



Research article

Models to distinguish effects of landscape patterns and human population pressures associated with species loss in Canadian national parks

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Abstract

It is widely accepted that large protected areas are required to effectively conserve historical species composition. However, recent analyses of mammal species loss in Canadian and African national parks contradict earlier conclusions that extent of local extinctions (i.e., extirpations) is strongly inversely related to park size, suggesting that park size alone is inadequate to predict reserve designs that may sustain biodiversity. To plan protected areas that will meet conservation goals, reserve-design models that incorporate other landscape-scale factors in addition to reserve area are needed; potential factors include the types and intensity of land use and habitat change, together with land cover types, in and around parks. Additionally, human population size around parks, and visitor density in parks may affect species loss. We quantified land use, land cover, and human population in and around 24 Canadian national parks to model effects of human disturbance and changes in natural habitats on known mammal extirpations. Multiple regression models were compared using the Akaike Information Criterion (AIC_c). The most parsimonious model (AIC_c weighting $w_i = 0.5391$) emphasized effective habitat area in and around parks and not visitor numbers nor human population size around parks. Our model suggests that parks with as little as 3140 km² of effective habitat area inside may be large enough to conserve historical mammal species composition if they are also surrounded by at least 18 000 km² of effective habitat within 50 km of park boundaries.

Introduction

Island biogeography (MacArthur and Wilson 1967) has long provided a theoretical framework to study species losses in protected areas (Diamond 1975; Soulé, Wilcox and Holtby 1979; Glenn and Nudds 1989; Burkey 1995; Newmark 1995, 1996; Woodroffe and Ginsberg 1998; Gurd and Nudds 1999; Wiersma and Nudds 2001). In Canada, estimated species' distributions of terrestrial mammals prior to widespread European settlement (Banfield 1974) have been used as the reference state to which present-day species richness in parks has been compared. Glenn and Nudds (1989) originally classified mammals in Canada as either disturbance-sensitive or disturbance-tolerant based on their tolerance of human

disturbance and/or presence on human-altered landscapes (*sensu* Humphreys and Kitchener 1982). For example, species requiring large tracts of wilderness, such as grizzly bears (*Ursus arctos*) were classified as disturbance-sensitive, while those found near human settlements or in agricultural landscapes, such as coyote (*Canis latrans*) were classified as disturbance-tolerant. The work of Glenn and Nudds (1989) and subsequent studies in Canadian protected areas has shown that some parks do not contain their historical complement of species, and the reduction in the number of disturbance-sensitive mammal species, in particular, is more severe in national and provincial parks in the southeast region of the country, which is also the region most densely populated by humans (Glenn and Nudds 1989; Gurd and Nudds 1999;

Wiersma and Nudds 2001). A significant correlation between the difference in present and historical species richness of disturbance-sensitive mammals and park size ($r^2 = 0.83$, $p = 0.0001$) has been reported for these parks (Gurd and Nudds 1999). The minimum size for parks as habitat 'islands' in this part of the country – below which they will no longer contain their historical number of mammals – has been estimated to be 5037 km² (CI: 2700–13 000 km²; Gurd, Nudds and Rivard 2001).

However, in a further study that measured changes between historical and present-day *composition* of disturbance-sensitive mammals within 24 national parks, a much weaker correlation between park size and species losses in the southeastern parks was found ($r^2 = 0.15$, $p = 0.30$; Wiersma and Nudds 2001). Thus, while island biogeography theory has provided a useful framework for thinking about species losses from protected areas, the discrepancies between the studies of mammals in Canadian parks cited here illustrate that island biogeography theory alone may not be sufficient to explain extirpations from parks (see also Rivard et al. 2000).

Recent advances in the field of landscape ecology have provided other avenues for considering the effects of landscape pattern and change on ecological processes (Naveh and Lieberman 1984; Turner, Gardner and O'Neill 2001). Several studies suggest a relationship between landscape pattern and biodiversity, citing in particular the importance of patch size, connectivity, edge effects, and degree of heterogeneity in land cover types (Miller, Brooks and Croonquist 1997; Aauri and deLucio 2001). Other studies have illustrated the link between land use (i.e., human disturbance on the landscape) and landscape patterns (Wickham, O'Neill and Jones 2000; Hobson, Bayne and Van Wilgenburg 2002), showing that, in general, increased human use leads to increased habitat fragmentation, which in turn may affect species losses and/or the composition of species within a region (Wickham, O'Neill and Jones 2000; Coppedge et al. 2001; Wagner and Edwards 2001; Foster et al. 2002; Gu, Heikkilä and Hanski 2002). Landscape ecology has also been linked with metapopulation theory on both real (Virgos 2001; Gu, Heikkilä and Hanski 2002) and artificial (With and King 2001) landscapes to show the effects of habitat fragmentation on source-sink population dynamics. These studies suggested that increases in habitat fragmentation might decrease persistence time and/or re-colonization rates in habitat patches within a metapopulation.

In addition to considering landscape patterns and their effect on species composition in parks, recent studies have also suggested that human population size around small parks might contribute more importantly to extirpations than park size (and related aspects of landscape pattern caused by humans) *per se* (Brashares, Arcese and Sam 2001; Harcourt, Parks and Woodroffe 2001; Parks and Harcourt 2002). These authors relied on the relative weights of r^2 statistics from multivariate analyses to infer the relative importance of highly correlated, and therefore confounded, variables. Alternate statistical approaches, such as information criteria (Burnham and Anderson 1998), are available to better deal with potentially inter-correlated data to choose best explanatory models. Here, we develop a model-based approach to assess the relative contributions of landscape pattern (i.e., land use and land cover) and human population size in and around 24 Canadian national parks to local extirpations, in an effort to move beyond simple island biogeography models to explain loss of mammals from protected areas. This research builds on past research on the effects of size and habitat alteration on species losses in Canadian national parks (Rivard et al. 2000; Gurd, Nudds and Rivard 2001) but uses improved Geographic Information Systems (GIS) capabilities to develop new methods for quantifying landscape patterns together with more detailed human use data to further refine our understanding of factors affecting species loss from parks.

Methods

The parks

To minimize the effect of a wide range of variables correlated with latitude (Rivard et al. 2000), we analyzed only parks ($n = 24$) south of the 60th parallel (with the exception of the recently-established Wapusk National Park on Hudson's Bay due to insufficient data on current species composition; Figure 1, Appendix 1); and we excluded parks composed of island archipelagos.

Species changes

'Species loss' for each park was the difference between historical species composition of disturbance-sensitive mammals in an area at the same site, the same size, and the same shape as a present-day park, and the current composition of disturbance-



Figure 1. The national park of Canada. Parks studied are shaded in black ($n = 24$). Parks are labeled with the four-letter code in Appendix 1.

sensitive mammals in that park (as reported in Wiersma and Nudds 2001). 'Net change' was the simple difference between current richness and historical richness of disturbance-sensitive species (synonymous with "species losses" as reported by Gurd and Nudds 1999). Models were also built to explain 'carnivore loss' and the 'appearances of disturbance tolerant species' (reported in Wiersma and Nudds 2001). We expected, as carnivores are considered a sensitive subset of disturbance-sensitive mammals, that the model predicting 'carnivore loss' would parallel that for disturbance-sensitive mammals, whereas we expected, in general, that factors that most affected losses of disturbance-sensitive species would be those

that most affected gains in disturbance-tolerant species (Foster et al. 2002).

Newmark (1995), and Rivard et al. (2000) measured extirpations since park establishment, and subsequent analyses to evaluate the relative contribution of landscape change vs. human density (Parks and Harcourt 2002) used this measure of extinction. This may not be the appropriate historical reference state. Although there are challenges to using historical data as a benchmark against which to measure change (e.g., Aplet and Keeton 1999), it is clear that by the time that many parks were created in the early to mid 20th century, landscapes in and around them had already undergone considerable change in habitat and human use prior to establishment. Thus, consist-

ent with Glenn and Nudds (1989), Gurd and Nudds (1999), and Wiersma and Nudds (2001), we preferred to measure faunal changes from before the time of park establishment.

Measuring land use

Land use was quantified by measuring the amount of human disturbance (human built infrastructure) within and surrounding parks using National Topographic Series (NTS) digital maps (scale 1:250 000). Maps were edited in ArcView™ (ESRI, version 3.2, Redlands, CA) to select human-built features (roads, trails, campgrounds, etc.), which were then exported to ArcInfo™ (ESRI, version 8.1, Redlands, CA) for analysis. In addition, a zone 50 km wide around each park was created in ArcView to represent the “study area” around the park in which landscape characteristics were measured; large bodies of water (such as oceans and the Great Lakes) located within this buffer area were excluded from the analysis.

Rivard et al. (2000) measured land use characteristics within 10 km and 100 km zones outside of park boundaries, and found that these were significantly correlated with land use characteristics within parks (Table 3 in Rivard et al. 2000). Although we measured different land use characteristics than did Rivard et al. (2000), we were reasonably sure that we would see a similar pattern of correlations, and thus we chose not to measure landscape characteristics at varying distances from park boundaries, as we felt this data would be redundant.

We chose a distance of 50 km for measurement of landscape characteristics outside of the parks, as we felt it best represented a distance from park boundaries within which it was practical to implement regional landscape management. Parks Canada has called for individual parks to manage within the context of greater park ecosystems (Canadian Heritage 1994) and has supplied a resource survey approach for defining greater park ecoregion boundaries based on abiotic, biotic and cultural features, known as the “ABC Approach” (Grigoriew et al. 1985). Even so, Zorn et al. (2001) examined ecosystem management programs in national parks in the province of Ontario, and concluded that greater park ecosystem boundaries were difficult to identify, and that the parks varied in their definitions of areas of cooperation. For example, Pukaskwa National Park followed the ABC approach in delineating their greater ecosystem boundaries, based largely on watersheds of influence,

geological patterns, and surrounding forestry activities (Skibicki 1995). The resulting greater park ecosystem was defined to be 8000–15 000 km² in size (Geomatix International 1996), which translates to a radius of approximately 45–65 km from the park boundary. Conversely, Georgian Bay Islands National Park defined its greater park ecosystem based on consultation with neighboring land managers (Walton 1998). The resulting greater ecosystem is largely confined to the Severn Sound watershed, and radiates approximately 30–50 km from the park boundary (Figure 1 in Walton 1998). Thus, while a study area outside the park defined by a 50 km distance may be somewhat arbitrary, we believe that the results of our analysis, and subsequent management implications, would not change substantially if another distance less than 100 km from the park boundary were chosen to define the study area.

We conducted an analysis of human-built infrastructure by calculating the “footprint” of human-built features within and outside each park. Instead of measuring total road length, which has been used as an index of landscape fragmentation (e.g., Rivard et al. 2000), we incorporated each feature’s proximal impact on the landscape (Forman 2003) by creating buffer widths in ArcInfo. Buffer widths represent the presumed effects of roads beyond the physical space that they occupy, and were determined using the “avoidance distances” of various mammals from Jalkotzy, Ross and Nasserden (1997). We selected values from Jalkotzy, Ross and Nasserden (1997) for species missing from parks, based on the comparison of historical mammal composition with present-day species data for each park (Wiersma and Nudds 2001). The median road avoidance distance for the disturbance-sensitive mammals observed to have gone missing from parks was 200 m for highways, and 100 m for paved roads (Jalkotzy, Ross and Nasserden 1997). Highways were defined as paved, multi-lane, primary highways. We assigned buffer widths of 50 m to limited-use gravel roads and 25 m to foot and horse trails (Jalkotzy, Ross and Nasserden 1997). The avoidance value for trails is consistent with values published elsewhere (Cole 1987). Railways are thought to have effects similar to low to medium-use roads (Jalkotzy, Ross and Nasserden 1997) and were assigned a buffer width of 100 m. Powerline corridors were not assigned a buffer width as they have not been shown to be barriers even to small mammals such as white-footed mice (*Peromyscus leucopus*) and short-tailed shrews (*Blarina brevicauda*) (Schreiber and Graves 1977).

Table 1. Pearson correlation coefficients for landscape and human population data used in the analysis. Data are log-transformed. *p*-values are indicated in parenthesis.

	Effective habitat area out	Visitors	Population
Effective habitat area in	0.410 (0.04)	-0.202 (0.34)	-0.295 (0.16)
Effective habitat area out		0.280 (0.18)	-0.283 (0.18)
Visitors			0.471 (0.02)

Buffered linear features were combined with area features such as built-up areas (town sites), campgrounds and golf courses. The cumulative “footprint” was then subtracted from the total area of the park to determine the “effective area” of the park. Similarly “footprints” of features outside the park were created and subtracted from the total area within 50 km of the park boundary.

Measuring land cover

The type and amounts of habitat inside and outside parks was measured using AVHRR (Advanced Very High Resolution Radiometry) satellite imagery with a pixel resolution of 1 km² in 13 different classes at a scale of 1:2 000 000. For each park, the area of each of the land cover types within the park, and within 50 km of each park boundary was measured using ArcInfo. The area of non-habitat was calculated by summing the total area of the land cover classes for bare rock, ice and snow, agricultural cropland, agricultural rangeland, and large bodies of water. We excluded urbanized land from our “non-habitat” category and accounted for it, instead, in the analysis of human disturbance using the larger-scale (more detailed) NTS maps. For each park, the “non-habitat” values were subtracted, respectively, from the total area of the park, and the total area within 50 km of the park boundary, to determine the “habitat area” inside and outside the park.

There exist a myriad of landscape indices to measure landscape pattern and habitat fragmentation (see summary in chapter 5 of Turner, Gardner and O’Neill 2001), many of which can be measured using advanced statistical packages (e.g., McGarigal and Marks 1995). Others have used more straightforward measures of landscape heterogeneity and fragmentation patterns. For example, Rivard et al. (2000) indexed fragmentation by counting the number and area of isolated polygons of natural cover within and outside of parks. Here, we measured the total area of habitat and non-habitat patches in and around parks;

we were less concerned about the particular configuration of the habitat, such as the extent of fragmentation. Fahrig (1997), for example, showed that the amount of habitat lost may be more important than the degree of fragmentation in determining how well species can disperse in a landscape; others (Malanson and Cramer 1995; Keitt, Urban and Milne 1997; With, Gardner and Turner 1997; Ney-Nifle and Mangel 2000) have suggested that degree of connectivity is difficult to assess in any case, because of complications of scale and variation in the dispersal ability of species.

Once we had analyzed land use and land cover to create maps of the “effective area” and “habitat area” respectively in and around each of the parks, we overlaid these to get maps of overall “effective habitat area” in and around parks, which was the measurement used in subsequent model building.

Human impact

We used data from Parks Canada about visitor density in parks (Canadian Heritage 1998). Outside of parks, we identified all population centers in the 50 km zone on NTS maps. The populations of these communities were taken from the most recent census data (1995) from the Statistics Canada Community Profiles database (www.statcan.ca) and summed to index the size of the human population in the region outside the park.

Model building

Previous studies about the effects of park size and surrounding human population have demonstrated that many of the features measured were highly correlated with each other, and inferred the magnitude of particular effects from r^2 values (Rivard et al. 2000; Parks and Harcourt 2002). Instead, to improve inferences about the relative contributions of land use, land cover, and human impact to species changes when these may be correlated, we built regression models in SAS (SAS Institute, Inc., version 8.2, Carey, NC) using the GENMOD procedure and evaluated them using Akaike’s

Table 2. Log-likelihood and Akaike Information Criterion (AIC_c ; Burnham and Anderson 1998) for the six best regression models for loss of disturbance-sensitive mammals in 24 Canadian national parks. K equals the number of parameters plus an intercept and error term. Δ_i values < 2 are considered credible best models. Weights (w_i) are a measure of the weight of evidence in favour of that particular model over all others. EH in: effective habitat area within a park; EH out: effective habitat area in a 50 km radius outside of the park boundary; visitors: number of visitors per year in a park; population: human population size in a 50 km radius outside of the park. Variables are log-transformed.

Model	Variables	Log-likelihood	K	AIC_c	Δ_i	w_i	r^2	p
6	EH in; EH out	-42.997	4	96.10	0.00	0.5391	0.65	<0.0001
2	EH in; visitors; EH out	-42.248	5	97.83	1.73	0.2270	0.67	<0.0001
4	EH in; EH out; population	-42.781	5	98.90	2.80	0.1332	0.66	<0.0001
1	Global model	-42.247	6	101.44	5.34	0.0374	0.67	<0.0001
8	EH in, visitors	-46.329	4	102.76	6.66	0.0193	0.54	<0.001
13	EH out	-47.864	3	102.93	6.83	0.0177	0.48	<0.001

Information Criterion (AIC; Burnham and Anderson 1998). Variables were first log-transformed to achieve normality. Data are not highly correlated (Table 1), increasing our confidence in the ability of the AIC selection to discriminate between models, without being confounded by highly inter-correlated predictor variables. Although landscape features can often show nonlinear relationships, an examination of our landscape data plotted against species changes suggested that they were robust to linear models. We constructed a global model with all four predictor variables (effective habitat area in parks; number of visitors in parks; effective habitat area outside parks; and human population outside parks) and then systematically evaluated all possible combinations of models with fewer than four predictor variables for each of the four species change variables (loss in disturbance-sensitive species, loss of carnivore species, net change in disturbance-sensitive species, and the number of appearances of disturbance-tolerant species). The residuals for each model were assessed for goodness-of-fit for normal distribution using a Kolmogorov–Smirnov goodness-of-fit test (Zar 1999). Because of the relatively low ratio of sample size to model parameters ($n/K = 24/4$ predictor variables, plus the error term, plus the intercept), we modified for small sample sizes (AIC_c ; Burnham and Anderson 1998). The goal of the model building was to identify the most parsimonious model explaining each of the four types of species changes. The lowest AIC_c value indicates the model that achieves the best tradeoff between variance and bias of the resulting parameter estimates.

In addition to calculating AIC_c values, Akaike weights (w_i) were calculated (Burnham and Anderson

1998). Weights sum to 1 and provide a measure of the weight of evidence in favour of one model over the others (White 2001). Parameter weights ($\sum w_i$ for all i models in which a given parameter appears) give the relative weights of each parameter within the range of models considered. We also calculated Δ_i , as the difference between the AIC_c for the i^{th} model in the set and the minimum AIC_c . Delta values can be used to gauge the relative plausibility of each model. Models with $\Delta_i < 2$ are strongly supported by the data. Models with $\Delta_i = 2-4$ are somewhat supported, and those with $\Delta_i > 7$ are weakly supported by the data (Burnham and Anderson 1998).

Results

Here we follow the protocols of Anderson et al. (2001) on the presentation of analyses that involve model selection. All best models exhibited good fit using Kolmogorov–Smirnov tests ($p > 0.15$). The best model for each measure of species change included different parameters; however there were some consistencies between the four sets of models. The predictor variables for either the amount of effective habitat inside or the amount of effective habitat outside of parks appears in each of the top six models for species losses (Tables 2–4) and in four of the best six models for the appearance of disturbance-tolerant species (Table 5). These habitat variables were included together in four of the best six models for loss of disturbance-sensitive mammals (Table 2) and the loss of carnivores (Table 3), and two of the best six models for the net change in richness of disturbance-sensitive

Table 3. Log-likelihood and Akaike Information Criterion (AIC_c; Burnham and Anderson 1998) for the six best regression models for loss of carnivores in 24 Canadian national parks. *K* equals the number of parameters plus an intercept and error term. Δ_i values < 2 are considered credible best models. Weights (w_i) are a measure of the weight of evidence in favour of that particular model over all others. EH in: effective habitat area within a park; EH out: effective habitat area in a 50 km radius outside of the park boundary; visitors: number of visitors per year in a park; population: human population size in a 50 km radius outside of the park. Variables are log-transformed.

Model	Variables	Log-likelihood	<i>K</i>	AIC _c	Δ_i	w_i	r^2	<i>p</i>
2	EH in; visitors; EH out	-31.066	5	75.47	0.00	0.4650	0.75	<0.0001
6	EH in; EH out	-33.366	4	76.84	1.37	0.2342	0.70	<0.0001
1	Global model	-30.873	6	78.69	3.22	0.0929	0.76	<0.0001
13	EH out	-35.826	3	78.85	3.39	0.0855	0.63	<0.0001
4	EH in; EH out; population	-33.107	5	79.55	4.08	0.6040	0.71	<0.0001
9	Visitors; EH out	-35.357	4	80.82	5.35	0.0320	0.65	<0.0001

Table 4. Log-likelihood and Akaike Information Criterion (AIC_c; Burnham and Anderson 1998) for the six best regression models for the net change in species richness of disturbance-sensitive mammals from 24 Canadian national parks. *K* equals the number of parameters plus an intercept and error term. Δ_i values < 2 are considered credible best models. Weights (w_i) are a measure of the weight of evidence in favour of that particular model over all others. EH in: effective habitat area within a park; EH out: effective habitat area in a 50 km radius outside of the park boundary; visitors: number of visitors per year in a park; population: human population size in a 50 km radius outside of the park. Variables are log-transformed.

Model	Variables	Log-likelihood	<i>K</i>	AIC _c	Δ_i	w_i	r^2	<i>p</i>
8	EH in; visitors	-59.490	4	129.09	0.00	0.2034	0.28	0.03
13	EH out	-61.410	3	130.02	0.93	0.1481	0.16	0.06
15	EH in	-61.640	3	130.48	1.39	0.1296	0.14	0.07
6	EH in; EH out	-60.617	4	131.34	2.25	0.1124	0.21	0.08
2	EH in; visitors; EH out	-59.234	5	131.80	2.72	0.0983	0.30	0.07
9	Visitors; EH out	-60.889	4	131.88	2.80	0.0566	0.19	0.11

mammals (Table 4). Number of visitors appeared in three of each of the best six models for species loss (Tables 2–4), and in only one of the best six models to explain the increase in appearance of disturbance-tolerant species (Table 5). Population size in communities outside parks appeared in two of the best six models for loss of disturbance-sensitive mammals (Table 2) and the loss of carnivores (Table 3), and in three of the best six models for the appearance of disturbance-tolerant species (Table 5). It was not included in any of the best six models for net change in species richness of disturbance-sensitive mammals.

The r^2 values do not allow for rigorous discrimination between the competing models, as the majority of models show similar fits (Tables 2–5). Thus, the relative AIC values (Δ_i) and corresponding Akaike weights (w_i) allow for better discrimination between competing models. The most parsimonious models for loss of disturbance-sensitive species and carnivore loss included only the predictor variables for effective habitat area inside and outside of parks ($\Delta_i = 0.0$ and 1.37, respectively). This same model was some-

what adequate for net change in disturbance-sensitive species richness ($\Delta_i = 2.25$), considering the small sample size (Burnham and Anderson 1998). None of the models were particularly strong for net change in disturbance-sensitive species richness or the appearance of disturbance-tolerant species as Akaike weights were less than 0.2 for even the best models in each set, and Δ_i values did not indicate strong discrimination between models. Akaike parameter weights (w_i) suggest that, overall; the land use/land cover variables have higher weights of evidence than the human-use variables (visitor and population densities) (Table 6).

Parameter estimates show a negative relationship between predictor variables and species change variables in all cases, except net change in richness of disturbance-sensitive mammals (Table 7). Thus, as effective habitat area increases within and outside a park, the number of disturbance-sensitive species (including carnivores) lost, or the number of disturbance-tolerant appearing, is expected to decline (i.e., the species composition of the park is not expected to change very much). In the case of net change in spe-

Table 5. Log-likelihood and Akaike Information Criterion (AIC_c; Burnham and Anderson 1998) for the six best regression models for the appearance of disturbance-tolerant mammals in 24 Canadian national parks. *K* equals the number of parameters plus an intercept and error term. Δ_i values < 2 are considered credible best models. Weights (w_i) are a measure of the weight of evidence in favour of that particular model over all others. EH in: effective habitat area within a park; EH out: effective habitat area in a 50 km radius outside of the park boundary; visitors: number of visitors per year in a park; population: human population size in a 50 km radius outside of the park. Variables are log-transformed.

Model	Variables	Log-likelihood	<i>K</i>	AIC _c	Δ_i	w_i	r^2	<i>p</i>
15	EH in	-49.979	3	107.16	0.00	0.1911	0.05	0.27
14	visitors	-50.265	3	107.73	0.57	0.1436	0.001	0.86
12	population	-50.281	3	107.76	0.60	0.1413	0.03	0.42
13	EH out	-50.373	3	107.95	0.79	0.1289	0.02	0.49
7	EH in; population	-49.148	4	108.40	1.24	0.1026	0.12	0.27
11	EH out; population	-49.741	4	109.59	2.43	0.0567	0.07	0.46

cies richness, both parameter estimates are positive. This indicates that net change increases (i.e., fewer species lost as net value becomes less negative) as the effective habitat area and number of visitors increase. In the two cases where the best model also included number of visitors as an explanatory variable (the best model for carnivores lost and for net change in disturbance-sensitive mammals), the magnitude of the parameter estimates for this variable was less than that of the landscape variables.

Discussion

Wiersma and Nudds (2001) reported that only 15% of the variation in loss of disturbance-sensitive species among nine parks in the highly populated south-eastern region of the country was explained by park size. However, once land use and land cover had been accounted for, the effective habitat area of parks, together with the effective habitat area outside parks yielded a good model for predicting loss of disturbance-sensitive species in 24 parks in southern Canada, with a relative Akaike weighting of 0.54, and an r^2 value of 0.65. Thus, it appears, at the scale studied here, that the amount of suitable habitat area in, and within a 50 km radius from, parks are the most important factors that have affected losses of disturbance-sensitive mammals.

When the effective habitat areas within, and in a 50 km zone outside of, park boundaries are plotted against one another (Figure 2), clear size thresholds emerge below which parks have lost disturbance-sensitive mammal species. The three parks which have not lost any disturbance-sensitive species all have amounts of effective habitat area within them greater

Table 6. Parameter weightings based on Akaike weights (w_i ; Burnham and Anderson 1998) for each model for mammalian species change in 24 Canadian national parks. Higher values indicate higher relative support for inclusion of a parameter in the model.

Parameter	w_i
<i>Loss of disturbance-sensitive mammals</i>	
Effective habitat in	0.9731
Effective habitat outside	0.9636
Number of visitors	0.2968
Population size	0.1854
<i>Carnivores lost</i>	
Effective habitat in	0.8549
Effective habitat outside	0.9975
Number of visitors	0.5994
Population size	0.1823
<i>Net disturbance-sensitive change</i>	
Effective habitat in	0.6319
Effective habitat outside	0.4598
Number of visitors	0.5030
Population size	0.2372
<i>Disturbance-tolerant appearing</i>	
Effective habitat in	0.4488
Effective habitat outside	0.3176
Number of visitors	0.3089
Population size	0.4004

than 3141 km² together with effective habitat area of at least 18 000 km² within 50 km. One park, Prince Albert National Park (PALB; Figure 2), although big enough to have sufficient effective habitat area within it, is not apparently surrounded by sufficient effective habitat, as it has lost at least one species. All of the remaining parks are below the minimum threshold for effective habitat area in parks, and none exceeded

Table 7. Parameter estimates for each of the best models (as identified using the Akaike Information Criterion (AIC_c); Burnham and Anderson 1998) measuring mammalian species change in 24 Canadian national parks.

Parameter	Estimate	Standard error	X^2	$p > X^2$
<i>Loss of disturbance-sensitive mammals</i>				
Intercept	10.572	1.1814	80.08	<0.0001
Effective habitat in	-0.6171	0.1787	11.93	0.0006
Effective habitat outside	-0.4574	0.1190	14.77	0.0001
<i>Carnivores lost</i>				
Intercept	10.0295	1.5722	40.70	<0.0001
Effective habitat in	-0.3737	0.1165	10.29	0.0013
Effective habitat outside	-0.3692	0.0791	21.76	<0.0001
Number of visitors	-0.2547	0.1131	5.07	0.0243
<i>Net change in disturbance-sensitive species richness</i>				
Intercept	15.1444	5.0454	9.01	0.0027
Effective habitat in	0.8425	0.3306	6.49	0.0108
Number of visitors	0.7333	0.3378	4.71	0.0300
<i>Disturbance-tolerant appearing</i>				
Intercept	4.9905	1.4406	12.00	0.0005
Effective habitat in	-0.2541	0.2179	1.36	0.2434

the threshold for effective habitat area outside, even though it is theoretically possible for some of the larger of these parks to be surrounded by as much as 18 000 km² of effective habitat within 50 km. For smaller parks, it is not possible to achieve the threshold for effective habitat outside the parks within 50 km simply because of geometric constraints. In addition there are other constraints imposed by, for example, proximity to large bodies of water.

The importance of effective habitat area outside of parks in the models for disturbance-sensitive species loss, net change in disturbance-sensitive species richness and carnivore loss is consistent with other research that has considered the effects of habitat fragmentation (e.g., Ranta et al. 1998; Malanson and Cramer 1999), or addressed issues of minimum viable populations for mega fauna (e.g., Landry, Thomas and Nudds 2001; Vasarhelyi, Thomas and Nudds 2001). Indeed, many have called for the need to improve the connectivity of protected areas through the use of corridors or other linkages (Noss and Harris 1986; Beier and Noss 1998). Although the specific mechanisms to re-establish or maintain connectivity have come under considerable scrutiny and debate (Simberloff and Cox 1987; Simberloff et al. 1992; Mann and Plummer 1995), we show that models that include effective habitat area outside parks can better account for species extirpations from parks than simply park size alone.

Our results are consistent with the idea that a large park will not be suitable to conserve mammals if it is

too isolated from the surrounding habitat matrix, but suggest also that neither may a small, but seemingly well-connected park conserve its historical complement of species. As an extreme example, even if Point Pelee National Park (PELE; Figure 2) were buffered with 50 km of unaltered habitat, the total area of the buffer and the park combined would still be far below the minimum size thresholds to conserve mammals in protected areas suggested here and elsewhere (e.g., Gurd, Nudds and Rivard 2001). While it might be informative to evaluate the extent to which wider buffers around small parks might be functionally equivalent to smaller buffers around large parks, in practice the point will often be moot. Nevertheless, where previously it has been hypothesized that less isolated parks will have suffered few extinctions, we have shown that, indeed, parks better buffered by natural habitat have experienced lower extinction rates of mammals. Furthermore, given that the Akaike weights for the landscape variables were generally higher than those for human use (Table 6), our analysis suggests that loss of habitat inside and outside of parks has contributed more to observed species losses than factors correlated with the presence of abundant humans, in or outside of parks.

Harcourt, Parks and Woodroffe (2001) and Parks and Harcourt (2002) analysed human population density outside African and American parks, respectively, and showed that small parks tended to be found in areas with high human densities. They proposed that

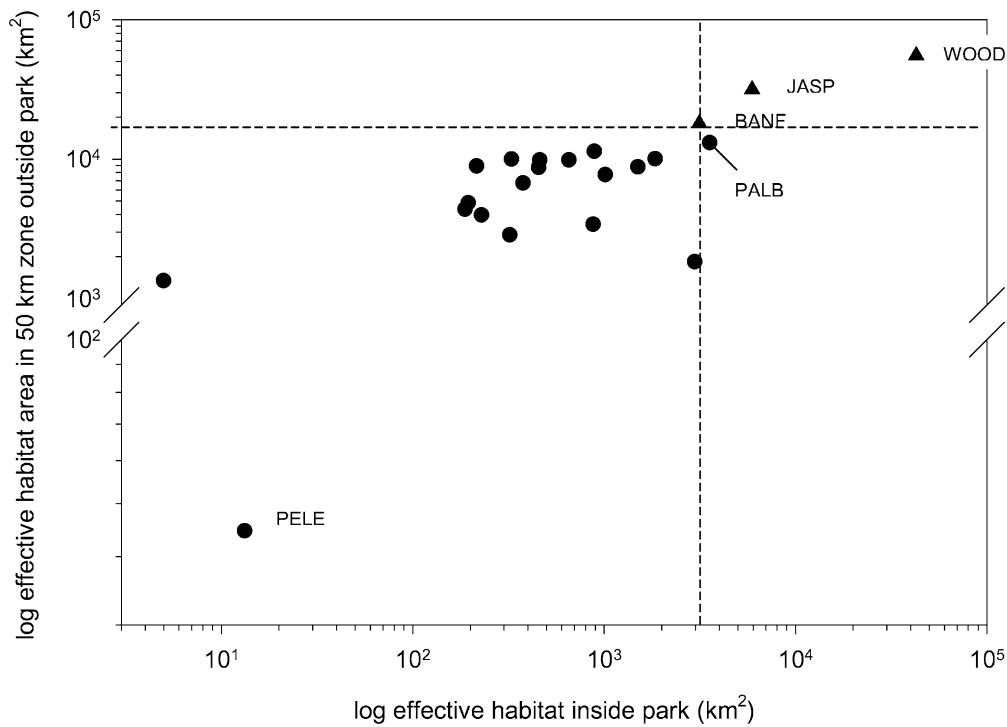


Figure 2. Plot of effective habitat area within and in a 50 km zone outside of 24 Canadian national parks. Triangles indicate parks that have had zero losses of disturbance-sensitive species. Dashed lines indicate intercepts for minimum effective habitat area within and surrounding parks at which loss of disturbance-sensitive species is predicted to be zero based on Akaike models. Effective habitat area is that left after land use and land cover types unsuitable as habitat is subtracted from the total areas within and around parks. Labeled points are discussed in text. See Appendix 1 for data values.

small parks might face a “double jeopardy” with respect to local extinction risk and predicted that species extinctions would be correlated with human density outside of parks. It is important to note that Parks and Harcourt (2002) carried out their analysis of American parks in buffer zones 50 and 100 km outside of park boundaries, while we confined our analysis to a 50 km buffer only. In our analysis of Canadian national parks, despite the perceived existence of a similar pattern of small parks in areas of the country with high human density (but see Table 1), number of visitors and human population did not have high Akaike weights in models for loss of carnivores or disturbance-sensitive species (Table 6). Moreover, in the two cases where the best model included number of visitors as a predictor variable, parameter estimates suggested (somewhat counter-intuitively) that increased visitors contributed to reducing the number of carnivore species lost and increasing the net change in richness of disturbance-sensitive mammals (i.e., more visitors = net change approaching 0). These observations are consistent with the idea that habitat change

has contributed more to species loss from reserves than has human activity, at least as indexed by human density in and outside of parks.

We can think of four reasons that we have arrived at a different conclusion than Harcourt, Parks and Woodroffe (2001) and Parks and Harcourt (2002) about the relative contribution of human activity to species extinction in reserves within a 50 km buffer zone. First, we used improved model selection procedures (Burnham and Anderson 1998) to infer the relative importance of potentially correlated explanatory variables, such as park size, habitat change and human density. Second, human density may not be an appropriate index of human activity. It is not inconceivable that on different continents, human density may correlate with different human activities. In some regions, like Africa, high human density may reflect increased specific activities like hunting and trapping which may differentially affect game species (Brashares, Arcese and Sam, 2001; Harcourt, Parks and Woodroffe 2001), but in other settled landscapes, such as urban and semi-rural North America, high human density may

correlate with different mortality agents, such as roads. Future models might be improved with the inclusion of variables that represent specific human activities in and around the parks (e.g., hunting and trapping, vehicular traffic) which might be more directly related to extirpations than the landscape variables measured here (see also Rivard et al. 2000). Third, we measured changes in mammal species composition from a time well before park establishment in all cases. Perhaps landscape changes better account for mammal extirpations over the time frame we analyzed, and human density better accounts for extirpations over the shorter time frames, such as since time of park establishment as analyzed by Parks and Harcourt (2002). Finally, Harcourt, Parks and Woodroff (2001) examined only extinctions of three carnivore species, and Parks and Harcourt (2002) examined only mammals > 5 kg of the orders Carnivora and Artiodactyla. In contrast, we looked at all disturbance-sensitive mammals of all sizes and from all orders. It is possible that the species examined by Harcourt, Parks and Woodroff (2001) and by Parks and Harcourt (2002) are more sensitive to human disturbance specifically than the aggregation of all species that we examined.

Thus, because there is reasonable weight of evidence for each, we do not fully resolve whether landscape patterns or human population size has a greater impact on extinctions of all species in all parks. Like Parks and Harcourt (2002), our results do show the need to move beyond simple biogeography models that consider park size in isolation of other factors. More importantly, our results show the value of using model selection procedures to tease out such factors in further studies. For example, had we used the same statistical approach as Parks and Harcourt (2002), we might have concluded, based on r^2 values, that human population size and number of visitors was a significant explanatory variable for species losses (Table 2). However, the AIC values show that the more parsimonious model includes only landscape factors. Thus, future studies should use model selection procedures to further distinguish among competing hypotheses about the relative impact of park size, landscape patterns and factors associated with human population size on species losses from protected areas.

There was no best overall model for explaining the appearances of disturbance-tolerant species (Table 5). The appearance of native North American disturbance-tolerant species may be related to other changes in habitat, such as the replacement of old growth forests in eastern Canada with second growth

forests following logging and land clearing for agriculture in the early 19th century (e.g., Hunt 1998; Foster et al. 2002), or changes in stand composition in the boreal forest as a result of fire suppression (e.g., Murphy and Lehnhausen 1998). Future study at the scales of individual parks with similar analyses may yield new insights into these compositional changes and could be done using buffer data for human-built features more appropriate to the specific species and landscape. In addition, analyzing patterns of landscape connectivity for a particular species is possible at the park scale, and might allow for tests of hypotheses concerning compositional turnover within a given park.

Finally, we caution that, like other attempts to estimate acceptable size thresholds (e.g., Gurd, Nudds and Rivard 2001), we based our analysis on data about species presence/absence, and that minimum landscape thresholds to protect viable populations might be much higher.

We documented that small parks do not contain the historical composition of disturbance-sensitive mammals consistent with previous investigations. Indeed, our results suggest parks should be much larger, since only a few met the minimum threshold for effective habitat area. However, we also showed that small parks might be insufficient to conserve such species, even if embedded in a relatively unaltered landscape matrix. Very large parks may also fail to conserve historical species richness and composition if they have a high degree of human development in or around them, contain mostly inhospitable habitat, or are isolated from the surrounding habitat matrix. If existing or planned parks can not be made large, an increase in the effective area of the park through the minimization and/or consolidation of certain visitor facilities and other park infrastructure may help to relieve extirpation risk for some species. For example, over the past three decades, Point Pelee National Park has substantially increased its effective habitat area by 12% (equal to an increase of 50% in the forested area of the park; M. Smith, Point Pelee National Park, pers. comm.) by the active removal of cottages and visitor facilities to outside the park boundaries. Adams and Nudds (1992) predicted that removal of infrastructure in Point Pelee would yield sufficient effective habitat to support the reintroduction of the previously extirpated flying squirrel (*Glaucomys volans*); recent surveys eight years after the reintroduction of *G. volans* support their prediction (Bednarczuk 2003). Similarly, as Banff National Park appears to be teetering on the edge of

thresholds for effective habitat both in and outside its boundaries, our analysis suggests that, to conserve Banff's historical complement of species, recent legislative and policy initiatives designed to result in no net increase in development in the park, to eliminate some land use/infrastructure barriers to movements of large mammals, and to engage neighboring jurisdictions in land use planning around the park, are appropriate. Others of Canada's national parks have lost, and may continue to lose, disturbance-sensitive mammals, but our results point to minimum thresholds for the landscape in and around the parks that may guard against further losses and promote the maintenance, and (to the extent possible) the restoration of historical species composition.

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Appendix 1. List of the National Parks examined in this study, together with four-letter code used in figures; park area; effective habitat area in park, and effective habitat area in a 50 km zone outside park.

Park	Code	Park area (km ²)	Effective habitat area in park (km ²)	Effective habitat area in a 50 km zone outside park (km ²)
Banff	BANF	6641.0	3141.0	18002.0
Cape Breton Highlands	CBH	948.0	877.6	3412.4
Elk Island	ELKI	194.0	173.6	0.0
Forillon	FORI	240.4	229.3	3981.0
Fundy	FUND	205.9	187.5	4358.5
Glacier	GLAC	1349.3	889.9	11363.7
Grasslands	GRAS	906.4	873.5	0.0
Gros Morne	GROS	1805.0	1502.9	8769.3
Jasper	JASP	10878.0	5928.0	31543.9
Kejimikujik	KEJI	403.7	328.5	10009.3
Kootenay	KOOT	1406.4	1013.5	7715.0
Kouchibouguac	KOUC	239.2	194.7	4850.0
La Mauricie	LAMA	536.1	455.3	8732.4
Mount Revelstoke	MREV	259.7	215.8	8885.1
Pacific Rim	PRIM	285.8	461.1	9819.4
Point Pelee	PELE	15.0	13.2	44.6
Prince Albert	PALB	3874.3	3562.3	13086.0
Prince Edward Island	PEI	26.0	4.9	1343.2
Pukaskwa	PUK	1877.8	1847.9	10040.8
Riding Mountain	RMTN	2973.5	2857.1	1836.2
Terra Nova	TERR	399.9	376.6	6721.7
Waterton Lakes	WLKS	505.0	322.0	2865.6
Wood Buffalo	WOOD	44802.0	42675.2	55307.1
Yoho	YOHO	1313.1	656.3	9871.3