

# Protected Areas and Prospects for Endangered Species Conservation in Canada

ISABELLE E. DEGUISE AND JEREMY T. KERR\*

Department of Biology, University of Ottawa, Box 450, Station A, Ottawa, ON K1N 6N5, Canada

**Abstract:** Reserve networks figure prominently in conservation strategies that aim to reduce extinction rates. We tested the effectiveness of the current reserve network at protecting species at risk in Canada, where relatively extensive wilderness areas remain. We compared numbers of terrestrial species at risk included in existing reserves to randomly generated networks with the same total area and number of reserves. Existing reserve networks rarely performed better than randomly selected areas and several included fewer endangered species than expected by chance, particularly in the most biologically imperiled regions. The extent of protected area and density of species at risk were unrelated at either broad (countrywide) or finer spatial scales (50 × 50 km grids), although there was a tendency for the most threatened regions of the country to have few or no protected areas (1.5% of areas with >30 endangered species were in reserves). Although reserves will play a useful role in conserving endangered species that occur within them, reducing extinction rates in a region with much of the world's remaining wilderness will require integrating conservation strategies with agricultural and urban land-use plans outside formally protected areas.

**Key Words:** endangered species, land use, nature reserves, null models, species at risk

Áreas Protegidas y Perspectivas para la Conservación de Especies en Peligro en Canadá

**Resumen:** Las redes de reservas figuran prominentemente en las estrategias de conservación que buscan reducir las tasas de extinción. Probamos la efectividad de la actual red de reservas para proteger especies en riesgo en Canadá, donde aun permanecen extensas áreas silvestres. Comparamos los números de especies terrestres en riesgo en reservas existentes con los de redes generadas aleatoriamente con la misma superficie total y número de reservas. Las redes de reservas existentes raramente se desempeñaron mejor que las áreas seleccionadas aleatoriamente y varias incluyeron menos especies en peligro que las esperadas al azar; particularmente en las regiones con mayor peligro. La extensión del área protegida y la densidad de las especies en riesgo no estuvieron relacionadas en escalas espaciales grandes (todo el país) ni más finas (cuadrículas de 50 × 50 km), aunque hubo una tendencia a tener menos o ninguna área protegida en las regiones más amenazadas del país (1.5% de áreas con >30 especies en peligro estaba en reservas). Aunque las reservas jugarán un papel útil en la conservación de especies en peligro que viven en ellas, la reducción de las tasas de extinción en una región con mucho de las áreas silvestres que quedan en el mundo requerirá de la integración de estrategias de conservación con planes de uso de suelo agrícola y urbana alrededor de las áreas formalmente protegidas.

**Palabras Clave:** especies en peligro, especies en riesgo, modelos nulos, reservas naturales, uso de suelo

## Introduction

Because most of the terrestrial surface of the Earth has been modified by humans (Vitousek et al. 1997; Sander-

son et al. 2002), it is no surprise that extinction rates have accelerated to mass extinction proportions (Heywood et al. 1994; Lawton & May 1994). This biodiversity decline extends to the loss of individual populations, which

\*Address correspondence to J. Kerr; email [jkerr@uottawa.ca](mailto:jkerr@uottawa.ca)  
Paper submitted August 4, 2004; revised manuscript accepted March 7, 2005.

reduces species' capacity to contribute to ecosystem services required by humans and adapt to rapid environmental change (Hughes et al. 1997; Chapin et al. 2000). Establishing reserve networks in regions of the world where "the last of the wild" yet remain will be critical to long-term conservation success (Sanderson et al. 2002).

To be effective, reserve networks must be able to ameliorate the effects of factors that threaten species with extinction, which have been well studied. In the United States, habitat loss is a primary cause of species endangerment (Dobson et al. 1997; Wilcove et al. 1998). Similarly, in a multiscale analysis, land-use conversion to agriculture was the best predictor of numbers of endangered species in Canada (Kerr & Cihlar 2004; Kerr & Deguise 2004). Introduced species and urbanization have also caused the decline of many species (Czech & Krausman 1997). Overhunting, even in the absence of serious land-use changes, is believed to be the primary threat to more than one-third of World Conservation Union (IUCN) red-listed mammals and birds (Bodmer et al. 1997; Rosser & Mainka 2002). These and other threats can act additively, act synergistically, or interact unexpectedly to deplete biodiversity (Laurance & Cochrane 2001; Balmford et al. 2003).

Reserve networks represent one of the leading strategies for reducing extinction rates (Lawler et al. 2003). The gap between the potential utility of reserves and their actual contribution, however, is sometimes substantial (Rodrigues et al. 2004), largely because relatively few reserves have been designated specifically to conserve biodiversity (Margules & Pressey 2000). Many species cannot maintain viable populations even within some of the largest reserves ever established (Burkey 1995; Gurd et al. 2001).

As human activities continue to expand into remaining wilderness areas, the need to establish protected areas in areas where they are most needed becomes progressively more acute. In Canada, where permanent land-use changes are still relatively concentrated and extensive wilderness areas persist (Kerr & Cihlar 2003, 2004), protected-areas networks are considered critical to the protection and recovery of endangered species and are integrated into new endangered species legislation (Species at Risk Act 2002). Many of Canada's endangered species are also threatened in the United States, and conserving peripheral populations of these species is particularly important for their long-term survival (Channell & Lomolino 2000).

The relationship between the extent of protected area and number of endangered species in a region can take three forms (Kerr & Cihlar 2004). First, a negative correlation might be observed if the reserve network had been effective at preventing species from becoming endangered or had successfully caused them to recover and be delisted. A negative relationship may also arise if reserves are established in areas with low species diversity, leaving species in more diverse areas to become endangered (Pressey et al. 2000; Scott et al. 2001). A positive relation-

ship (i.e., more reserved lands in areas with many endangered species) might be observed if the reserve network had been established responsively (deliberately or otherwise) with new reserves placed in areas where there were many endangered species that had not recovered sufficiently to be delisted. We expected to observe this pattern for Canada's reserve system. A third possibility, however, is no correlation between protected area extent and numbers of endangered species that might be observed if reserves had not been established to address endangered species conservation priorities (Kerr & Burkey 2002).

We used new data on endangered species and protected areas in Canada to address two questions. First, given the distribution of terrestrial endangered species within each of Canada's 15 ecozones, how effectively does the existing reserve system include endangered species relative to randomly situated reserves? We constructed a null model to address this question. Second, we tested for a relationship between patterns of species endangerment and the extent of protected areas across Canada. A significant proportion of the world's remaining wilderness is in Canada (Sanderson et al. 2002), so measurements of the effectiveness of biodiversity conservation strategies there could inform conservation planning for the world's remaining wilderness frontiers.

## Methods

Digital geographic data for all protected areas in Canada falling within IUCN categories I-III were obtained from the World Wildlife Fund in 2001 (H. Alidina, personal communication) and rasterized. Terrestrial reserves range in size from  $<1 \text{ km}^2$  to  $>50,000 \text{ km}^2$  and extend across approximately 10.1% of country's surface (Table 1; Fig. 1).

Species distribution data for species at risk (categorized as endangered, threatened, or of special concern) were obtained from the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; <http://www.cosewic.gc.ca>). As of May 2003, COSEWIC listed 243 species at risk that were predominantly terrestrial. Taxa included birds ( $n = 46$ ), mammals ( $n = 34$ ), lepidopterans ( $n = 7$ ), reptiles ( $n = 15$ ), amphibians ( $n = 13$ ), and plants, lichens, and fungi ( $n = 128$ ). We excluded several reptiles and amphibians considered primarily aquatic (Environment Canada; <http://www.speciesatrisk.gc.ca>). Within each of Canada's 15 terrestrial ecozones (Fig. 1), we determined the total area of the reserve network, the mean area of each reserve, and the number of endangered species (Table 1).

To compare the effectiveness of existing reserves in Canada to a randomly generated network of parks, we constructed a null model for Arc/Info Grid in Arc Macro Language (ESRI 2001; Fig. 2). Within each ecozone, this algorithm generated reserve networks with the same

**Table 1. Summary data on ecozones of Canada used in the analyses of protected areas and null model results.<sup>a</sup>**

Ecozone	Mean area (km <sup>2</sup> ) of reserves (no. of reserves/ecozone)	Area protected (%)	No. of endangered species in random reserve network	No. of endangered species in existing reserve network (p <sup>b</sup> )
Northern Arctic	3,262 (33)	7.6	8.0	7 (0.068)
Arctic Cordillera	2,375 (23)	22.7	8.9	8 (0.048) <sup>c</sup>
Southern Arctic	7,776 (17)	17.8	7.6	7 (0.47)
Taiga Cordillera	6,774 (4)	10.8	4.7	4 (0.34)
Taiga Plains	1,229 (20)	4.5	9.0	7 (0.044) <sup>c</sup>
Boreal Cordillera	1,719 (37)	14.9	8.0	8 (0.99)
Taiga Shield	2,233 (32)	6.2	9.4	11 (0.87)
Pacific Maritime	110 (170)	10.0	31.8	28 (0.096)
Boreal Plains	169 (395)	10.2	20.8	20 (0.28)
Montane Cordillera	274 (274)	15.6	41.0	34 (<0.004) <sup>c</sup>
Boreal Shield	165 (1189) <sup>d</sup>	11.4 <sup>c</sup>	47.4	50 (0.88)
Hudson Plains	239 (193)	13.0	9.0	7 (<0.004) <sup>c</sup>
Prairies	21 (299)	1.4	34.0	33 (0.18)
Mixed Wood Plains	6.3 (77)	0.4	58.2	51 (0.032) <sup>c</sup>
Atlantic Maritime	110 (110)	6.0	24.7	23 (0.14)

<sup>a</sup>Also presented are mean numbers of species at risk protected by randomly generated parks in each of the 15 terrestrial ecozones compared with the number of species protected by existing reserves in Canada.

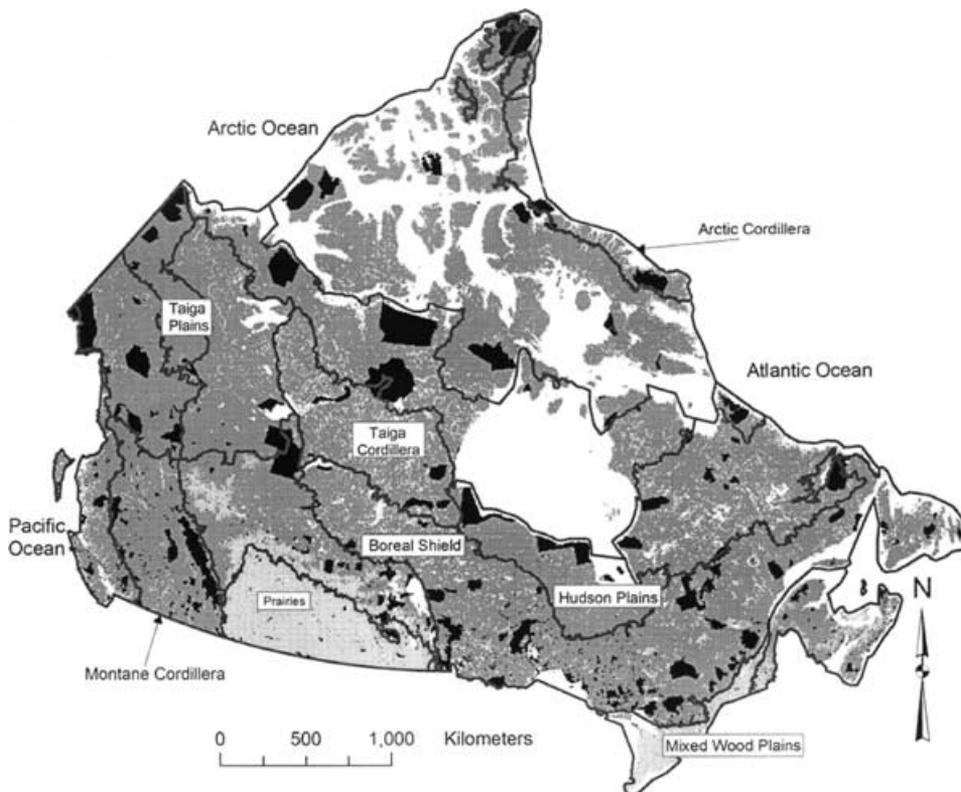
<sup>b</sup>Probability that the real reserve network performs as well as areas chosen randomly in the null model.

<sup>c</sup>Ecozones where the existing reserve network includes fewer species at risk than expected by chance (significance = 0.05).

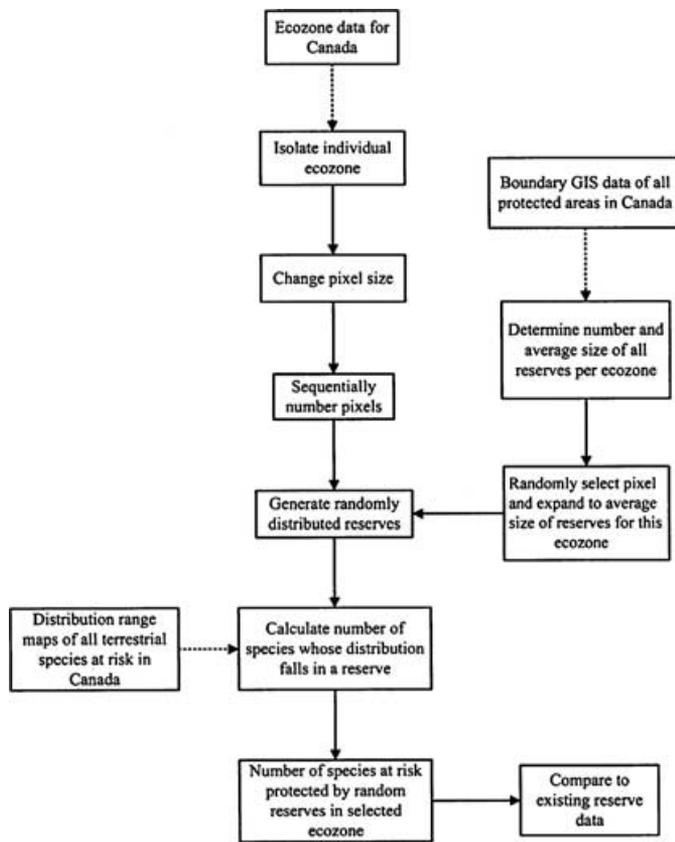
<sup>d</sup>Area of 559 km<sup>2</sup> within 346 reserves used for null model.

number of reserves and total area as the real network but with reserves whose locations were randomized spatially (human-modified lands were considered valid locations for null-modeled reserves because these areas usually have the greatest numbers of endangered species;

human-modified lands can be identified from satellite land use/land cover data from the SPOT4/Vegetation sensor; Kerr & Cihlar 2003). The area of each null-modeled reserve was the mean area of reserves actually found within that ecozone (accurate to within less than the size of one



**Figure 1. Protected areas (black), ecozones (black lines), extent of human-dominated lands (light gray), or lands with limited human dominance (dark gray) in Canada. Areas in white are water or outside Canadian territory. Human-dominated lands were detected using satellite-based land-use data. More information about Canada's ecozones can be found at <http://www.ccea.org/ecozones/terr.html>.**



*Figure 2. The null-model algorithm used to randomly generate reserve networks for each of Canada's ecozones. Randomly generated networks have the same number of reserves and same total area as the real network.*

pixel for the ecozone—null-modeled reserve boundaries lined up with pixel edges and therefore the area of these reserves varied slightly from the mean reserve size for the ecozone). Reserve locations were randomized and not selected to conserve the spacing patterns of the real reserve network. The latter approach would have addressed a different question than the one we focused on here: Does the existing reserve network include endangered species as effectively as a randomly generated network with the same number of reserves and total protected area? We repeated the random reserve generation routine many times to produce a null distribution of numbers of endangered species that would be protected by randomly placed reserves. The effectiveness of each ecozone's actual reserve network could then be compared with that of randomly generated reserves by calculating the proportion of randomly generated reserve systems that included fewer endangered species than the actual reserve network. This value corresponds to the probability that the real reserve network performs at least as well as randomly situated reserves (Table 1).

To allow the null models to run within an acceptable period of time, we resampled GIS data to 4600-m resolution in most ecozones (actual computer runtime on three dual processor, 3 GHz Pentium 4 systems with 1 gigabyte of RAM was about 4 months for all ecozones). The value of 4600 m was selected empirically to allow null models to run in a reasonable time but still detect the presence of relatively small-ranged endangered species. If pixel resolution is too large, endangered species with ranges that are smaller than the pixel size are not detected by ArcGIS in null-modeled reserve networks. It would have been possible to inflate the ranges of very range-restricted species to equal that of a single  $4600 \times 4600$  m pixel but this could have caused resampling errors in ArcGIS such that these species' ranges would have occupied parts of adjacent pixels. Accordingly, we used pixel sizes of 2200 m for the Prairies and 500 m for the Mixed Wood Plains because these ecozones include endangered species with very small distributions. These values were also selected empirically to ensure that all endangered species could be detected while holding processing time down to a practical level. At the end of each run the algorithm determined the number of species at risk whose ranges intersect at least one of the random reserves. This process was repeated 250 times in each ecozone to generate statistical distributions of endangered species protection by random reserve networks.

We reclassified the protected areas in the Boreal Shield ecozone. This ecozone contained 1189 separate protected areas, many of which were contiguous. Processing this many reserves over such a broad extent ( $>1.7 \times 10^6$  km<sup>2</sup>) was impractical, so we merged spatially contiguous, but administratively distinct, protected areas. We also eliminated spatially isolated reserves that occupied  $< 10$  km<sup>2</sup>. The concessions made to process this ecozone are biologically reasonable—endangered species in the Boreal Shield are broadly distributed, are typically large bodied (e.g., woodland caribou [*Rangifer tarandus caribou*]), and cannot maintain viable populations in small reserve isolates. Omitting such areas reduced the total extent of the protected areas network by 1.1%, from 195,756 km<sup>2</sup> to 193,565 km<sup>2</sup>. These concessions increased the apparent inclusiveness of the real reserve system relative to the randomly generated networks. Had the randomization routine treated spatially contiguous reserves as separate entities instead of single, larger reserves, random reserve networks generated by the null model would have spread over a larger area of the ecozone and probably included more of the ecozone's endangered species.

We used linear regression to test the relationship between the number of endangered species and extent of protected area at two respective resolutions: ecozones and  $50 \times 50$  km grid cells. For both analyses, we measured the number of endangered species and extent of protected area within each sampling unit (an ecozone or grid cell). We also tested for a relationship between

mean reserve size and numbers of endangered species (log transformed to stabilize residual variance) per ecozone. Because ecozones in Canada differ in their areas (Table 1), we included ecozone area in regression models to ensure that area effects did not obscure our conclusions (Ricketts et al. 1999; Kerr & Deguisse 2004).

All geographic data were processed using ArcInfo Grid (ESRI 2003). Statistical analyses were conducted using S-Plus Version 6.2 (Insightful Corporation 2003).

## Results

The distribution and size of protected areas varied across Canada (Fig. 1). Throughout Canada, 2863 protected areas were included with a combined area of approximately  $8.99 \times 10^5$  km<sup>2</sup> and an average size of 314 km<sup>2</sup>. The Mixed Wood Plains was least protected, with few reserves and the smallest total area protected (77 reserves extend across 0.42% of the area of the ecozone, or about 482 km<sup>2</sup>). This ecozone also had the most endangered species (101 out of the 243 species at risk in Canada). The Boreal Shield had the largest number of reserves and the greatest reserve area, with approximately  $1.96 \times 10^5$  km<sup>2</sup> of protected land (Table 1).

Reserve networks in most ecozones included endangered species about as often as randomly placed areas with notable exceptions. In the Mixed Wood Plains and Montane Cordillera, both with large numbers of species at risk, existing reserve systems were significantly less inclusive than randomly placed areas (Table 1). In the Mixed Wood Plains, the mean number of species at risk within random reserve networks was 58.2 (SD = 2.9), whereas the existing reserves in this region protected 51 endangered species (Table 1; Fig. 3a). The Montane Cordillera reserve network included 34 species at risk, which was fewer than any network consisting of spatially randomized reserves. The Taiga Plains, Hudson Plains, and Arctic Cordillera also included significantly fewer endangered species than expected by chance ( $p < 0.05$ ). Randomized reserve networks included one or two more species than the existing reserve network in these ecozones, a small but statistically significant difference. The reserve networks of most other ecozones performed no worse than randomly chosen areas (Fig. 3b), although these ecozones include, at present, relatively few species at risk.

There was no relationship between the total area protected per ecozone and the total number of species at risk found within each ecozone ( $R^2 = 0.001$ ,  $p > 0.90$ ). When we subdivided Canada into  $50 \times 50$  km grid cells, our results remained consistent at this higher resolution (Fig. 4;  $R^2 < 10^{-5}$ ,  $p = 0.63$ ,  $n = 5323$ ). Among areas with the greatest need for protection, defined arbitrarily as any grid cell with 10 or more endangered species, the extent of protected area was small (3.6% of this 662,000 km<sup>2</sup> area

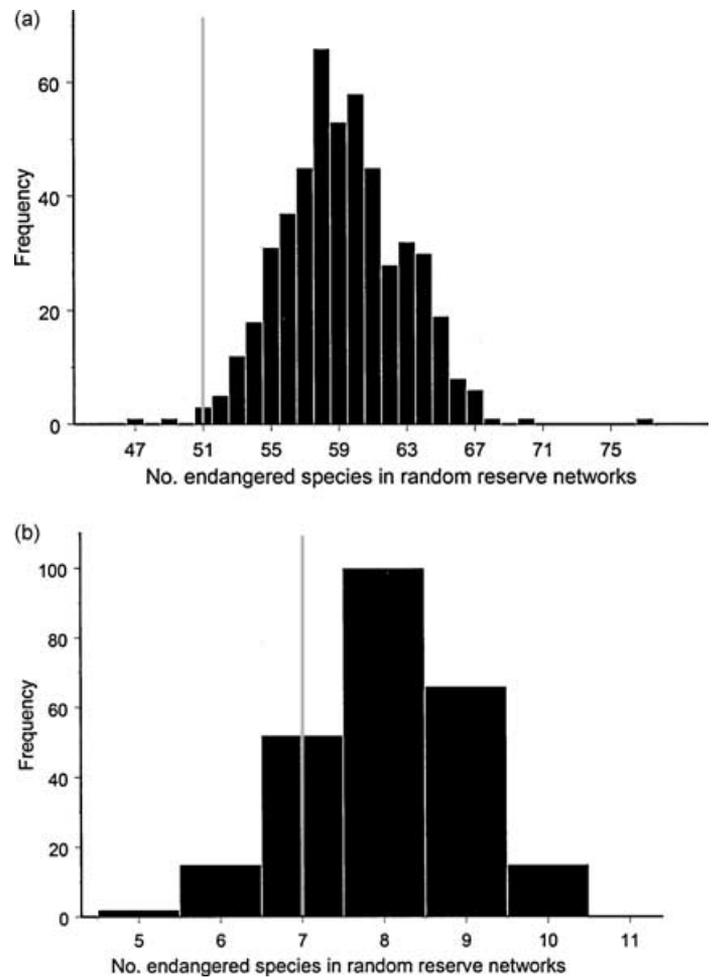


Figure 3. Distribution of numbers of endangered species that would be protected by randomly placed reserves in (a) the Mixed Wood Plains (southeastern Canada) and (b) the Southern Arctic (northern Canada) (vertical line is the number of endangered species protected by the existing reserve network).

is protected). Mean reserve size declined strongly in ecozones where there were many species at risk (Fig. 5,  $R^2 = 0.76$ ,  $p < 10^{-4}$ ). Ecozone area, which could potentially influence this relationship, was unrelated to numbers of endangered species alone ( $F = 0.255$ ,  $p = 0.622$ ) or in multiple regression models with mean reserve size (variable  $p = 0.108$ ).

## Discussion

Among Canada's ecozones, existing reserve networks most commonly included no more endangered species than expected by chance. In the most seriously degraded ecozone, the Mixed Wood Plains, randomly generated reserve networks included more endangered species than expected by chance (Fig. 3b). This area is the most

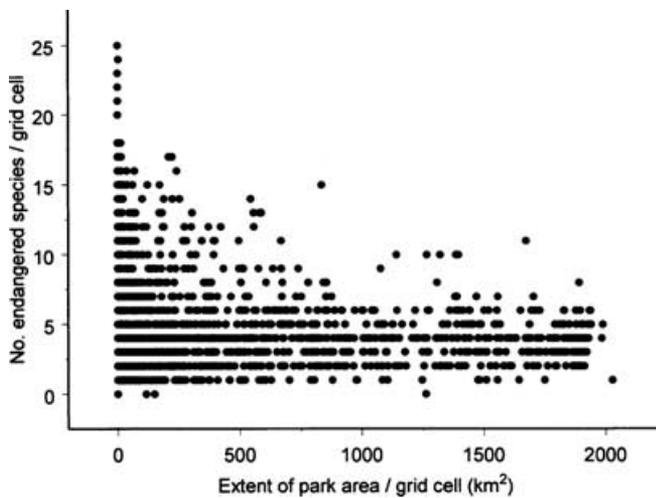


Figure 4. The relationship between the number of terrestrial endangered species and the extent of protected area within  $50 \times 50$  km grid cells ( $n = 5323$ ) across Canada.

densely populated in Canada, includes extensive urban and agricultural land uses, has the greatest concentration of endangered species, and is for many taxa the most diverse region in the country (Kerr & Packer 1997; Kerr 2001). There were also many endangered species in the Montane Cordillera, where the existing reserve network included fewer endangered species than any randomly generated network. Land uses that inhibit reserve establishment in this ecozone include extensive forestry activities and agriculture, which are concentrated in the south.

The benefits of reserves in the most threatened regions of Canada are limited by their small size: mean reserve size in Canada declined sharply as numbers of endangered species per ecozone increased (Fig. 5). Patterns

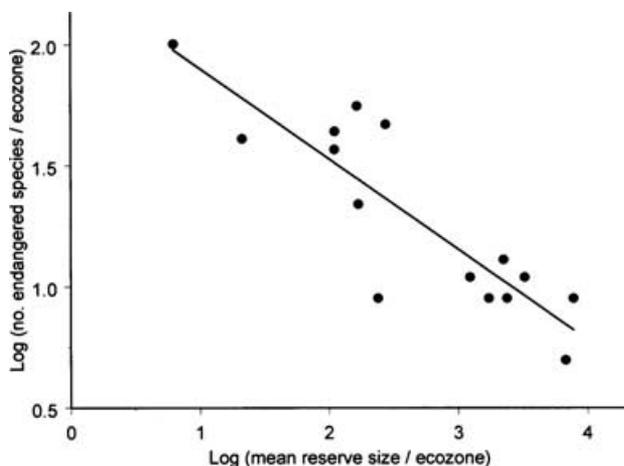


Figure 5. The relationship between mean reserve size and numbers of endangered species per ecozone (log transformed;  $R^2 = 0.76$ ,  $p < 10^{-4}$ ,  $n = 15$ ).

of habitat loss in Canada's ecozones are positively related to natural patterns of species richness (Seabloom et al. 2002; Kerr & Cihlar 2003) and endangered species numbers (Kerr & Deguise 2004). This pattern likely arises because of longstanding land use conflicts. Areas with the highest diversity are now dominated by agricultural land uses (Kerr & Cihlar 2003), which makes it difficult to establish new reserves or expand existing, small reserves. Similar patterns of skewed reserve distributions have been found across the Western Hemisphere (Andelman & Willig 2003). Canada's Species at Risk Act provides little additional habitat protection in areas with the largest numbers of endangered species (and therefore the smallest reserves), although it promotes cooperative conservation measures in these areas of mostly privately owned land. These efforts have not yet been widely implemented and their effects cannot yet be evaluated.

Species in some northern ecozones (e.g., Taiga Shield and Boreal Cordillera) were included in existing reserves relatively completely, although there were few endangered species in these areas and low species richness overall. Range sizes among northern endangered species are broad and most of the north is considered "wilderness" (there are fewer land-use conflicts; Sanderson et al. 2002), so including endangered species in reserve networks should be easier. Even in Canada's wilderness areas, however, reserve systems in three ecozones (Arctic Cordillera, Taiga Plains, and Hudson Plains; Table 1) included significantly fewer endangered species than expected by chance. In the Boreal Shield, the ecozone for which adjacent reserves were fused and small reserve isolates eliminated from the null model, randomly generated sets of reserves were usually less inclusive than the existing reserve network. Had it been practical to treat adjacent reserves distinctly, however, then randomly placed reserves would most likely have included as many or more endangered species because the random reserve networks would have been sampled more evenly throughout the geographic space of the Boreal Shield ecozone than they were for the model run here.

The null model we have constructed is conservative. First, the null model counted all endangered species with ranges that intersected even a tiny portion of a single reserve. Furthermore, null reserve networks were based on mean reserve size per ecozone and not the actual reserve size distribution. This concession to processing speed, although necessary, probably lowered the number of endangered species included in random reserve networks (in the null model all reserves were equal in size, so it was impossible for a particularly large reserve to be placed randomly over the area with the greatest numbers of endangered species). In the Mixed Wood Plains, where every reserve is small and there is little variability in reserve size, this concession is unlikely to have any practical consequence. Null model assumptions are biologically unrealistic but necessary to test for the presence

of an effect, in this case, whether reserves and areas chosen at random included endangered species (Gotelli & Graves 1996; Colwell et al. 2004). Had we employed more realistic biological constraints on the null model, such as counting endangered species in the null reserves only if they were viable populations or even requiring that species had to be found in more than one reserve to be counted, then both actual and null reserve systems would have performed less well.

Canada's reserves are far from the level of protection called for by coarser-resolution global gap analysis (Rodrigues et al. 2004) or by analyses of endangered species distributions in Canada (Kerr & Cihlar 2004). There is little chance of achieving more ambitious objectives of representing genetic or phylogenetic diversity (Rodrigues et al. 2004) or distinct populations of individual species (Hughes et al. 1997; Ceballos & Ehrlich 2002) in the reserve systems of Canada. It would be useful to assess the extent to which such aspects of diversity are currently represented within reserves. The null expectation for such a study would be that genetic and phylogenetic diversity are represented within reserves with the same proportion as species' distributions.

Reserve networks in Canada might include unexpectedly few endangered species for two reasons. First, endangered species are concentrated in areas with extensive human land use, clearly inhibiting reserve establishment or expansion. This cannot explain why reserve networks in ecozones consisting predominantly of wilderness include fewer endangered species than expected by chance (although land claims and traditional land uses by aboriginal Canadians influence reserve placement). A second reason for poor reserve performance, however, is that protected areas have simply not been established to protect biodiversity. National parks, for example, are intended to maintain areas for the "benefit, education and enjoyment" of Canadians (National Parks Act 2000). It is only in the later Species at Risk Act that an endangered species protection role is firmly established for national parks (Species at Risk Act 2002). Canadian parks include significant and vast tracts of wilderness, although diversity for most taxa is lower (e.g., Kerr & Packer 1997; Kerr et al. 2001) and far less threatened (Kerr & Cihlar 2004; Fig. 4) in such areas.

Conserving biodiversity in Canada will require solutions to this conflict with human land uses, perhaps led by complementarity analyses that could identify areas with inadequate protection, formal or otherwise (Luck et al. 2004; Warman et al. 2004), or by expanding small reserves to include surrounding areas, an approach that has seen some success (e.g., in privately held lands around Waterton National Park in Alberta, <http://www.natureconservancy.ca>; around St. Lawrence Islands National Park, G. Giffin, personal communication). Given that reserves include fewer endangered species than expected by chance in the Mixed Wood Plains, Montane

Cordillera, and even some ecozones that lack extensive permanent human land uses, protected areas networks alone are unlikely to provide effective endangered species protection in Canada.

Conservation activities outside reserves, especially efforts that involve private landowners, should be a high priority. Tax incentives and conservation easements may prove effective in this respect (Scott et al. 2001) and would reduce the land-use conflicts that would arise from—and probably scuttle—efforts to establish large protected areas in the midst of privately held lands. Even had existing reserve networks included more endangered species than expected by chance, reserve area is far smaller in areas with many endangered species (Fig. 5). Thus, we emphasize the importance of distinguishing between inclusiveness and effectiveness. The small reserves in ecozones with many endangered species are unlikely to maintain viable populations of most endangered species (e.g., Gurd et al. 2001). Even species that can reach high population densities (e.g., invertebrates) in small reserves cannot be reliably conserved in such areas—environmental stochasticity is likely to eliminate population isolates over long periods (e.g., the Karner blue butterfly [*Lyceides melissa samuelis*], extirpated from southern Ontario; Packer 1994). Integrating conservation into agricultural and urban land-use practices (e.g., James 2002) will be critical for reducing the loss of species in Canada given the wide gap between the effectiveness of reserves and the needs of endangered species.

## Acknowledgments

We are grateful to the Natural Sciences and Engineering Research Council of Canada for Discovery Grant support to J.T.K. and summer scholarship support to I.E.D. The Canadian Foundation for Innovation, Ontario Innovation Trust, and the University of Ottawa generously provided funds for research infrastructure to J.T.K. and the Canadian Facility for Ecoinformatics Research. Comments by D. Currie, T. R. E. Southwood, and R. M. May improved this research, as did detailed and constructive commentary by R. Pressey and three anonymous reviewers.

## Literature Cited

- Andelman, S. J., and M. R. Willig. 2003. Present patterns and future prospects for biodiversity in the Western Hemisphere. *Ecology Letters* 6:818–824.
- Balmford, A., R. E. Green, and M. Jenkins. 2003. Measuring the changing state of nature. *Trends in Ecology & Evolution* 18:326–330.
- Bodmer, R. E., J. F. Eisenberg, and K. H. Redford. 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology* 11:460–466.
- Burkey, T. V. 1995. Faunal collapse in East African game reserves revisited. *Biological Conservation* 71:107–110.
- Ceballos G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. *Science* 296:904–907.

- Channell, R. and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. *Nature* **302**:84–86.
- Chapin, F. S., III, et al. 2000. Consequences of changing biodiversity. *Nature* **105**:234–242.
- Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist* **163**:E1–E23.
- Czech, B., and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. *Science* **277**:1116–1117.
- Dobson, A., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. *Science* **275**:550–553.
- ESRI (Environmental Systems Research Institute). 2003. Arc/Info for Windows NT. Version 8.2.3. ESRI Limited, Redlands, California.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C.
- 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.
- Heywood, V. H., G. M. Mace, R. M. May, and S. N. Stuart. 1994. Uncertainties in extinction rates. *Nature* **368**:105.
- Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 1997. Population diversity: its extent and extinction. *Science* **278**:689–692.
- Insightful Corporation. 2003. S-Plus, academic site release. Version 6.2. Murray Hill, New Jersey.
- James, S. M. 2002. Bridging the gap between private landowners and conservationists. *Conservation Biology* **16**:269–271.
- Kerr, J. T. 2001. Global biodiversity: from description to understanding. *Trends in Ecology & Evolution* **16**:424–425.
- Kerr, J. T., and T. V. Burkey. 2002. Endemism, diversity, and the threat of tropical moist forest extinctions. *Biodiversity and Conservation* **11**:695–704.
- Kerr, J. T., and J. Cihlar. 2003. Land use and cover with intensity of agriculture for Canada from satellite and census data. *Global Ecology & Biogeography* **12**:161–172.
- Kerr, J. T., and J. Cihlar. 2004. Patterns and causes of species endangerment in Canada. *Ecological Applications* **14**:167–175.
- Kerr, J. T., and I. Deguise. 2004. Habitat loss and the limits to endangered species recovery in Canada. *Ecology Letters* **7**:1163–1169.
- Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high energy areas. *Nature* **385**:252–254.
- Kerr, J. T., T. R. E. Southwood, and J. Cihlar. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences of the United States of America* **98**:11265–11370.
- Laurance, W. F., and M. A. Cochrane. 2001. Synergistic effects in fragmented landscapes. *Conservation Biology* **15**:1488–1489.
- Lawler, J. J., D. White, and L. L. Master. 2003. Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. *Ecological Applications* **13**:1762–1772.
- Lawton, J. H., and R. M. May. 1994. Estimating extinction rates. *Philosophical Transactions of the Royal Society of London Series B* **344**:1–104.
- Luck, G. W., T. H. Ricketts, G. C. Daily, and M. Imhoff. 2004. Alleviating spatial conflict between people and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **101**:182–186.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243–253.
- National Parks Act. 2000. Government of Canada, Minister of Public Works and Services, Ottawa.
- Packer, L. 1994. The extirpation of the Karner blue butterfly in Ontario. Pages 143–151 in D. A. Andow, R. J. Baker, and C. P. Lane, editors. *Karner blue butterfly: a symbol of a vanishing landscape*. Minnesota Agricultural Experiment Station, St. Paul.
- Pressey, R. L., et al. 2000. Using abiotic data for conservation assessments over extensive regions: quantitative methods applied across New South Wales, Australia. *Biological Conservation* **96**:55–82.
- 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.
- Rodrigues, A. S. L., et al. 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* **428**:640–643.
- Rosser, A. M., and S. A. Mainka. 2002. Overexploitation and species extinctions. *Conservation Biology* **16**:584–586.
- Sanderson, E. W., J. Malanding, M. A. Levy, K. H. Redford, A. V. Wannebo, and G. Woolmer. 2002. The human footprint and the last of the wild. *BioScience* **52**:891–904.
- Scott, J. M., et al. 2001. Nature reserves: do they capture the full range of America's biological diversity? *Ecological Applications* **11**:999–1007.
- Seabloom, E. W., A. P. Dobson, and D. M. Stoms. 2002. Extinction rates under non-random patterns of habitat loss. *Proceedings of the National Academy of Sciences of the United States of America* **99**:11229–11234.
- Species at Risk Act. 2002. Government of Canada, Minister of Public Works and Services, Ottawa.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Warman L. D., D. M. Forsyth, A. R. E. Sinclair, K. Freemark, H. D. Moore, T. W. Barrett, R. L. Pressey, and D. White. 2004. Species distributions, surrogacy, and important conservation regions in Canada. *Ecology Letters* **7**:374–379.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperilled species in the United States. *BioScience* **45**:607–615.