

Use of Estimated “Pristine” Species-Area Relations as Null Models For Evaluating Size and Integrity Standards for Protected Areas: An Update

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Abstract

Sizes and locations of protected areas often have been based on convenience and/or compromise with competing land-uses. Increasingly, protected area networks are required to conserve species diversity efficiently and to serve as ecological benchmarks against which to judge effects of anthropic disturbances. Yet, it is difficult to judge how large an area is large enough to meet this objective. We improved on earlier analyses that used species-area relations as null models – to control for the effect of habitat size on species diversity – for estimating minimum reserve areas (MRAs) for interior forest songbirds in woodlots and mammals in provincial and national parks. MRA is defined as the size of a protected area above which species richness is not distinguishable from that in non-fragmented habitat of the same size. Early null models violated statistical assumptions of independence because they were constructed by sequentially sampling species richness in nested plots of increasing area. Further, the forms of the models were assumed to be the same over all sizes of area, and were thus used to extrapolate expected species richness for areas much smaller than those used to generate the model. New null models for songbirds had steeper slopes and lower intercepts than previous models; for mammals, the reverse was true. Thus, earlier tests for faunal collapse in habitat fragments for birds were liberal and the estimate of MRA was conservative; the reverse was true for mammals. Nevertheless, the estimated MRAs were robust, if only due to the wide confidence intervals on the new estimates. For forest interior birds, the MRA was 55 hectares (95% CI: 22-138). This was 22% smaller than the 70 hectares estimated previously. Earlier analyses tended to overestimate the number of species locally extinct in fragments smaller than this. For mammals, estimated MRA was 505,800 hectares (95% CI: 272,500-1,190,400). Earlier analyses tended to underestimate the number of mammal species locally extinct in parks below this threshold.

Introduction

Sizes and locations of protected areas, like provincial and national parks, often have been based on convenience and/or compromise with competing land-uses (Pressey et al., 1993). Sometimes parks were designated “by default”, such as those with high topographic relief like Riding Mountain National Park and Turtle Mountain, Moose Mountain and Duck Mountain Provincial Parks and those unsuitable for agriculture in the prairies like Cypress Hills Provincial Park. These parks appear nevertheless to conserve intact, indigenous mammal faunas (Glenn and Nudds 1989). Still other parks, especially in heavily-settled regions like

southern Ontario (Glenn and Nudds 1989), and perhaps in other areas (Newmark, 1987, but see Van Riper and Quinn 1988), appear to have lost significant fractions of their initial mammal fauna in direct proportion to their sizes. The smaller the park, the greater the loss of species. Though the application of island biogeographic theory (MacArthur and Wilson, 1963) to reserve design has, in some respects, been controversial (e.g., Margules et al., 1982; Zimmerman and Bierregaard, 1986), this latter observation is entirely consistent with its predictions (Nudds, 1993).

Increasingly, protected area networks are required to conserve species diversity efficiently (Leader-Williams et al., 1990; Noss and Cooperrider, 1994; Pressey et al., 1993) and to serve as ecological baselines – i.e., intact and functioning natural areas – against which to gauge the effects of anthropocentric disturbance elsewhere (Nudds, 1998; Sinclair, 1983; Arcese and Sinclair, 1997). Yet, it is difficult to judge the adequacy of existing and proposed protected areas with respect to fulfilling these roles. This is because, though much research has gone into questions about representation in reserve systems, considerably less has addressed the thornier and perhaps more important issue of how big a protected area must be to enable what is represented to persist.

The research that has addressed this issue often comprises estimates of minimum dynamic, or minimum critical, areas based on population viability projections, or minimum viable population estimates (e.g., Wilcox, 1984; Nunney and Campbell, 1993) for individual rare, endangered, or 'flagship' species. If that single species happens also to be an 'umbrella species' – i.e., one whose viability in an area is considered to indicate that many others will also persist (Hager, 1997) – then an area deemed large enough to conserve it might be large enough to consider intact. This approach is controversial (Hager, 1997; Simberloff, 1997), however. For example, in Algonquin Provincial Park, a putative 'umbrella species' – timber wolves (*Canis lupus*) – and their associated mammal fauna appear to do quite well (Glenn and Nudds, 1989). But, Algonquin was once extremely altered by anthropic disturbance and is still exploited by forestry that might nevertheless have local-scale effects on other flora and fauna.

A different approach, not without its own controversial aspects, involves instead estimating the minimum size of a protected area above which any effects of area on the number of species in it are not detectable relative to an intact area the same size in a non-fragmented landscape (Nudds, 1993). This is referred to as the minimum reserve area (MRA) in order to distinguish it from other kinds of estimates of minimum areas. Estimating this area requires an appropriate 'null model' for the effect of area reduction and/or isolation of a protected area on the number of species in it – i.e., faunal collapse. For this purpose, we have used the species-area relation, referred to by Schoener (1976) as probably the closest thing to a 'law' in ecology.

The choice of an appropriate species-area relation to use as a standard for comparison is tricky. The parameters of such relations (i.e., the slopes and intercepts of plots of numbers of species against area) vary considerably by taxa, with scale (i.e., over areas from as small as 0.001 m² to whole continents), and geography (McLaughlin, 1997; McLaughlin and Nudds, in review). However, given an appropriate scale and taxon, species-area relations are robust null models for testing for faunal collapse (Glenn and Nudds, 1989; Schmiegelow,

1990, 1992; Gurd and Nudds, in review; Henschel, 1998; McLaughlin, 1998) and thus for estimating MRAs (Nudds, 1993; Gurd et al., in review; Henschel, 1998). Until recently, we were familiar with just three systems where this approach had been applied: plants at very small spatial scales (Cowling and Bond, 1991), mammals in Canadian provincial and national parks (Glenn and Nudds, 1989) and songbirds in woodlots in southern Ontario (Schmiegelow, 1990).

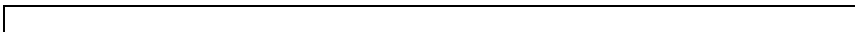
Each of these last two studies made novel use of large, existing databases to try to test rigorously for faunal collapse in natural habitat remnants. Nudds (1993) went further to infer from these studies the MRAs for each of the taxa. However, several aspects of these attempts required improvement before we could be confident that estimates of MRA were robust. Here we report on and synthesize recent studies (Gurd and Nudds, in review; Gurd et al., in review; Henschel 1998) in this regard.

Mammals in Parks

Glenn and Nudds (1989) constructed 'null' species-area curves, for the effects of isolation and area reduction on the numbers of species of mammals in provincial and national parks, using historical maps of species' ranges from the period prior to widespread landscape alteration by European settlement. However, species' distributions from these maps were removed by using a very coarse system of 100 x 100 km grid squares. Thus, the smallest area in which mammal species richness was estimated was 10,000 km² – much larger than many of the parks for which they had current estimates of numbers of mammal species. Glenn and Nudds assumed that the form of the relation was the same over all areas and extrapolated their null curve to the lower range of park sizes in order to compare the slopes and intercepts of their null model with that from the parks (Figure 1).

Further, the null curve was constructed by sampling sequentially larger aggregations of 1,000 km² plots, but mammal species counted in sequentially larger areas were added to totals from smaller areas nested within the larger areas. This presented two potential problems. First, the procedure violated assumptions of statistical independence and what effect this had on the estimates of slopes and intercepts of the null models was unknown. Second, the procedure resulted in inflated error degrees of freedom and biased the confidence intervals on the null model to being too narrow. Finally, Nudds (1993) did nothing more elaborate than to 'eyeball', very conservatively, the MRA as the intersection of the lower 95% confidence interval on the null model with the regression line for the parks.

Gurd and Nudds (in review) and Gurd et al. (in review) instead used finer grid resolution (10 x 10 km) and non-nested sampling of the historical range maps to avoid the problems of extrapolation and statistical non-independence. Further, they estimated the point of intersection of the regressions, and the confidence interval around that point, by more sophisticated statistical methods. Their analyses resulted in qualitatively similar results to those of Glenn and Nudds (1989) with respect to the hypothesis that parks in the Alleghanian-Illinoian mammal provine had lost mammal species due to isolation and reductions in area.



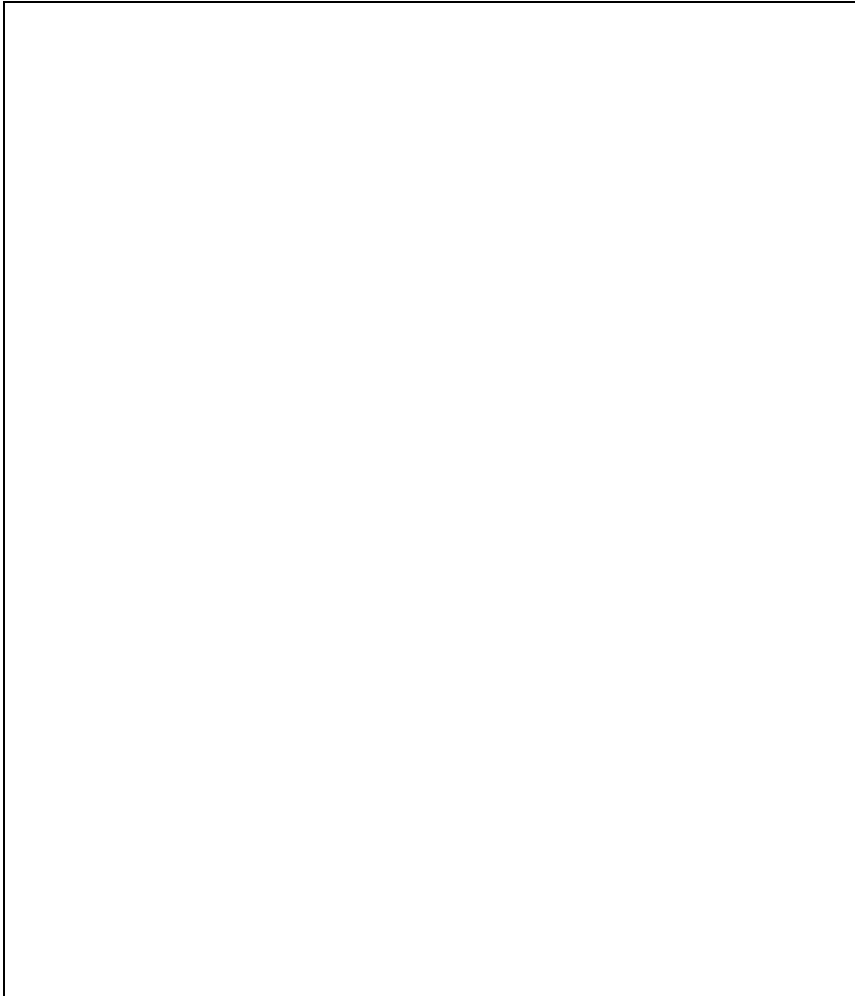


Figure 1. (Upper). The null species-area relation for mammals in the Alleghanian-Illinoian mammal province, estimated by sampling historical geographical range data (smallest sampling unit = 1,000 km²) and extrapolated to the sizes of provincial and national parks, with the species-area relation for parks. The smallest park is Point Pelee National Park and the largest is Algonquin provincial Park. The park curve appears to intersect the lower 95% confidence limit on the null model at about 100,000 ha. From Nudds (1993) after Glenn and Nudds (1989). (Lower) The null species-area relation for mammals estimated by sampling plots over the same size range as the parks (smallest sampling unit = 100 km²), with the species-area relation for parks. The curves intersect at 505,800 ha (95% CI: 272,500-1,190,400). From Gurd et al. (in review). Redrawn from Gurd and Nudds (in review).

However, the new null model was based on fewer, but independent, data points, and consequently had wider confidence intervals (Figure 1). Further, the slope was less steep and the intercept larger, on the null model, than that

estimated by Glenn and Nudds (1989).

Songbirds in Forest Fragments

Schmiegelow's (1990, 1992) approach to test for faunal collapse among songbirds in forest fragments in southwestern Ontario was analogous to that of Glenn and Nudds' (1989) for testing for faunal collapse among mammals in parks (Figure 2). Further, however, she had to use relatively recent bird atlas data, collected from an already fragmented landscape. She corrected for the effect of remaining forested area in the grid squares she sampled, but had to assume – reasonably – that, for the songbirds of interest, species presence/absence had not changed since before widespread European settlement in Ontario – though abundances of individual species quite likely had.

Henschel (1998) instead studied in a landscape in eastern Ontario where he could find forest fragments and large contiguous forest blocks in close geographic proximity. He constructed a null species-area relation with data from areas of various sizes within the contiguous forest, assuring also statistical independence and thereby avoiding extrapolation, and compared it to a similar curve for adjacent forest fragments (Figure 2). As in the case for mammals, the results of the two studies were qualitatively similar; in particular both found evidence consistent with the hypothesis that songbirds undergo faunal collapse in small forest fragments. However, the slope of Henschel's null model was less steep and the intercept lower than Schmiegelow's.

Conclusion

The potential severity of the shortcomings of Glenn and Nudds (1989) and Schmiegelow (1990) notwithstanding, these studies were still among the first to attempt to investigate faunal collapse in a rigorous fashion by making reference to a 'control' state, thereby also allowing for inferences about MRAs. Many early studies asserted that faunal collapse happened in remnant patches of natural habitat, but they were compromised by the absence of appropriate controls for the effect of area on floral and faunal diversity in the absence of fragmentation. The mere observation that fewer species reside in smaller patches of remnant habitat than in larger patches is not necessarily indicative of species loss from the smaller patches as a result of area reduction and/or isolation; small patches are expected to have fewer species anyway (Nudds, 1993). To test adequately for an effect of fragmentation on species diversity in remnant patches requires knowledge of the shape of the species-area relation that would be obtained in a non-fragmented landscape. For landscapes already fragmented, this isn't easy. Neither could many early studies – because of the absence of controls for the effect of area – be used to infer the MRA necessary to conserve natural species diversity in protected areas; in the absence of one of the species-area relations, it is not possible to estimate their intersection.



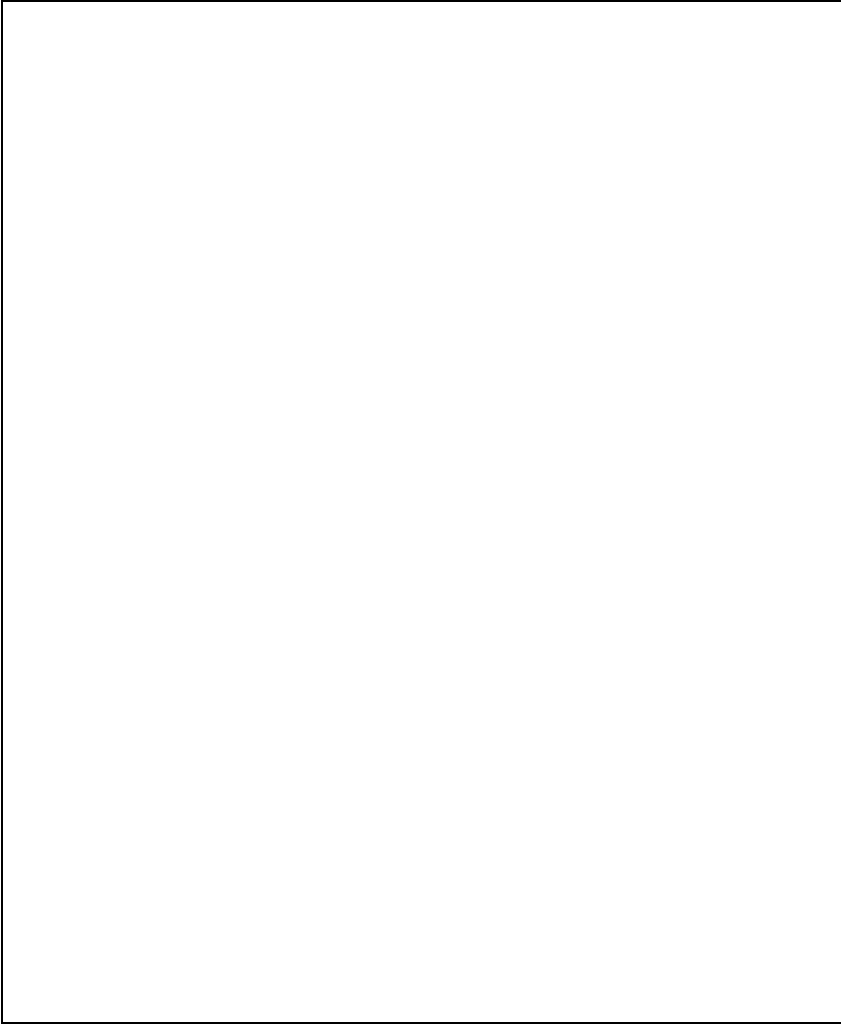


Figure 2. (Upper) The null species-area relation for forest songbirds (with 95% confidence limits) estimated by sampling from bird atlas data (smallest sampling unit = 100 km²) in southern Ontario and extrapolated to the size ranges of woodlots, with the species-area relation for forest songbirds in woodlots. The curves appear to intersect at about 70 ha. From Nudds (1993) after Schmiegelow (1990). (Lower) The null species-area relation for forest interior birds in contiguous forest in eastern Ontario, generated by sampling over the same range of plot sizes as the woodlot data, with the species-area relation for forest interior birds in woodlots. These curves intersect at 55 ha (95% CI: 22-138). From Henschel (1998).

Still, inability to estimate well the species-area relation to which habitat fragments could be compared created potential for Type I or II statistical errors with respect to the hypothesis that protected areas, or other natural habitat remnants, might nevertheless undergo faunal collapse (Schmiegelow, 1992). These errors, in

turn, have important ecological and economic implications for management (Schmiegelow, 1992). Schmiegelow's test for faunal collapse of songbirds in remnant patches of forest in southwestern Ontario was too liberal (i.e., biased to Type I error). Use of Henschel's (1998) null model resulted in a more conservative test of the hypothesis that songbirds experienced faunal collapse in eastern Ontario woodlots. That is, it was more difficult for Henschel to conclude, for a given small woodlot, that it contained fewer species than it would have if it were part of a contiguous forest landscape, than it was for Schmiegelow. On the other hand, use of Henschel's model resulted in a slightly more liberal estimate of the MRA (55 hectares) for forest interior birds. That is, Henschel estimated that a forest fragment could be slightly smaller than that inferred (70 hectares) by Nudds (1993) and still not contain fewer species than it would contain if it was part of a large, contiguous forest.

The opposite pattern obtained from the re-analysis of Glenn and Nudds'(1989) test for faunal collapse among mammals in parks. Gurd and Nudds (in review) concluded that Glenn and Nudds' test was biased to Type II error (too conservative) with respect to the hypothesis that small parks had undergone faunal collapse. That is, Glenn and Nudds had underestimated the extent to which mammals had gone locally extinct in small parks. Further, Nudds (1993) used a different, and much too liberal, definition of MRA than that used in subsequent analyses. He estimated the point at which the species-area relation for parks intersected the lower 95% CI on the regression for the null species-area relation to be approximately 100,000 hectares. Gurd et al. (in review) estimated the same point more rigorously at 169,000 hectares (95% CI: 43,000 - 745,000). Thus, even by that too-liberal standard, the new analysis indicates that a park large enough to contain the same number of mammal species that it would have had in a large, contiguous natural landscape would have to be larger than 100,000 hectares. If the intersection of the two regressions is instead used to estimate the MRA for mammals, then it is about five times larger, at 505,800 hectares (95% CI: 272,550 - 1,940,000) than that previously reported.

Despite re-analyses, MRAs for forest songbirds and mammals appear robust in the neighbourhoods of the old estimates, if only because the confidence intervals on the new estimates of MRAs are so wide as to include the old estimates. Nudds' (1993) earlier estimate of MRA for mammals converged on others in the literature derived from consideration of minimally viable populations of large carnivores (Schonewald-Cox et al., 1988 [108,000 hectares], Belovsky, 1987 [100,000 hectares]), seeming to lend some legitimacy to it. However, those analyses appear also to seriously underestimate the minimum area to conserve entire mammal faunas, whether or not they would be sufficient to conserve populations of individual species of mammal.

We reached the same general conclusions about the relative sizes of MRAs for forest birds and for mammals, namely, that the MRA for mammals was several orders of magnitude greater than for songbirds. This difference is largely attributable to differences in dispersal abilities between the taxa; birds are better able to overcome the effects of isolation and distance among protected areas, so species loss from small protected areas is better offset by colonization than it is for mammals (Schmiegelow and Nudds, 1987). This has led to the notion that mammals should be the target taxon for estimating minimum sizes for reserves, since protected areas large enough to contain an intact mammal fauna should

also be large enough to contain intact faunas of everything else. Plants, by this score, would be a very poor target taxon for planning reserve designs. They typically have very shallow species-area relations (e.g., Nudds et al., 1996). A protected area of minimum size to include all plant species is unlikely to include viable populations of many other kinds of organisms, though protected area networks based on plants may include a large fraction of species of other taxa (Hager, 1997; Hager and Nudds, in review).

In the five years since Nudds (1993) first reported on the numbers of Ontario's parks, in the regions corresponding to the Alleghanian-Illinoian mammal province, that met the MRAs for birds or mammals, a number of parks and conservation reserves have been added. 26 have been added (Ontario Ministry of Natural Resources, 1997), but only an existing park that was enlarged (Wabakimi Provincial Park, 892,061 hectares) exceeded the MRA for mammals. It is clear that there is virtually no opportunity to establish reserves that would meet the MRA for mammals in the south of the province. There, however, ecologically-justified reserve designs could still be based on MRAs for other flora or fauna, such as birds, with full acknowledgement that they could not be designed to conserve all of what was once naturally present.

However, in the Canadian shield region of Ontario, there is ample opportunity – indeed, there is a need in order to sustain a renewable resource industry there (Nudds et al., 1998) – to establish reserves large enough to satisfy the MRA for mammals. At this time, it is our best guess that this coarse-filter approach might result in reserves large enough to function as intact, ecological baseline controls against which to measure success at managing for sustained ecosystem function in the intervening matrix.

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