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The relative effects of road traffic and forest cover on anuran populations

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ABSTRACT

Road traffic and the loss of forests are both known to have negative effects on anurans. However, the relative importance of these two predictors is poorly understood because forest cover in the landscape is usually negatively correlated with the density of roads and traffic. To evaluate the independent effects of traffic and forest cover, we selected 36 ponds near Ottawa, Canada, at the center of four landscape types: low forest/low traffic; low forest/high traffic; high forest/low traffic; and high forest/high traffic, where traffic and forest cover were measured within 100–2000 m of the edge of each pond. We surveyed all ponds in 2005 and re-surveyed a 23-pond subset in 2006. The negative association between species richness and traffic density was stronger (partial $R^2 = 0.34$; $P < .001$) than the positive association of species richness with forest cover (partial $R^2 = 0.10$; $P > .05$) in the landscape. Three of six common species showed stronger associations with traffic density than with forest cover – *Bufo americanus*, *Rana pipiens*, and *Hyla versicolor*; two species – *Pseudacris crucifer* and *Rana sylvatica* – showed stronger associations with forest cover than with traffic; while *Rana clamitans* showed similar associations with traffic and forest cover. Our results show that the overall negative effect of traffic on anuran populations in northeastern North America is at least as great as the negative effect of deforestation, and also that the relative effects of these two predictors on anuran abundance vary between species.

1. Introduction

Two of the most important landscape scale predictors of anuran presence and abundance are forest cover and roads, particularly high traffic roads (Fahrig et al., 1995; Vos and Chardon, 1998; Cushman, 2006). However, the relative importance of forest cover and roads or traffic in the landscape is poorly understood, mainly because road density and forest cover are usually correlated (Houlahan and Findlay, 2003). Understanding the relative importance of the traffic density and forest cover in the landscape on anuran populations has important management implications. For example, the main conservation priority for a species relatively unaffected by forests but negatively affected by traffic would be to preserve landscapes with low traffic densities irrespective of forest cover. Our goal in this study was to quantify the relative effects of traffic density and forest cover on the anuran species richness and relative abundances near Ottawa, Canada.

Amphibian populations are declining globally, mainly due to the loss and degradation of natural habitat (Stuart et al., 2004). Many species require forest habitat in the landscape for part of their life cycle (Wilbur, 1980). In addition, many

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populations are thought to exhibit metapopulation dynamics (Hecnar and M'Closkey, 1996; Pope et al., 2000; Marsh and Trenham, 2001), so moist forest habitats allowing dispersal among local populations are important for long-term population persistence (deMaynadier and Hunter, 1999). Indeed, forest cover within a landscape extending 100–3000 m from breeding ponds and wetlands is positively associated with the presence and abundance of many species of amphibians (e.g. Laan and Verboom, 1990; Hecnar and M'Closkey, 1998; Knutson et al., 1999; Guerry and Hunter, 2002; Houlahan and Findlay, 2003; Herrmann et al., 2005).

The necessity of moving between multiple habitats and of re-colonizing breeding sites means that many amphibians are also vulnerable to roads in the landscape. Studies have shown negative correlations between: amphibian species richness in breeding sites and paved road density (e.g. Findlay et al., 2001); anuran pond occupancy and road density (Vos and Chardon, 1998); and anuran relative abundance and traffic density (Fahrig et al., 1995; Carr and Fahrig, 2001).

The negative effect of roads on anurans is probably due mainly to direct mortality (roadkill). Fahrig et al. (1995) showed that high traffic two-lane paved roads had a much larger effect on anuran abundance than low traffic two-lane paved roads. Mortality rates for anurans on high traffic roads are higher than on low traffic roads (Hels and Buchwald, 2001), and forestry roads with very low traffic have no effect on anuran movements (deMaynadier and Hunter, 2000). In addition, incidences of very large numbers of road-killed anurans are well-documented (e.g. Ashley and Robinson, 1996), and studies have shown strong population-level effects of traffic density (Carr and Fahrig, 2001) and high traffic roads on anurans (Van Gelder, 1973; Vos and Chardon, 1998). Therefore, total traffic on roads in the landscape likely has a greater effect on anurans than total length of roads in the landscape.

There are several reasons why the relative importance of the effects of roads and forest loss on anuran populations is largely unknown. Numerous landscape scale studies have looked at both effects (Findlay and Houlahan, 1997; Hecnar and M'Closkey, 1998; Knutson et al., 1999; Lehtinen et al., 1999; Houlahan and Findlay, 2003; Herrmann et al., 2005), but as Houlahan and Findlay (2003) point out, forest cover and paved road density are frequently highly correlated, making it impossible to determine which has the greater effect. Studies that include urban areas (e.g. Knutson et al., 1999; Lehtinen et al., 1999; Trenham et al., 2003) inevitably result in high correlations between road density and urbanization. Urbanization has severe negative effects on anuran populations (e.g. Rubbo and Kiesecker, 2005; Gagné and Fahrig, 2007), due to a variety of factors of which roads are only one. Low variation among sites in predictor variables can also bias conclusions regarding relative effects of roads versus forest loss. In southwestern Ontario, forest cover in the landscape had a larger effect on amphibian species richness than the distance to the nearest paved road (Hecnar and M'Closkey, 1998). Paved road density and forest cover were uncorrelated in this study; however, most of these sites were far from high traffic roads, so the full potential effect of traffic was not measured. Finally, all previous studies of the effects of both roads and forest loss on anurans used road density (e.g. Lehtinen et al., 1999; Findlay et al., 2001) or distance from roads (Hecnar and M'Closkey, 1998) to measure road effects, which likely underestimates the full effect of road traffic on anurans.

Our purpose was to quantify the relative importance of the full effects of deforestation and roads on anuran populations. We accomplished this by selecting landscapes in which forests and traffic were uncorrelated and in which there was a large range in variation of both forest cover and traffic, and by using traffic density rather than road density to measure the road effects.

2. Methods

2.1. Site selection

We conducted this study in rural areas of eastern Ontario and western Quebec within 100 km of Ottawa, Ontario, Canada in the spring and summer of 2005 and 2006. We surveyed 36 permanent ponds in 2005 and a 23 pond subset of these in 2006 (Fig. 1). Ponds were at the center of 1500 m radius landscapes with varying amounts of forest cover and traffic density. Fifteen hundred metres contains the dispersal range of most species examined (Oldham, 1966; Schroeder, 1976; Berven and Grudzien, 1990; Seburn and Seburn, 1998). Sampling ponds were at least 3 km apart to avoid overlap of landscapes and thus avoid pseudoreplication. To minimize the correlation between forest and traffic, we selected ponds in four landscape types: low forest/low traffic, low forest/high traffic, high forest/low traffic, and high forest/high traffic (Fig. 2). 'Low forest' landscapes had ⩽35% forest cover and 'high forest' landscapes had ⩾60% forest cover within 1500 m of the pond. 'Low traffic' landscapes contained only two-lane municipal and county roads (paved and unpaved), and 'high traffic' landscapes contained at least one major intercity highway or motorway within 1500 m of the pond (Appendix A).

2.2. Anuran field surveys

Nine anuran species are present in the study area: wood frog (*Rana sylvatica*), spring peeper (*Pseudacris crucifer*), western chorus frog (*P. triseriata*), northern leopard frog (*R. pipiens*), American toad (*Bufo americanus*), gray treefrog (*Hyla versicolor*), green frog (*R. clamitans*), mink frog (*R. septentrionalis*) and bullfrog (*R. catesbeiana*).

In 2005 we conducted three visual day surveys and eight auditory night chorus surveys to assess the relative population sizes of all anuran species at or near the sample ponds. Chorus surveys were conducted between April 12 and July 27, with at least two surveys during each species' peak breeding season. Chorus surveys followed a modified version of the Marsh Monitoring Protocol (Bishop et al., 1997). Surveys started 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 four abundance classes: 0 – no individuals calling; 1 – individuals can be counted and calls are not overlapping; 2 – calls of <15 individuals, some overlap of calls; 3 – calling individuals too numerous to count or ⩾15 individuals calling, calls over-

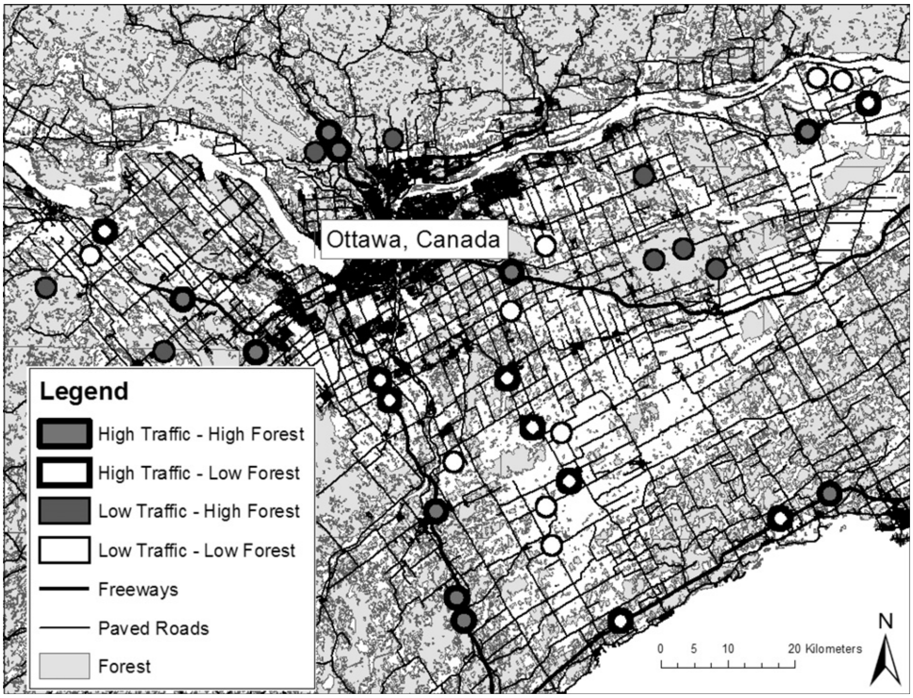


Fig. 1 – Study area, showing all sites (*n* = 36) surrounded by a buffer 1500 m in radius.

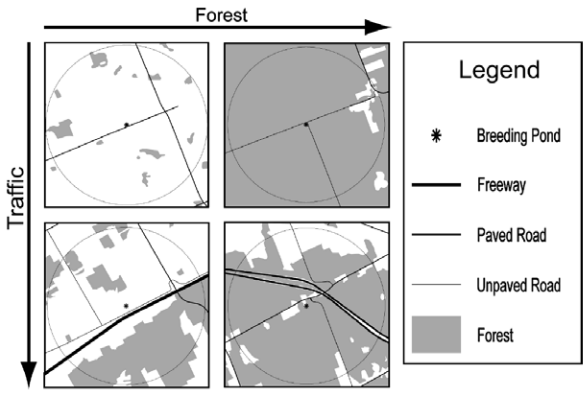


Fig. 2 – Sampling design, with an example of each of the four types of landscapes: low forest–low traffic, high forest–low traffic, low forest–high traffic, high forest–high traffic. Only four of the 36 landscapes are shown.

lapping. The ponds were divided into nine survey routes, and were surveyed over four nights that were as close to consecutive as weather conditions permitted. Surveys were only conducted on warm evenings (average survey temperature April to mid-May 8.3 °C ± 3.3 SD; mid-May to mid-June 16.0 °C ± 5.6 SD; July 22.2 °C ± 2.6 SD) with little wind (average Beaufort wind scale reading 0.93 ± 1.14 SD). The order in which the routes were done within a survey was randomized, and the order in which ponds were surveyed within a route was alternated among forwards, backwards, starting at the middle of the route and moving forwards, and starting at the middle and moving backwards, to vary the survey time for each pond. One pond was only surveyed seven times due to lack of access for the last survey. In 2006, we conducted eight chorus surveys of the 23 pond subset. The only difference in the protocols between 2005 and 2006 was that we divided the ponds into six routes in 2006, rather than the nine routes we used in 2005. One pond was only surveyed seven times in 2006.

We conducted the visual surveys between 3 May and 12 June 2005 to correspond with the peak breeding season of leopard frogs and green frogs (Carr and Fahrig, 2001). While we recorded all anurans seen during the surveys, we focused on green frogs and leopard frogs as visual surveys produce better relative abundance estimates for green frogs than call surveys (Nelson and Graves, 2004), and leopard frog presence may be underestimated from call surveys alone (de Solla et al., 2005). Each survey was conducted between 09:00 and 18:00 h over 4 days. Adult and juvenile frogs were counted as a surveyor slowly walked along the pond edge or through shallow emergent vegetation. The time spent at each pond varied from 9 to 108 min, with more time spent at ponds with greater perimeter and higher amounts and densities of emergent vegetation. We did not perform visual surveys in 2006 due to logistic constraints.

2.3. *Landscape and local variables*

We quantified three landscape variables – percent forest, percent wetland, and traffic density – in nested landscapes of 100–2000 m radii from the edge of the sampling ponds at 100 m intervals. We obtained forest and wetland cover in the landscapes from digital 1:50,000 Natural Resources Canada topographic maps; wetland cover was included to control for its effect on anuran populations (e.g. Vos and Chardon, 1998; Findlay et al., 2001). We obtained digital maps of all public roads from the National Road Network of Canada vector road datasets for Ontario and Quebec (Natural Resources Canada, 2003). We obtained traffic volumes, measured as average annual daily (24-h) traffic (AADT), for most roads from the City of Ottawa transportation department, the City of Gatineau transportation department, the Regional Municipality of Ottawa-Carleton transportation department, township and county public works departments, and the Ontario and Quebec Ministries of Transportation. However, for some roads AADT counts did not exist. When these roads were minor, we estimated 250 AADT for two-lane gravel roads, 25 for one-lane gravel roads, 500 for paved roads, and 50 for dead-end roads (paved or gravel), based on AADT counts for similar roads in the study area. We also did traffic counts for seven mid-sized (paved, two-lane, centre-line) roads for two 15 min periods on consecutive weeknights between 1900 and 2130 h. These counts were immediately preceded or followed by 15 min traffic counts on roads with known AADT counts. We then estimated AADT for the roads with unknown traffic volumes by assuming the same ratio of the 15 min count to AADT as for the roads with known AADT. The values for the two nights were averaged. We calculated traffic density ($\sum$AADTm/m^2) in each landscape as the length of each road in the landscape multiplied by its traffic volume, summed over all the road segments in the landscape, divided by the landscape area (Carr and Fahrig, 2001). GIS analyses were done using ArcGIS 9.0 (Environmental Systems Research Institute, Redlands, California, USA).

We quantified six local pond variables to control for their effects in the statistical models: average conductivity, average pH, pond perimeter, percent cover of emergent and floating vegetation within 2 m of the pond edge (all measured in spring/summer 2005), amount of overhanging vegetation and degree of insolation (sun exposure) (measured in 2006). Conductivity and pH, which can significantly affect anurans (e.g. Weyrauch and Grubb, 2004; Babbitt et al., 2006), were measured at four points at each pond. Pond perimeter, which is positively correlated with species richness (Hecnar and M'Closkey, 1998), was measured using a handheld GPS unit with sub-meter resolution (Trimble GeoExplorer, Trimble Navigation Ltd., Westminster, Colorado USA). Overhanging vegetation may provide calling sites for treefrogs, and also affects the amount of sunlight at a pond, which, together with the amount of emergent and floating vegetation near the pond edge has been shown to affect leopard and green frog abundances (Pope et al., 2000; Carr and Fahrig, 2001). These variables were measured with systematic surveys using line transects perpendicular to the pond edge at evenly spaced intervals (19 m, 38 m, 56 m or 76 m) using a modification of the protocol of Gagné and Fahrig (2007). Between 4 and 15 transects were taken at each pond, depending on pond size, and incorporating all habitat types at the pond edge. At each transect we recorded whether or not there were trees overhanging the pond edge, degree of insolation within 2 m of the pond edge (full sun all day, shaded part of the day, shaded all day), emergent vegetation and surface vegetation percent cover at 1 m and 2 m from the pond's edge. We averaged the values for each variable over all transects at each pond.

2.4. Statistical analysis

Chorus surveys are a good relative abundance indicator for many anuran species (Shirose et al., 1997; Stevens and Paszkowski, 2004). We used summed chorus counts as the response variable for all species except leopard frogs and green frogs (reasons below). Summed chorus counts give weight to ponds with both consistent calling and high numbers of calling individuals (Pope et al., 2000). However, de Solla et al. (2005) showed that chorus surveys alone can underestimate leopard frog presence. Thus, in 2005 for leopard frogs, we used summed chorus counts, but if no leopard frogs were heard calling but at least one individual was seen during a day survey, we recorded a count of one rather than zero, to indicate a small breeding population. Since visual surveys have been shown to provide better green frog population estimates than chorus surveys (Nelson and Graves, 2004) and this species is very conspicuous in visual surveys (Hecnar and M'Closkey, 1997a), we used the maximum number of adults seen at a pond during the visual surveys as the response for this species in 2005. Only six anuran species were sufficiently common for species-level analyses. Species richness was defined as the total number of anuran species seen or heard during all surveys at each pond in 2005, and the total number of anuran species heard during call surveys at each pond in 2006.

We used generalized linear models (GLMs) to determine the relative effects of traffic density and forest amount on species richness and relative abundances of individual species. We used the *glm* function in R 2.2 (R Development Core Team, 2005), and the *glm.nb* function in the *MASS* package (Venables and Ripley, 2002) in R 2.2. We used a Gaussian, Poisson or negative binomial link function depending on the response distribution of each species. Model assumptions were checked by examining the model deviance residuals as well as the partial residual plots for significant and borderline significant predictors. The green frog numbers were log-transformed to fit the normality assumption of the Gaussian model.

Statistical models were built for species richness and for each species at each of the 20 spatial scales. Each model included traffic density, percent forest and percent wetland as predictors. In addition, the statistical models for each species included any local pond variable that was significant at $\alpha = .05$ in the last step of a stepwise multiple regression with all local variables (Table 1), using the *stepAIC* function in *MASS*. We compared the relative effects of traffic and forest by comparing the deviance explained by each term after controlling for the effects of all other predictors. The significance ($\alpha = .05$) of the explained deviance was tested using a χ^2-test for the Poisson and negative binomial models, and an *F*-test for the Gaussian models with the *Anova* function in the *car* package in R 2.2 (Fox, 2006). We also calculated the percentage of deviance explained by traffic and forest (the explained deviance of the term divided by the null deviance of the model (Crawley, 1993)) as an estimate of the predictor's explanatory power.

We built statistical models as described above using just the 2005 data. We then ran the same models using the 2006 data to ensure that the patterns we found in 2005 were not simply a statistical artifact of the year in which sampling occurred.

3. Results

All nine anuran species in the regional species pool were present at our sites. Occurrence frequencies are given in Appendix

Table 1 – Model structure of GLM models for determining the relative effect of traffic density and forest cover (2005 data)

Species	Type of model	Response	Local predictors	Landscape scale predictors
Wood frog	Poisson	SC	Conductivity, floating vegetation, emergent vegetation	Wetland, forest, traffic
Spring peeper	Gaussian	SC	pH, pond perimeter	Wetland, forest, traffic
American toad	Negative binomial	SC	None	Wetland, forest, traffic
Leopard frog[a]	Poisson	MSC	Pond perimeter, overhanging vegetation, surface vegetation	Wetland, forest, traffic
Gray treefrog	Negative binomial	SC	Pond perimeter	Wetland, forest, traffic
Green frog[b]	Gaussian	Max # of adults	None	Wetland, forest, traffic
Species richness[c]	Gaussian	species richness	Pond perimeter	Wetland, forest, traffic

The same model structure was used with the 2006 data unless indicated otherwise. *Notes:*SC, summed chorus counts; PA, presence/absence; MSC, modified summed chorus counts (summed chorus count, unless no frog was heard, but at least one was seen during a day survey in which case a value of 1 is recorded rather than 0).

a In 2006 the response was summed chorus counts.

b In 2006 the response was summed chorus counts and a Poisson model was used.

c In 2005 the response was number of species seen or heard in visual and chorus surveys. In 2006 the response was based only on the number of species heard in chorus surveys.

B. Species richness ranged from 3 to 7 species per pond in 2005 (average 5.1 ± 1.19 SD) and from 2 to 6 species in 2006 (average 4.6 ± 1.19 SD). The range of the percentage of forest and traffic density in the landscape at all spatial scales was 1–99% and 0.1–21.5$\sum$AADTm/m^2, respectively, and the correlation between them was less than ±0.20 at all scales (Appendix C).

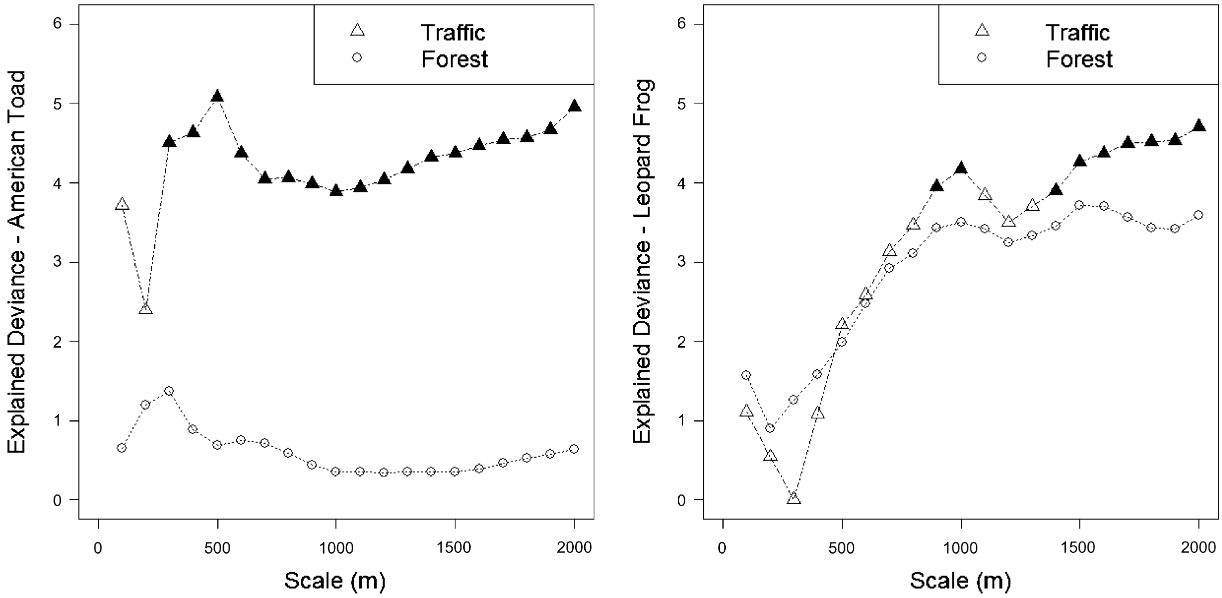
The association between species richness and traffic density was more than three times the association between species richness and forest cover in the landscape (Fig. 3). Statistical models were built for six individual species (wood frog, spring peeper, leopard frog, American toad, gray treefrog and green frog). For American toad, leopard frog and gray treefrog, relative abundance was more strongly associated with traffic density than with percentage of forest in the landscape (Fig. 3). Green frog relative abundance was approximately equally associated with traffic density and forest cover. Spring peeper and wood frog abundances were much more strongly associated with forest cover than with traffic density (Fig. 3).

In 2005, we found significant negative associations between traffic density and species richness ($P = 0.0003$, partial $R^2 = 0.34$ at the 500 m scale), and the relative abundances of American toads ($P = 0.024$, 12.3% deviance explained at the 500 m scale) and leopard frogs ($P = 0.03$, 7% deviance explained at the 2000 m scale). There were borderline significant negative associations between traffic density and relative abundances of green frogs ($P = 0.058$, partial $R^2 = 0.11$ at the 300 m scale), wood frogs ($P = 0.067$, 7% deviance explained at the 2000 m scale), and gray treefrogs ($P = 0.097$, 5% deviance explained at the 200 m scale). There were significant positive associations between forest cover and relative abundances of spring peepers ($P = 0.0006$, partial $R^2 = 0.33$ at the 100 m scale) and wood frogs ($P = 0.018$, 12% deviance explained at the 100 m scale). Species richness ($P = 0.075$, partial $R^2 = 0.10$ at the 500 m scale), and green frog abundance ($P = 0.09$, partial $R^2 = 0.08$ at the 400 m scale) showed borderline significant positive associations with forest cover. We observed a borderline significant negative association between leopard frog relative abundance and forest cover ($P = 0.054$, 6% deviance explained at the 1500 m scale) (Fig. 3). The abundances of all six common species were negatively correlated with traffic in 2005, but both positive and negative relationships between species abundances and forest cover in the landscape were present (Fig. 4).

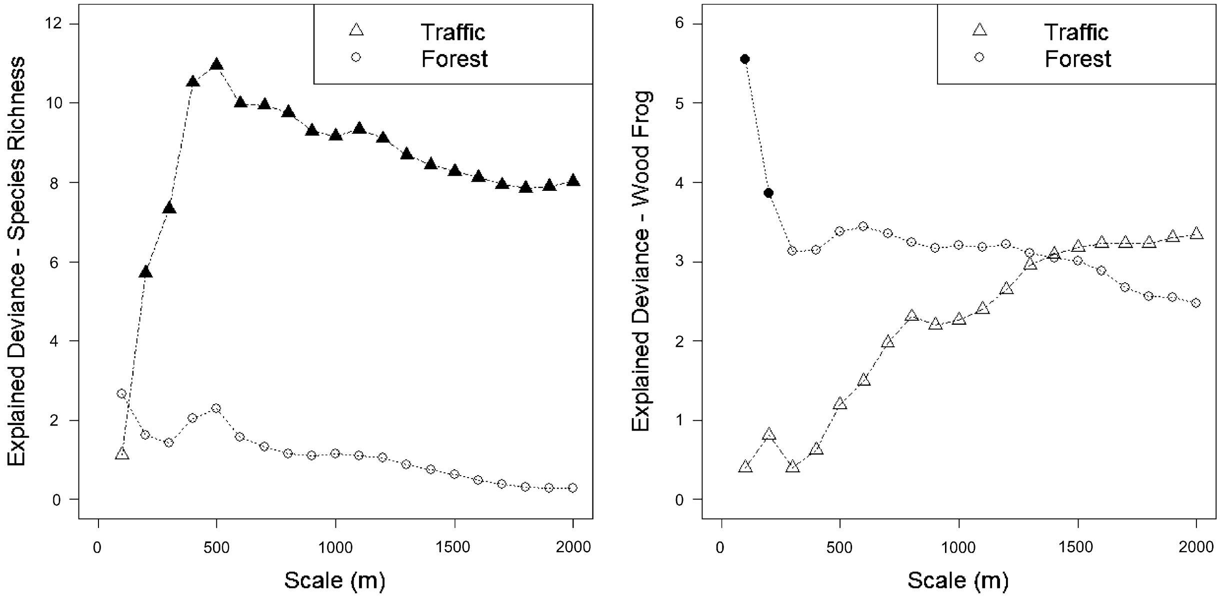
Results from 2006 (Appendix D) were generally consistent with those from 2005 (Fig. 3), with no change in the relative effects of traffic and forest for any species or for species richness. However, wood frogs showed a much stronger positive association with forest cover in 2006 (56% deviance explained at the 100 m scale) than in 2005 (12% deviance explained at the 100 m scale). Wood frogs also showed a significant positive association with traffic in 2006 ($P = 0.017$, 15% deviance explained at the 100 m scale), but a (non-significant) negative association with traffic at all scales in 2005. In addition, leopard frogs were not significantly associated with traffic density in 2006, unlike in 2005. Finally, American toad abundance was significantly negatively associated with forest cover in 2006 ($P = 0.037$, 13% deviance explained at the 100 m scale) but not in 2005.

4. Discussion

This is the first study to evaluate the relative importance of road traffic and forest cover on amphibian species richness and abundance. We found that the negative effect of traffic on anuran populations in eastern Ontario is at least as large as the effect of forest cover in the landscape. We expect that similar patterns would be found throughout eastern Canada and the northeastern United States. Our findings confirm the suggestions of Houlahan and Findlay (2003) and Cushman (2006) that the detrimental effect of roads on amphibians can be as severe as the effect of deforestation, and strengthen the case (Fahrig et al., 1995; Vos and Chardon, 1998; Hels and Buchwald, 2001) that landscapes with low traffic are required for anuran conservation. However, our results also show that the relative importance of traffic density and forest cover varies enormously among species. Traffic density generally had a larger impact than forest cover on the relative abundances of species with weak or negative affinities with forest cover in



Negative response to forest and negative response to traffic

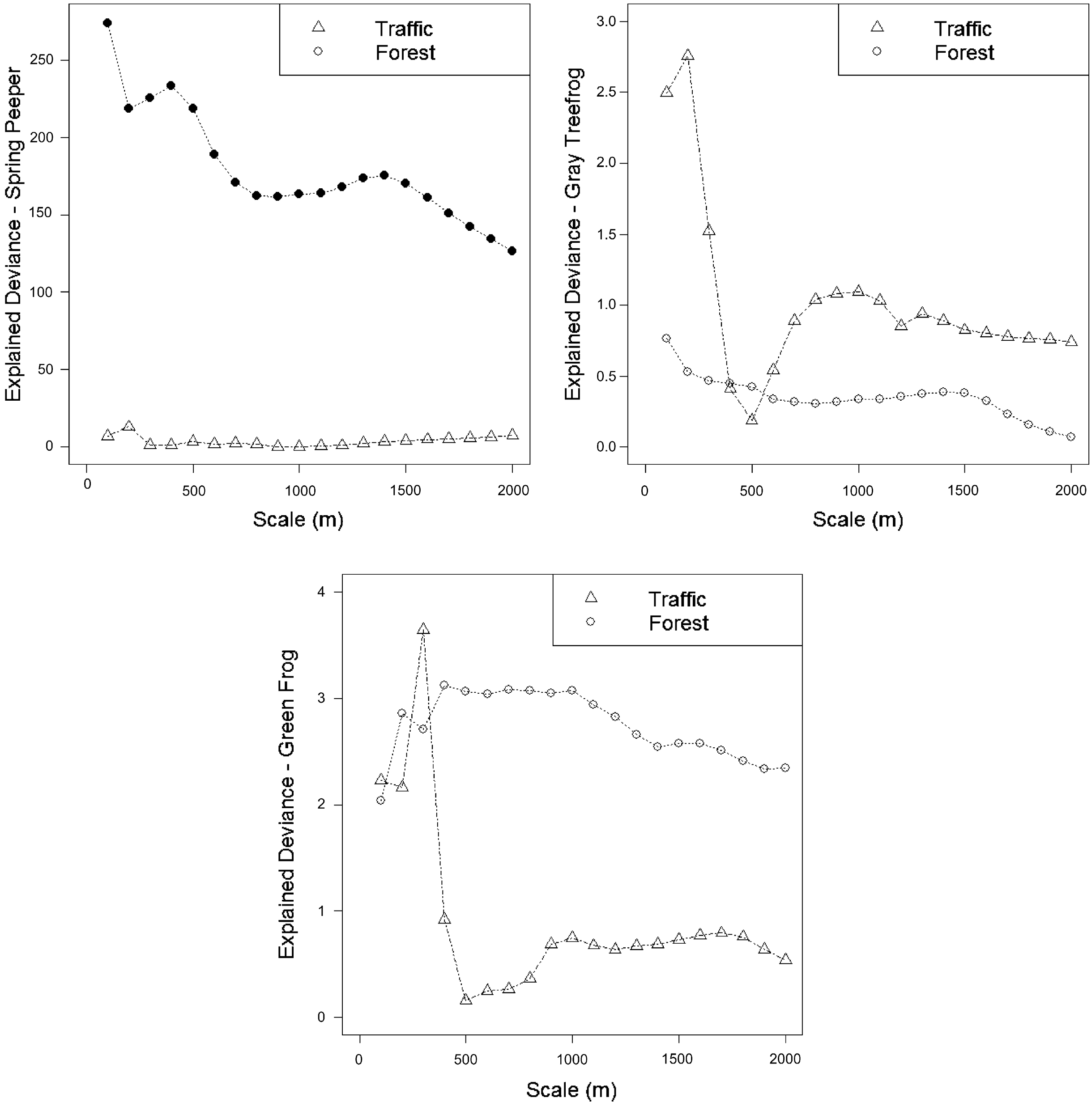


Positive response to forest and negative response to traffic

Fig. 3 – Relative effects of traffic density and forest cover at 100–2000 m radius (scale) from the edge of sampling ponds (2005 data; *n* = 36). Panels are organized according to the type of response of each species or species richness (positive or negative) to the two predictors. The filled-in symbols indicate significant effects at $\alpha = .05$; hollow symbols are non-significant. Note that explained deviance should not be compared between species.

the landscape, while for the two forest specialist species, the positive association between forest cover and relative abundance was much stronger than the negative association with traffic density.

A major and somewhat unexpected finding was that the negative association between anuran species richness and traffic density was much larger than the positive association between species richness and forest cover. Generally, positive associations between species richness and forest cover are at least as large as negative associations with road density (Hecnar and M'Closkey, 1998; Findlay et al., 2001; Houlahan and Findlay, 2003). Lehtinen et al. (1999) do show that road density is the best predictor of species richness in Minnesota, but many of the landscapes in this study had high amounts of urbanization, which is usually correlated with paved road density. It is likely that the very strong impact of roads on spe-



Positive response to forest and negative response to traffic

Fig. 3 – *continued*

cies richness we observed is because we used traffic density, a more precise measure of road effects on anurans than road density (Fahrig et al., 1995).

The weak positive association of species richness with forest cover (also found by Knutson et al., 2004) was due to different species showing positive and negative associations with forest cover (Gagné and Fahrig, 2007). In most studies forest cover in the landscape has a strong positive association with amphibian species richness (Hecnar and M'Closkey, 1998; Kolozsvary and Swihart, 1999; Lehtinen et al., 1999; Findlay et al., 2001; Houlahan and Findlay, 2003; Herrmann et al., 2005). Some of these relationships may be partly due to correlations between forest cover and roads or traffic (Houlahan and Findlay, 2003). Differences in the observed effects of forest cover on species richness may also be due to variations in forest configuration in the landscape (Guerry and Hunter, 2002), or regional differences in forest cover between studies (Hecnar and M'Closkey, 1998).

Most species showed the highest associations with forest cover and/or traffic within 500 m of the breeding ponds, indicating that this is the scale at which most anurans in the study area interact with the landscape surrounding breeding pools. This is similar to the 750 m scale of effect found by Vos and Chardon (1998) and Findlay et al. (2001), but less than the 2–3 km scale observed by Houlahan and Findlay (2003) and Price et al. (2004). However, we found that the association

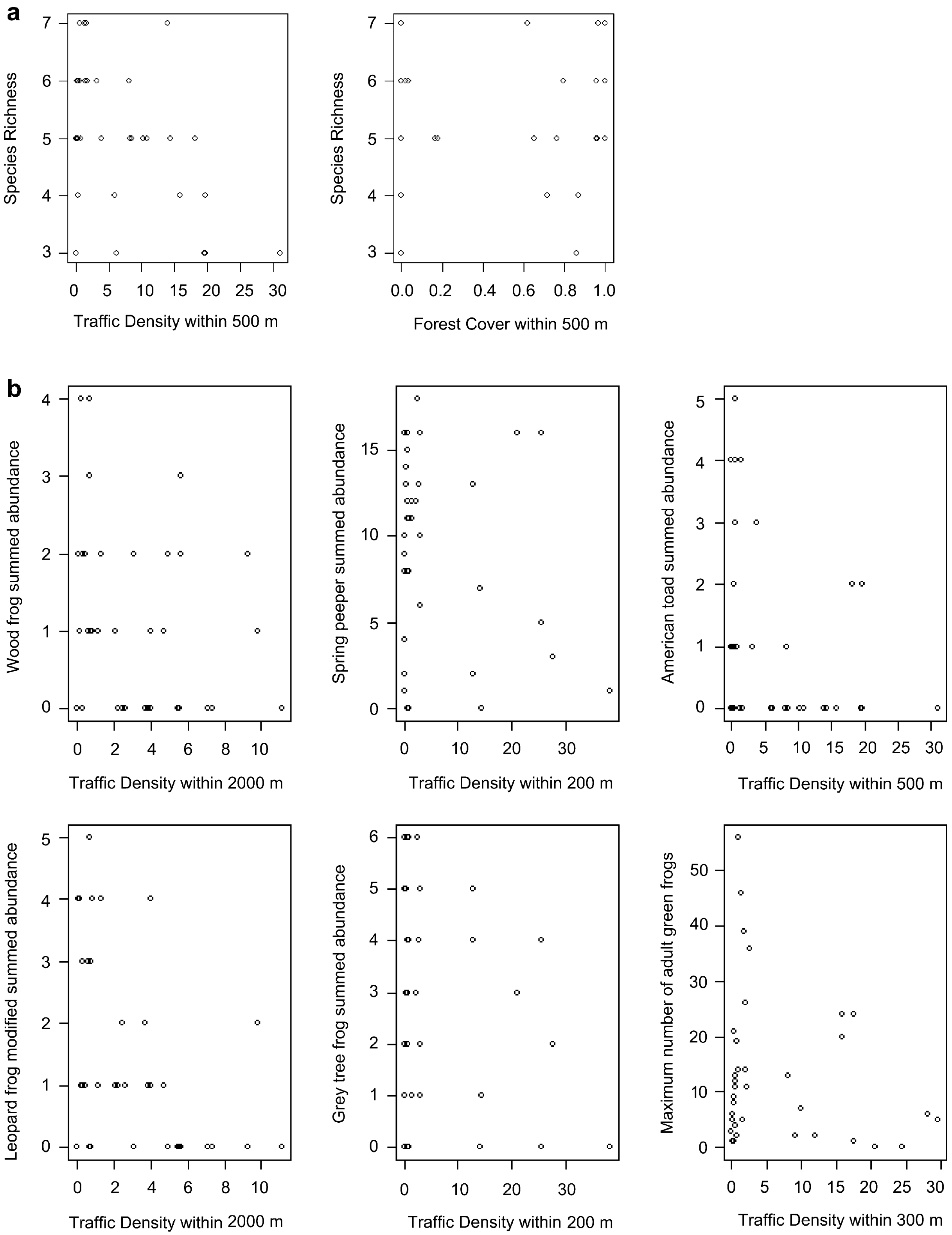


Fig. 4 – The relationship species richness and traffic density ($\sum$AADTm/m^2) and percent forest cover (a); the relationship between the relative abundance of six species of anurans and traffic density (b) and forest cover (c). All relationships are shown at the scale of the maximum effect for each species (2005 data).

between traffic density and leopard frog abundance peaked at the 2 km scale, which is similar to the findings of Carr and Fahrig (2001).

American toads and leopard frogs, the two species which were significantly negatively associated with traffic density in this study, also showed weak negative associations with

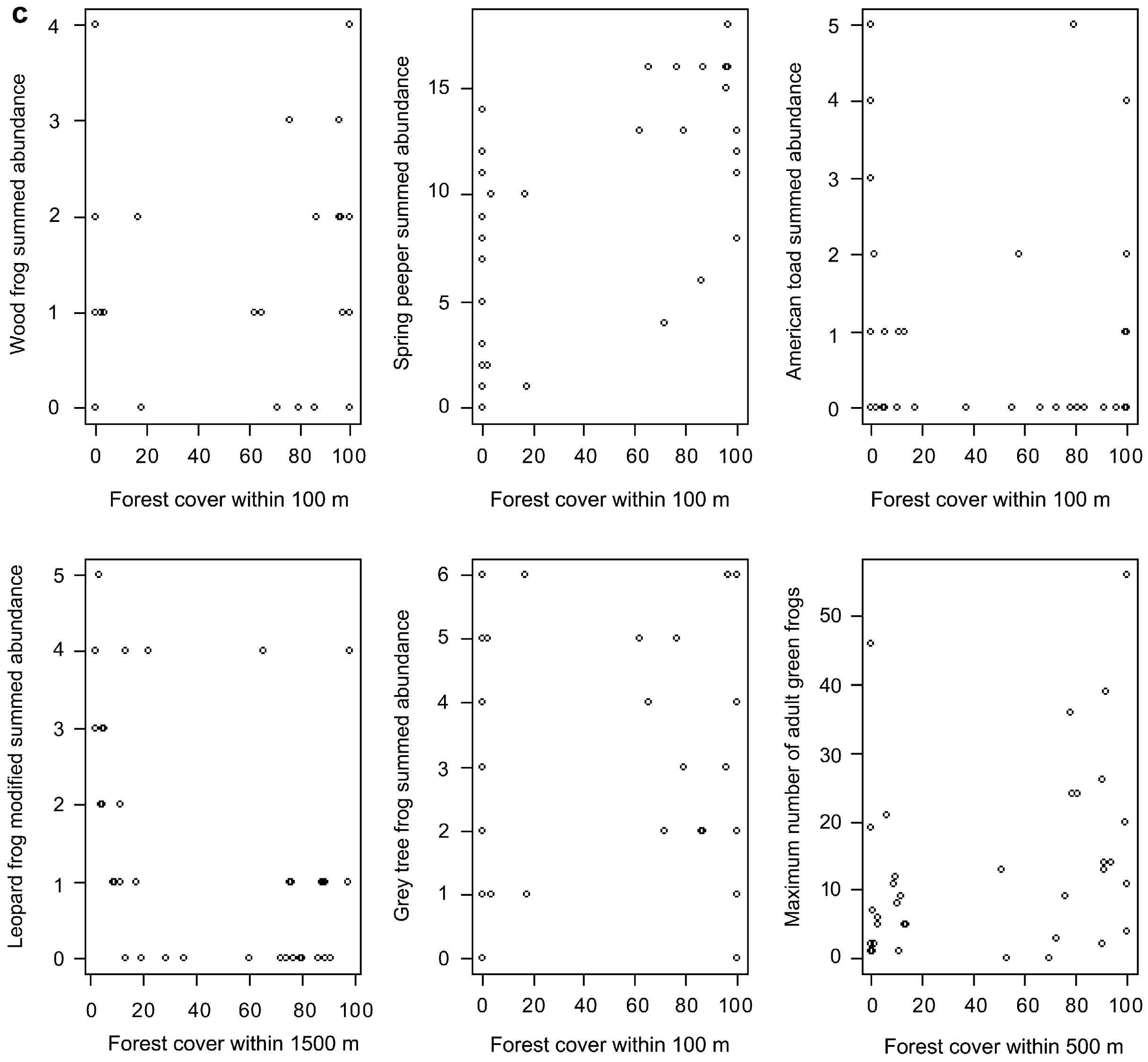


Fig. 4 – *continued*

forest cover in the landscape. Both toads and leopard frogs are known to be vagile, dispersing up to 5–6 km (Hamilton, 1934; Seburn and Seburn, 1998). Toads commonly use landscapes up to 1 km from breeding ponds (Forester et al., 2006), while leopard frogs are thought to routinely move up to 8 km during yearly migrations (Seburn and Seburn, 1998). It is thus not surprising that both species are vulnerable to high traffic densities in the landscape, and indeed other studies found that the related European toad *Bufo bufo* is vulnerable to traffic mortality (e.g. Van Gelder, 1973; Schlupp and Podloucky, 1994) and that leopard frogs are negatively affected by traffic density in the landscape (Carr and Fahrig, 2001). While both toads and leopard frogs have been shown to have a negative affinity with forest cover (Guerry and Hunter, 2002; Gagné and Fahrig, 2007), positive associations with forest cover also exist for both (Gibbs et al., 2005; Houlahan and Findlay, 2003), so the weak negative associations we saw in this study with forest cover for these two species are not surprising.

Although we did not find a significant association between green frog or gray treefrog abundances and traffic density, there is probably a biologically significant negative effect of very high traffic densities on these species, which would have been apparent if we had more ponds in landscapes with very high traffic densities (see Fig. 4b). This suggests that high traffic roads can have negative effects on species that are relatively unaffected by moderate traffic densities, as both green frogs and gray treefrogs are known to be largely unaffected by paved road densities in the landscape (Trenham et al., 2003; Weyrauch and Grubb, 2004) (but see Houlahan and Findlay, 2003). However, Carr and Fahrig (2001) found that traffic had no significant effect on green frog populations; again it is possible that traffic densities were not sufficiently high in this study to demonstrate a negative effect. The lack of a significant association between the abundance of these two species and forest cover is supported by the literature (Trenham et al., 2003; Herrmann et al., 2005; Gagné and Fahrig, 2007), though positive associations with forest cover also exist for both species (e.g. Houlahan and Findlay, 2003).

The strong positive association between the abundance of spring peepers and wood frogs and forest cover in the landscape, and the lack of a significant association with traffic density in the landscape are both supported by the literature. Both species have strong positive associations with forest cover (Hecnar and M'Closkey, 1998; Houlahan and Findlay, 2003; Regosin et al., 2003; Homan et al., 2004; Porej et al., 2004), while only two studies (Findlay et al., 2001; Houlahan and Findlay, 2003) indicate significant negative associations with traffic for these species. We are unable to explain our significant positive relationship between traffic density and wood frog abundance in 2006. A previously published positive association between paved road density and wood frog occupancy (Trenham et al., 2003) suggests that our result is not a statistical artifact, and that some feature associated with high traffic roads (perhaps roadside ditches) has a positive effect on wood frog abundance.

We are confident that we correctly identified the relative importance of the effects of traffic density and forest cover on anuran species richness and relative abundances, as there was no change in relative effects from 2005 to 2006. However, wood frogs, leopard frogs, and American toads all showed between-year differences in the magnitude of their associations with traffic and/or forest cover. The 2006 results for wood frogs are likely to be more accurate than the 2005 results, because the early spring of 2005 was characterized by large temperature fluctuations resulting in unusually erratic and localized peaks in wood frog breeding and calling activity (Fred Schueler, pers. comm.). The lack of an association between leopard frog abundance and traffic density in 2006 was surprising, as in addition to the significant negative association with traffic density we observed in 2005, Carr and Fahrig (2001) also showed a negative association for this species. Leopard frogs were more abundant in 2006 than in 2005, indicating that this species may establish populations in high traffic landscapes during peak years, which are then unable to persist due to the high traffic. We have no explanation for why we observed a significant negative association between American toads and forests in 2006, but not in 2005.

Predatory fish negatively affect many anurans (Hecnar and M'Closkey, 1997b; Smith et al., 1999), and as we were unable to control for their presence, it is possible that this may have confounded our results. We compensated for this by including all calling from within 100 m of the pond edge, as fish-free vernal pools and wetlands were nearly ubiquitous in the forests near our ponds. Vernal pools are important breeding habitat for the anurans in our study region that are also the most negatively affected by predatory fish – wood frogs, spring peepers, and gray treefrogs (Hecnar and M'Closkey, 1997b; Skelly et al., 1999). It is, however, possible that the relatively weak relationship we observed between traffic density and leopard frog abundance as compared to Carr and Fahrig (2001) is due to a correlation between traffic density and fish presence, as the latter study was conducted entirely in fish-free ponds and leopard frogs rarely use vernal pools as breeding sites.

This study has important implications for conservation. Our results show that landscapes with low traffic densities – especially within 500 m of breeding ponds – are vital for anuran conservation in our area. Landscapes with high forest cover within 100 m of breeding ponds are also crucial for wood frog and spring peeper population maintenance, and even heavily forested landscapes with moderate traffic densities should have some conservation value for the maintenance of these forest obligate species. However, the conservation value of landscapes with low forest cover will be greatly reduced if traffic densities are high within 2000 m of breeding ponds, as the species particularly associated with open habitats – American toads and leopard frogs – are also the most vulnerable to road traffic. In conclusion, we agree with Gagné and Fahrig (2007) that a mosaic of high and low forest landscapes surrounding wetlands is needed for anuran conservation, but add that land managers should ensure that at least some ponds and wetlands are away from high traffic roads for the maintenance of high regional anuran diversity.

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Appendix A. Supplementary data

Supplementary data associated with this article (Appendices A, B, C and D) can be found, in the online version, at doi:10.1016/j.biocon.2007.08.025.

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