

UC Davis

Recent Work

Title

Effect of road traffic on two amphibian species of differing vagility

Permalink

<https://escholarship.org/uc/item/16p368zz>

Authors

Carr, Laurie W.

Fahrig, Lenore

Publication Date

2001-08-04

Peer reviewed

Effect of Road Traffic on Two Amphibian Species of Differing Vagility

LAURIE W. CARR AND LENORE FAHRIG

Ottawa-Carleton Institute of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada, email lfahrig@ccs.carleton.ca

Abstract: *Vehicular traffic can be a major source of mortality for some species. Highly vagile organisms may be at a disadvantage in landscapes with roads because they are more likely to encounter roads and incur traffic mortality. To test this prediction, we assessed the population abundance of two anuran species of differing vagility, the leopard frog (*Rana pipiens*, more vagile) and the green frog (*Rana clamitans*, less vagile), at 30 breeding ponds. Traffic density, an index of the amount of potential traffic mortality, was measured in concentric circles radiating from the ponds out to 5 km. We conducted multiple linear regressions relating population abundance to traffic density, pond variables, and landscape habitat variables and found that leopard frog population density was negatively affected by traffic density within a radius of 1.5 km. There was no evidence that the presence of vehicular traffic affected green frog populations. These results suggest that traffic mortality can cause population declines and that more vagile species may be more vulnerable to road mortality than less vagile species.*

Efectos del Tráfico Carretero sobre Dos Especies de Anfibios de Diferente Movilidad

Resumen: *El tráfico vehicular puede ser una causa importante de mortalidad para algunas especies. Organismos altamente móviles pueden estar en desventaja en paisajes con carreteras, debido a que su probabilidad de encontrar carreteras e incurrir en mortalidades por tráfico es mayor. Para probar esta predicción, evaluamos la abundancia de dos especies de anuros de diferente movilidad, la rana leopardo (*Rana pipiens*, más móvil) y la rana verde (*Rana clamitans*, menos móvil), en tres estanques de reproducción. La densidad del tráfico como un índice de la cantidad potencial de mortalidad por tráfico fue medida en círculos concéntricos radiando de los estanques hacia afuera y hasta los 5 km. Llevamos a cabo regresiones lineales múltiples relacionando la abundancia poblacional con la densidad del tráfico, las variables del estanque y las variables del hábitat del paisaje. Encontramos que la población de rana leopardo estuvo negativamente afectada por la densidad del tráfico dentro de un radio de 1.5 km. No hubo evidencias de que la presencia de tráfico vehicular afectó a las poblaciones de rana verde. Estos resultados sugieren que la mortalidad por tráfico puede ocasionar declinaciones poblacionales y que las especies más móviles pueden ser más vulnerables a la mortalidad carretera que las especies menos móviles.*

Introduction

The presence of vehicular traffic and the continuous, linear nature of roads can be a significant physical barrier to movement for many species (small mammals: Oxley et al. 1974; Garland & Bradley 1984; Mader 1984; Merriam et al. 1989; snails: Baur & Baur 1990; arthropods: Mader et al. 1990) and a major source of mortality. For

example, over 2 years, 32,000 amphibians, reptiles, birds, and mammals were found as roadkill on the 3.6-km Long Point causeway adjacent to Big Creek Wetland, Lake Erie, Canada (Ashley & Robinson 1996). Ehmann and Cogger (1985) estimate that road traffic kills 5.48 million reptiles and frogs in Australia each year. The loss of individuals due to traffic mortality can have an effect on two levels: reduced population sizes and reduced movement between complementary resources and conspecific populations (Carr et al. 2000). As barriers to movement, roads create smaller patches and increase patch isolation. Smaller

Paper submitted February 4, 2000; revised manuscript accepted September 26, 2000.

populations are at a greater risk of extinction by chance from demographic, genetic, and environmental stochastic events (Wilcox & Murphy 1985; Schoener & Spiller 1992). Isolated populations also have a higher chance of extinction without the demographic and genetic input of immigrants and a lower chance of recolonization after extinction (Lande 1988; Sjögren-Gulve 1994).

Roads and traffic mortality are ubiquitous in landscapes modified by humans. The survival of populations in such landscapes depends on the interaction between the spatial pattern of roads and the dispersal characteristics of the organisms (Fahrig & Grez 1996). One such dispersal characteristic is vagility. *Vagility* is defined as “the inherent power of movement possessed by individuals” (Allaby 1994). We used this term instead of *dispersal distance* or *dispersal capability* because it encompasses both movement distance and movement frequency. More vagile species are more likely to encounter roads unless there is some behavioral mechanism for road avoidance. We therefore expect a vagile species to be more prone to traffic mortality than a less vagile species.

We examined the effect of road traffic on the population abundance of two sympatric amphibian species of differing vagility, the green frog (*Rana clamitans*, less vagile) and the leopard frog (*Rana pipiens*, more vagile). Anurans are well known victims of vehicular mortality (van Gelder 1973; Fahrig et al. 1995). They are particularly susceptible because their life histories require them to go between habitats, which often means they must cross roads.

Breeding populations of green and leopard frogs are spatially separated (Rittschof 1975; Breden 1987; Berven & Grudzien 1990), and recolonization of areas of local extinction depends on long-distance dispersal of juvenile frogs (Gill 1978; Sjögren 1991; Hecnar and M'Closkey 1996). Both species move seasonally among distinct habitats. Green frogs occupy two different habitats, for overwintering and breeding (Gilhen 1984), and leopard frogs occupy three habitats, for overwintering, breeding, and summer feeding (Merrell 1977). Both species move long distances between these habitats, although once in a habitat they are relatively sedentary (Martof 1953; Dole 1965). Available dispersal information suggests that leopard frogs cover greater distances in the landscape than green frogs because of longer dispersal and migration distances for juveniles and adults, and more frequent movements between habitat types (Dole 1967, 1971; Oldham 1967; Rittschof 1975; Schroeder 1976; Merrell 1977; Hine et al. 1981; Seburn et al. 1997). Therefore, leopard frogs should encounter roads more often than green frogs, and incur greater traffic mortality.

We used population abundance in ponds in relation to traffic density in the surrounding landscapes to compare the effect of roads on leopard frogs and green frogs. We hypothesized that traffic-related mortality is sufficient to negatively affect populations of both species. Because

the leopard frog is a more vagile species, however, it should experience a greater decline in population abundance in relation to traffic density than green frog populations. Our goals were to relate the population abundance of green frogs and leopard frogs to traffic density in the surrounding landscape and to determine the distance at which traffic density has the greatest effect on population abundance.

Methods

We conducted this study in the Ottawa-Carleton region, Ontario, Canada. Agriculture, roads, and urban development have caused loss and fragmentation of forest, and wetland drainage has reduced aquatic habitat from about 45.8% of the Ottawa area in 1890 to about 12.6% in 1982 (Snell 1987).

We surveyed 30 permanent ponds in a region of about 50 × 50 km. To reduce variation in the data due to variation in landscape composition, we chose ponds in similar landscapes (mostly agricultural fields). To reduce pseudoreplication, we selected sample ponds at least 1 km apart and interspersed higher- and lower-traffic ponds as much as possible (Fig. 1). Selected ponds had a clearly defined vegetated edge, were not connected to other ponds or wetlands, and did not support fish. Twenty-nine of the 30 ponds were human-made. We excluded new quarries and concrete pools as potential sites. All ponds were over 10 years of age, except one that was 6 years old.

We conducted two types of population surveys, chorus and visual, to increase the accuracy of estimates of

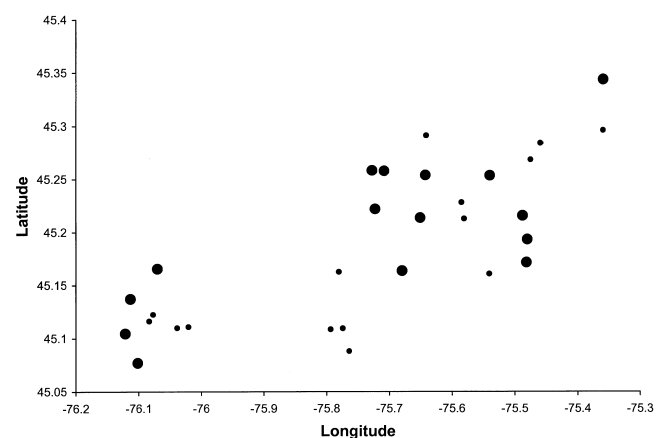


Figure 1. Distribution of the 30 sampled ponds, showing the 15 ponds in lower-traffic landscapes as small circles and the 15 ponds in higher-traffic landscapes as large circles. Ponds were deliberately selected so that higher-traffic and lower-traffic landscapes were interspersed as much as possible.

relative population size. Chorus surveys count the number of calling breeding males, and visual surveys count the number of frogs (male, female, and juvenile) seen in the ponds.

We conducted six chorus surveys during the peak breeding season of leopard frogs, between 17 April and 12 May 1998, and four chorus surveys during the peak breeding season of green frogs, between 1 June and 3 July 1998. The number of surveys completed was twice the number needed to detect presence or absence. For example, there were no new ponds with calling leopard frogs after three surveys, so we conducted six surveys. The number of individual calling leopard and green frog males was counted over a period of 5 minutes for each survey. The ponds were divided into four survey routes that we drove in four different sequences to vary the time of the survey for each pond: forward, backward, or starting from a midpoint and moving forward or backward (Pope 1996). We began the surveys 0.5 hours after sunset and finished them before midnight (Gartshore et al. 1997). We initiated surveys for leopard frogs when the air temperature was $>8^{\circ}\text{C}$ (Hine et al. 1981; Gartshore et al. 1997) and for green frogs at $>21^{\circ}\text{C}$ (Gartshore et al. 1997).

We conducted four visual surveys during the peak breeding season of leopard frogs, between 5 and 17 May 1998, and three visual surveys during the peak breeding season of green frogs, between 11 and 26 June 1998. Ponds were divided into two routes that were covered from 0900 hours to 1700 hours over 2 days. We alternated between driving routes backward and forward to vary survey times for each pond. Leopard and green frogs were counted as a surveyor walked slowly along the waterline, stopping approximately every 2 m to scan the waterline, shore, and water ahead (Olsen et al. 1997). Search effort was proportional to the perimeter of the pond and the density of vegetation. Thick vegetation precluded the scanning method and required the surveyor to adopt a zigzag pattern so that the vegetated area could be searched adequately. We adopted this same pattern when the shore was flooded, making ideal conditions for leopard frogs. We surveyed the entire pond perimeter for each pond, except for two ponds where a portion of the perimeter was impassable. During the day, leopard and green frogs are usually found at the waterline, at the water surface, or in moist vegetation on the shore (Olsen et al. 1997), so they were readily visible. We conducted the surveys on sunny, windless days because cold and windy conditions depress the surface activity of many frog species (Olsen et al. 1997).

We quantified local pond attributes (pH and length of spawning habitat [m]) and landscape attributes (area of forest, forested wetland, human development, agriculture fields, water bodies [km^2] and the length of streams [km]) to control for habitat differences in statistical

models. We used three classes of spawning habitat for leopard and green frogs so as to encompass gradation in habitat quality and to acknowledge that "low-quality" habitat might still constitute suitable habitat. Green and leopard frogs preferentially lay eggs in vegetation in shallow water, with leopard frogs preferring warmer water (Martof 1956; Merrell 1977; Wells 1977; Hine et al. 1981; Gilbert et al. 1994). For leopard frogs, we defined optimal-quality spawning habitat as unshaded, shallow (<65 cm water depth) shoreline with narrow-leaved emergent vegetation; suboptimal habitat as shoreline with emergent vegetation in full sun or shallow water (<65 cm); and low-quality habitat as shoreline that did not meet the criteria for optimal or suboptimal habitat.

For green frogs, we defined optimal spawning habitat as shallow shoreline (<65 cm water depth) with submergent and emergent vegetation, suboptimal habitat as shallow shoreline (<65 cm) that had either submergent or emergent vegetation, and low-quality habitat as shoreline that did not fit the criteria of optimal or suboptimal habitat. We quantified landscape variables within a radius of 1.5 km from the center of the pond. This distance was based on the observation that ponds containing leopard frogs (the more vagile species) are most likely to have sources of summer feeding habitat within 1–1.6 km (Hine et al. 1981; Pope et al. 2000).

The predictor variable of primary interest was traffic density, an index of the potential amount of road mortality. We calculated traffic density in concentric circles surrounding each pond with increasing radii of 0.25, 0.5, 0.75, 1, 1.25, 1.5, 1.75, 2, 2.5, 3, 3.5, 4, 4.5, and 5 km. Traffic density in each circle was calculated as the sum of the length of each road in the circle multiplied by the traffic volume for that road, divided by the area of the circle. Traffic volume was measured as average annual daily (24-hour) traffic (AADT) counts. The AADT counts were supplied by Ottawa-Carleton townships, the Regional Municipality of Ottawa-Carleton Transportation Department, and the Ontario Ministry of Transportation Eastern Region Traffic Section. Road length and landscape variables were measured from digital Government of Canada 1:50,000 topographic maps (1979–1989) through the digitizing feature in MapInfo Pro (MapInfo Corporation 1997).

We summed the frog abundance counts for each of the visual and chorus surveys over all surveys (7 and 10 respectively) to give weight to ponds that had both consistent calling and high calling numbers (Pope et al. 2000). The summed abundance counts were square-root-transformed and then standardized; thus, they followed a distribution with zero mean and unit variance. Population abundance counts from the visual and chorus surveys were correlated for both leopard frogs ($r = 0.43$, $p = 0.0175$) and green frogs ($r = 0.74$, $p < 0.0001$) and were therefore combined to produce one abundance measure for each species in each pond.

To determine the influence of traffic density on the population abundance of green and leopard frogs, we used stepwise multiple linear regression analysis in SAS (SAS Institute 1996). The multiple regression proceeded in three steps: (1) all local and landscape variables (but not traffic density) were included to produce the most significant habitat model; (2) each traffic-density variable was substituted consecutively into the model from step 1 to determine the most significant radius for traffic density in terms of the partial F value; (3) all two-way traffic-density interaction terms were included with the model from step 2 in a stepwise multiple regression. Variables were included in the final model if their partial F value was significant at $\alpha = 0.05$.

Results

Leopard frogs were absent from 4 ponds (no calling or visual records), 12 ponds had no calling, and 5 had no visual records. Green frogs were present in all ponds, but 2 had no calling and 3 had no visual records. Leopard frogs were present in the surveys from 17 April to 26 June; green frogs were present from 5 May to the last survey date of 3 July. For both species, calling was more active during the peak breeding season.

Traffic density within a radius of 1.5 km of the ponds had a significant negative effect on leopard frog abundance ($F_{1,30} = 9.680, p = 0.0046$) (Table 1; Figs. 2 & 3). On the other hand, there was no evidence that green frog abundance was correlated with traffic density at any scale (Figs. 2 & 4). These results supported our hypothesis that the more vagile species (leopard frog) would incur greater population decline with increasing traffic density compared with a less vagile species (green frog). It was unexpected that green frogs did not experience some population decline in relation to traffic density.

Only the length of streams within 1.5 km of the pond contributed significantly (positively) to the observed variation in green frog abundance ($F_{1,30} = 6.787, p = 0.015$). Amount of forested wetland within 1.5 km and pond pH both had marginal significant negative effects on green frog abundance, pH, length of optimal spawning habitat, and interaction between traffic density and

amount of human development had significant effects on leopard frog abundance (Table 1). Increasing pH was related to decreases in leopard frog abundance, whereas increasing length of optimal spawning habitat was related to increases in leopard frog abundance. Examination of the interaction plot for traffic density and human development showed that the negative effect of traffic density on leopard frog abundance was only evident at low levels of development. Traffic density at 1.5 km was significantly correlated with area of water bodies and human development. Length of streams in the landscapes was significantly correlated with area of forest and agricultural fields.

Discussion

Our results qualitatively support our hypothesis, that the more vagile species, the leopard frog, is more strongly affected by road traffic than the less vagile species, the green frog. We hypothesize that green frogs move less through the landscape and therefore are less likely to encounter roads. This remains speculative, however, because of several shortcomings in the available demographic and movement data for these two species.

We selected the two species for this study based on their apparent similarities in demography and their apparent differences in vagility. Available data suggest that green frogs and leopard frogs have similar mean clutch sizes, 3750 and 4000 eggs, respectively (Hecnar & M'Closkey 1997), similar patterns of mortality with respect to age class (Hine et al. 1981; Shirosé & Brooks 1995), similar time to sexual maturity (usually 2 years) (Gilbert et al. 1994; Wells 1977), and decreased larval growth rates in crowded conditions (Gromko et al. 1973; Skelly 1995). These similarities in demography suggest that these two species should have similar capacities for compensating for increased mortality from road traffic, but we have no estimates of demographic parameters of the particular populations in our study. We would need this information to rule out the possibility that some environmental factor(s) unknown to us negatively affect leopard frog population growth rates in our area, making them more vulnerable than green frogs to additional mortality from roads.

Table 1. Analysis of variance of the regression model relating leopard-frog abundance to local, landscape, and traffic-density variables.*

Source of variation	l	df	Type III sums of squares	Partial F	p
Intercept	4.524	1			
pH	-0.616	1	12.317	6.537	0.0170
Amount of optimal leopard-frog habitat	0.016	1	27.978	14.850	0.0007
Traffic density at 1.5 km	-5.4×10^{-05}	1	18.238	9.680	0.0046
Traffic density at 1.5 km \times area of human development at 1.5 km	9.1×10^{-05}	1	9.680	5.138	0.0323

*Model $R^2 = 0.42, p = 0.006, n = 30$.

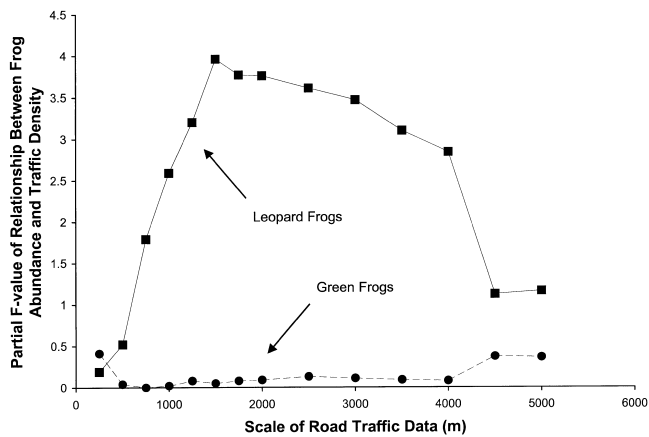


Figure 2. Partial F values for effect of road-traffic density on leopard frog and green frog population abundances in 30 ponds versus scale of landscape (radius) used for traffic-density calculation. Models included other significant habitat variables: pH and amount of optimal leopard frog habitat at the pond edge (for leopard frog models) and length of stream within 1.5 km of the ponds (for green frog models).

The available information on vagility is also limited. Dispersal data are highly sensitive to sampling scheme and landscape characteristics, and to date there has been no study of leopard frog and green frog dispersal at the same site. Therefore it is possible that our a priori categorization of the two species as more and less vagile was incorrect. Furthermore, a low road-encounter rate for green frogs could result if they bypass roads by moving along streams. There are several reports of large amounts of leopard frog road mortality (Bovbjerg &

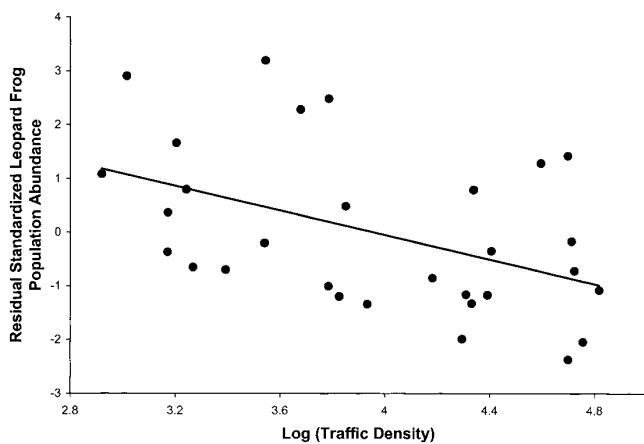


Figure 3. Relationship between traffic density and population abundance of leopard frogs in 30 ponds. Residuals from leopard frog abundance regressed against pH and amount of optimal leopard frog habitat are plotted against traffic density within 1.5 km of the ponds.

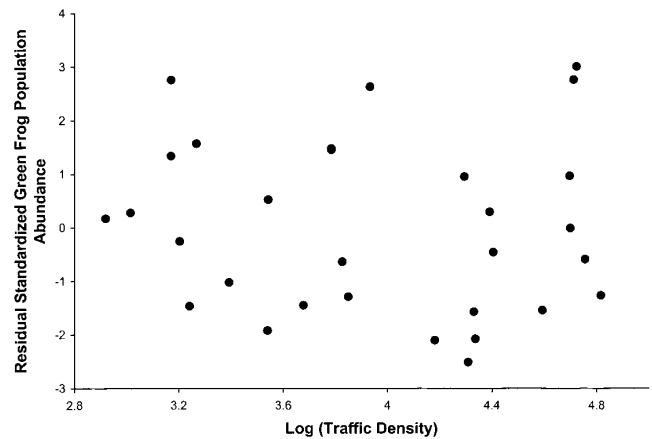


Figure 4. Relationship between traffic density and population abundance of green frogs in 30 ponds. Residuals from green frog abundance regressed against stream length are plotted against traffic density within 1.5 km of the ponds.

Bovbjerg 1964; Rittschof 1975; Merrell 1977; Ashley & Robinson 1996; M. H. Link, unpublished data) but only one report of a relatively small amount of green frog road mortality (Ashley & Robinson 1996). The observed effect of stream length on green frog abundance in our study might provide a clue to green frog movement. Green frogs feed along stream banks (Martof 1953), and drainage ditches have been noted as major dispersal routes for green frogs (Schroeder 1976). Streams bypass roads by crossing under rather than over them and could reduce green frog traffic mortality.

It is also possible that the lack of an apparent effect of traffic density on green frog populations is due to a time-lag between the increase in traffic in the Ottawa region and the effect of traffic on the frog populations. Findlay and Bourdages (2000) suggest that the full effect of roads on herpetile populations could take decades to become apparent if the initial populations were reasonably high. We have no information on historic populations of the two species in our study area.

Because our study is correlational, we cannot say for certain that the significant relationship between traffic density and leopard frog abundance was caused by traffic mortality. Pollution, in the form of vehicular emissions and road runoff that contains toxic chemicals, petroleum, de-icing salts, and sediment, can also have a negative effect on amphibian populations (Mahaney 1994; Lefcort et al. 1998; Welsh & Ollivier 1998). Because traffic density was correlated with developed areas, the observed decrease could also be due in part to increased urbanization. Indirect evidence suggests, however, that traffic mortality per se was at least partly responsible for our results. For example, estimates of the survival rate of toads crossing roads with 24–40 cars per

hour (624–960 AADT) vary from zero (Heine 1987) to 50% (Kuhn 1987). Based on these estimations, at least 30% of roads in our landscapes had traffic volumes sufficient to cause significant amounts of amphibian mortality. Road surveys of migrating amphibians in our study region found a higher proportion of dead frogs and toads on roads with higher traffic intensity (Fahrig et al. 1995). This differential mortality suggests that road mortality at least contributed to our observed decrease in the local population abundance of leopard frogs with increasing traffic density.

Although most fragmentation-amphibian studies have not taken roads into account, a growing body of work suggests that roads negatively affect anuran population persistence (Vos & Chardon 1998). Amphibians appear to be especially vulnerable to traffic mortality because they readily attempt to cross roads, but they are slow-moving and small and thus not easily avoided by drivers. It has been shown that traffic level or density is negatively correlated with (1) abundance of roadside anuran populations (Fahrig et al. 1995), (2) leopard frog (but not green frog) population abundance (our study), and (3) pond-occupation probability of the moor frog (*Rana arvalis*) (Vos & Chardon 1998). Also, the number of roads or paved road density is related to (1) genetic isolation of the common frog (*Rana temporaria*) (Reh & Seitz 1990; Hitchings & Beebee 1997) and the common toad (*Bufo bufo*) (Hitchings & Beebee 1998), (2) herpetile species richness in wetlands (Findlay & Houlahan 1997), and (3) presence of wood frogs (*Rana sylvatica*) and mink frogs (*Rana septentrionalis*) (but not presence of leopard or green frogs) in wetlands (C. S. Findlay et al., unpublished data). The lack of correlation between the presence of leopard frogs and paved road density in the study by Findlay et al. (unpublished data) could be attributed to the fact that road density was not measured beyond 1 km and the response variable was presence or absence, which is a coarser measure than abundance.

We measured traffic density at several different scales to determine the size of the landscape unit with the largest effect on anuran population abundance. Our results suggest that traffic can influence the population abundance of leopard frogs out to at least 1.5 km from the population (Fig. 2). This is similar to the traffic-effect distances of 750 m (Vos & Chardon 1998), 1 km (Findlay & Houlahan 1997), and 2 km (Findlay et al., unpublished data) found in other amphibian-road studies. A road effect out to 1.5 km for leopard frogs implies that the majority of leopard frog movement occurs within this distance. Because leopard frogs are probably the most vagile anuran in Ontario (Hecnar & M'Closkey 1997), a landscape unit of 1.5 km in radius could provide a guideline for measuring the effect of landscape variables on anuran populations in general.

Forman and Alexander (1998) coined the term, *road-effect zone* for the maximum distance at which signifi-

cant ecological effects of roads occur. Forman (2000) estimated that the road-effect zone varies from 200 to 800 m in the United States and that about one-fifth of the U.S. land area is therefore directly affected by road. Our results suggest that leopard frogs are affected by roads up to distances of almost twice Forman's (2000) maximum assumed road-effect zone. This difference may be due to the different approaches used to detect the scale of road effects. Forman used a road-centered approach, whereas we used a habitat-centered (in our case, pond-centered) approach. We suggest that our method allowed us to detect the combined effects on each focal population of all roads in the surrounding landscape. The combined effect of a road network depends on the number of roads and their traffic volumes, and their placement relative to one another and to the various habitats in the landscape (Carr et al. 2000).

Most metapopulation or metapopulation-like models of patchy populations do not directly include the effects of dispersal mortality on population dynamics (e.g., Hanski 1994; With & Crist 1995; Lindenmayer & Possingham 1996). Based on these models, it has become a widely held notion that more vagile species have a higher tolerance to habitat loss and fragmentation than less vagile species. But models that include dispersal mortality predict exactly the opposite: more vagile species should be more vulnerable to habitat loss and fragmentation because they are more susceptible to dispersal mortality (Fahrig 1998; Casagrandi & Gatto 1999). This prediction is supported by Gibbs (1998), who examined the presence-absence of five amphibian species across a gradient of habitat loss. He found that species with low dispersal rates are better able than more vagile species to persist in landscapes with low habitat cover. Gibbs (1998) postulated that the land between habitats serves as a demographic "drain" for many amphibians. Furthermore, Bonnet et al. (1999) found that snake species that use frequent long-distance movements have higher mortality rates than do sedentary foragers.

Whether vagility is an advantage or a disadvantage in the face of habitat loss and fragmentation appears to depend on the level of mortality experienced by dispersing individuals in the nonhabitat or "matrix" portion of the landscape. We suggest that, where roads represent a large mortality factor in the matrix, high vagility can place a population at risk.

Acknowledgments

We thank D. Bender, J. Brennan, S. Brady, M. Lynne Charron, A. Goncalves DaSilva, B. Goodwin, T. Goodwin, K. Henein, J. Joynt, M. Lee, K. Lo, A. Mitchel, S. Peters, S. Pope, S. Moola, L. Tischendorf, and A. Wong for assistance with the data collection. This work was supported by a scholarship from the Natural Sciences and

Engineering Research Council of Canada (NSERC) to L.W.C. and a grant from NSERC to L.F.

Literature Cited

- Allaby, M. 1994. Oxford concise dictionary of ecology. Oxford University Press, New York.
- Ashley, E. P., and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. *Canadian Field-Naturalist* **110**:403-412.
- Baur, A., and B. Baur. 1990. Are roads barriers to dispersal in the land snail *Arianta arbustorum*? *Canadian Journal of Zoology* **68**:613-617.
- Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* **22**:2047-2056.
- Bonnet, X., G. Naulleau, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* **89**:39-50.
- Bovbjerg, R. V., and A. M. Bovbjerg. 1964. Summer emigration of the frog *Rana pipiens* in northwestern Iowa. *Iowa Academy of Science* **71**:511-518.
- Breden, F. 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* **2**:386-395.
- Carr, L. W., S. E. Pope, and L. Fahrig. 2000. Impacts of landscape transformation by roads. In K. J. Gutzwiller, editor. Concepts and applications of landscape ecology in biological conservation. Springer-Verlag, New York.
- Casagrandi, R., and M. Gatto. 1999. A mesoscale approach to extinction risk in fragmented habitats. *Nature* **400**:560-562.
- Dole, J. W. 1965. Summer movements of adult leopard frogs *Rana pipiens* Schreber, in northern Michigan. *Ecology* **46**:236-254.
- Dole, J. W. 1967. Spring movements of leopard frogs, *Rana pipiens* Schreber, in Northern Michigan. *The American Midland Naturalist* **78**:167-181.
- Dole, J. W. 1971. Dispersal of recently metamorphosed leopard frogs, *Rana pipiens*. *Copeia* **2**:221-228.
- Ehmann, H., and H. Cogger. 1985. Australia's endangered herpetofauna: a review of criteria and policies. Pages 435-447 in G. Grigg, R. Shine, and H. Ehmann, editors. *Biology of Australasian frogs and reptiles*. Surrey Beatty & Sons and Royal Zoological Society of New South Wales, Sydney.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**:273-292.
- Fahrig, L., and A. Grez. 1996. Population spatial structure, human-caused landscape changes and species survival. *Revista Chilena de Historia Natural* **69**:5-13.
- Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Talyor, and J. F. Wegner. 1995. Effect of road traffic on amphibian density. *Biological Conservation* **74**:177-182.
- Findlay, C. S., and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. *Conservation Biology* **14**:86-94.
- Findlay, C. S., and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* **11**:1000-1009.
- Forman, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* **14**: 31-35.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* **29**:207-231.
- Garland, T., Jr., and W. G. Bradley. 1984. Effects of highway on Mojave desert rodent populations. *American Midland Naturalist* **111**:47-56.
- Gartshore, M. E., M. J. Oldham, R. van der Ham, F. W. Scheuler, C. A. Bishop, and G. C. Barrett. 1997. Amphibian road call counts participants manual. Ontario Task Force on Declining Amphibian Populations and the Canadian Wildlife Service, Ontario.
- Gibbs, J. P. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. *Landscape Ecology* **13**:263-268.
- Gilbert, M., R. Leclair, and R. Fortin. 1994. Reproduction of the northern leopard frog (*Rana pipiens*) in floodplain habitat in the Richelieu River, P. Québec, Canada. *Journal of Herpetology* **28**:465-470.
- Gilhen, J. 1984. Amphibians and reptiles of Nova Scotia. Nova Scotia Museum, Halifax, Canada.
- Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* **48**:145-166.
- Gromko, M. H., F. S. Mason, and S. J. Smith-Gill. 1973. Analysis of crowding effect in *Rana pipiens* tadpoles. *Journal of Experimental Zoology* **186**:63-72.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151-162.
- Hecnar, S. J., and R. T. M'Closkey. 1996. Regional dynamics and the status of amphibians. *Ecology* **7**:2091-2097.
- Hecnar, S. J., and R. T. M'Closkey. 1997. Patterns of nestedness and species association in a pond-dwelling amphibian fauna. *Oikos* **80**:1-10.
- Heine, G. 1987. Einfache Meß- und Rechenmethode sur Ermittlung der überlebenschance wandernder Amphibien beim überqueren von Straßen. *Beih. Veröff. Naturschutz und Landschaftspflege in Baden-Württemberg* **41**:473-479.
- Hine, R. L., B. L. Les, and B. F. Hellmich. 1981. Leopard frog populations and mortality in Wisconsin, 1974-1976. Technical bulletin 122. Department of Natural Resources, Madison, Wisconsin.
- Hitchings, S. P., and T. J. C. Beebee. 1997. Genetic substructuring as a result of barriers to gene flow in urban *Rana temporaria* (common frog) populations: implications for biodiversity conservation. *Heredity* **79**: 117-127.
- Hitchings, S. P. and T. J. C. Beebee. 1998. Loss of genetic diversity and fitness of common toad (*Bufo bufo*) in populations isolated by inimical habitat. *Journal of Evolutionary Biology* **11**:269-283.
- Kuhn, J. 1987. Straßentod der Erdkröte (bufo bufo L.): Verlustquoten und Verkehrsaufkommen, Verhalten auf der Straße. *Beih. Veröff. Naturschutz und Landschaftspflege in Baden-Württemberg* **41**:175-186.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* **241**:1455-1460.
- Lefcort, H., R. A. Meguire, L. H. Wilson, and W. F. Ettinger. 1998. Heavy metals alter the survival, growth, metamorphosis, and anti-predatory behavior of Columbia spotted frog (*Rana luteiventris*) tadpoles. *Archives of Environmental Contamination and Toxicology* **35**:447-456.
- Lindenmayer, D. B., and H. P. Possingham. 1996. Modeling the inter-relationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in southeastern Australia. *Landscape Ecology* **11**:79-105.
- Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. *Biological Conservation* **29**:81-96.
- Mader, H. J., C. Schell, and P. Kornacker. 1990. Linear barriers to arthropod movements in the landscape. *Biological Conservation* **54**: 209-222.
- Mahaney, P. A. 1994. Effects of freshwater petroleum contamination on amphibian hatching and metamorphosis. *Environmental Toxicology and Chemistry* **13**:259-265.
- MapInfo Corporation. 1997. MapInfo Pro. Version 4.5. MapInfo, Troy, New York.
- Martof, B. S. 1953. Home range and movements of the green frog, *Rana clamitans*. *Ecology* **34**:529-543.
- Martof, B. S. 1956. Factors influencing size and composition of populations of *Rana clamitans*. *American Midland Naturalist* **56**:224-243.
- Merrell, D. J. 1977. Life history of the leopard frog, *Rana pipiens*, in Minnesota. Occasional paper 15. Bell Museum of Natural History and University of Minnesota, Minneapolis.
- Merriam, G., K. Michal, E. Tsuchiya, and K. Hawley. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Landscape Ecology* **29**:227-235.

- Oldham, R. S. 1967. Orienting mechanisms of the green frog, *Rana clamitans*. *Ecology* **48**:477-491.
- Olsen, D. H., W. P. Leonard, and R. B. Bury. 1997. Sampling amphibians in lentic habitats. Northwest fauna 4. Society for Northwestern Vertebrate Biology, Olympia, Washington.
- Oxley, D. J., M. B. Fenton, and G. R. Carmody. 1974. The effects of roads on populations of small mammals. *Journal of Applied Ecology* **11**:51-59.
- Pope, S. E. 1996. The relative roles of landscape complementation and metapopulation dynamics in the distribution and abundance of leopard frogs (*Rana pipiens*) in Ottawa-Carleton. M. S. thesis. Carleton University, Ottawa.
- Pope, S. E., L. Fahrig, and H. G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* **81**:2498-2508.
- Reh, W., and A. Seitz. 1990. The influence of land use on the genetic structure of populations of the common frog *Rana temporaria*. *Biological Conservation* **54**:239-249.
- Rittschof, D. 1975. Some aspects of the natural history and ecology of the leopard frog, *Rana pipiens*. Ph.D. thesis. The University of Michigan, Ann Arbor.
- SAS Institute. 1996. SAS user's guide: statistics. Version 6.12. Cary, North Carolina.
- Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. *The American Midland Naturalist* **95**:471-474.
- Schoener, T. W., and D. A. Spiller. 1992. Is extinction rate related to temporal variability in population size? An empirical answer for orb spiders. *The American Naturalist* **139**:1176-1207.
- Seburn, C. N. L., D. C. Seburn, and C. A. Paskowski. 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. Pages 64-72 in D. M. Green, editor. *Amphibians in decline: Canadian studies of a global problem. Herpetological conservation 1*. Society for the Study of Amphibians and Reptiles, St. Louis, Missouri.
- Shirose, L. J., and R. J. Brooks. 1995. Age structure, mortality, and longevity in syntopic populations of three species of ranid frogs in central Ontario. *Canadian Journal of Zoology* **73**:1878-1886.
- Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* **42**:135-147.
- Sjögren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* **75**:1357-1367.
- Skelly, D. K. 1995. Competition and the distribution of spring peeper larvae. *Oecologia* **103**:203-207.
- Snell, A. 1987. Wetland distribution and conversion in southern Ontario. Working paper 48. Canada Land Use Monitoring Program, Inland Waters and Lands Directorate, Environment Canada, Ottawa.
- van Gelder, J. J. 1973. A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. *Oecologia* **13**:93-95.
- Vos, C. C., and J. P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* **35**:44-56.
- Wells, K. D. 1977. Territoriality and male mating success in the green frog (*Rana clamitans*). *Ecology* **58**:750-762.
- Welsh, H. H., Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecological Applications* **8**:1118-1132.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist* **125**:879-887.
- With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* **76**:2246-2459.

