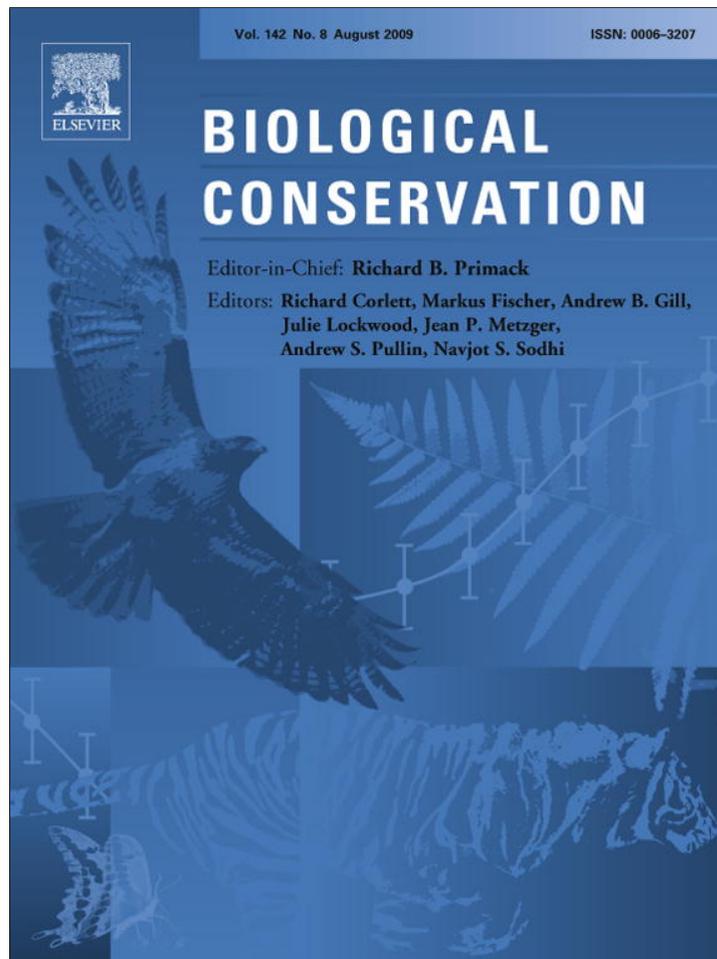


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## Efficiency and effectiveness in representative reserve design in Canada: The contribution of existing protected areas

Yolanda F. Wiersma<sup>a,\*</sup>, Thomas D. Nudds<sup>b</sup>

<sup>a</sup> Department of Biology, Memorial University, St. John's NL, Canada A1B 3X9

<sup>b</sup> Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1

### ARTICLE INFO

#### Article history:

Received 31 July 2008

Received in revised form 17 February 2009

Accepted 24 February 2009

Available online 25 March 2009

#### Keywords:

Algorithms

Canada

Gap analysis

Mammal conservation

Reserve planning

### ABSTRACT

To be effective, reserve networks should represent all target species in protected areas that are large enough to ensure species persistence. Given limited resources to set aside protected areas for biodiversity conservation, and competing land uses, a prime consideration for the design of reserve networks is efficiency (the maximum biodiversity represented in a minimum number of sites). However, to be effective, networks may sacrifice efficiency. We used reserve selection algorithms to determine whether collections of existing individual protected areas in Canada were efficient and/or effective in terms of representing the diversity of disturbance-sensitive mammals in Canada in comparison to (1) an optimal network of reserves, and (2) sites selected at random. Unlike previous studies, we restricted our analysis to individual protected areas that met a criterion for minimum reserve size, to address issues of representation and persistence simultaneously. We also tested for effectiveness and efficiency using historical and present-day data to see whether protected area efficiency and/or effectiveness varied over time. In general, existing protected areas did not effectively capture the full suite of mammalian species diversity, nor are most existing protected areas part of a near-optimal solution set. To be effective, Canada's network of reserves will require at minimum 22 additional areas of >2700 km<sup>2</sup>. This study shows that even when only those reserves large enough to be effective are considered, protected areas systems may not be representative, nor were they representative at the time of establishment.

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### 1. Introduction

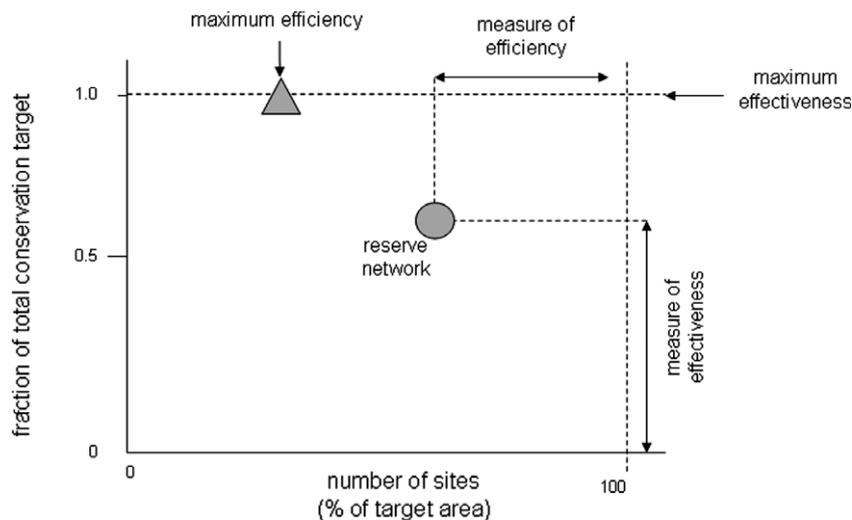
It is well known that protected areas planning in North America and elsewhere has historically been carried out on an ad hoc basis. Many of the earliest protected areas were designated for their scenic, recreational, and tourism values (Runte, 1997; Sellars, 1997), while others were designated to provide employment opportunities in impoverished regions (Runte, 1997; MacEachern, 2001). Today, however, protected areas are assumed to play an important role in preserving representative samples of ecosystem and species diversity (e.g., Parks Canada Agency, 2000). Recent research suggests that existing protected areas do not perform well in this capacity (e.g., Pressey and Nicholls, 1989; Rebelo and Siegfried, 1992; Saetersdal et al., 1993; Lombard et al., 1995; Pressey et al., 1996; Williams et al., 1996; Khan et al., 1997; Freitag et al., 1998; Jaffre et al., 1998; Nantel et al., 1998; Sarakinos et al., 2001; Heikkinen, 2002; Stewart et al., 2003; Branquart et al., 2008). An analysis of what particular gaps exist in current protected areas networks in relation to biodiversity representation can

help planners identify priorities for establishment of new protected areas and/or restoration of existing ones. With limited resources for conservation, it is prudent to prioritize the siting of protected areas in places where they will be efficient and effective (Fig. 1). In contrast to ad hoc planning for protected areas, reserve selection algorithms can be used to identify sets of protected areas that capture all species, communities or other biological units of interest at least once within a pre-defined region (Margules et al., 1988; Pressey et al., 1996; Branquart et al., 2008). The commonly used heuristic algorithms generally are based either on maximizing species richness (richness-based) or the presence of rare species (rarity-based) (Pressey et al., 1996). These types of approaches have recently been applied in regional protected areas planning in various parts of Canada, for example in the central coast of British Columbia (Gonzales et al., 2003).

The goal of reserve selection algorithms is to identify an efficient solution to the challenge of *representation* of biodiversity within reserves; efficiency is defined as achieving representation of all species with the lowest cost, often measured as the fewest number of sites (e.g., Pressey and Nicholls, 1989). Targets for representation within the network of protected areas may include, for example, all of the species in a region, or all of the variety of ecosystem types or vegetation/landform complexes (Pressey

\* Corresponding author. Tel.: +1 709 737 7499; fax: +1 709 737 3068.

E-mail addresses: [ywiersma@mun.ca](mailto:ywiersma@mun.ca) (Y.F. Wiersma), [tnudds@uoguelph.ca](mailto:tnudds@uoguelph.ca) (T.D. Nudds).



**Fig. 1.** Illustration of the concepts of *efficiency* and *effectiveness*. Efficiency is larger when the number of sites in the protected areas network is smaller. Maximum efficiency is obtained by the minimum set. Effectiveness is a measure of how close a protected areas network is to attaining the representation target. Thus efficiency is measured based on the size of the network (X-axis), while effectiveness is measured based on the performance of the network relative to the representation target (Y-axis). (Figure and caption adapted from Rodrigues et al. 1999.)

et al., 1993). However, if individual protected areas within a network that is nevertheless representative are too small, then the network may be rendered unrepresentative over time by the loss of individual species within reserves. Thus, algorithms should also include criteria that enhance species *persistence*; ensuing networks should then effectively conserve and efficiently represent the regional diversity of species (Rodrigues et al., 2000; Cabeza, 2003; Kerley et al., 2003; Pressey et al., 2003; Solomon et al., 2003).

In Canada, Wiersma and Nudds (2006) postulated an efficient and effective reserve network for representing all disturbance-sensitive mammals using individual reserves that were expected to allow mammals to persist, even in the face of habitat insularization. The individual reserves showed little overlap with existing protected areas in Ontario (Nudds and Wiersma, 2004), indicating that existing protected areas, in their entirety as a network, are ineffective and/or inefficient (Rodrigues et al., 1999; Stewart et al., 2003). Nevertheless, it might be that combinations of existing and new and/or expanded areas, while necessarily constrained with respect to *efficiency* (that is, result in more sites than required for maximum representation) could be as *effective* in ensuring persistence (Rodrigues et al., 1999). Thus, it is important to evaluate the contribution of existing protected areas to the efficiency and effectiveness of reserve networks. The goal of this study was to evaluate the efficiency and effectiveness of existing protected areas across Canada for representation of disturbance-sensitive mammals, and where necessary, identify how many additional protected areas might be necessary to achieve an effective network.

Wiersma and Nudds (2006) used heuristic reserve selection algorithms to delineate efficient and effective networks of protected areas for disturbance-sensitive mammals in each of eight mammal provinces of Canada (Hagmeier, 1966; Fig. 2), based on both historical (Banfield, 1974) and current (Patterson et al., 2003) species' ranges. (Wiersma (2007a) showed that similar results are obtained when analyses are conducted across other biologically-relevant regions, such as terrestrial ecozones.) The analysis of species data from two different points in time allowed for a comparison of representation requirements for a historical "benchmark" condition to the representation requirements at present. The first resulted in estimates of where protected areas might have been optimally located prior to widespread European

settlement, and the second identified optimal sites that account for species range shifts that may have occurred during the intervening years. Both solutions were comprised of proposed protected areas that met a minimum reserve area (MRA) criterion for mammals, and thus species are expected to persist within them (Gurd et al., 2001). Here, we build on this work by assessing how well existing protected areas represent mammals compared to these optimal networks.

Instead of a simple contrast of the optimal sites in the proposed networks with existing MRA-sized protected areas, we "seeded" the algorithms with the existing protected areas that were sufficiently large to allow for long-term species persistence, and then identified where additional minimally-sized protected areas (if any) should be located to represent all species in each mammal province. If the existing suite of protected areas is an efficient (or nearly-efficient) and effective network for meeting representation targets in each mammal province, then there should be no difference in the number of protected areas required in the optimal network when existing protected areas are included, compared to the proposed optimal network when they are excluded. Further, if existing protected areas are an important component of near-optimal solutions to representation, then even in cases where more protected areas might be needed, these should be fewer than the number required to represent species when existing protected areas are excluded from the algorithms. This is the case observed with a representative protected areas analysis for reptiles and amphibians in north eastern India (Pawar et al., 2007). However, given the historical documentation attesting that establishment of many national and provincial parks was motivated by scenic, recreation, and economic values (Runte, 1997; Sellars, 1997; MacEachern, 2001), we expected that existing protected areas would not necessarily contribute parts of an efficient solution to effective biodiversity representation. Other regions globally have shown a bias to over-representation of high altitude habitats (Oldfield et al., 2004; Martinez et al., 2006) and less populated areas (Sarakinov et al., 2001). Evidence in Canada of a bias towards large protected areas at northern latitudes (Rivard et al., 2000), and historical and anecdotal evidence that many parks were located in areas with high scenic value (and not necessarily high ecological value), lead us to expect that existing protected areas may not even be effective, let alone efficient.



**Fig. 2.** The mammal provinces of Canada (Hagmeier, 1966). For this study, the Eastern and Western Hudsonian, the Ungavan, and the Eastern Eskimoan mammal provinces were excluded as they have low mammalian diversity. The Saskatchewanian mammal province was excluded because it did not contain any large protected areas. The western portion of the Alleghenian mammal province was analyzed separately, and the eastern portion of the Alleghenian mammal province was combined with the Illinoian.

## 2. Methods

### 2.1. Target regions and mammal data

Analysis was carried out in ecologically defined target regions (mammal provinces) in Canada (Fig. 2). The Alleghenian–Illinoian mammal province in Canada spans east and west of the Great Lakes and so was analyzed as two provinces. The Saskatchewanian mammal province did not include any existing MRA-sized protected areas and was excluded, yielding a total of seven mammal provinces for analysis. Northern mammal provinces were excluded because of low mammalian diversity. Historical data on mammal distributions were obtained from Banfield's Mammal Atlas of Canada (Banfield, 1974), which represents the ranges of disturbance-sensitive mammals prior to widespread European settlement. Recent atlas data (Patterson et al., 2003) were used to account for those species whose ranges may have contracted or expanded in response to human-induced habitat changes. Only those species defined by Glenn and Nudds (1989) as sensitive to human disturbance (*sensu* Humphreys and Kitchener, 1982) were included in the analysis, as disturbance-insensitive mammals (e.g., racoons, coyotes) were deemed not to be a high priority for protection from anthropogenic landscape change.

### 2.2. Existing protected areas data

Data on existing protected areas were obtained from the North American Conservation Areas Database (NCAD) and Canadian Conservation Areas Database (CCAD), available online from the Canadian Council on Ecological Areas ([www.ccea.org](http://www.ccea.org)). We also assembled polygon coverages of national and provincial parks for use in a GIS from a Government of Canada website (source: [www.geogratis.gc.ca](http://www.geogratis.gc.ca)). The NCAD and CCAD data sets included spatially referenced points identifying the location and attributes of all protected areas. We selected those areas in IUCN classes I–VI (national, provincial, and territorial parks, as well as wildlife manage-

ment areas, game preserves, and biosphere reserves; hereafter referred to as “existing protected areas”). Only those areas that met or exceeded the lower 95% confidence interval for the minimum reserve area (MRA) estimate (i.e., >2700 km<sup>2</sup>; Gurd et al., 2001) were used in the analysis ( $n = 29$ ). We used the total protected area published in the above databases. Thus we considered the total area as the MRA threshold, even though in some cases, the non-habitat areas (built infrastructure and unsuitable habitat) might push the effective size of the protected area below the MRA (e.g., Wiersma et al., 2004). Time and data constraints did not allow us to measure effective area of all 29 sites, nor did Gurd et al. (2001) use effective area in their analysis. Thus, we are confident that the MRA threshold is reasonable as a *minimum* size criterion for effective protected areas. However, there will be some variation in the effectiveness of the individual protected areas in meeting conservation goals. This variation will be due in part to management strategies, amount of visitation, external ecological stressors, etc. Although IUCN categories classify on strength of protection, they do not comment on management effectiveness (CCEA, 2008), and thus, we have not attempted to further classify the existing protected areas based on conservation effectiveness. Given the variation in effectiveness, it is possible that additional protected areas may be required.

### 2.3. Heuristic reserve selection

Following Wiersma and Nudds (2006), we ran rarity-based heuristic algorithms on the candidate MRA plots in each mammal province, but “seeded” each of the runs (three replicates each of three MRA size estimates) with existing protected areas for a total of nine runs per mammal province. MRA estimates (2700 km<sup>2</sup>, 5000 km<sup>2</sup>, 13,000 km<sup>2</sup>) were based on values determined from analysis of disturbance-sensitive mammals in Canada (Gurd et al., 2001). We did not discriminate between existing protected areas above the larger thresholds because previous work (Wiersma and Nudds, 2006) suggests that variation in the “grain” (i.e., above

the minimum 2700 km<sup>2</sup> MRA size as estimated by Gurd et al. (2001)) of the analysis does not vary the number of sites in the optimal solution. We included runs using the larger MRA sizes to boost the number of replicates for comparison to the existing network. Restricting the protected areas used to “seed” the algorithms to those above the 5000 km<sup>2</sup> and 13,000 km<sup>2</sup> thresholds would have minimized the difference between sites needed when existing protected areas were included or excluded, since there are fewer existing protected areas above the larger MRA thresholds. Ultimately, we are interested in the contribution of existing protected areas that meet the minimum MRA threshold, thus all existing protected areas >2700 km<sup>2</sup> were included in all runs. Mammalian species richness within each mammal province was compared to the aggregate species composition of the existing protected areas within that province to identify which species were not yet represented. Additional sites needed to capture each species at least once were identified using a rarity-based heuristic reserve selection algorithm (Margules et al., 1988; Pressey et al., 1993). Additional sites were selected iteratively, prioritizing those with species with the smallest extent of occurrence. Reserves were selected and added to the system until all species were represented at least once in a reserve.

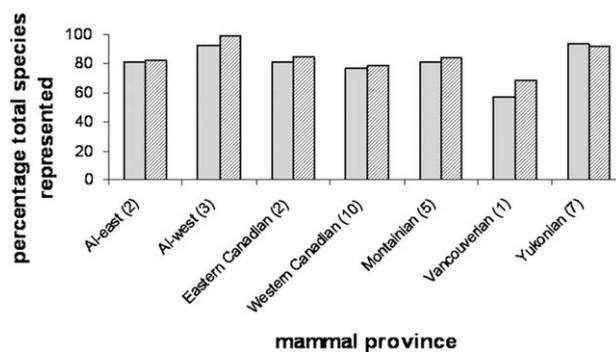
#### 2.4. Comparison with the optimal reserve network

Within each mammal province, the reserve network generated after “seeding” with existing protected areas was compared to the results of nine runs that generated the optimal reserve network without existing protected areas (Wiersma and Nudds, 2006). Network efficiency (total number of protected areas needed to represent all disturbance-sensitive mammals at least once in the network) with and without existing protected areas was compared with Student's *t*-test (Zar, 1999).

To compare the effectiveness of existing protected areas to that of the optimal network within each mammal province, species-accumulation curves for the optimal network and the existing protected areas were constructed. Curves were plotted in the order in which the optimal sites were selected, and the chronological order in which the existing protected areas were established, respectively. To test whether either resulted in more effective networks than random site selection, curves based on equivalent numbers of random sites as in each optimal set ( $n = 9$ ) were compared. More effective networks should represent a higher number of disturbance-sensitive mammals for a given number of sites than less effective ones.

### 3. Results

The number of existing protected areas in each mammal province deemed sufficiently large for persistence of mammal diversity ranged from 1 to 10; no existing sets of reserves in any mammal province captured the full range of mammal diversity. Existing protected areas captured between 57% and 94% of the total historical species richness in each province and between 68% and 99% of the total modern-day species richness in each mammal province (Fig. 3). Between 1 and 7 additional MRA-sized sites (for a total of ~22 across all mammal provinces) were required to represent all mammals at least once in each network within a mammal province when the analysis was applied to the historical distribution data (Table 1), and between 0 and 7 (for a total of ~23 across all mammal provinces) additional plots had to be added when the analysis was applied to the modern distribution data (Table 2). Numbers of protected areas required in reserve systems were significantly higher when existing protected areas were included in all cases (Tables 1 and 2).



**Fig. 3.** Effectiveness of existing protected areas. The number of protected areas in each mammal province is given in parenthesis on the X-axis. Effectiveness is expressed as a percentage of the total species richness of mammals in each mammal province based on historical (grey bars) and modern-day (hatched bars) species data.

Effectiveness of optimal, existing, and random sets of sites was similar only in the western portion of the Alleghenian mammal province (Fig. 4b), likely due to the small size of this province, and hence the small number of candidate plots, compared to the other mammal provinces. In all other mammal provinces, neither existing protected areas nor random sets of the same number of sites were 100% effective (Fig. 4a, c–g). Of six mammal provinces with more than one existing protected area, those areas were more effective than sites selected at random in three cases: eastern Alleghenian (Fig. 4a), Eastern Canadian (Fig. 4c), and Western Canadian (Fig. 4d). Effectiveness differed little between existing protected areas and random sites in the western Alleghenian (Fig. 4b) and the Yukonian (Fig. 4g); existing protected areas were less effective than sites selected at random in the Montainian mammal province (Fig. 4e).

With respect to the location of sites identified by reserve selection algorithms when existing protected areas were included and excluded, two additional patterns were examined. The location of optimal sites with and without the inclusion of existing protected areas was examined to see whether it differed when existing protected areas were included. In the majority of cases, the same optimal locations were identified for inclusion in the representative network when protected areas were included and excluded from the analysis. In addition, optimal sites were overlaid with existing protected areas that fell below the MRA threshold; the optimal sites overlapped with 540 existing smaller protected areas (table available in the Supplementary material).

### 4. Discussion

As expected, existing large protected areas in Canada do not represent the full suite of disturbance-sensitive mammals, and thus function as parts of neither effective nor efficient networks. Interestingly, existing protected areas did a slightly better job of representing the modern species assemblage than the historical one (Fig. 3). This may be due to the fact that some of the more recently-established protected areas were designated for conservation of a specific species, or were established with ecological values, rather than scenic or economic values in mind. Certainly some of the protected areas in the latter half of the twentieth century attempted to represent ecosystems other than the scenic mountain ranges that were the focus of the earliest sites (Runte, 1997; Sellars, 1997).

In three mammal provinces, existing protected areas were either less, or no more, effective than sites selected at random. Significantly more protected areas were required to achieve full representation in each mammal province when the algorithms

**Table 1**

Number of additional MRA-sized protected areas needed to capture all mammals in at least one protected area, derived by applying the rarity-based algorithm to the historical data. Results are shown when existing MRA-sized protected areas are excluded and included in the minimum set. Values reported are the mean from three replicates of three MRA estimates (total nine replicates). Significance was tested using Student's *t*-test (Zar, 1999).

Mammal province	Mean number of sites needed based on rarity-based algorithms ( <i>n</i> = 9 runs)	Number of MRA-sized protected areas	Mean number of additional sites needed ( <i>n</i> = 9 runs)	Mean number of sites needed including existing protected areas ( <i>n</i> = 9 runs)	Difference between number of sites with and without existing protected areas	
					<i>t</i>	<i>p</i>
Alleghenian–Illinoian (eastern)	3.56	2	3.33	5.33	4.22	<0.001
Alleghenian–Illinoian (western)	2.67	3	0.56	3.56	2.27	0.05
Eastern Canadian	2.89	2	2.67	4.67	4.79	<0.001
Western Canadian	8.56	10	5.89	15.89	14.99	<0.001
Montanian	5.22	5	4.00	9.00	8.40	<0.001
Vancouverian	4.00	1	4.00	5.00	2.35	0.05
Yukonian	2.89	7	1.00	8.00	10.49	<0.001

**Table 2**

Number of additional MRA-sized protected areas needed to capture all mammals in at least one protected area, derived by applying the rarity-based algorithm to the modern data. Results are shown when existing MRA-sized protected areas are excluded and included in the minimum set. Values reported are the mean from three replicates of three MRA estimates (total nine replicates). Significance was tested using Student's *t*-test (Zar, 1999).

Mammal province	Mean number of sites needed based on rarity-based algorithms ( <i>n</i> = 9 runs)	Number of MRA-sized protected areas	Mean number of additional sites needed ( <i>n</i> = 9 runs)	Mean number of sites needed including existing protected areas ( <i>n</i> = 9 runs)	Difference between number of sites with and without existing protected areas	
					<i>t</i>	<i>p</i>
Alleghenian–Illinoian (eastern)	3.00	2	2.67	4.67	7.07	<0.001
Alleghenian–Illinoian (western)	2.11	3	0.22	3.22	5.55	<0.001
Eastern Canadian	3.11	2	2.22	4.22	6.03	<0.001
Western Canadian	6.33	10	4.33	14.33	33.94	<<0.001
Montanian	6.11	5	4.22	9.22	11.94	<0.001
Vancouverian	3.44	1	3.33	4.33	8.00	<0.001
Yukonian	3.00	7	1.78	8.78	26	<<0.001

included the existing protected areas. Thus, inclusion of existing protected areas decreases the efficiency of a reserve network relative to when they are excluded, at least with respect to representing mammalian diversity.

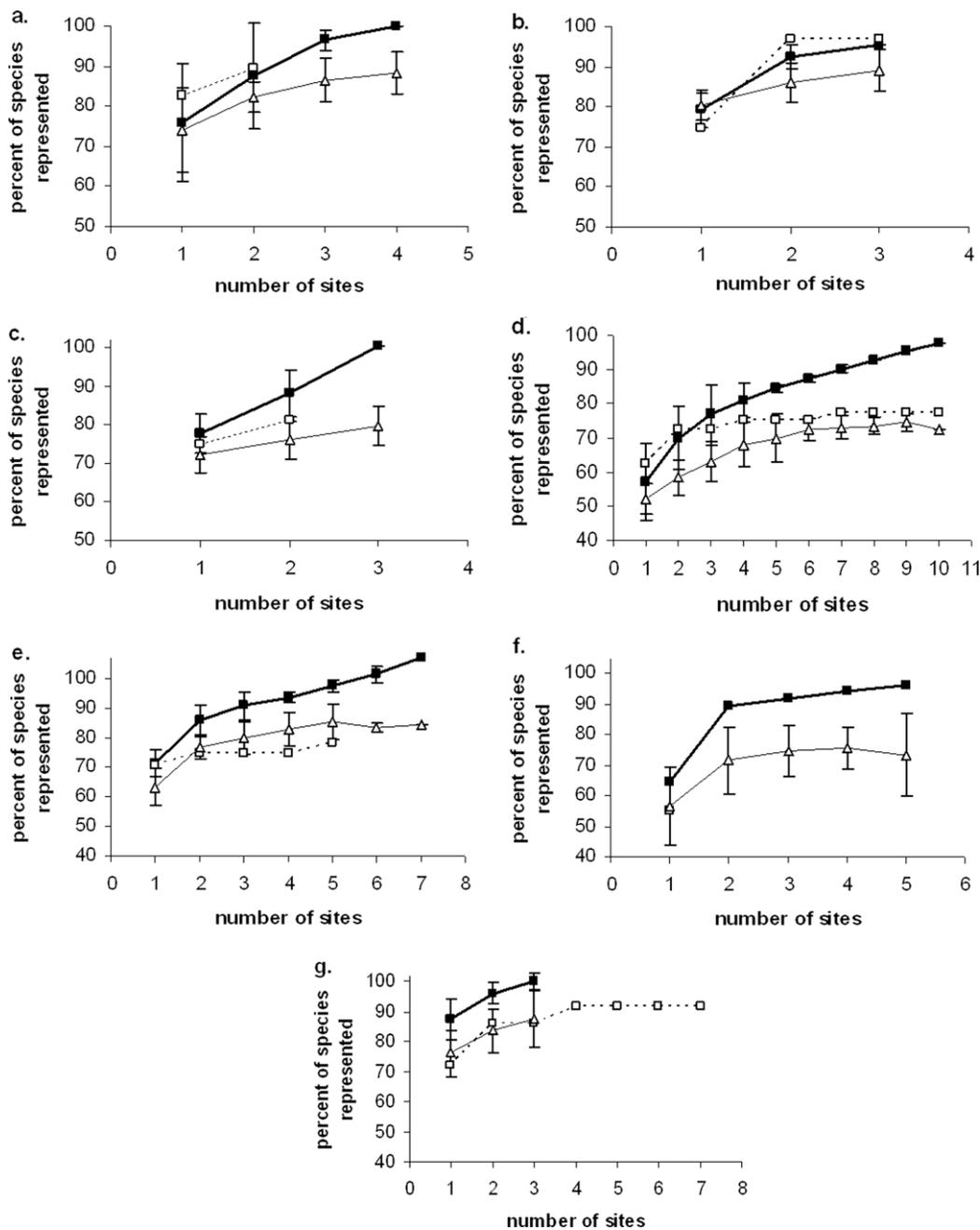
The locations for optimal sites did not differ in the majority of cases when protected areas were included and excluded from the network. This suggests that when considered in combination with the optimal sites, existing protected areas are almost completely redundant with respect to mammalian diversity. That is, the optimal sites appear to have high irreplaceability (*sensu* Ferrier et al., 2000), perhaps because they contain unique species not found in any of the existing protected areas.

Protected areas might be rendered redundant when considered in combination with the optimal sites due to the historical motivations for protected areas designation. The median year of establishment for the existing protected areas is 1975 (mean year of establishment: 1960), which is well before the concept of minimum representation and reserve selection algorithms first appeared in the literature in the early 1980s (Kirkpatrick, 1983). Thus, the majority of the protected areas were not designated with the goal of biodiversity representation in mind. Certain features of the landscape (such as mountain ranges in the western mammal province) are over-represented, while other features (such as prairie ecosystems) are not captured. In Europe, representation and design criteria for protected areas were developed in the 1980s and onwards. A recent survey there showed that land managers and practitioners often are unaware of systematic approaches for reserve selection or can not or will not apply them because of data, time and resource constraints, scepticism about their effectiveness, or lack of coordination at a policy level (Branquart et al., 2008).

A similar comparison of existing protected areas to an optimum set in Québec yielded similar results. The Québec study examined

representative sites for 394 species at risk (both flora and fauna) in candidate plots that were 65–80 km<sup>2</sup> (Sarakinis et al., 2001). The remote northern part of the province was over-represented and areas in the south were under-represented (Sarakinis et al., 2001). These results are not unique to Canada. Low elevation areas were under-represented, and high elevation areas over-represented, by protected areas in England (Oldfield et al., 2004). However, a reserve network which over-represented high elevation areas in Spain nevertheless adequately represented threatened lichen species confined to high elevation forests (Martinez et al., 2006). However, even where there is a relatively high proportion of a protected area, representation may not be adequate (Tognelli et al., 2008). Over 20% of the Chile's land area is set aside for conservation, yet a recent study found 13% of terrestrial vertebrates were unrepresented and approximately 45% were under-represented in the current assemblage of protected areas. When the analysis included proposed protected areas, which were selected based on expert scientific opinion, there was still a significant number of vertebrate species unrepresented (Tognelli et al., 2008).

Results of other studies which measured the overall effectiveness of existing protected areas at representing biodiversity elements, are similar to ours. Pawar et al. (2007) examined representation of reptiles and amphibians in India and found that they were not adequately represented in existing protected areas in India. They similarly “seeded” algorithms with existing protected areas, but found that fewer additional reserves were required for adequate representation than when existing protected areas were not included (Pawar et al., 2007). In Finland, existing protected areas contributed significantly to the network, although there was a gap in representation of certain types of forests along waterways, which sometimes contained regionally rare species (Heikkinen, 2002). Thus, it appears that worldwide, protected areas do



**Fig. 4.** Species accumulation curves generated from modern species' distribution data for: optimal sites (closed squares, thick lines) selected via a rarity-based heuristic algorithm; existing protected areas (open squares, dashed lines) selected in chronological order; and a random sample of sites (open triangles, thin lines) in the mammal provinces of Canada. (a) Alleghenian (eastern portion); (b) Alleghenian (western portion); (c) Eastern Canadian; (d) Western Canadian; (e) Montanian; (f) Vancouverian; (g) Yukonian.

make contributions to biodiversity representation, but that no matter what the target organism or ecosystem analyzed, there appear to be gaps in the system and additional protected areas are necessary to have effective biodiversity representation.

Many of the optimal sites for representing mammals in Canada are located near borders of mammal provinces consistent with an “edge effect” (greater diversity in transition zones between ecologically defined regions) of biogeographical proportions as noted by others (Glenn, 1990; Araújo and Williams, 2001; Gaston et al., 2001). Thus, the presence of optimal sites on both sides of the boundary of a mammal province might in fact render either one of them redundant from the perspective of efficiency and effectiveness. For example, Wiersma (2007b) completed an analysis of the

minimum representative set for these data at a larger extent, with all mammal provinces combined, and identified which transition zones should be designated as priority areas for biodiversity representation. However, it is debated whether to site protected areas along transition zones (Araújo, 2002). Alternatively, it may be more appropriate to disregard arbitrary regional boundaries (political or ecological) altogether and to instead use patterns in species distribution to assist in identification of representative sites (Wiersma and Urban, 2005; Gove et al., 2008). If “edge effects” are taken into account, and redundancies in representative protected areas are eliminated, then the existing suite of protected areas may be rendered relatively less effective than under the current analysis.

Sites identified as parts of near-optimal solutions using the heuristic algorithms overlapped with 540 existing protected areas that are smaller than the minimum reserve area (MRA) estimate. Thus, a prudent management strategy might be to expand the boundaries of these sites and or establish/maintain connectivity around them to bring their size at least to the estimated lower threshold of MRA (i.e., 2700 km<sup>2</sup>; Gurd et al., 2001).

Across Canada, it appears that the existing protected areas that are large enough to conserve mammals are generally not located in the places where they can efficiently or effectively represent the diversity of mammals in each region. That they are not located in the most efficient locations based on historical data may not be surprising, given that many protected areas were established after much of the landscape had been altered by widespread European settlement. However, neither are they optimally located with respect to the modern distributions of mammals. If representation of all species in each mammal province is a policy goal, then the results of heuristic algorithms such as the ones described here may be useful to identify locations where protected areas should be established (or in the case where small protected areas exist, where they can be expanded) to efficiently create an effective representative network of protected areas expected to enable the persistence of species in them.

### Acknowledgements

Historical mammal data was digitized using a grant from Parks Canada to TDN. Modern mammal data was provided by NatureServe in collaboration with Bruce Patterson, Wes Sechrest, Marcelo Tognelli, Gerardo Ceballos, The Nature Conservancy – Migratory Bird Program, Conservation International – CABS, World Wildlife Fund – US, and Environment Canada – WILDSPACE. E. Boulding, R. Corry, K. Lindsay, R. Pressey, J. Shuter, D. Sleep, W. Yang, and three anonymous reviewers provided helpful comments on the manuscript. This work was supported with funding to YFW from the Canadian Council on Ecological Areas, and an Ontario Graduate Scholarship, and by NSERC support to TDN.

### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.02.034.

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