Conservation of Mammals in Eastern North American Wildlife Reserves: How Small Is Too Small?

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Abstract: *A common objective of methods of systematic reserve selection has been to maximize conservation benefits—frequently current species richness—while reducing the costs of acquiring and maintaining reserves. But the probability that a reserve will lose species in the future is frequently not known because the minimum area requirements for most species have not been estimated empirically. For reserves within the Alleghenian-Illinoian mammal province of eastern North America, we empirically estimated the minimum area requirement of terrestrial mammals such that reserves should not lose species because of insularization. We compared this estimate to the actual size of 2355 reserves and reserve assemblages within the mammal province. The estimated minimum area requirement was 5037 km^2 (95% CI: 2700–13,296 km^2). Fourteen reserves and reserve assemblages were >2700 km^2, 9 were >5037 km^2, and 3 were >13,296 km^2. These 14 reserves accounted for 73% of the total area of reserves and 10% of the total area of the mammal province. Few reserves appear large enough to avoid loss of some mammal species without the additional cost of active management of habitat or populations. Immigration corridors and buffer zones that combine small reserves into assemblages totaling at least 2700 km^2 may be the most efficient means of conserving mammals in these reserves.*

Conservación de Mamíferos en Reservas de Vida Silvestre de Norteamérica Oriental: Que tan Pequeño es Muy Pequeño

Resumen: *Un objetivo común de los métodos de la selección sistemática de reservas ha sido maximizar los beneficios de la conservación—frecuentemente riquezas de especies actuales—mientras que se reducen los costos de adquisición y mantenimiento de las reservas. Sin embargo, la probabilidad de que las reservas pierdan especies en el futuro es frecuentemente sabido puesto que los requerimientos mínimos de área para la mayoría de las especies no ha sido estimada empíricamente. Para las reservas que se encuentran dentro de la provincia de mamíferos Alleghenian-Illinoian de Norteamérica oriental, estimamos empíricamente los requerimientos mínimos de área para mamíferos terrestres de tal manera que las reservas no perdiesen especies debido al aislamiento. Comparamos estas estimaciones con los tamaños actuales de 2355 reservas y ensamblajes de reservas dentro de la provincia de mamíferos. El requerimiento de área mínima estimado fue de 5037 km^2 (95% CI: 2700–13,269 km^2). Catorce reservas y ensamblajes de reservas fueron mayores a 2700 km^2, 9 fueron mayores a 5037 km^2, y 3 fueron mayores a 13,296 km^2. Estas 14 reservas correspondían al 73% del área total de las reservas y 10% del área total de la provincia de mamíferos. Pocas reservas son lo suficientemente grandes como para evitar pérdidas de algunas especies de mamíferos sin los costos adicionales de un manejo activo de hábitat o de poblaciones. Los corredores de inmigración y las zonas de amortiguamiento que combinen pequeñas reservas dentro de ensamblajes que tengan por lo menos un total de 2700 km^2 podría ser la estrategia más eficiente para conservar mamíferos en estas reservas.*

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Introduction

Efficient in situ conservation requires that the conservation benefit of reserves be maximized while costs are reduced (Glenn 1990; Vane-Wright et al. 1991; Georgiadis & Balmford 1992). This trade-off between conservation benefit and cost is a central consideration of algorithms proposed to aid the design of reserve systems (Margules et al. 1988; Rebelo & Siegfried 1992; Pressey et al. 1993, 1994; Rothley 1999). In general, these algorithms consider a number of candidate sites and select an optimal subset based on a number of criteria. The criteria vary and can be complex, although a common objective is to maximize species richness while reducing the total area to be conserved.

But optimality algorithms have primarily considered current species richness, which may not be constant. Future changes to the habitat surrounding a reserve may eliminate the periodic immigration necessary to maintain populations (Brown & Kodric-Brown 1977; Lomolino et al. 1989). Reserves currently situated in habitat isolates may continue to lose species even without changes to the surrounding habitat due to time lags between isolation and species loss (Brooks et al. 1999). For example, Margules et al. (1994) compared plant species richness on limestone pavements to test whether an "optimal" system of pavement reserves created to protect rare and uncommon plant species based on data from 1974 would still meet its objective in 1985. Although the optimal system of 14 reserves contained more target species than random selections of 14 reserves or the 14 largest reserves, the optimal reserve system nevertheless lost 18 of 50 species by 1985. Knowledge of each reserve's potential to maintain its 1974 species richness may have led to selection of different reserves and a more robust reserve system. Thus, the ability of reserves to maintain species following reserve establishment is at least as important as the number of species present at establishment (Simberloff & Abele 1982; Shaffer & Samson 1985; Soulé & Simberloff 1986).

How can one know if a reserve will maintain its species complement? Numerous studies of oceanic islands, land-bridge islands and terrestrial isolates have shown that species-area relationships for isolated patches of habitat have lower intercepts and steeper slopes than habitat patches of equal size within a much larger area of habitat (MacArthur & Wilson 1967; Brown 1971; Lawlor 1986; Rosenzweig 1995; Turner 1996). This pattern is ubiquitous: Rosenzweig (1995) could not give an example that contradicts it. Because species-area relationships for isolates have steeper slopes and lower intercepts than those of non-isolates, there must be a point at which these two relations intersect. At this point an isolate will contain as many species as a non-isolate. The area coordinate of this intersection is the minimum area required to avoid loss of species due to isolation (Bond et al. 1988; Cowling & Bond 1991).

Seven of 10 parks in the extensively developed Canadian portion of the Alleghenian-Illinoian mammal province (Hagmeier 1966) contained fewer terrestrial mammal species than were estimated to have been present prior to European settlement (Glenn & Nudds 1989; Gurd & Nudds 1999). We compared the species-area relationships of these parks to estimated species-area relationships of the Alleghenian-Illinoian mammal province prior to European settlement and estimated the minimum area requirement below which we expect terrestrial mammals to become extirpated from isolated reserves. We also compared the size of reserves throughout the Alleghenian-Illinoian mammal province to our estimate of the minimum area requirement to evaluate the future potential of present reserves in Canada and the United States to conserve terrestrial mammals.

Methods

Glenn and Nudds (1989) first provided estimates of the historical species-area relationships for six mammal provinces in Canada prior to extensive habitat alteration by European settlers. Gurd and Nudds (1999) improved their methods, and we use their data here. A brief description of the methods follows, but readers are referred to the original references for further details.

Gurd and Nudds (1999) generated historical species-area relationships separately for two groups of mammal species following habitat descriptions in Banfield (1974): disturbance-tolerant species that persist in human-dominated landscapes and disturbance-intolerant species that do not. Introduced species and marine mammals were not considered. To generate historical species-area relationships, we digitized historical range maps for each species (Banfield 1974) with a geographical information system and compiled them to create a composite species-richness map. This map was "sampled" through 14 randomly placed, non-overlapping plots of 10, 100, 1000, and 10,000 km^2 ($n = 56$). The species richness of each plot was estimated as the number of species' ranges that intersected each plot. Lists of mammal species currently present within Canadian parks and the size of each park were taken from Glenn and Nudds (1989). Although the analysis by Gurd and Nudds (1999) considered five mammal provinces and two species groups, we present data only on disturbance-intolerant species in the Alleghenian-Illinoian mammal province (Fig. 1). A maximum of only three parks in each of the other nine province-group analyses contained fewer species than expected historically, too few for the present analysis.

We fitted a power model to both the range and park data, as follows: $S = cA^z$, where S represents the number of species, A represents the plot or park area (km^2), and c and z are constants. The values of c and z were estimated by least-squares regression following logarithmic
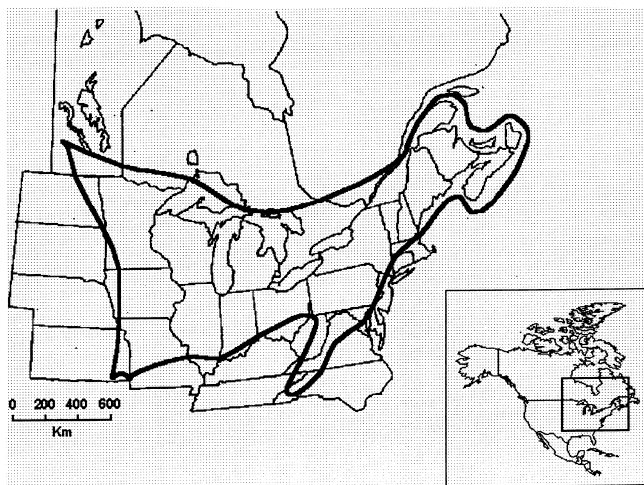
Figure 1. Thick line shows the extent of the Alleghenian-Illinoian mammal province in Canada and the United States (figure redrawn from Hagmeier 1966).

transformation of the data. The regression of the range data was analyzed for lack of fit (Draper & Smith 1981) to test the assumption that the data could be adequately summarized with a linear model.

We estimated the minimum area requirement at the intersection of the species-area curve of habitat fragments with the historical species-area curve for similar but contiguous habitat. Using 2000 iterations of a bootstrap resampling method (Efron 1981), we estimated the 95% confidence intervals around the intersection of the two regression lines.

We used these data for four reasons. First, the historical species-area curve was constructed from historical range maps with many data points. This allows for estimation of the variation about the curve and is essential to rigorous testing for loss of species from the parks (for a discussion of the implications of Type I and II errors for reserve design, see Schmiegelow 1992). Second, the separate treatment of disturbance-tolerant and -intolerant species prevented losses of disturbance-intolerant species from being masked by increases in numbers of disturbance-tolerant, invasive species (Diamond 1975; Humphreys & Kitchener 1982; Blake & Karr 1984). Third, the historical and park data were compared within faunistically homogenous regions (mammal provinces) and over relatively similar time frames, reducing the possibility that differences were due to effects other than habitat fragmentation. Our method (Gurd & Nudds 1999), therefore, compared the current state of species richness in parks with a "best guess" for an area of the same size and location, but from a period prior to the appearance of the presumed effect on diversity (i.e., widespread habitat loss and insularization). As such, this approach makes use of a controlled "natural experiment." Fourth, mammals have significantly different species-area curves than

other taxa (Brown 1978; Humphreys & Kitchener 1982; Murphy & Wilcox 1986a, 1986b; Schmiegelow & Nudds 1987) because of lower dispersal abilities and population densities. Consequently, they may require larger areas than other taxa to conserve the same fraction of initial species richness (Schmiegelow & Nudds 1987). The lack of empirical estimates of the minimum area required to avoid loss of mammals may lead to large inefficiencies in conservation planning, with potential negative effects on mammals and other species.

We compared our estimate of the minimum area requirement for terrestrial mammals to the sizes of existing reserves in the Alleghenian-Illinoian mammal province. We compiled data on national, state, and provincial parks; national, state, and provincial forests; national, state, and provincial wildlife refuges; state and provincial fish and wildlife management areas; and state, provincial, and nongovernmental nature reserves in Canada and the United States. We concentrated on reserves for which wildlife conservation was a management objective. Reserves that preserve historical sites or cater to high-impact recreational activities were excluded.

For each reserve, we attempted to determine its size, location, and whether it was adjacent to any other reserves. In cases where reserves consisted of more than one separate tract of land, we attempted to collect data on each separate tract. If reserves were adjacent to one another, we combined the area of the adjacent reserves and refer to them specifically as reserve assemblages, but generically as reserves. We included in the analysis the total area of reserves that crossed the boundary of the mammal province, but we did not include adjacent reserves located entirely outside of the mammal province. We collected data primarily from websites or literature provided by the various agencies responsible for managing reserves. We also consulted atlases and road maps to identify reserves and determine their boundaries. If area data for a reserve was not available from these sources, we requested it from the managing agency directly.

We noted errors in the reserve area data when we were aware of them. Errors occurred for two reasons. First, our list of reserves was not exhaustive, and we were unable to determine the area of all the reserves we identified. In cases where data for adjacent reserves were unavailable, the size of the reserve assemblage was underestimated. Second, some reserves consisted of more than one separate tract, particularly national and state forests in the United States. Data on the size of individual tracts composing a reserve often were not available. The majority of our data consist of the total area of all tracts, which overestimates the area of contiguous protected habitat in some reserves. Both sources of error affected some reserve assemblages. We used maps to visually estimate net error and determine if it had the potential to affect the comparison with the estimate of the minimum area requirement.
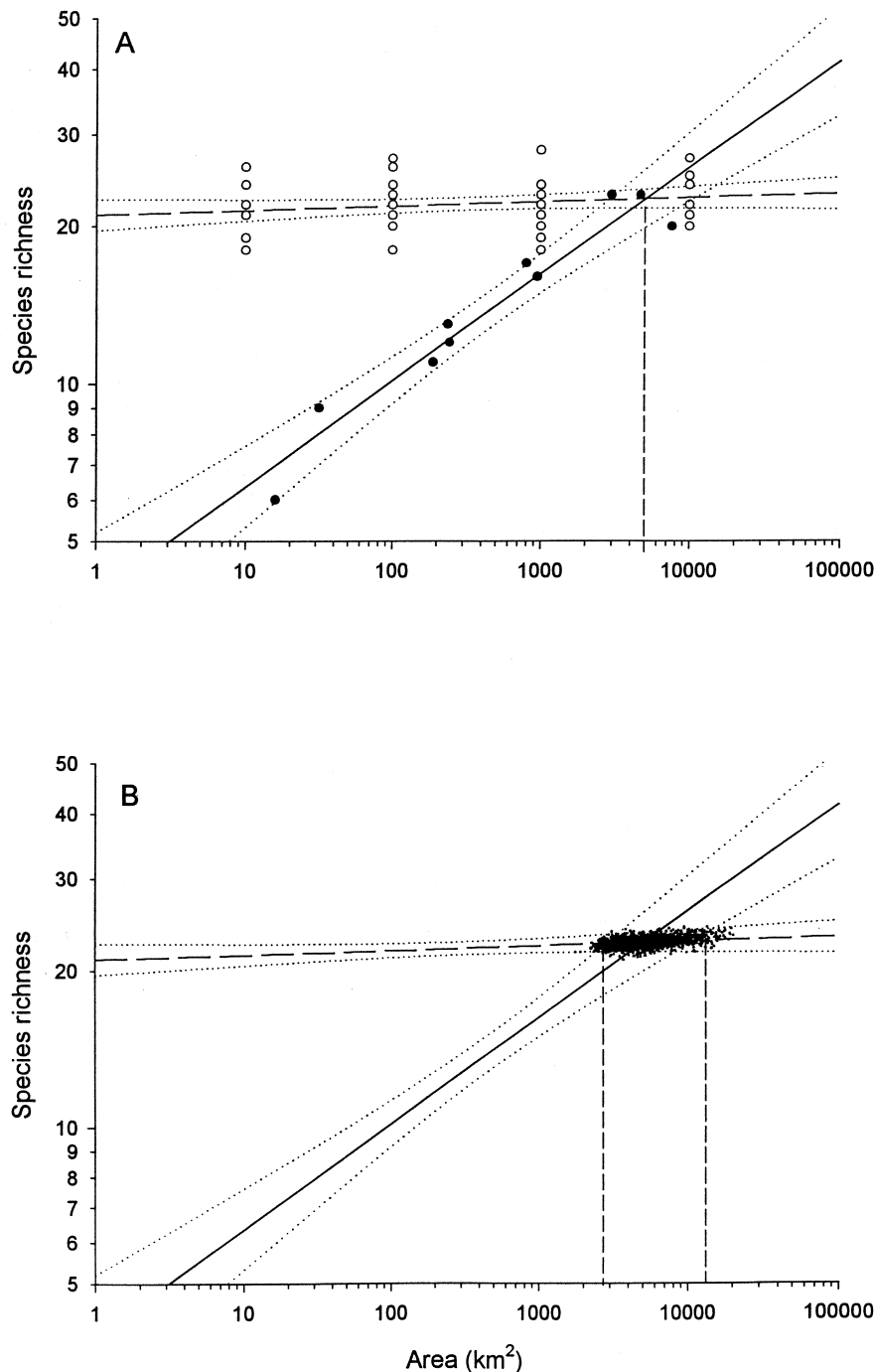
Figure 2. Point of intersection of the species-area regression line for mammals in some national and provincial parks in Canada (●, solid line) with the historical species-area regression line (○, dashed line). Dotted lines are 95% confidence intervals for the species-area regression lines. (a) The intersection point provides an estimate of the expected minimum area requirement for mammals of 5037 km² (vertical line). Some of the historical species-area data points overlap. The parks, in increasing order of size, are Point Pelee, Prince Edward Island, Turtle Mountain, Kouchibouguac, Forillon, Gaspésie, Cape Breton Highlands, Riding Mountain, Quetico, and Algonquin. (b) The distribution of 2000 bootstrapped estimates of the intersection of the species-area regression lines for the parks and the historical range data. The vertical lines show the lower (2700 km²) and upper (13,262 km²) 95% confidence intervals of the expected minimum area requirement for mammals.

Results

The historical species-area relationship was $S = 1.3223A^{0.0086}$. The intercept ($p = 0.0001$), but not the slope ($p = 0.13$, $r^2 = 0.043$), was significantly different from zero (Fig. 2a). The species-area regression equation for the parks was $S = 3.966A^{0.20}$, and both the slope ($p = 0.0001$) and intercept ($p = 0.0001$, $r^2 = 0.93$) were significantly different from zero (Fig. 2a).

The minimum area requirement estimated from the intersection of the two regression lines was 5037 km² (95% CI: 2700–13,296 km²) (Fig. 2). The bias between the mean of the bootstrapped estimates (5,140 km²) and the intersection estimate was small (103 km², or 2%). The mean minimum area requirement represented 0.29% (95% CI: 0.15–0.75%) of the total area of the Alleghenian-Illinoian mammal province (1,761,825 km², excluding the area of the Great Lakes).

We identified 3169 individual reserves throughout the Alleghenian-Illinoian mammal province. We were unable to determine the area of 548 of these reserves, leaving a total sample of 2621 individual reserves. Of these, 363 were combined into 97 reserve assemblages consisting of between 2 and 45 individual reserves, leaving 2355 reserves and reserve assemblages of 178,542 km², or 10.13% of the Alleghenian-Illinoian mammal province. These reserves and reserve assemblages ranged in size from 0.002 to 24,300 km², with a mean of 68.1 km² (Fig. 3).

Fourteen reserves and reserve assemblages were larger than 2700 km², 8 were larger than 5037 km², and 3 were larger than 13,296 km² (Table 1). These 14 reserves totaled 129,841 km², 73% of the total area of all reserves (Fig. 4). Three other reserves and reserve assemblages were less than 600 km² smaller than the lower confidence interval of the minimum area requirement (Table 1). The next largest reserve was only 1628 km².

Discussion

We estimated the mean minimum area requirement to conserve the historical assemblage of mammals in the Alleghenian-Illinoian mammal province at 5037 km², but reserves as small as 2700 km² may not experience species losses. Candidate reserves in this range have greater conservation value for mammals and should receive greater consideration for inclusion in reserve systems. Fourteen reserves out of 2355 are larger than 2700 km² and appear capable of maintaining their historical mammal fauna, even in the event of insularization. These reserves repre-

sent only 0.5% of those we identified, but they account for 72% of the total area of reserves. Our analysis suggests that species absent from these reserves were likely extirpated by forces other than insularization and that species may persist in these reserves if they are reintroduced and adequately protected.

A majority of the reserves in the Alleghenian-Illinoian mammal province are smaller than our estimate of the minimum area requirement and may conserve only a fraction of their historical mammal fauna in the absence of active management of habitat or populations. In most parts of the mammal province, it is unlikely that many reserves can be enlarged to meet the minimum area requirement given current land use and ownership. Creation of corridors and buffer zones to connect individual reserves below the minimum area requirement into reserve assemblages of a total area greater than the minimum area requirement may be the most efficient use of these strategies to aid mammal conservation (but see Hobbs 1992). Along the northern edge of the mammal province, many reserves are not isolated. In these areas, management directed toward enlarging reserves above the minimum area requirement or toward managing land-use activities outside reserves so that isolation of the reserve does not occur may have the greatest positive effect on mammal conservation.

There are assumptions inherent in our estimation of the minimum area requirement, and the accuracy of our results relies on the validity of these assumptions. The most important assumption is that the numbers of species present in the Canadian parks are at equilibrium at the present park sizes, particularly in the three largest
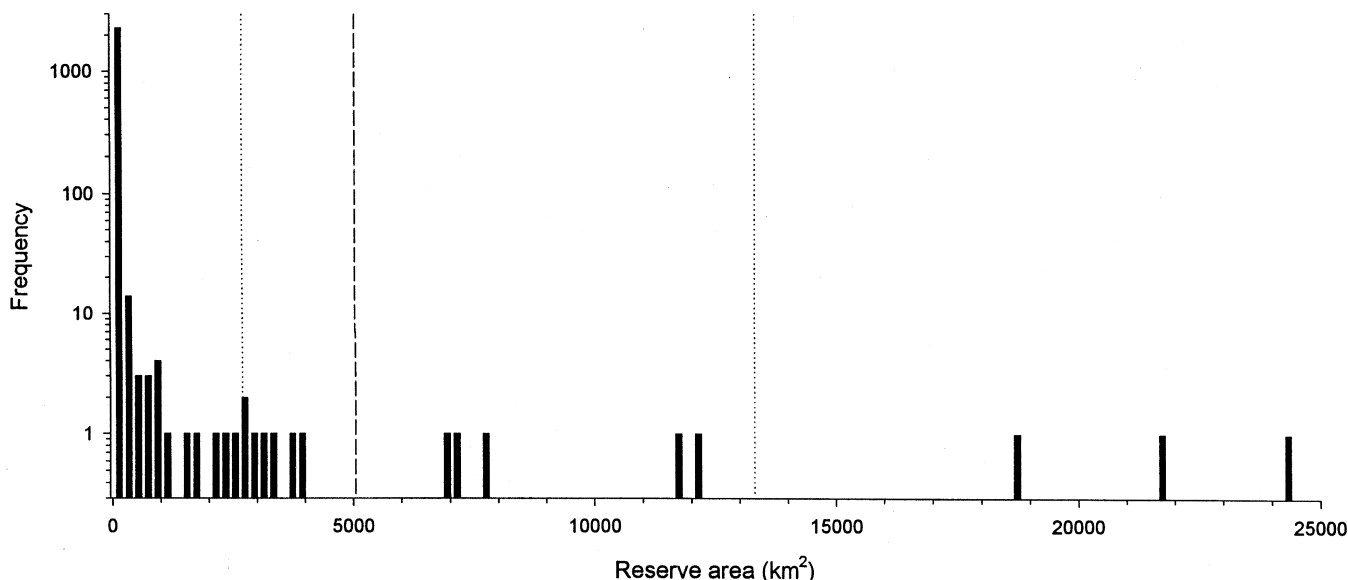

Figure 3. The size-frequency distribution of 2355 reserves and reserve assemblages in the Alleghenian-Illinoian mammal province of eastern North America. The expected minimum area required to conserve terrestrial mammals (dashed line) and the 95% confidence intervals (dotted lines) are indicated.

Table 1. The 17 largest reserves and reserve assemblages in the Alleghenian-Illinoian mammal province.[a]

Location (province/state)	No. of reserves[b]	Name	Area (km²)
Québec	2	La Mauricie National Park assemblage	2,110.00
Minnesota	3	Agassiz National Wildlife Refuge assemblage	2,579.87[c]
New York	1	Catskills State Park	2,632.50
Manitoba	1	Whiteshell Provincial Park	2,737.15[c]
Manitoba	1	Riding Mountain National Park	2,978.00
New York, Pennsylvania	10	Allegheny National Forest assemblage	3,002.56[c]
New Hampshire, Maine	7	White Mountain National Forest assemblage	3,288.56[d]
Québec	5	Chic-chocs Provincial Wildlife Reserve assemblage	3,713.20
Wisconsin	3	Cheauamegon National Forest assemblage	4,758.75[e]
Michigan, Wisconsin	6	Ottawa National Forest assemblage	6,990.5[c]
Pennsylvania	45	Sproul State Forest assemblage	7,085.08[f]
Ontario	1	Algonquin Provincial Park	7,725.00
Michigan	7	Hiawatha National Forest assemblage	11,790.53[d]
Michigan	8	Manistee National Forest assemblage	12,154.58[d]
Kentucky, North Carolina, Tennessee, Virginia, West Virginia	21	George Washington and Jefferson National Forest assemblage	18,603.57[d]
Ontario, Minnesota	14	Quetico Provincial Park–Superior National Forest assemblage	21,624.28[c]
New York	1	Adirondack State Park	24,300.00[g]

[a] *The area of Richard J. Dorer State Forest in Minnesota was unavailable. This forest, combined with adjacent reserves, may be larger than 2700 km².*
[b] *Reserve assemblages are composed of adjacent reserves.*
[c] *Some adjacent reserves are not included. Reserve area is underestimated.*
[d] *Some reserves consist of separate tracts, and some adjacent reserves are not included. Contiguous reserve area is overestimated but is larger than 2700 km².*
[e] *Some reserves consist of separate tracts. Contiguous reserve area is overestimated but is larger than 2700 km².*
[f] *Sproul State Forest assemblage consists of many similarly sized tracts of land, each of which may be substantially smaller than the total area of the assemblage.*
[g] *Private and public property.*

parks, which will otherwise anchor the upper end of the species-area relationship. The effect of future loss of species would be to move our estimated minimum area requirement further to the right, so we caution that our estimated minimum area requirement may be too low.

Biotas that are not in equilibrium are likely (1) if the parks are not isolated and immigration maintains more species than the park area can support independently (Brown & Kodric-Brown 1977), or (2) if the parks are isolated but the extirpation rate is slow, such that the
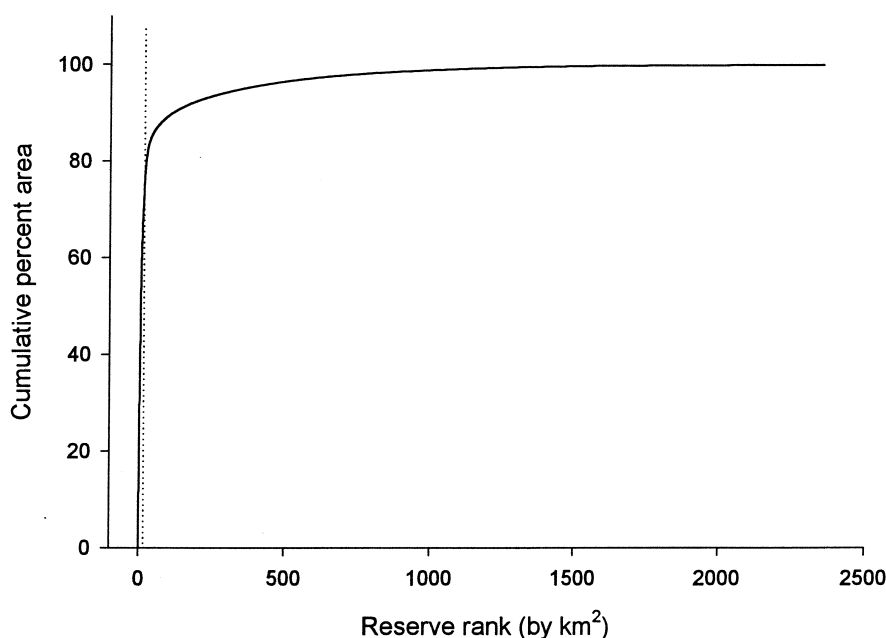

Figure 4. Cumulative percent area of 2355 reserves and reserve assemblages in the Alleghenian-Illinoian mammal province of eastern North America. The 14 reserves to the left of the dotted vertical line are larger than the lower 95% confidence interval of the minimum area requirement for mammals (2700 km²).

parks will continue to lose species in the future. For example, two of the largest parks, Algonquin and Quetico, are located in landscapes that consist primarily of forest. This forest matrix likely supports many, if not all, the disturbance-intolerant species, and individuals can still move into and out of these parks. Riding Mountain National Park is surrounded by an agricultural landscape, however, and contains as many species as expected based on the historical range data (Fig. 2a).

Few data or theories predict, a priori, extirpation rates for mammalian fauna following the relatively abrupt isolation of parks compared to land-bridge islands. Soulé et al. (1979) calculated that it would take 500 years for the number of large mammal species in East African reserves to reach equilibrium, but the 95% simultaneous prediction intervals spanned orders of magnitude (Boecklen & Gotelli 1984). Current methods still require extrapolation of species richness estimates taken over time (Brooks et al. 1999), which are not available for the Canadian parks. Other critical information, such as when a park became isolated from immigration of species is also unknown, may vary between species, and is not necessarily related to the time at which a park was established. Future research is required to determine if the number of species present in the parks has stabilized and which species continue to maintain immigration into the parks.

In the face of an uncertain future and potential losses of species in parks that have not become completely isolated, the value of our results lies, perhaps, not so much in their interpretation as to the minimum area above which mammals will be conserved, but as a minimum below which we suspect mammal species will almost certainly be lost. On the other hand, the confidence intervals around our estimate of the minimum area requirement are wide, so it may be that future changes in species richness would not substantially change our estimate.

We assume also that the loss of species from the parks is due to the effects of insularization. This is unlikely to be true for all species in all parks. For example, southern flying squirrels (*Glaucomys volans*) were reintroduced to Point Pelee National Park in 1992 (Adams 1995) and are still present. The extirpation of the squirrels was apparently due to habitat modification and pest management to benefit migratory birds. Predator-control programs have been carried out in Canadian national parks (Dunlap 1991) and may have contributed to the extirpation of some species from parks. Loss of species due to other factors will result in the "true" park regression lying above our estimate and an overestimation of the minimum area requirement. Although erring on the side of caution (against species' losses) may not have detrimental effects on the individual performance of future reserves, it could result in an inefficient distribution of resources for conservation.

We made no attempt to categorize reserves based on other anthropogenic influences such as timber extraction, hunting, mining, or forest-fire management. We did not consider these activities to be fundamentally inconsistent with mammal conservation, although they may, if poorly managed, influence the persistence of mammals in reserves (e.g., Woodroffe & Ginsberg 1998; Rivard et al. 2000). Many of these activities occur in the Canadian parks, so to some extent their effects are included in our data.

By calculating the minimum area requirement in the northern portion of the Alleghenian-Illinoian mammal province and comparing this estimate to the size distribution of reserves throughout the mammal province, we assumed that the mammal province is faunistically homogeneous. Seven species of disturbance-intolerant mammals (one lagomorph, four rodents, and two chiropterans) do not occur in the Canadian portion of the Alleghenian-Illinoian mammal province. We doubt that any of these species have a minimum area requirement larger than 2700 km^2, so it is unlikely that this omission affects the validity of our contrast between the sizes of existing reserves and our estimate of the minimum area requirement.

There is little evidence that the apparent loss of species from the Canadian parks is an artifact of inherent biases between the park and the historical range data. Biases may occur because species lists for parks tend to be minimum estimates of richness because species are likely to have been missed, whereas range data may overestimate local species richness because species are not ubiquitous throughout their range (Van Riper & Quinn 1988; Robinson & Quinn 1992). If our results were due to such an artifact, species loss would be pervasive in all parks, but Gurd and Nudds (1999) found that only 20 of 72 parks contained fewer species than expected historically, and 9 of these were located in the highly modified Alleghenian-Illinoian mammal province.

Any estimate of a minimum area requirement is likely to prove controversial, but confidence is increased if different methods produce similar estimates. Burkey (1995), based on data from Newmark (1987), estimated that large-mammal extinctions from national parks in western North America would be zero for parks of 12,000 km^2 or larger. Beier (1993) modeled cougar (*Felis concolor*) population dynamics and estimated that there was very low extinction risk over 100 years for areas of 2200 km^2 and larger. Shaffer and Samson (1985) estimated the minimum area requirement for grizzly bears (*Ursus arctos*) to be between 1,000 and 13,500 km^2. Schonewald-Cox et al. (1988) empirically estimated the minimum area required to conserve gray wolves (*Canis lupus*) for an undetermined amount of time at 1080 km^2. Wolves that colonized Isle Royale (544 km^2) in the late 1940s may not persist due to low population size and high demographic stocasticity (Peterson 1999). Our data indicate that wolves have not persisted in parks smaller than 950 km^2. These independent estimates of the minimum area requirement for some large mammals generally fall in the range of our estimate, 2,700–13,262 km^2.

Reserves that are large enough to support their complement of historical species are a benefit to reserve systems beyond their conservation value. As ecological controls with which test for the effects of human activities, large reserves can play a role in directing future management (Arcese & Sinclair 1997; Huff & Varley 1999; Peterson 1999; Porter & Underwood 1999; Wright 1999). As controls, large reserves should be as free from anthropogenic effects as possible and should maintain as many ecological processes as possible. Maintenance of a complete biota is an important step toward ensuring that the full diversity of trophic dynamics is present in reserves.

Acknowledgments

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