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RESEARCH ARTICLE

Accessible habitat: an improved measure of the effects of habitat loss and roads on wildlife populations

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Abstract Habitat loss is known to be the main cause of the current global decline in biodiversity, and roads are thought to affect the persistence of many species by restricting movement between habitat patches. However, measuring the effects of roads and habitat loss separately means that the configuration of habitat relative to roads is not considered. We present a new measure of the combined effects of roads and habitat amount: accessible habitat. We define accessible habitat as the amount of habitat that can be reached from a focal habitat patch without crossing a road, and make available a GIS tool to calculate accessible habitat. We hypothesize that accessible habitat will be the best predictor of the effects of habitat loss and roads for any species for which roads are a major barrier to movement. We conducted a case study of the utility of the accessible habitat concept using a data set of anuran species richness from 27 ponds near a motorway. We defined habitat as forest in this example. We found that accessible habitat was not only a better predictor of species richness than total habitat in the landscape or distance to the motorway, but also that by failing to consider accessible habitat we would have incorrectly concluded that there was no effect of habitat amount on species richness.

Keywords Habitat fragmentation · Accessible habitat · Road ecology · Ontario · Amphibians · Species richness · Habitat loss · GIS · Barriers · Deforestation

Introduction

Habitat loss has negative consequences for populations and communities (reviews in Andren (1994) and Fahrig (2003)). In addition, the replacement of habitat with certain matrix cover types can create barriers or filters to the movement of individuals between habitat patches. Roads are thought to be a particularly strong barrier or filter for many species (Forman and Alexander 1998; Trombulak and Frissell 2000).

The effects of the loss of habitat and of roads on wildlife populations are usually evaluated using separate variables in landscape-scale studies. The effect of habitat loss is generally measured by the correlation between the amount of habitat in the landscape and species distribution or abundance, while the effects of roads are generally evaluated by the correlation between the density of roads/traffic in the landscape or the distance to the nearest road and

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species distribution or abundance (e.g., Gutzwiller and Barrow 2003; Johnson and Collinge 2004; Marchand and Litvaitis 2004). However, by considering habitat loss and roads as separate predictors, investigators do not account for the fact that habitat that can be accessed from a focal habitat patch without crossing a road is more likely to contribute to a population than habitat on the other side of the road. In addition, a road that needs to be crossed to access other habitat patches is likely to have a much greater negative effect on the population than one that does not restrict habitat access. Therefore, we hypothesize that measuring habitat loss and road effects on wildlife populations separately can lead to an underestimate of the effects of both stressors on wildlife populations.

In this paper, we introduce a new landscape variable, 'accessible habitat', to measure the combined effects of habitat loss and roads which accounts for the location of habitat in relation to roads. We define accessible habitat as the amount of habitat that can be reached from a focal patch of habitat without crossing a road (Fig. 1); note that other types of linear barriers (railroads, rivers, etc) could also be used to delineate accessible habitat.

The type of road (or barrier) used to delineate accessible habitat will be species-dependent. If a species avoids crossing any paved roads, paved roads should be used to delineate accessible habitat. However, if a species or taxon attempts to cross most or all roads, then only high-traffic roads should be used to delineate accessible habitat as smaller roads will only have a weak barrier effect.

We hypothesize that accessible habitat will be more strongly related to wildlife population persistence than total habitat amount and/or road density/distance to a road when populations are negatively affected both by habitat loss and roads. We present a

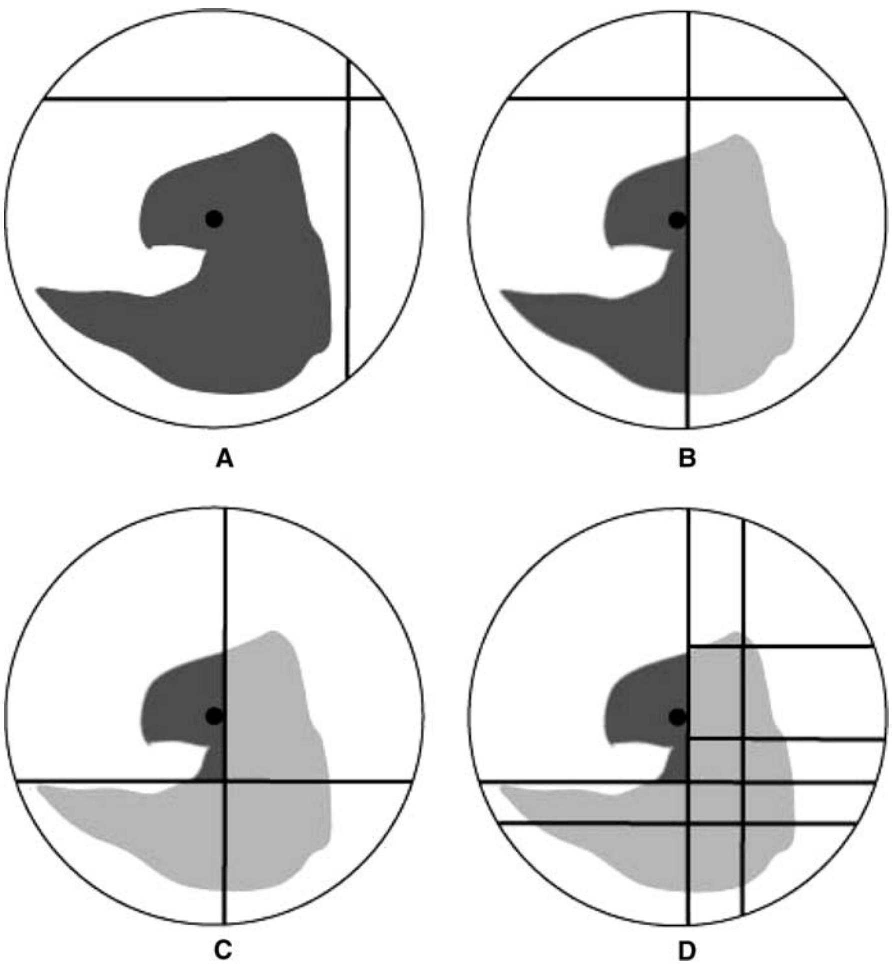

Fig. 1 Hypothetical landscapes illustrating accessible habitat. In **A**, all habitat (dark grey) is accessible by some species from a focal sampling point (small black circle) without crossing a road (thick black line). In **B**, **C** and **D** accessible habitat (dark grey) is less than total habitat (light grey + dark grey). Distance to the nearest road is the same in landscapes **B**, **C** and **D**, but accessible habitat is lower in landscapes **C** and **D**. Road density is higher in landscape D than in landscape C but accessible habitat remains the same in both landscapes

case study of the utility of the accessible habitat concept using a data set of anuran species richness near a motorway in eastern Ontario, Canada.

Case study: the effect of accessible forest on the species richness of frogs and toads near a major motorway

Both the amount of forest and roads/traffic in the landscape are known to be important predictors of amphibian species richness, distribution and abundance. Many species of amphibians require upland habitat in the landscape along with ponds or wetlands for breeding (Wilbur 1980). Forests can provide both upland habitat and help maintain the moist microclimate that facilitates the dispersal of amphibians (deMaynadier and Hunter 1999), and the amount of forest in the landscape around breeding ponds and wetlands is known to be positively associated with amphibian species richness (e.g., Laan and Verboom 1990; Hecnar and M'Closkey 1998; Knutson et al. 1999; Findlay et al. 2001; Houlahan and Findlay 2003; Herrmann et al. 2005). The necessity of moving between multiple habitats and dispersing to re-colonize breeding sites means that many amphibians are also vulnerable to roads in the landscape. Studies have shown negative correlations between anuran species richness and paved road density (e.g., Findlay et al. 2001); between anuran pond occupancy and road density (Vos and Chardon 1998); and between anuran relative abundance and traffic density (Fahrig et al. 1995; Carr and Fahrig 2001). High-traffic roads have a greater negative effect on anurans than low-traffic roads (Van Gelder 1973; Fahrig et al. 1995; Vos and Chardon 1998). We define habitat to be forest in our case study, and define accessible habitat (forest) to be the percentage of forest in the landscape that can be reached from sampling ponds without crossing a major motorway.

The purpose of this case study was to answer the following question: Is accessible forest a better predictor of anuran species richness than either (1) the total amount of forest in the landscape; or (2) distance to the motorway; or (3) the total amount of forest in the landscape and the distance to the motorway? Given the vulnerability of anurans to both loss of forests and high-traffic roads, we predicted that accessible forest would be a better predictor of anuran species richness than total forest and/or distance to the motorway.

Methods

Study design

We selected 27 ponds located 35–3250 m away from a 58 km section of Highway 401 in a rural part of eastern Ontario, Canada (Fig. 2). Highway 401 is the main route connecting the two largest cities in Canada—Toronto and Montreal. In the study area, it is a limited access, four-lane divided highway (motorway) with an average traffic volume of 18,300 vehicles/day in September 2006 (personal communication, Mary Anne Griepsma, Ontario Ministry of Transportation). Traffic volumes at night are high (30% of traffic travels between 8 pm and 8 am) largely due to truck traffic: trucks constitute 56% of the night-time traffic volume, and 40% of the total daily traffic volume. Average traffic volumes on Highway 401 are relatively low compared to suburban highways where traffic volumes of 50,000–150,000 vehicles/day are not unusual (Forman and Deblinger 2000; Ontario Ministry of Transportation 2003). However, as most anuran movements are at night (Todd and Winne 2006), the high night-time traffic volumes mean that Highway 401 is likely to have a much greater negative effect on anuran populations than commuter routes with higher average daily traffic volumes, but lower night-time traffic volumes.

We defined accessible habitat (forest) as the amount of forest within 1000 m from the edge of a sampling pond that could be accessed without crossing Highway 401. The 1000 m distance is biologically relevant because it encompasses the majority of the migration and dispersal movements of the anuran species in our study area (Guerry and Hunter 2002). In addition, significant associations with the amount of forest in the landscape have been observed for most anuran species found in the study area at this scale (Findlay et al. 2001; Houlahan and Findlay 2003; Knutson et al. 2004; Price et al. 2004; Herrmann et al. 2005). All study ponds were at least 1 km apart to ensure independence of the sampling sites (Petranka et al. 2004). As a result, only 4.7% of the total area of all landscapes was overlapping

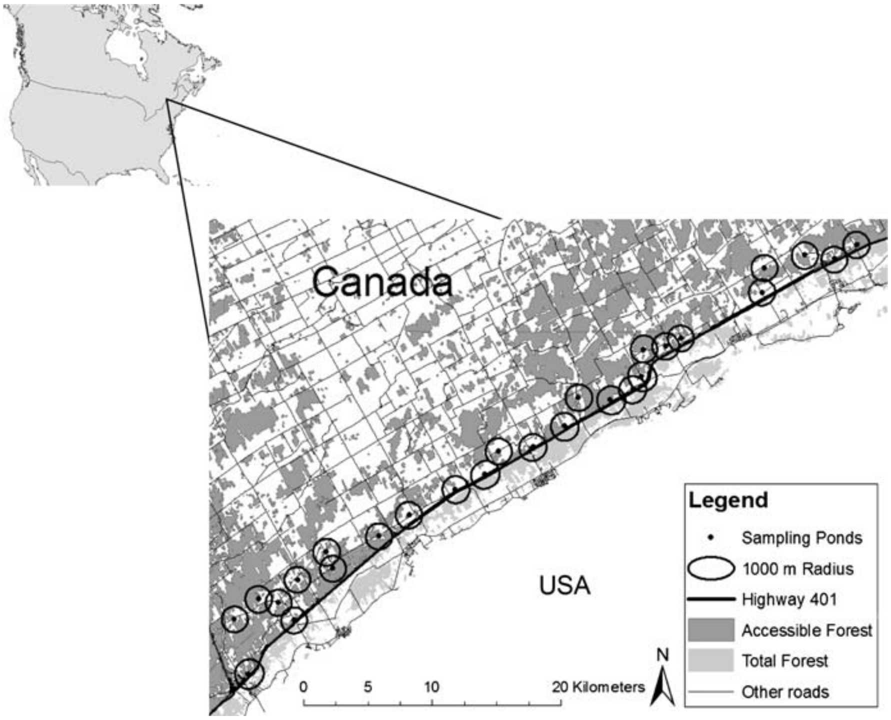

Fig. 2 Study area, showing sampling ponds, total forest cover and accessible forest cover (i.e., forest that can be reached from sampling ponds without crossing highway 401)

(Fig. 2). In addition, all study ponds were suitable for anuran breeding (no quarries, no fish hatcheries, at least some shallow water with emergent vegetation). We used every suitable pond in our study area within 500 m of the highway (14 in total) to minimize the correlation between total and accessible forest (which is 100% beyond 1 km from the highway), thus maximizing the statistical power of our analyses. The remaining 13 ponds were located up to 3250 m from the edge of the highway to maximize our ability to detect an effect of distance to Highway 401 on anuran populations.

Anuran field surveys

We conducted eight auditory night chorus surveys and four visual day surveys to assess the species richness of anurans at or near the sampling ponds in 2006. Nine of the 14 anuran species found in the Great Lakes Basin (Harding 1997) are present in the study area: wood frog (*Rana sylvatica*), spring peeper (*Pseudacris crucifer*), western chorus frog (*Pseudacris triseriata*), northern leopard frog (*Rana pipiens*), American toad (*Bufo americanus*), gray treefrog (*Hyla versicolor*), green frog (*Rana clamitans*), mink frog (*Rana septentrionalis*) and bullfrog (*Rana catesbeiana*).

Chorus surveys were conducted between April 1 and July 12, and were timed so that there were at least two surveys during the peak breeding season of each species present in the region. Chorus surveys followed a modified version of the Marsh Monitoring Protocol (Bishop et al. 1997). We began surveys half an hour after sunset and finished before midnight. We surveyed each pond for 5 min, and recorded the number of calling males at or within 100 m of the pond in one of four abundance classes: 0—no individuals calling; 1—individuals can be counted and calls are not overlapping; 2—calls of <15 individuals can be distinguished, some overlap of calls; 3—calling individuals too numerous to count or ≥ 15 individuals calling, calls overlapping. We included calling from within 100 m of the pond to account for the preference of several species (wood frog, spring peeper, gray treefrog), to breed in ephemeral vernal pools—which were very common in the forests adjacent to our sampling ponds—in addition to permanent ponds (Skelly et al. 1999). The ponds were divided into four routes, and were surveyed over two nights that were as close to consecutive as weather conditions permitted. Surveys were only conducted on warm evenings (average survey temperature April 1st–May 9th 9.3°C ± 4.1 SD; May 24th–July 12th 20.3°C ± 3.7 SD) with little wind (average Beaufort wind scale reading 1.04 ± 1.15 SD). The order in which the routes were sampled within a survey was randomized, and the order in which ponds were surveyed within a route was alternated between forwards, backwards, starting at the middle of the route and moving forwards, and starting at the middle and moving backwards to vary the time of the survey for each pond.

We conducted the visual surveys between May 8 and July 8, 2006 to correspond with the peak breeding season of aquatic frogs (leopard frog, green frog, mink frog, bullfrog). These species are conspicuous during their breeding seasons in visual surveys, but are easily missed using call surveys alone (de Solla et al. 2005). Each survey was conducted between 0900 and 1800 h over 4 days. Adult and juvenile frogs were counted as a surveyor slowly walked along the edge of pond or through shallow emergent vegetation. Search effort was proportional to the density of emergent vegetation. The total time spent at each pond varied from 2 to 121 min, with more time spent at ponds with a greater pond perimeter and higher amounts and densities of emergent vegetation.

Measurement of landscape variables

We quantified two landscape variables—percentage of forest and percentage of accessible forest—in landscapes of 1000 m radii from the edge of the sampling ponds. We also calculated the distance from the listening point at each pond to Highway 401, the amount of forest within 100 m of the edge of each pond, and the area of each pond. We did not quantify road density in our landscapes as Highway 401 was the only road within 1000 m of any of the sampling ponds with sufficient traffic volumes to present a significant barrier to anurans, and thus road density of major roads would have been redundant with distance to Highway 401. We calculated pond area in ArcGIS after measuring pond perimeter using a handheld GPS unit with sub-meter resolution (Trimble Geo-Explorer, Trimble Navigation Ltd, Westminster, Colorado USA). We obtained the amount of forest in the landscape from digital 1:50 000 Natural Resources Canada topographic maps. All GIS work was performed with the ArcGIS 9.0 geographic information system (Environmental Systems Research Institute, Redlands, California, USA), mostly using custom tools written in the open source scripting language Python 2.1 (http://www.python.org). An ArcGIS tool written in Python for calculating accessible habitat can be downloaded from the Geomatics and Landscape Ecology Research Laboratory (GLEL) website: http://www.glel.carleton.ca/RESEARCH/accessiblehabitat.php This tool can be run within ArcGIS without any knowledge of the Python language.

Statistical analysis

Species richness was defined as the total number of species of anurans seen or heard during all surveys at each pond. We used multiple regression models to determine whether accessible forest, distance to Highway 401 or the combined effects of distance to Highway 401 and the total amount of forest or accessible forest in the landscapes was a better predictor of anuran species richness. All statistical models were run using the *lm* function in R 2.2 (R Development Core Team 2005).

We built eight statistical models containing pond area, amount of forest cover within 100 m of the pond, and (1) accessible forest; (2) total forest; (3) distance to Highway 401; (4) total forest + distance to Highway 401; (5) accessible forest + distance to Highway 401; (6) total forest + distance to Highway 401 + total forest × distance to Highway 401 (7) total forest + accessible forest + distance to Highway 401; (8) total forest + accessible forest + distance to Highway 401 + total forest × accessible forest. We included pond area in all models as large ponds tended to extend farther away from the highway than small ponds located the same distance from the highway, and to control for the positive association between pond area and anuran species richness (Hecnar and M'Closkey 1998). We included the amount of forest within 100 m of the pond edge in all models to account for between-pond differences in forested vernal pool habitat adjacent to the pond. We compared the adjusted R^2 of the models, and also calculated the partial R^2 (amount of variation explained by each predictor after controlling for the variation explained by the other predictors in the model) (Zar 1999) of each of the predictors of interest. The statistical significance ($\alpha = 0.05$) of each predictor after controlling for the effects of the other predictors in the models was tested using an F-test with Type II SS using the *Anova* function in the *car* package (Fox 2006) within R 2.2. Type II SS conform to the principle of marginality and are more appropriate than Type III SS when interactions are present in the model. If no interactions are present, Type II SS are equivalent to Type III SS (Fox 2002). We log-transformed total forest, accessible forest and distance to Highway 401 to meet the assumption of homogeneity of variance.

Results

The Pearson correlation between log(total forest) and log(accessible forest) was 0.56; the correlation between log(accessible forest) and log(distance to Highway 401) was 0.71; and the correlation between log(total forest) and log(distance to Highway 401) was 0.007.

Accessible forest was the best landscape predictor of anuran species richness, explaining 50% of the variation in species richness after controlling for local variables (Fig. 3a; Table 1). The best overall model included all variables and the interaction between total forest and accessible forest; this model explained 67% of the variation in species richness (adjusted R^2 of 0.57) (Table 1). Accessible forest was a much better predictor of the effect of forest cover than total forest, which explained only 1% of the variation in species richness (Fig. 3c; Table 1). Accessible forest remained a significant predictor of species richness even after total forest and/or distance to Highway 401 was included in the model.

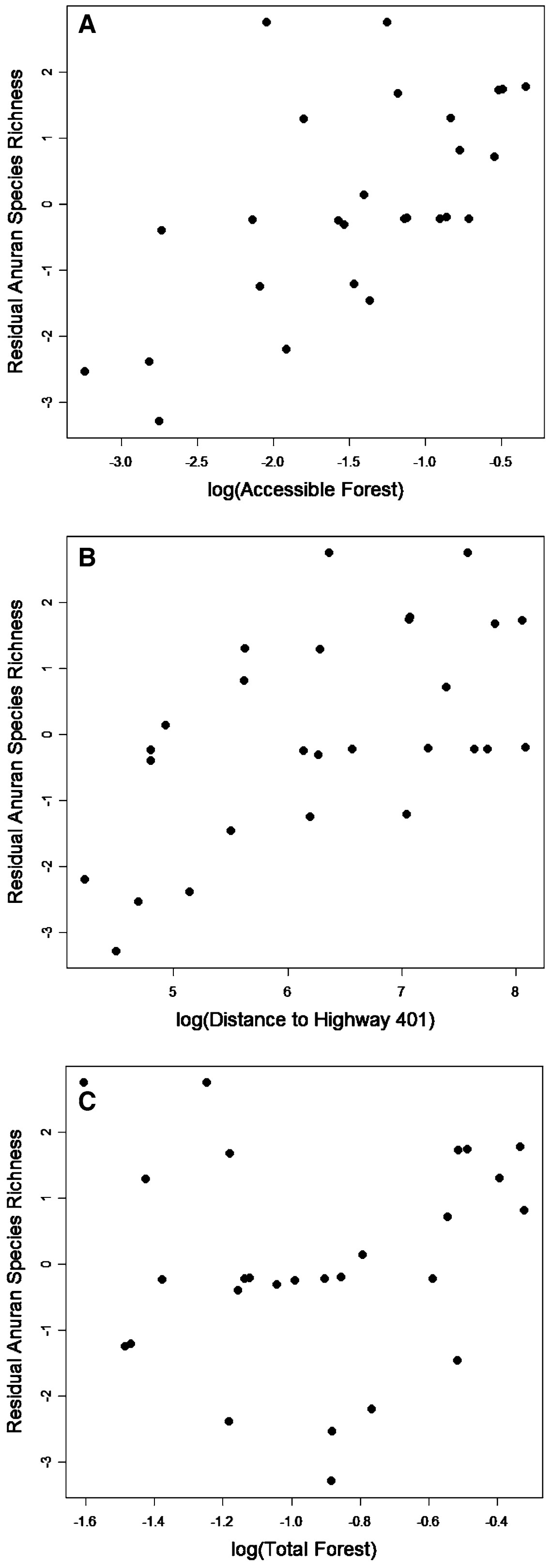

Fig. 3 Relationship between residual anuran species richness ▶ and log-transformed (**a**) accessible forest within 1000 m of sampling ponds; (**b**) distance to highway 401 (m); (**c**) total forest within 1000 m of the sampling ponds ($n = 27$). Residuals are from anuran species richness regressed against pond area and forest cover within 100 m of the pond edge. Residuals represent variation in the response not explained by the predictor variables, so this approach allows us to show the relationship between species richness and the landscape predictors (total forest, accessible forest and distance to the highway) independently of the effects of the local variables (pond area and amount of forest within 100 m of the pond) on species richness

Table 1 Summary of statistical models ($n = 27$)

Model	Adjusted R^2 of model	Predictor	Coefficient	Partial R^2	F
1	0.33	log(Distance to Highway)	0.90 ± 0.23	0.40	15.13***
2	<0.00	log(Total Forest)	0.42 ± 0.94	0.01	0.18
3	0.44	log(Accessible Forest)	1.61 ± 0.34	0.50	22.93***
4	0.30	log(Distance to Highway)	0.9 ± 0.23	0.40	14.49***
		log(Total Forest)	0.34 ± 0.79	<0.00	0.19
5	0.44	log(Distance to Highway)	0.32 ± 0.32	0.04	0.97
		log(Accessible Forest)	1.23 ± 0.51	0.21	5.68*
6	0.28	log(Distance to Highway)	1.27 ± 0.85	0.40	13.97**
		log(Total Forest)	−2.32 ± 5.87	0.01	0.18
		log(Distance to Highway) × log(Total Forest)	0.40 ± 0.88	0.01	0.21
7	0.48	log(Distance to Highway)	−0.06 ± 0.38	0.00	0.02
		log(Total Forest)	−1.61 ± 0.94	0.12	2.91
		log(Accessible Forest)	2.04 ± 0.69	0.30	8.83**
8	0.57	log(Distance to Highway)	0.15 ± 0.36	0.00	0.18
		log(Total Forest)	1.86 ± 1.71	0.12	3.53
		log(Accessible Forest)	3.89 ± 1.01	0.30	10.71**
		log(Total Forest) × log(Accessible Forest)	2.47 ± 1.06	0.21	5.46*

The response variable for all models is species richness; pond area and amount of forest within 100 m of the pond edge are also included as predictors in all models. Statistical significance the F-statistic is indicated as: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

There was no significant interaction effect between total forest and distance to Highway 401, but there was a significant interaction between total forest and accessible forest (Table 1), such that the relationship between total forest and species richness shifted from negative to positive with increasing accessible forest.

Discussion

Case study

Our results indicate that not measuring accessible habitat can lead to incorrect conclusions about the effects of habitat loss near barriers on wildlife populations. Total forest cover in the landscape was a very poor predictor of species richness, both in isolation and in combination with distance to the highway, while accessible forest was a strong predictor of species richness, even after controlling for distance to the highway. If we had not considered accessible forest we would have mistakenly concluded that there was no effect of forest cover on anuran species richness.

The significant interaction between accessible forest and total forest was caused by a negative effect of total forest on species richness when accessible forest was low, and a positive effect of total forest when accessible habitat was high. This occurred because there was frequently a large amount of forest on the far side of Highway 401 within 1000 m of the sampling ponds even when accessible forest was low (Fig. 2), resulting in relatively high total forest but low accessible forest. This non-accessible forest happened to be higher at sites with low species richness, leading to what was most likely a spurious negative correlation between total forest and species richness when accessible forest was low. On the other hand, at sites where both accessible forest and total forest were high, most of the forest in the landscape was accessible (total forest and accessible forest were nearly identical), and thus total forest (and accessible forest) were both positively correlated with species richness.

The strength of the association (adjusted R^2 and partial R^2 values) of species richness with accessible forest and distance to Highway 401 suggests that this highway is a near-complete barrier to anurans, either because they avoid moving onto the highway and/or because of very high mortality rates when they attempt to cross. Unfortunately, we were unable to verify this by directly observing anuran mortality and behavior on the highway, due to the high traffic volumes on the road. This supports findings showing genetic differentiation of anuran populations separated by major highways (Reh and Seitz 1990; Lesbarreres et al. 2006). It is likely that the barrier effect of Highway 401 is due to mortality when crossing is attempted, as it is known that anurans often attempt to cross busy roads and that this results in very high mortality rates (Van Gelder 1973; Hels and Buchwald 2001).

The significant positive association between accessible forest and species richness after we controlled for distance to Highway 401 supports numerous other studies showing positive associations between forest cover and the species richness of this group of anurans (e.g., Houlahan and Findlay 2003; Herrmann et al. 2005). Interestingly, Gagné and Fahrig (2007) did not find a significant effect of forest cover on species richness in a study in the same region on the effects of urbanization on anurans. It is possible that inaccessibility of some of the forest in their study led to a reduction in the observed effect of this predictor. We suggest that future studies investigating the effects of forest cover on amphibians at the landscape scale in areas with major roads should include accessible forest as a predictor variable to evaluate the full effect of habitat amount and major roads on these species.

General implications of accessible habitat for wildlife conservation

Accessible habitat has important implications for the conservation of many species of wildlife. An increasingly large body of literature shows that roads are barriers to the movement of a wide variety of species and taxa in addition to amphibians. These include ground beetles (e.g., Keller and Largiader 2003), bumblebees (Bhattacharya et al. 2003), European badgers (Clarke et al. 1998), small mammals (e.g., Oxley et al. 1974), turtles (e.g., Steen and Gibbs 2004), bobcats and coyotes (Riley et al. 2006), roe deer (Kuehn et al. 2007), bighorn sheep (Epps et al. 2005) and grizzly bears (Mace et al. 1996).

Our results suggest that accessible habitat is likely to be a better measure of habitat loss when barriers are present in the landscape than the total amount of habitat for species for which linear landscape elements present major barriers to movement. If the accessible fraction of the habitat is sufficient to support the needs of a species, it does not matter whether or not roads prevent use of the habitat on the other side of the road, but including this non-accessible habitat in the analysis can obscure the effect of the biologically meaningful accessible habitat, as occurred in our case study.

Indeed, the importance of using accessible habitat versus total habitat will depend on the relationship between the non-accessible habitat and the accessible habitat. If the two are highly positively correlated, then including non-accessible habitat in the analysis (i.e., using total habitat as a predictor) should be nearly as good a measure of the effects of habitat loss on a species than if accessible habitat is used as the predictor. If, however, the non-accessible habitat is poorly or negatively correlated with accessible habitat (as occurred in our case study), then including it in the analysis (by using total habitat rather than accessible habitat as a predictor) can obscure the biologically real effect of accessible habitat by adding noise to the analysis. Consequently, failing to consider the location of habitat relative to the location of major barriers such as roads can lead to an underestimation of the effects of habitat loss in landscapes near roads (Fig. 1). This could lead investigators to then falsely conclude that habitat near roads is of little value to conservation.

A failure to consider accessible habitat could also lead to an underestimation of the effects of roads on wildlife populations, though this was not the case in our study. For example, if roads are complete barriers, road density is likely to be a poor measure of the effects of roads as only the first road an animal reaches will be important. Likewise, distance to the nearest road will only be an appropriate measure of the effects of roads if a single road is delineating accessible habitat in all landscapes as multiple roads close to a focal patch are likely to have a greater negative effect on wildlife than a single road and this will not be accounted for by measuring the distance to the nearest road (Fig. 1).

The utility of accessible habitat in measuring the combined effects of roads/barriers and habitat loss on wildlife populations will depend on the response of individual species to roads or barriers. Accessible habitat will be at least as good a measure of the effects of habitat loss as the total amount of habitat in the landscape and may be a better measure of the effects of roads than road density/distance to the nearest road when roads are a complete or near-complete barrier to movement. Based on the examples given earlier in the discussion, highways are likely to act as major barriers to movement for many if not most terrestrial animals, either due to avoidance of the road or due to very high mortality rates when crossings are attempted, as has been observed for frogs (Hels and Buchwald 2001), turtles (Aresco 2005) and European badgers (Clarke et al. 1998). However, even minor roads may be a major barrier to movement for some species, such as salamanders (deMaynadier and Hunter 2000), invertebrates (Mader 1984), small mammals (Swihart and Slade 1984), and some snakes (Shine et al. 2004), due to the behavioral response of these species to the road surface. Accessible habitat is likely to be less useful for measuring the effects of roads and habitat loss if individual roads only have a small negative effect on a species. In this case, road density is likely to be the best measure of the (cumulative) effect of roads in the landscape, and the total amount of habitat in the landscape may be a better measure of the effects of habitat loss than accessible habitat. Accessible habitat should be a worse predictor of the abundance or distribution of a species than the total amount of habitat in the landscape if linear features that are not barriers are used to delineate accessible habitat, as this will result in an underestimate of the amount of biologically useful habitat in the landscape. Measuring accessible habitat in addition to habitat amount and roads for different types of linear barriers can give an indication of the way in which a species responds to a particular type of road/barrier, because accessible habitat delineated by major barriers should be a better predictor of species abundance/persistence than accessible habitat delineated by weak barriers.

In conclusion, habitat loss and the effects of roads/linear barriers should not just be considered in isolation for species affected by both predictors, because doing so can lead to an underestimation of the effects of habitat loss and may also lead to an underestimation of the effects of roads/barriers on wildlife populations. We recommend that landscape ecologists should include accessible habitat in studies of the effects of both habitat loss and linear barriers on wildlife populations.

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