpreted in terms of a combination size (Ferrier et al. 2000). For maximum comparability of irreplaceability values between data sets, the initial combination size for each data set was fixed relative to the minimum number of selection units needed to satisfy targets for each data set.

To compare irreplaceability values between different selection units, we intersected two sets of selection units for each pairwise comparison, effectively subdividing one grid of planning units with the other. This intersection produced a common set of spatial units that had a larger number of units than either of the two original data sets separately. Initial irreplaceability values were calculated for the original units in the two original data sets and then allocated to subunits in the intersected grid. Irreplaceability values in each subunit were compared between each pair of data sets with the Spearman rank correlation because the values were not normally distributed. We determined the significance of each correlation by randomizing one of the data sets in each pairwise comparison 2000 times and calculating the Spearman rank coefficient. The data set with the greater total number of units was randomized for comparisons between different selection-unit data sets. Significance testing by randomization of the data was necessary because the data sets being compared were not independent.

Results

Selection Units

The most efficient selection unit was the 0.16-km^2 hexagon, which is the smallest regular grid (Table 2; Fig. 2). Efficiency is based on the area of selected sites relative to all selection units in the region (Pressey & Nicholls 1989). Although minimum sets selected with the larger hexagonal units were only slightly less efficient than the smallest hexagonal unit, the area included in the selected sites was much greater (Table 2). The larger units comprised a greater total regional area than the smaller units. If the total area of each data set was restricted to the area within the actual regional boundary, the difference in efficiency would be greater.

The 10-km^2 hexagons, the largest selection units, produced the most contiguous minimum set, which had the fewest contiguous groups of sites with the lowest mean perimeter-to-area ratio (Table 2; Fig. 2d). The number of contiguous groups and mean perimeter-to-area ratio increased, whereas mean and median group size decreased with a decrease in size of the hexagonal selection units (Table 2). However, only median group size was significantly correlated with selection-unit size ($r = 1.00$, $p < 0.001$). The minimum set identified with TEM polygon

Table 2. Comparison of minimum sets of sites resulting from variation in size and shape of the selection unit, features of biodiversity, and magnitude of the conservation targets.

Algorithm trials	*Total area of minimum set (km^2)*	*Number of sites selected*	*Total number of sites available*	*Efficiency of sites selected*	*Number of contiguous groups of sites*	*Mean size of contiguous groups of sites (km^2)*	*Median size of contiguous groups of sites (km^2)*	*Mean perimeter-to-area ratio (km:km^2)*
Selection unit								
TEM[a] polygon	261.18	524	10125	0.83	285	0.92	0.53	9.06
0.16-km^2 hexagon	239.01	1542	10930	0.86	275	0.87	0.31	7.85
2-km^2 hexagon	304.00	152	963	0.84	29	10.48	4.00	2.12
10-km^2 hexagon	360.00	36	233	0.84	11	32.73	20.00	0.97
Biodiversity feature								
red- and blue-listed species	360.00	36	233	0.84	11	32.73	20.00	0.97
red-listed species	310.00	31	233	0.87	11	28.18	10.00	1.01
Conservation target								
MVP[b] estimate	2310.00	231	233	0.01	1	2310.00	2310.00	0.16
current populations	890.00	89	233	0.62	4	222.50	40.00	0.83
half populations	360.00	36	233	0.84	11	32.73	20.00	0.97

[a] *TEM, terrestrial ecosystem map.*
[b] *MVP, minimum viable population.*

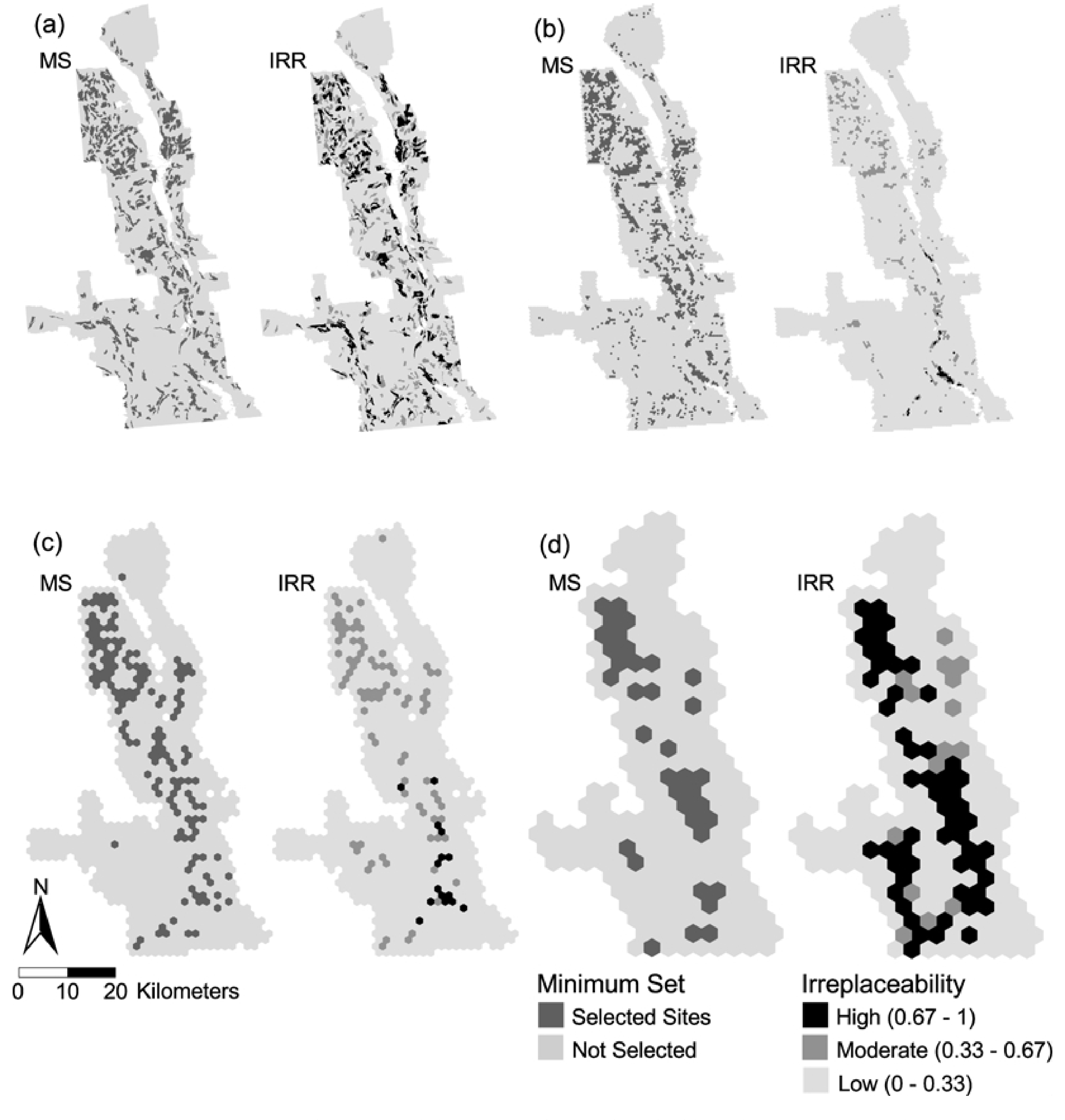

Figure 2. Minimum sets (MS) and irreplaceability (IRR) of sites identified based on (a) terrestrial ecosystem map polygons, (b) 0.16-km^2 hexagons, (c) 2-km^2 hexagons, and (d) 10-km^2 hexagons for 29 red- or blue-listed vertebrate species.

selection units had the lowest contiguity—the highest perimeter-to-area ratio and number of contiguous groups of sites.

All similarity coefficients between minimum sets were significantly higher than those between randomly selected sets of sites (Table 3). However, similarity between minimum sets with different selection units was low ($\leq$40.3%). Irreplaceability values of the sites in each of the selection-unit data sets were weakly but significantly correlated (Table 3; Fig. 2). The highest correlation coefficients were between different hexagon data sets, and the lowest coefficients were between the hexagon data sets and the TEM polygon data set. The Jaccard similarity coefficients and irreplaceability correlations for the pairwise comparisons were positively correlated ($r = 0.96$; $p < 0.01$).

Table 3. Comparisons of minimum sets and irreplaceability values for different selection units, biodiversity features, and conservation targets.[a]

	0.16-km^2 hexagon	*2-km^2 hexagon*	*10-km^2 hexagon*
Selection unit			
minimum-set overlap			
TEM[b] polygon	0.300**	0.239**	0.234**
0.16-km^2 hexagon	—	0.403**	0.337**
2-km^2 hexagon	—	—	0.388**
irreplaceability correlation[c]			
TEM polygon	0.350** (50,359)	0.270** (19,015)	0.231** (13,855)
0.16-km^2 hexagon	—	0.670** (17,467)	0.402** (13,707)
2-km^2 hexagon	—	—	0.523** (2,008)
	Red-listed species		
Biodiversity feature			
minimum-set overlap			
red- and blue-listed species	0.590**		
irreplaceability correlation ($n = 233$)			
red- and blue-listed species	0.837**		
	Current populations	*Half populations*	
Conservation target			
minimum-set overlap			
MVP[d] estimate	1.000 ns	1.000 ns	
current populations	—	0.946**	
irreplaceability correlation ($n = 233$)			
MVP estimate	0.160*	0.160*	
current populations	—	1.000**	

[a] *Minimum-set overlap was measured with Jaccard's similarity coefficient. The probability that each similarity coefficient is different from random was calculated with 1000 random selections of the equivalent total number of sites or with area for polygon selection units. Significant coefficients for minimum set comparisons are higher on average than similarity values between randomly selected sets of sites. Irreplaceability correlations are Spearman rank, and significance was determined by randomizing one of the data sets in each pairwise comparison 2000 times and calculating the Spearman rank coefficient. Probabilities: ns, not significant;* *$p < 0.05$; **$p < 0.001$.

[b] *TEM, terrestrial ecosystem map.*

[c] *A conversion factor of 1.65 times the number of sites in each minimum set was used to standardize the irreplaceability calculations across all data sets. Sample sizes are given in parentheses.*

[d] *MVP, minimum viable population.*

Biodiversity Features

The total area required to represent half populations of the 11 red-listed species was 50.0 km^2 less (14%; five sites) than that needed to represent half populations of all 29 vertebrate species (Table 2; Fig. 3). Spatial overlap of the minimum sets was lower than the irreplaceability correlation for the two sets of biodiversity features (Table 3). The high irreplaceability correlation indicates that sites were initially ranked similarly for different sets of vertebrates (Fig. 3). Furthermore, the minimum set identified with only red-listed species represented 93.1% of the conservation targets for all 29 vertebrate species. The American Bittern (*Botaurus lentiginosus*) and Sandhill Crane (*Grus canadensis*), both blue-listed species, were not represented at their conservation targets.

Conservation Targets

The variation in conservation targets resulted in corresponding differences in the number of sites selected in each minimum set (Table 2; Fig. 4). The MVP conservation targets were not achieved for 5 of the 29 species: American Bittern, Ferruginous Hawk, Sandhill Crane, White-headed Woodpecker (*Picoides albolarvatus*), and Western Screech Owl (*Otus kennicottii macfarlanei*). However, the American Bittern would likely have sufficient habitat if large lake polygons were included in the analyses.

Spatial overlap was highest between minimum sets that had similar conservation targets (Table 3). Of the 36 sites selected for half populations, only one site was different from the 89 selected for current populations. The spatial overlap of the minimum set using MVP targets with the other two minimum sets was high but not significantly different from similarity coefficients between randomly selected sets of sites. The trend in correlation values for irreplaceability was opposite to the trend in Jaccard similarity values (Table 3). The ranking of irreplaceability values was identical between half and current populations, but both of these rankings differed from the ranking for MVP targets (Table 3; Fig. 4).

Discussion

Our results demonstrate the sensitivity of systematic reserve-selection procedures to changes in scale-related

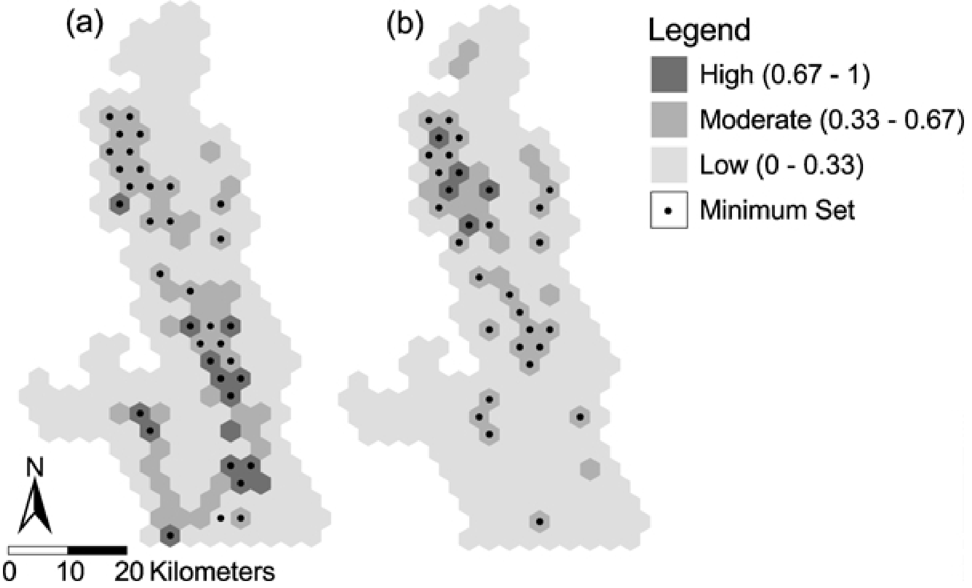

Figure 3. Minimum sets and irreplaceability of sites identified based on (a) 29 red- or blue-listed vertebrate species and (b) 11 red-listed vertebrate species.

variables. In the process of comparing different data sets, we used two different measures, the Jaccard similarity coefficient that measured the spatial overlap of minimum sets and the correlation of irreplaceability values for all sites in the region. Although the irreplaceability correlations are based directly on the distribution of species, and the Jaccard Coefficient is based on the spatial location of sites selected with species distributions, there is a positive relationship between the two measures for comparisons among different selection-unit data sets. However, the irreplaceability correlation likely provides the better information for comparing sites for conservation because it is based on where species are found and not on the attributes of single minimum sets and the particular rules used to select sites (Pressey et al. 1994; Hopkinson et al. 2001). Nevertheless, the irreplaceability correlation ignores the problem of actually selecting a set of sites for conservation. Therefore, both measures are informative.

Our results indicate that the scale of both the spatial and biological data influences the distribution, number, and total area of sites selected by a systematic reserve-selection algorithm (see also Andelman & Willig 2002, Rouget 2003). Although the intended conservation targets were achieved in each of the minimum sets of sites

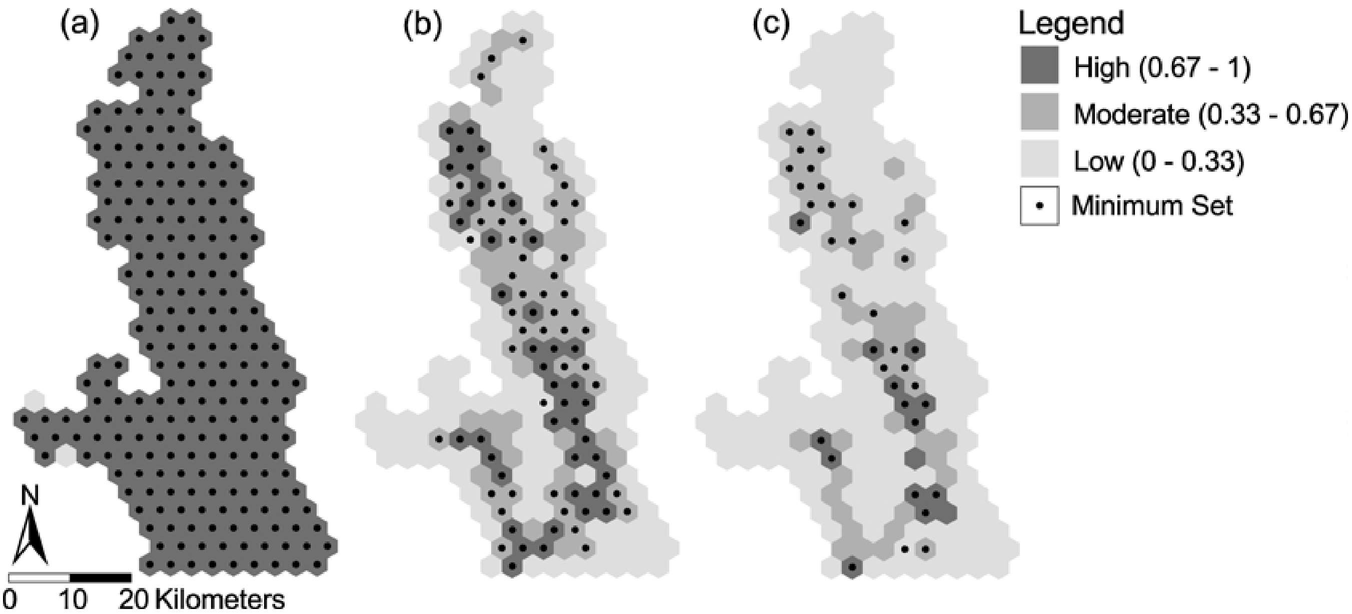

Figure 4. Minimum sets and irreplaceability of sites identified based on (a) minimum viable populations, (b) current population sizes, and (c) half the current population sizes for 29 red- or blue-listed vertebrate species.

(except when general minimum viable population estimates were used), differences in the spatial distribution and number of sites identified are important considerations for reserve selection. Although there is poor spatial congruence between minimum sets resulting from changes to scale-related variables, which emphasizes the need for caution in interpreting sites derived from selection algorithms, the irreplaceability of sites in different data sets was more similar (Table 3).

In general there was a significant positive correlation of irreplaceability between different sets of selection units, but the maximum similarity between data sets was 67%. The regular hexagons show higher correlations with each other than those between irregular TEM polygons and hexagons, likely because of the high variability in sizes of the TEM polygons. Also, correlations between hexagons at some scales (i.e., 2 km^2 vs. 0.16 km^2) were greater than those between other scales, indicating that scale does have some influence on the irreplaceability of sites within a region. Furthermore, different selection units resulted in different minimum sets of sites, with low spatial overlap ($\leq$40%). Therefore, before recommendations are implemented from studies that identify systematically selected conservation sites, it is important to consider the reasons a particular selection-unit size was used. This is a particular issue to consider when making the transition from planning for whole regions and large selection units to implementation within ownership parcels (Rouget 2003).

At fine spatial scales it is important that resulting conservation sites are large enough to provide adequate contiguous habitat area to meet the life requisites of each species, in the event they are isolated from other sites (Pressey & Logan 1995). Large selection units can be used to abate this problem in the selection stage of conservation planning, because they resulted in fewer and larger contiguous groups of sites than small units and increased the contiguity of the reserve system (Table 2). Alternatively, smaller selection units can be used with reserve-selection algorithms that amalgamate sites too small to meet the life requisites of species on their own (Possingham et al. 2000; McDonnell et al. 2002). Although both these methods lead to a higher cost for implementation of the reserve system (Bedward et al. 1992; Nicholls & Margules 1993; Lombard et al. 1995; Pressey & Logan 1998), they also tend to overrepresent conservation targets for regional biota, which is beneficial for the long-term conservation of species.

It is difficult, nonetheless, to determine the selection-unit size that is most appropriate for regional conservation planning using systematic reserve-selection techniques (see also Rouget 2003). Decisions on selection-unit size cannot rely solely on broad recommendations without consideration of the scale of the regionally mapped data (Fotheringham 1989). For example, recommendations for conserving mammals in North America (Gurd et al. 2001) and for maintaining vertebrate richness in an ecosystem similar to the South Okanagan (Stoms 1994) would not be feasible in the small region used for our study. And although the TEM polygons that map precise boundaries of vegetation are the most ecologically meaningful selection unit used in our study, they are variable, and some are likely to be too small for effective implementation of conservation areas within the region. Therefore, it is essential to examine both the habitat complexity of the region and the scale of the data available for reserve selection before deciding the size and shape of the selection unit.

Differences in biodiversity features did not have as dramatic an effect on the spatial configurations of minimum sets as did different selection units. The spatial overlap of the minimum sets with different biodiversity features was only 59% (Table 3), but the conservation targets for 17 of the 19 blue-listed vertebrate species were satisfied in the minimum set identified with only the 11 red-listed vertebrate species. Furthermore, the irreplaceability of sites within the region was ranked similarly for each data set. Therefore, conservation sites identified based on a subset of threatened vertebrate species, which is not restricted to an individual taxonomic group (Ricketts et al. 1999), can provide a reasonable surrogate for identifying conservation sites for other vertebrate species in the region (see also Brooks et al. 2001). These analyses could be applied to other taxonomic groups, such as plants and invertebrates, when appropriate data are available to determine whether a more diverse set of surrogates could represent all biodiversity within the region. However, both the selection unit and conservation targets used to assess such surrogates may affect how well they represent biodiversity (Rouget 2003), but we did not address this issue in our analyses.

The geopolitical boundary of the South Okanagan region presents difficulties in identifying conservation targets for species. Many of the species included in our study are on the peripheries of their range and interact with conspecifics south of the U.S.–Canadian border. Although potentially inaccurate, we identified conservation targets that represent populations of species rather than arbitrarily identifying a set number of grid cells to represent species, because the results of the minimum-set comparisons are more relevant to management decisions likely to take place.

In our study, conservation targets altered the total area selected but did not have a strong effect on the distribution of sites selected in minimum sets (Table 3). The irreplaceability of individual sites, however, was affected by variation in conservation targets. The results for the minimum-set overlap suggest that the sites selected with the MVP target are slightly more similar to those selected with other targets, whereas the irreplaceability correlations suggest the opposite and have large differences between values (Table 3). Because the minimum set identified for MVP targets covered most of the study area (99.1%), there was a high spatial overlap with any other minimum set for the region, since the Jaccard similarity calculation was limited by the smaller minimum set. The irreplaceability correlations between MVP targets and both current and half populations were lower because the MVP conservation targets for species were disproportionately different from the other conservation targets. Current populations were twice the size of half populations, whereas MVP estimates were not related by a constant value to either of the former two conservation targets. Conservation targets are important considerations in systematic reserve selection, and the effect of changes in target values on site selection should be examined with other regional data.

Although the measure used to evaluate similarity can alter the conclusions drawn about the sensitivity of systematic reserve selection to changes in scale-related variables, both measures we used indicate that spatial scale has a strong influence. Therefore, sites identified as priorities for conservation with systematic reserve-selection techniques must be considered cautiously. We recommend that regional data be analyzed at more than one scale to determine the variability in regional conservation priorities, particularly for fine-scale analyses where reserves are likely to be implemented (Rouget 2003). The utility of systematic reserve-selection algorithms for identifying conservation areas will increase when the consequences for site selections of choosing particular variable values are fully understood. Until then, these procedures provide a fundamental step in conservation planning and the development of effective reserve networks for regional biodiversity, as long as users are aware that systematically selected sites may need refinement to accomplish this goal.

Acknowledgments

This work was funded by the Habitat Conservation Trust Fund (BC), Environment Canada, Friends of Ecological Reserves (BC), and the National Science and Engineering Research Council of Canada. The Ministry of Water, Land and Air Protection in British Columbia, in particular O. Dyer, T. Ethier and G. Boughton, provided the data for this project and in-kind support. The National Parks and Wildlife Service in New South Wales, Australia, provided C-Plan software and technical support. A. Blachford provided technical support for analyses involving randomization of data. B. Foster and I. McTaggart-Cowen provided guidance for this research.

Literature Cited

Andelman, S. J., and M. R. Willig. 2002. Alternative configurations of conservation reserves for Paraguayan bats: considerations of spatial scale. Conservation Biology **16:**1352–1363.

Ando, A., J. Camm, S. Polasky, and A. Solow. 1998. Species distributions, land values and efficient conservation. Science **279:**2126–2128.

Araújo, M. B., and P. H. Williams. 2000. Selecting areas for species persistence using occurrence data. Biological Conservation **96:**331–345.

Bedward, M., R. L. Pressey, and D. A. Keith. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. Biological Conservation **62:**115–125.

Brooks T., A. Balmford, N. Burgess, J. Fjeldså, L. A. Hansen, J. Moore, C. Rahbek, and P. Williams. 2001. Toward a blueprint for conservation in Africa. BioScience **51:**613–624.

Canadian Ferruginous Hawk Recovery Team. 1994. National recovery plan for the Ferruginous Hawk. Environment Canada, Ottawa.

Committee on the Status of Endangered Wildlife in Canada. 2002. Canadian species at risk. Environment Canada, Hull, Ontario.

Ferrier, S., R. L. Pressey, and T. W. Barrett. 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biological Conservation **93:**303–325.

Fotheringham, A. S. 1989. Scale-independent spatial analysis. Pages 221–228 in M. Goodchild and S. Gopal, editors. The accuracy of spatial data bases. Taylor and Francis, London, United Kingdom.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–150 in M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer Associates, Sunderland, Massachusetts.

Freemark, K. E., H. Moore, D. Forsyth, A. R. Sinclair, T. Barrett, D. White, and R. Pressey. 2000. Identifying sites for conserving biodiversity across Canadian landscapes using a complementarity approach. On compact disk, D. J. Brunckhorst and D. A. Mouat, editors. Landscape futures: examining innovations and advances in research for natural resource planning and management across regional landscapes that might lead us towards a sustainable future. Proceedings of the 1st international symposium on landscape futures. UNESCO Institute, University of New England, Armidale, New South Wales, Australia.

Gurd, D. B., T. D. Nudds, and D. H. Rivard. 2001. Conservation of mammals in eastern North American wildlife reserves: how small is too small? Conservation Biology **15:**1355–1363.

Hopkinson, P., J. M. J. Travis, J. Evans, R. D. Gregory, M. G. Telfer, and P. H. Williams. 2001. Flexibility and the use of indicator taxa in the selection of sites for nature reserves. Biodiversity and Conservation **10:**271–285.

Kiester, A. R., J. M. Scott, B. Csuti, R. F. Noss, B. Butterfield, K. Sahr, and D. White. 1996. Conservation prioritization using GAP data. Conservation Biology **10:**1332–1342.

Klinkenberg, B. 2002. Spatial analysis of the coincidence of rare vascular plants in the Carolinian Zone of Canada: implications for protection. Canadian Geographer **46:**194–203.

Krebs, C. J. 1999. Ecological methodology. Benjamin/Cummings, Menlo Park, California.

Lombard, A. T., A. O. Nicholls, and P. V. August. 1995. Where should nature reserves be located in South Africa? A snake's perspective. Conservation Biology **9:**363–372.

Lombard, A. T., R. M. Cowling, R. L. Pressey, and P. J. Mustart. 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conservation Biology **11:**1101–1116.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405:**243–253.

McDonnell, M. D., H. P. Possingham, I. R. Ball, and E. A. Cousins. 2002. Mathematical methods for spatially cohesive reserve design. Environmental Modeling and Assessment **7:**107–114.

Ministry of Environment, Lands and Parks. 1999. British Columbia wildlife habitat rating standards. Version 2.0. Resources Inventory Branch, Victoria, British Columbia, Canada.

National Parks and Wildlife Service (NPWS). 1999. C-Plan: conservation planning software. User manual. Version 2.2. NPWS, Armidale, New South Wales, Australia.

Nicholls, A. O., and C. R. Margules. 1993. An upgraded reserve selection algorithm. Biological Conservation **64:**165–169.

Possingham, H. P., I. Ball, and S. Andelman. 2000. Mathematical methods for reserve system design. Pages 291–306 in S. Ferson and M. A. Burgman, editors. Quantitative methods for conservation biology. Springer-Verlag, New York.

Pressey, R. L. 1998. Algorithms, politics and timber an example of the role of science in a public, political negotiation process over new conservation areas in production forests. Pages 73–87 in R. Wills and R. Hobbs, editors. Ecology for everyone: communicating ecology to scientists, the public and the politicians. Surrey Beatty and Sons, Sydney, New South Wales, Australia.

Pressey, R. L., and V. S. Logan. 1995. Reserve coverage and requirements in relation to partitioning and generalization of land classes: analyses for Western New South Wales. Conservation Biology **9:**1506–1517.

Pressey, R. L., and V. S. Logan. 1998. Size of selection units for future reserves and its influence on actual versus targeted representation of features: a case study in western New South Wales. Biological Conservation **85:**305–319.

Pressey, R. L., and A. O. Nicholls. 1989. Efficiency in conservation evaluation scoring versus iterative approaches. Biological Conservation **50:**199–218.

Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vane-Wright, and P. H. Williams. 1993. Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology & Evolution **8:**124–128.

Pressey, R. L., I. R. Johnson, and P. D. Wilson. 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. Biodiversity and Conservation **3:**242–262.

Pressey, R. L., H. P. Possingham, and J. R. Day. 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biological Conservation **80:**207–219.

Price, O., J. C. Z. Woinarski, D. L. Liddle, and J. Russell-Smith. 1995. Patterns of species composition and reserve design for a fragmented estate: monsoon rainforests in the northern territory, Australia. Biological Conservation **74:**9–19.

Reyers, B., and A. S. van Jaarsveld. 2000. Assessment techniques for biodiversity surrogates. South African Journal of Science **96:**406–408.

Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. Loucks. 1999. Who's where in North America? Patterns of species richness and the utility of indicator taxa for conservation. Bioscience **49:**369–381.

Rouget, M. 2003. Measuring conservation value at fine and broad scales: implications for a diverse and fragmented region, the Agulhas Plain. Biological Conservation **112:**217–232.

Saetersdal, M., J. M. Line, and H. J. B. Birks. 1993. How to maximize biological diversity in nature reserve selection: vascular plants and breeding birds in deciduous woodlands, western Norway. Biological Conservation **66:**131–138.

Schmutz, J. K. 1984. Artificial nests for Ferruginous and Swainson's Hawks. Short communication. Journal of Wildlife Management **48:**1009–1013.

Scott J. M., H. Anderson, F. Davis, S. Caicoo, B. Csuti, T. C. Edwards Jr, R. Noss, J. Ulliman, C. Groves, and R. G. Wright. 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs **123**.

Soulé, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, United Kingdom.

Stoms, D. M. 1994. Scale dependence of species richness maps. Professional Geographer **46:**346–358.

Strittholt, J. R., and R. E. J. Boerner. 1995. Applying biodiversity gap analysis in a regional nature reserve design for the edge of Appalachia, Ohio (U.S.A.). Conservation Biology **9:**1492–1505.

Vanderklift, M. A., T. J. Ward, and J. C. Phillips. 1998. Use of assemblages derived from different taxonomic levels to select areas for conserving marine biodiversity. Biological Conservation **86:**307–315.

van Jaarsveld, A. S., S. Freitag, S. L. Chown, C. Muller, S. Koch, H. Hull, C. Bellamy, M. Kruger, S. Endrody-Youga, M. W. Mansell, and C. H. Scholtz. 1998. Biodiversity assessment and conservation strategies. Science **279:**2106–2108.

Vennesland, R., A. Harcombe, S. Cannings, and L. Darling. 2002. One fish, two fish, red fish, blue fish: species ranking in British Columbia. Brochure. Ministry of Water, Land, and Air Protection, Victoria, British Columbia, Canada.

Warman, L. D. 2001. Identifying priority conservation areas using systematic reserve selection and GIS at a fine spatial scale: a test case using threatened vertebrate species in the Okanagan, British Columbia. M.S. thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Warman, L., S. Robertson, A. Haney, and M. Sarell. 1998. Habitat capability and suitability models for 34 wildlife species; using terrestrial ecosystem mapping (1:20,000) in the South Okanagan and lower Similkameen study area and forest cover mapping (1:20,000) in the Penticton Forest District. Ministry of Environment, Lands and Parks, Penticton, British Columbia, Canada.

White, D., A. J. Kimerling, and W. S. Overton. 1992. Cartographic and geometric components of global sampling design for environmental monitoring. Cartography and Geographic Information Systems **19:**5–22.

Williams, P., M. Wisz, C. Rahbek, J. Moore, L. Hansen, N. Burgess, T. Brooks, and A. Balmford. 2000. Quantitative methods at the Congolese forest priority-setting workshop. World Wildlife Fund–US, Libreville, Gabon.