INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA

UMI®
800-521-0600

The impact of vehicular traffic on two frog populations of
differing vagility, *Rana pipiens* and *Rana clamitans*.

Laurie W. Carr, B.Sc.F.

A thesis submitted to
the Faculty of Graduate Studies
in partial fulfillment of
the requirements for the degree of

Master of Science

Carleton University
Ottawa, Ontario
September 15, 1999

© copyright
1999, Laurie W. Carr

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file *Votre référence*

Our file *Notre référence*

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-48488-2

Canada

The undersigned recommend to
the Faculty of Graduate Studies
acceptance of the thesis

The impact of vehicular traffic on two frog populations of
differing vagility, *Rana pipiens* and *Rana clamitans*.

submitted by Laurie W. Carr, B.Sc. F.
in partial fulfillment of the requirements for
the degree of Master of Science

Chair, Department of Biology

Thesis supervisor

Carleton University

September, 1999

ABSTRACT

Vehicular traffic can be a major source of dispersal related mortality for some species. Highly vagile organisms should be at a disadvantage in landscapes with roads because they are more likely to encounter roads and incur traffic mortality. Population abundance of two sympatric anuran species of differing vagility, *Rana pipiens* (vagile) and *Rana clamitans* (less vagile) was assessed at 30 breeding ponds. Traffic density, an index of the amount of potential traffic mortality, was measured in concentric circles radiating from the pond, out to 5 km. Multiple linear regressions relating population abundance to traffic density, pond and landscape variables concluded that *Rana pipiens* populations were negatively affected by traffic within a radius of 1.5 km, while *Rana clamitans* populations were not correlated with traffic density. These results imply that vagile species are vulnerable to traffic mortality which can cause population decline.

ACKNOWLEDGMENTS

I am going to start my "thank-yous" from the beginning. The first person on the list is Dr. Dawn Bazely from York University, who gave me my first taste of ecology and the academic life. She has been a wonderful source of support and has been a key element in my development as an ecologist. In short, she is a mentor and also a good friend.

Second on the list would be those forces that unknowingly colluded into my taking up residence in the basement of the Tory building. Those forces would be my husband, Shiraz Moola, Dr. Jay Malcolm, University of Toronto, and the authors of the article "Effects of road traffic on amphibian density" (Fahrig et al. 1995) (Bio.Conserv. 74:177-182). Thank you also to Dr. D.N. Roy and Dr. Vic Timmer, University of Toronto, for endlessly filling out scholarship applications.

Besides the people that got me to my Masters, there are many more that were essential to its completion. A grateful and heartfelt thank you goes to the froggers that voluntarily splashed about in the dark and mosquitoes gathering my data. I hope in return that they had fun, learnt a little about frogs, and had the satisfaction of doing science. A special thank you to Sarah Peters, my field assistant, who put in long hours despite her otherwise busy training schedule. Frogging volunteers: Darren Bender, Julie Brennan, Sheanna Brady, Maria Lynne Charron, Angelika Goncalves DaSilva, Brett Goodwin, Trina Goodwin, Kringen Henein, Janet Joynt, Michelle Lee, Ky Lo, April Mitchel, Sarah Peters, Shealagh Pope, Shiraz Moola, Lutz Tischendorf, and Alex Wong. Special

recognition should also be given to the thirty landowners that took an interest in my study and went out of their way to let me trample through their backyard and splash in their ponds.

I was fortunate to be in a lab that was a great source of support, knowledge, fun, friendship and scientific discussion. Thanks to Michelle, who with surprising calm, taught me how to drive standard; to Darren for enhancing my thesis with his computer skills; to Julie for always looking out for me; and to Shealagh for sharing her ponds, papers, and advice. Thanks to Tom Contreras, Brett Goodwin, Kringen Henein, Dave Omond, and Lutz Tischendorf for always being ready with help, discussion, and conversation.

I was truly lucky to have been under the tutelage of Dr. Lenore Fahrig, who introduced me to the wide wide world of Landscape Ecology. Her patience, interest and confidence in her students resulted in a very gratifying experience. I could not imagine a better supervisor. Pat Weatherhead and Scott Findlay advised me throughout my thesis while significantly increasing my understanding of amphibians, statistics and ecology.

Lastly I would like to thank my Aunt Phyllis and Uncle Bernhard for providing a home away from home, Saewan for being next door, and my family for putting up with me. I dedicate this thesis to my husband (obligatory mutualism), Shiraz, who missed me when I was away and gave me shoulder rubs when I wasn't.

TABLE OF CONTENTS

	Page
Abstract	iii
Acknowledgements	iv
Table of Contents	vi
List of Tables	vii
List of Figures	viii
List of Appendix	ix
Introduction	1
Background	5
Methods	9
Results	23
Discussion	31
Appendix	41
References	46

LIST OF TABLES

	Page
Table 1 Dispersal distances of <i>Rana pipiens</i> and <i>Rana clamitans</i>	6
Table 2 Variables included in statistical analysis	14
Table 3 Transect criteria for optimal and sub-optimal habitats are marked for combination A and combination B. Low quality spawning habitat is any combination not listed.	16
Table 4 Presence and peak counts of <i>Rana pipiens</i> and <i>Rana clamitans</i> population abundance in chorus and visual surveys of breeding ponds, Ottawa-Carleton 1998.	24
Table 5 Analysis of variance of best model relating <i>Rana clamitans</i> abundance to local, landscape, and traffic density variables.	25
Table 6 Analysis of variance of best model relating <i>Rana pipiens</i> abundance to local, landscape, and traffic density variables.	26

LIST OF FIGURES

	Page
Figure 1	4
Hypothesized effects of road traffic density abundance of <i>Rana pipiens</i> and <i>Rana clamitans</i>. <i>Rana pipiens</i> should incur a greater population decline (steeper slope) with increasing traffic density compared to <i>Rana clamitans</i>. <i>Rana pipiens</i> is a more vagile species than <i>Rana clamitans</i> and should incur greater traffic mortality. Initial population sizes are arbitrary.	
Figure 2	10
The study area in the Ottawa-Carleton region, southern Ontario, Canada. The distribution of the breeding ponds is indicated.	
Figure 3	18
Example of a digital landscape in which the landscape habitat variables and traffic density were measured. Concentric circles of radii 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0 km are indicated.	
Figure 4	29
Plot showing the decline of <i>Rana pipiens</i> population abundance with increasing traffic density. There was no significant relationship between <i>Rana clamitans</i> population abundance and traffic density. The residuals of green frog abundance regressed against STREAMS and the residuals from leopard frog abundance regressed against pH and LEOPARD OPTIMAL are plotted against traffic density within 1.5 km.	
Figure 5	30
Semivariance plots for <i>Rana pipiens</i> (A) and <i>Rana clamitans</i> (B) showing no evidence of spatial dependence of population abundance for either species. Semivariance of abundance is plotted against distance between ponds (lag).	

LIST OF APPENDICES

	Page
Appendix 1	
Data- Total chorus and visual survey counts for each pond	41
Data continued- Local variables	42
Data continued- Landscape habitat variables	43
Data continued- Traffic density variables 0.25-1.75 km	44
Data continued- Traffic density variables 2.0-5.0 km	45

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 and Bradley 1984, Mader 1984, Merriam et al. 1989; snails: Baur and Baur 1990; arthropods: Mader et al. 1990), as well as a major source of mortality. For example, over two years, 32,000 amphibians, reptiles, birds and mammals over the 3.6-km Long Point causeway adjacent to Big Creek Wetland, Lake Erie, Canada, were found as road-kill (Ashley and Robinson 1996). Ehmann and Cogger (1985) estimate that 5.48 million reptiles and frogs are killed in Australia each year by road traffic. The loss of individuals due to traffic mortality has an impact on two levels: first, a reduction in population size, and second, a reduction of dispersing individuals that essentially reduces connectivity between complementary resources and conspecific populations. As barriers to movement, roads effectively create smaller patches and increase patch isolation.

Roads and vehicular mortality are ubiquitous in landscapes that have been modified by humans. Population spatial structure, and therefore population survival, of organisms in such landscapes depends on the interaction between the spatial pattern of roads and the dispersal characteristics of the organisms (Fahrig and Grez 1996). Two dispersal characteristics that should determine the impact of vehicular traffic on population spatial structure are dispersal behaviour and vagility. Vagility is defined as "the inherent power of movement possessed by individuals" (Allaby 1994). It is used in this study instead of "dispersal distance" or "dispersal capability" to encompass both movement distance and

frequency. Dispersal behaviour will determine when, how, and if organisms cross roads. Vagility will determine the frequency with which organisms encounter roads and incur vehicular collisions. I expect a more vagile species to be more sensitive to traffic mortality than a less vagile species for this reason. The optimal dispersal distance for organisms that cross roads is then dependent on the distance between habitat patches and also on the mortality rate incurred during dispersal.

In this study, I evaluated the impact of vehicular traffic on the population abundance of two sympatric amphibian species of differing vagility, *Rana clamitans* (green frog) and *Rana pipiens* (leopard frog). Amphibians are well known victims of vehicular mortality (van Gelder 1973, Fahrig et al. 1995) due to the importance of dispersal in anuran population dynamics. Breeding populations are spatially separated so that the long-distance dispersal of juvenile frogs is the major source of gene flow between populations (Rittschof 1975, Breden 1987, Berven and Grudzien 1990), colonizations and recolonizations of local extinctions (Gill 1978, Sjögren 1991). *Rana clamitans* and *Rana pipiens* experience a seasonal shift in habitat that necessitates movement between distinct habitat types in order to fulfill overwintering, reproduction and foraging requirements (Gilhen 1984). *Rana pipiens* is considered a more vagile species because it undertakes three rather than two yearly migrations between habitats, and has longer adult and juvenile dispersal distances compared to *Rana clamitans*. As such, *Rana pipiens* should encounter roads more often than *Rana clamitans* and incur greater traffic mortality.

I used population abundance in relation to traffic density in the surrounding landscape to compare the impact of potential road mortality on *Rana pipiens* (more vagile) and *Rana clamitans* (less vagile). I hypothesized that vehicular related mortality is sufficient to significantly negatively impact population abundance and therefore population persistence of both *Rana clamitans* and *Rana pipiens*. However, because *Rana pipiens* is a more vagile species, it should experience a greater decline in population abundance in relation to traffic density than *Rana clamitans* (steeper slope in Figure 1).

The goals of this study were to relate population abundance of *Rana clamitans* and *Rana pipiens* to traffic density in the surrounding landscape and to determine the distance at which traffic density has the greatest effect on population abundance.

Figure 1. Hypothesized effects of road traffic density abundance of *Rana pipiens* and *Rana clamitans*. *Rana pipiens* should incur a greater population decline (steeper slope) with increasing traffic density compared to *Rana clamitans*. *Rana pipiens* is a more vagile species than *Rana clamitans* and should incur greater traffic mortality. Initial population sizes are arbitrary.

BACKGROUND

Rana clamitans and *Rana pipiens* have broadly sympatric ranges (McAlpine and Dilworth 1989). Green frogs range throughout eastern North America (Behler and King 1995) while Leopard frogs have a greater range which extends across Canada (Gilhen 1984), and from northern Canada to Panama, a range far more extensive than that of any other North American anuran (Dole 1965). Green and Leopard frogs have been observed in the Ottawa-Carleton region since 1883 (Mike Oldham- Ontario Herpetofaunal Summary, personal communication). Where their ranges overlap, they are commonly found in the same breeding ponds (Collins and Wilbur 1979, Hecnar and M'Closkey 1997, Martof 1953a).

Life cycle and movement

Green and leopard frogs experience a shift in habitat related to the seasons and distinct phases of their life history. Green frogs occupy two distinct habitats, overwintering and breeding (Gilhen 1984). Leopard frogs occupy three distinct habitats, overwintering, breeding and summer feeding (Merrell 1977). While both frogs undergo long-distance migration between these habitats, once in the habitat they are relatively sedentary (Martof 1953b, Dole 1965). Overall, leopard frogs cover greater distances in the landscape than green frogs. This is a combined factor of longer dispersal distances and more movements between habitat types (Table 1).

Table 1. Dispersal distances of *Rana pipiens* and *Rana clamitans*¹

	<i>R. pipiens</i> (km)	<i>R. clamitans</i> (km)
Observed distance between habitats	up to 2	< 1.6
Number of migrations in a year	3	2
Max. total dispersal distance of adults in a year	6	2-3
Max. juvenile dispersal distance observed	8	4.8

¹ Based on Dole 1967, Oldham 1967, Dole 1971, Rittschof 1975, Schroeder 1976, Merrell 1977, Hine et al. 1981, and Seburn et al. 1997.

Adult green frogs have been observed to move 140-640 m during seasonal migration. between overwintering and breeding habitat with movements probably under 1.6 km (Oldham 1967). Green frog tadpoles overwinter in the breeding pools and transform the following summer at which point they disperse to overwintering sites. The majority of observed distances for this dispersal range from 184-448 m, with rare dispersal events of 2.5 and 4.8 km (Schroeder 1976). In natural populations green frogs usually reach maturity in the year following transformation (Wells 1977). Once mature, green frogs are philopatric to the breeding sites. However, some movement between breeding ponds has been observed for green frogs either to meet reproductive demands, or to avoid desiccation (Martof 1953b).

For leopard frogs, breeding ponds should ideally be within 1.6 km of hibernaculum sites (Hine et al. 1981). This finding is similar to that of Merrell (1977) who found that overwintering, breeding and summer habitats were separated by one to two kilometers. However, much shorter distances (0-400m) between breeding and summer habitats have also been observed (Dole 1967, Hine et al. 1981). It is possible that an adult leopard frog may move up to 3 to 6 kilometers a year (Merrell 1977). Leopard frog tadpoles transform at the end of summer (young-of-the-year) and have been noted to move 5-800 m overland and 2.1 km downstream from natal ponds (Dole 1971, Rittschof 1975, Seburn et al. 1997). Leopard frogs usually mature the second year after transformation (Hine et al. 1981) and have been found in their adult residence, over 1 km (Rittschof 1975), 5.2 km (Dole 1971), and 8 km from their natal ponds one year later (Seburn et al. 1997).

Habitat

Green frogs overwinter in the mud and debris in the bottom of streams about a meter deep and forage along the stream banks before and after breeding (Martof 1953b). During breeding, green frogs preferentially occupy permanent aquatic habitats with a medium to high density of emergent and floating aquatic vegetation, muddy and silty bottoms, and shrubby habitats (Courtois et al. 1995, McAlpine and Dilworth 1989). Females preferentially oviposit in dense *Elodea* mats, other submerged aquatic plants, or sedges in shallow (12.2-44 cm) water near shore (Martof 1956, Wells 1977).

Leopard frogs overwinter in large lakes, spillways below dams at the outlet of lakes, streams, and rivers (Merrell and Rodell 1967, Merrell 1977). In the summer, leopard frogs prefer wet meadows that are close to water and that are not heavily grazed or mowed (Dole 1967, Merrell 1977, Beauregard and Leclair 1988). Leopards frogs have been observed in wet forests during the summer although the extent to which this habitat type is used is unknown (Dole 1965, Hine et al. 1981). During breeding, leopard frogs preferentially occupy temporary or permanent ponds that do not support fish (Merrell 1968), and that have a strong predominance of narrow-leaved and robust emergent vegetation (Gilbert et al. 1994, Beauregard and Leclair 1988). Egg masses are attached to herbaceous non-emergent (e.g. *Carex*) and robust emergent vegetation (e.g. *Typha*) in shallow water (65cm) that has been warmed by sunlight (Merrell and Rodell 1967, Merrell 1977, Hine et al. 1981, Gilbert et al. 1994).

Methods

Study region

This study was conducted in the Ottawa-Carleton region, Ontario, Canada. The region is primarily agricultural with forest remnants and some urban settlements. Agriculture, roads and urban development have fragmented the terrestrial landscape, while wetland drainage has reduced aquatic habitat from 45.8 % of the Ottawa area in 1890 to 12.6% in 1982 (Snell 1987).

Pond selection

Thirty permanent ponds were surveyed within the Ottawa-Carleton region (Figure 2). Ponds were spaced at least 1 km apart, to reduce pseudo-replication. Two criteria were used to reduce variation in the data due to landscape composition 1) ponds with similar landscapes (mostly agricultural fields) were chosen and, 2) ponds with a low and a high traffic road within 1 km were paired in each area. However, there were more ponds with low traffic density when traffic density was summed over a 5 km radius. This was due to the relative paucity of high traffic roads (such as major highways) in the region surveyed. Ponds had a clearly defined vegetated edge and were not connected to other ponds or wetlands, resulting in 29 out of 30 ponds being man made. New quarries and concrete pools were excluded as potential sites. All ponds were fishless and over 10 years of age except for one that was 6 years old.

Figure 2. The study area in the Ottawa-Carleton region, southern Ontario, Canada. The distribution of the breeding ponds is indicated.

Population abundance surveys

Two types of surveys, chorus and visual, were conducted to increase the accuracy of determining a relative measure of population size. Chorus surveys count the number of calling breeding males, while visual surveys count the number of frogs (mostly males but also females and juveniles) seen in the breeding ponds.

Chorus surveys

Six chorus surveys were conducted during the peak breeding season of leopard frogs between April 17 to May 12, and four surveys were conducted during the peak breeding season of green frogs between June 1 to July 3, 1998. The number of surveys completed was determined as twice the number of surveys that were necessary to detect presence or absence. For example, there were no new ponds with calling after three surveys for the leopard frog. Therefore six surveys were conducted. Volunteers and myself counted the number of individual calling leopard and green frog males over a period of 5 minutes for each survey. Three minutes is sufficient to detect presence and intensity of calling (Shirose et al. 1997), but not necessarily to count individuals. Where traffic levels were high, the 5 minutes were the sum of pauses in the background noise (Fahrig et al. 1995). Volunteers were trained to count anuran breeding calls using the Marsh Monitoring Program Training audio tape produced by the Canadian Wildlife Service. Inter-observer agreement of breeding surveys is generally high, although novices tend to underestimate the number of individuals calling (Shirose et al. 1997).

The ponds were divided into four routes that were driven in four different sequences to vary the beginning time of the survey for each pond. Routes were driven forwards, backward, or starting from a midpoint and moving forwards or backward (Pope 1996). Each survey was conducted by a new pair of surveyors to avoid observer bias. Surveys began 1/2 hour after sunset and finished before midnight (Gartshore et al. 1997). Attempts were made to have all four routes surveyed on the same night and during nights of light precipitation (Gartshore et al. 1997), but the use of volunteers made this impossible. Surveys were initiated for leopard frogs when the air temperature was greater than 8° (Hine et al. 1981, Gartshore et al. 1997) and for green frogs when the air temperature was above 21° (Gartshore et al. 1997).

Visual surveys

Four visual surveys were conducted during the peak breeding season of leopard frogs between May 5 and 17, and three surveys were conducted during the peak breeding season of green frogs between June 11 and June 26, 1998. Ponds were divided into two routes that were covered by an assistant and myself during the hours of 9 am and 5 p.m. over a period of two days. Routes were driven alternately backwards and forwards to vary survey times for each pond.

Leopard and green frogs were counted by the surveyors as they each walked slowly along half the waterline, stopping approximately every 2m 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 the 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. This same pattern was adopted when the shore was flooded making ideal conditions for leopard frogs. The entire pond perimeter was surveyed, except for two ponds, where a portion of the perimeter was impassable. Frogs were readily visible during the day, as *Rana spp.* are usually found at the waterline, at the water surface, or in moist vegetation on the shore (Olsen et al. 1997). Surveys were conducted on sunny calm days, as cold and windy conditions depress surface activity of many species (Olsen et al. 1997).

Habitat variables

Local pond attributes - pH, perimeter, spawning habitat (m) – and, landscape attributes - area of forest, wetland, human development, agriculture fields, waterbodies (km²) and the length of streams (km) - were quantified to control for habitat differences in statistical models (Table 2).

Pond pH

Mean pond pH was based on eight electronic pH meter readings taken at a depth of 5cm, 1 m out from the shore for the entire pond (Pope 1996). For one pond mean pH was based on 6 readings. The pH measurements were taken over three days July 30, 31 and August 1 1998.

Table 2. Variables included in statistical analysis

Variable	Description
Dependent	
LEOPARD ABUNDANCE	standardized population abundance, which is the sum of the visual and chorus survey counts.
GREEN ABUNDANCE	standardized population abundance, which is the sum of the visual and chorus survey counts.
Independent - Local	
pH	mean pH of pond water
LEOPARD OPTIMAL	length (m) of optimal spawning habitat
LEOPARD SUB-OPTIMAL	length (m) of sub-optimal spawning habitat
LEOPARD LOW	length (m) of low quality spawning habitat
GREEN OPTIMAL	length (m) of optimal spawning habitat
GREEN SUB-OPTIMAL	length (m) of sub-optimal spawning habitat
GREEN LOW	length (m) of low quality spawning habitat
Independent - Landscape	
	measured within 1.5 km of the centre of the pond
FOREST	area (km ²) of forested land
WETLAND	area (km ²) of forested and non-forested
BUILT-UP	area (km ²) of human developments including building complexes, paved areas, residential areas, and cemeteries
AGRICULTURE	area (km ²) of new and old agricultural land
WATER	area (km ²) of waterbodies including lakes, ponds, and rivers
STREAM	length (km) of streams including ditches
Independent - Traffic	
TRAFFIC	cumulative traffic density (traffic/km ²) in concentric circles of 0.25, 0.5, 0.75, 1, 1.25, 1.5, 1.75, 2, 2.5, 3, 3.5, 4, 4.5, 5 km radius, from the centre of the pond

Perimeter

Pond perimeter was paced and related to a measurement in meters for 28 ponds. Two pond perimeters were measured using topographic maps and aerial photographs.

Spawning habitat

Depending on the size of the pond, 4 to 16 equally spaced line transects that extended 3 m perpendicular from the shoreline into the water, were assessed per pond. For each transect I noted the proportion of the transect length that was covered by each vegetation type (emergent, submergent, and floating), water depth at 1m intervals, distance from shoreline at which the water depth was 65 cm., and insolation. Insolation was measured as the amount of sun received during the day (sun all day, shaded part of the day, and shaded all day).

Three classes of spawning habitat were derived to encompass gradation in habitat quality and to acknowledge that "low" quality habitat might still constitute suitable habitat. The total perimeter was multiplied by the proportion of transects with optimal, sub-optimal, or low spawning habitat (Table 3) so that the point samples were converted into estimates of the length of each quality of spawning habitat for leopard and green frogs (Pope 1996).

Table 3. Transect criteria for optimal and sub-optimal habitats are marked for combination A and combination B. Low quality spawning habitat is any combination not listed.

Transect criteria	<i>Rana pipiens</i> spawning habitat				<i>Rana clamitans</i> spawning habitat			
	Optimal		Sub-optimal		Optimal		Sub-optimal	
	A	B	A	B	A	B	A	B
Insolation: Full sun	X	X	X					
>1.5 m shallow water (< 65 cm)	X	X		X	X		X	X
> 1 m of shallow water with narrow-leaved emergent vegetation cover more than: a) 30% b) 5%	X	X	X	X		X		X
> 1 m of shallow water with submergent and/or floating vegetation cover more than: a) 30% b) 5%					X	X	X	

Landscape variables

I quantified the area of forest, open and forested wetland, human developments, new and old agriculture fields, waterbodies (km^2), and the length of streams (km) within a 1.5 km radius from the centre of each pond (Figure 3). Ponds with frogs are most likely to have other sources of habitat within 1-1.6 km (Pope 1996, Hine et al. 1981). Measurements were taken from digital Government of Canada 1:50,000 topographic maps (1979-1989) using the digitizing feature in MapInfo Pro (MapInfo Corporation 1997). Forest cover is fairly accurately represented on topographic maps (J. Houlahan, personal communication). To check this and other landcovers, I ground-truthed the area around each pond during the month of August by noting the land use that could be seen from the side of the road.

Traffic density

The predictor variable of primary interest in this study was traffic density, an index of potential amount of road mortality that combines road density and traffic volume on each road (Equation 1). I calculated the cumulative 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, 5 km (Figure 3). Road length was measured from digital Government of Canada 1:50,000 topographic maps (1979-1989) using MapInfo Pro (MapInfo corporation 1997). Traffic volume was measured as Average Annual Daily (24h) Traffic (AADT) counts. AADT counts were supplied by Ottawa-Carleton townships, the

Figure 3. Example of a digital landscape in which the landscape habitat variables and traffic density were measured. Concentric circles of radii 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0 km are indicated.

Regional Municipality of Ottawa-Carleton Transportation department, and the Ontario Ministry of Transportation Eastern Region Traffic Section. For minor roads that lacked traffic counts, the township provided an estimate. For residential areas I multiplied total road length by an average AADT count for the residential area. AADT counts for gravel and residential roads (69% of all roads), minor paved roads (17%), major paved roads (11%), and highways (3%) were, respectively, 0-990, 1000-4990, 5000-9990, and 10,000-16000.

Equation 1.

$$\text{Traffic density (traffic/km}^2\text{)} = [\sum_{i=1}^{i=n} (l_i * AADT_i)] / ACC$$

where n = the total number of roads

l_i = length of road _{i}

$AADT_i$ = Average Annual Daily Traffic for road _{i}

ACC = Area of concentric circle (km²)

Statistical Analysis

Dependent variable

The abundance counts for each of the visual and chorus surveys were summed over all surveys (7 and 10 respectively) to give weight to those ponds that had consistent calling as well as high calling numbers (Pope 1996). This method avoids using a "maximum count value" that could be sensitive to differences in climatic conditions during different

survey nights. Population abundance counts from the visual and chorus surveys were highly correlated for both leopard frogs ($r^2 = 0.19$, $p = 0.0175$) and green frogs ($r^2 = 0.054$, $p = 0.001$) and were therefore combined. The summed abundance counts were each square root transformed then standardized (distribution of zero mean and unit variance) so they would be equally weighted when added together. The transformed standardized visual and chorus counts were added together to produce one abundance measure for each pond for each of green and leopard frogs.

Model Building

In order to determine the influence of traffic density on population abundance of green and leopard frogs, I used stepwise multiple linear regression in SAS (SAS Institute 1996). The multiple regression proceeded in three steps. In the first step, all local and landscape variables were included to produce the most significant habitat model. In the second step, each traffic density (TRAFFIC) variable (Table 2) was substituted consecutively into the model from step 1 to determine the most significant radius of TRAFFIC in terms of the partial F-value. In the third step, all two-way TRAFFIC interaction terms were included with the model from step 2 in a stepwise multiple regression. All variables were included in the final model when their partial F-value was significant at $\alpha = 0.05$.

In all analyses, the assumptions of linear regression were checked through visual examination of residual plots. Residuals were plotted against each of the independent

variables, and the predicted values to test for homogeneity of variance and independence. Residual histogram plots were examined for normality.

Spatial dependence

Spatial dependence could exist in the data if ponds located close together were more similar in species abundance than ponds farther apart. This could be due to biotic or abiotic features that influence more than one pond or if frogs undertook extensive movements between ponds during breeding. Spatial dependence would indicate that each pond was not representative of an independent population and there was pseudoreplication in the data (Legendre and Fortin 1989, Hinch et al. 1994).

I explored spatial dependence in the data using semivariance, a method that measures the degree of similarity between observations separated by varying distances (lags).

Semivariance is the sum of squared differences between all possible pairs of points separated by distance h (Burrough 1995) (Equation 2). Semivariograms plot the semivariance against lag distance h , and allow the visualization of the scale of landscape pattern (Legendre and Fortin 1989, Turner 1991). If the difference between observations increases over lag distance, then semivariance increases (increasing slope). This increase continues until the observations are so far apart they become unrelated to each other and the semivariance equals the average variance of all the samples, and the slope of the semivariogram becomes zero (see Figure 5) (Gustafson 1998). Least squares regression

was used to fit a model to the semivariogram plot and determine the significance of the slope.

Equation 2

$$\text{Semivariance at lag } h = \sum_{i=1}^n [Z(x_i + h) - Z(x_i)]^2 / [2(n)]$$

where h = lag

n = number of observations in sample separated by lag h

$Z(x)$ = the value of attribute Z at point x

RESULTS

Surveys

Leopard frogs were absent from four ponds, twelve ponds had no calling, and five had no visual records. Green frogs were present in all ponds, but two had no calling and three had no visual records. The presence of juvenile leopard frogs in the visual surveys could have resulted in more ponds with visual records compared to ponds with calling. One of the ponds lacked optimal or sub-optimal leopard frog spawning habitat although this was not the case for the other ponds. Leopard frogs were present in the surveys from April 17 to June 26, while green frogs were present from May 5 to the last survey date, July 3. Calling was more active during the appropriate peak breeding season as defined in the methods section (Table 4).

Models

There was no evidence of a relationship between green frogs and the presence of TRAFFIC in the surrounding landscape. Only the length of streams (STREAMS) within 1.5 km of the pond significantly contributed to the observed variation in green frog abundance ($F_{1,30} = 6.787$, $p = 0.015$) (Table 5). On the other hand, leopard frogs were significantly negatively affected by the amount of TRAFFIC within a radius of 1.5 km ($F_{1,30} = 9.680$, $p = 0.0046$) (Table 6). These results supported my hypothesis that the more vagile species (leopard frog) would

Table 4. Presence and peak counts of *Rana pipiens* and *Rana clamitans* population abundance in chorus and visual surveys of breeding ponds, Ottawa-Carleton 1998.

Species	Chorus survey		Visual survey	
	Present in survey	Peak counts	Present in survey	Peak counts
<i>Rana pipiens</i>	April 17- June 18	April 30- May 12	May 5-June 26	May 5- 17
<i>Rana clamitans</i>	May 5-July 3	June 1 -July 3	May 5-June 26	June 11- 26

Table 5. Analysis of variance of best model relating *Rana clamitans* abundance to local, landscape, and traffic density variables.

Number of observations = 30

	coefficient	d.f.	type III SS	F stat	Pr (F)
intercept	-1.359	1			
STREAM (km)	0.2653	1	18.235	6.787	0.015

model $r^2 = 0.19$, $p = 0.015$

Table 6. Analysis of variance of best model relating *Rana pipiens* abundance to local, landscape, and traffic density variables.

Number of observations = 30

	coefficient	d.f.	type III SS	Partial r^2	Partial F stat	Pr (F)
intercept	4.524	1				
pH	-0.616	1	12.317	0.151	6.537	0.0170
LEOPARD OPTIMAL (m)	0.016	1	27.978	0.342	14.850	0.0007
TRAFFIC at 1.5 km (traffic/ km ²)	-5.4 E -05	1	18.238	0.223	9.680	0.0046
TRAFFIC at 1.5 km (traffic/ km ²) * Built-up (km ²)	9.1 E -05	1	9.680	0.118	5.138	0.0323

model $r^2 = 0.42$, $p = 0.006$

incur greater population decline with increasing traffic density compared to a less vagile species (green frog). However, it was unexpected that green frogs did not experience some population decline in relation to traffic amount (Figure 4).

The leopard frog model also included local habitat variables, pH (pH) and the length of optimal spawning habitat (LEOPARD OPTIMAL), and the interaction between TRAFFIC and the area of human developments (BUILT-UP). Increasing pH (more basic water) was related to decreases in leopard frog abundance while increasing length of optimal spawning habitat was related to increases in leopard frog abundance.

Examination of the interaction plot for TRAFFIC * BUILT-UP showed that TRAFFIC had a negative effect on leopard frog abundance for low levels of BUILT-UP, but did not have a negative impact at the highest levels of BUILT-UP.

TRAFFIC at 1.5 km was significantly correlated with area of waterbodies (WATER) and BUILT-UP (Pearson's product moment correlation, 0.385, $p = 0.0357$ and 0.459, $p = 0.0107$ respectively). STREAM was significantly correlated with forest area (FOREST) and agricultural fields (AGRICULTURE) (Pearson's product moment correlation, -0.0457, $p = 0.0112$ and 0.507, $p = 0.0043$ respectively).

Spatial dependence

Visual examination of the semivariogram did not show the characteristic rising slope that would indicate spatial dependence at some scale. A line fit by least squares regression

had a slope close to zero for leopard frogs and a decreasing slope for green frogs. This indicates a lack of evidence for spatial dependence at all distance between ponds (Figure 5). The physical implication of this is that the sample spacing was too large to resolve any pattern for species abundance distribution in the landscape.

Figure 4. Plot showing the decline of *Rana pipiens* population abundance with increasing traffic density. There was no significant relationship between *Rana clamitans* population abundance and traffic density. The residuals of green frog abundance regressed against STREAMS and the residuals from leopard frog abundance regressed against pH and LEOPARD OPTIMAL are plotted against traffic density within 1.5 km.

Figure 5. Semivariance plots for *Rana pipiens* (A) and *Rana clamitans* (B) showing no evidence of spatial dependence of population abundance for either species. Semivariance of abundance is plotted against distance between ponds (lag).

DISCUSSION

As predicted, leopard frogs (more vagile species) incurred greater population decline with increasing traffic density than green frogs (less vagile species). However, it was unexpected that green frog population abundance did not exhibit any relationship with road traffic in the landscape. There are two possibilities for this. One possibility is that green frogs incurred large amounts of road mortality but the population was able to overcome the mortality. Another possibility is that green frogs did not incur large amounts of road mortality because of a low road crossing rate. The first possibility seems unlikely since green and leopard frogs have similar mean clutch size, 3750 and 4000 eggs respectively (Hecnar and M'Closkey 1997), and thus similar capabilities of expanding their population in response to increased mortality. A low road crossing rate could result if green frogs were indeed less vagile and/or because they bypass roads by moving along streams. Interestingly, there are several reports of high leopard frog road mortality (Bovbjerg and Bovbjerg 1964, Rittschof 1975, Merrell 1977, Ashley and Robinson 1996, Linck 1998) but only one report of relatively low green frog mortality (Ashley and Robinson 1996). The explanatory strength of STREAM on green frog abundance might provide a clue to green frog movement. Green frogs feed along stream banks (Martof 1953b) and drainage ditches have been noted as major dispersal routes for green frogs (Shroeder 1976). Ditches also play an important role in gene flow as movement corridors for the common frog (*Rana temporaria*) (Reh and Seitz 1990). Streams bypass roads by crossing under rather than over roads and could reduce green frog mortality.

Traffic density was measured at several different scales to determine the size of the landscape unit that had the greatest effect on anuran population abundance. A landscape unit of 1.5 km for leopard frogs in this study implies that the majority of leopard frog movement occurs within this distance. Since leopard frogs are the most vagile anuran in Ontario (Hecnar and M'Closkey 1997), a landscape unit of 1.5 km in radius could provide a guideline for measuring the impact of landscape variables on anuran populations.

Following this reasoning, ponds should have been placed at least 3 km apart to avoid overlapping landscapes. Ten ponds were less than 3 km apart, and this could have resulted in some pseudoreplication. However, the possibility of pseudoreplication is countered by the lack of spatial dependence in the data as measured by the semivariance.

Determining a causal relationship between traffic density and leopard frog abundance, and length of streams and green frog abundance was not possible since traffic density and length of streams were correlated with other landscape features. It is not surprising that traffic density increased with increasing area of waterbodies and area of human developments. In the study region, major developments tended to be near large sources of water and would result in greater road density and traffic volume. The relationship between the length of streams (includes ditches) and area of forest (negative) and area of agricultural areas (positive) can be explained by the replacement of forests with agriculture fields in the Ottawa-Carleton region and the subsequent increase of drainage ditches.

Leopard frogs had a lower incidence than green frogs in this study, perhaps due to a greater sensitivity to local pond variables, pH and length of spawning habitat. It has been shown that a lower pH and a greater amount of spawning habitat are positively related to presence or abundance of anurans (Loman 1988, Pope 1996, Vos and Chardon 1998). For the green frog, however, "practically any body of fresh water is potential habitat..., whether small or large, temporary or permanent, and with or without vegetation (Gilhen 1984).

Relative measures (call and visual counts) of amphibian population abundance were used in place of the more labour intensive mark-and-recapture method of estimating population abundance. Call counts appear to represent an index of chorus size, whether chorus size reflects population abundance seems to depend on the species (Shirose et al. 1997). The relationship between chorus size and population abundance has not been evaluated for *Rana clamitans* and *Rana pipiens*. The fact that the visual and chorus survey counts were highly correlated suggests that an index of population size was attained in this study.

Impact of vehicular traffic on anuran populations

Roads are a potential source of dispersal related mortality in all anthropogenically fragmented landscapes as roads are required for human access. My results provide evidence that traffic can influence leopard frog population abundance out to at least 1.5 km. This is similar to the traffic-effect distances, 750 m (Vos and Chardon 1998), 1 km

(Findlay and Houlahan 1997), and 2 km (Findlay et al. in press), found in other amphibian-road studies. The traffic-effect distance is dependent on the movement distance of the organism and traffic density. Several studies have shown a negative correlation of survival probability and traffic volume for crossing amphibians (van Gelder 1973, Heine 1987, Khun 1987, Fahrig et al. 1995). Estimations of the survival rate of crossing toads at 24-40 cars per hour (624 - 960 AADT) varies from zero (Heine 1987) to 50% (Khun 1987). At least 30% of roads in this study had AADT values over 600. Therefore traffic volume should be sufficient to cause large amounts of amphibian mortality in the Ottawa-Carleton region. Road surveys of migrating amphibians in the Ottawa-Carleton region found a higher proportion of dead frogs and toads on high-intensity roads (Fahrig et al. 1995). The differential mortality found by Fahrig et al. (1995) suggests that road mortality contributed to the observed decrease in population abundance of leopard frogs with increased traffic level.

While most fragmentation-amphibian studies have not taken roads into account (Vos and Chardon 1998), there is a growing body of studies that have shown a negative correlation of roads on anuran population persistence. It has been shown that traffic level or density is negatively correlated with abundance of roadside anuran populations (Fahrig et al. 1995), leopard frog (*Rana pipiens*) but not green frog (*Rana clamitans*) populations (this study), and pond occupation probability of the moor frog (*Rana arvalis*) (Vos and Chardon 1998). The number of roads or paved road density has also been shown to be related to the genetic isolation of the common frog (*Rana temporaria*) (Reh and Seitz 1990), herptile species richness in wetlands (Findlay and Houlahan 1997), and the

presence of wood frogs (*Rana sylvatica*) and mink frogs (*Rana septentrionalis*) but not leopard or green frogs (Findlay et al. in press). The lack of correlation between leopard frogs and paved road density in the Findlay et al. (in press) study could be attributed to the fact that road density was not measured beyond 1 km and the response variable was presence/absence rather than abundance.

Amphibians appear to be vulnerable to the fragmenting effect of roads and road traffic (Findlay et al. in press). Terrestrial amphibians are characteristically slow moving and not cognizant of the danger of traffic (Ashley and Robinson 1996, Vos and Chardon 1998). Unlike salamanders, anurans do not appear to avoid roads (deMaynardier and Hunter 1995). Mass migrations result in mass mortality and as Merrell (1977) describes, "At such times, the slaughter may be so great that the highway becomes slippery because of the numerous carcasses". Amphibians however, are not the only species that have are vulnerable to road mortality. Vehicular collisions have been recorded for insects, mammals, reptiles and birds (Forman 1988).

The loss of individuals through traffic mortality impacts leopard frog populations at both the local and regional level. At the local level, the population to which the individuals belong could be reduced in size. At the regional level, traffic mortality is a filtering process where a proportion of individuals does not successfully cross the road. This essentially fragments habitat and reduces landscape connectivity. If killed individuals are juveniles, then dispersal between populations, recolonizations of local extinctions, and occupation of new sites could be reduced (Rittschof 1975). Overall, the consequences of

traffic mortality are smaller and more isolated populations. Smaller populations are at a greater risk of extinction by chance, due to demographic, genetic, and environmental stochastic events (Wilcox and Murphy 1985). Isolated populations also have a lower chance of survival without the demographic and genetic input of immigrants, and of recolonization after extinction (Lande 1988).

Amphibian decline

Amphibian populations may be declining worldwide. The cause is presumed to be a complex mixture of local (agricultural pollution, habitat destruction and fragmentation) and possibly global (acid rain, ultra-violet radiation, climate change) conditions (Blaustein et al. 1994, Blaustein and Wake 1995, Pounds and Crump 1994).

More specifically, the genus *Ranidae* has experienced population declines through the 1970s and early 1980s followed by an increasing trend to the present (based on 891 amphibian populations mostly in Western Europe and North America) (Houlahan in press). This fluctuation could be attributed to the wide oscillations in population size characteristic of amphibians (Pechmann et al. 1991). Leopard frog populations have declined or become locally extinct over most of the frog's range over the last 20 years in North America (Beauregard and Leclair 1988, Gilbert et al. 1994). While some populations in Manitoba, Canada showed recovery in the 80s (Koonz 1992), the prairie populations of *Rana pipiens* in Alberta, Saskatchewan, and Manitoba were classified as vulnerable in 1998, and the southern mountain populations in British Columbia were

classified as endangered in 1998 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 1999). Speculated causes of the decline are overharvesting for research and teaching (Merrell 1977), environmental stress (Koonz 1992), habitat loss (Gilbert 1994), and increases in predatory fish and waterfowl (Orchard 1992). Habitat destruction leading to increased habitat fragmentation is cited as one of the most important factors causing amphibian decline in industrialized regions (Blaustein et al. 1994). My results suggest that traffic could be a contributing factor to amphibian declines in roaded landscapes.

Reducing anuran traffic mortality can be achieved by either modifying anuran behavior or reducing the amount of traffic. "Toad tunnels" are a popular method of increasing landscape connectivity and consist of drift fences that funnel amphibians through a tunnel that passes under the road. This measure has shown some success with dispersing amphibians (Langton 1989, Jackson 1998), although it is still not clear to what extent the tunnels are used and whether they can alleviate the impacts of traffic mortality at the population level. Another option is to create habitat on one side of the road so that crossing the road is unnecessary (Langton 1989, G. Venbass, personal communication). This is unlikely to work with leopard frogs, as they do not necessarily use the closest available habitat (Pope 1996). Still another option is to collect and physically move dispersing frogs over the road (Linck 1998). Reducing traffic can be achieved by seasonal road closures (Straker 1998), reducing the number of roads with high traffic volumes (C.F. Jaarsma, personal communication.) or reducing the dependency of humans on vehicles.

Implications for landscape ecology

Landscape connectivity is a functional measure, integrating landscape structure and the ability of an organism to move through and between landscape elements (Taylor et al. 1993). A highly vagile species should have a greater ability to move between landscape elements and thus perceive a fragmented landscape as still functionally connected (With and Crist 1995). However, a landscape structure that results in dispersal-related mortality might alter the ability of an organism to move between landscape elements, especially for a highly vagile species. This seems to be the case for amphibians in highly fragmented landscapes, where high terrestrial mortality is one of or the limiting factor in determining population size rather than the size of the breeding site (Vos and Chardon 1998). In this study, traffic mortality incurred during overland dispersal seems to be the cause for local population declines in the vagile species *Rana pipiens*. Gibbs (1998) found a similar result with amphibians where dispersal ability was inversely related to abundance in habitat patches that were fragmented due to habitat loss. Gibbs (1998) postulates that land between habitats serves as a demographic "drain" for many amphibians and that species that rely on dispersal are at a disadvantage in landscapes with large amounts of intervening habitat. Dispersal-related mortality could affect the ability of individuals to utilize heterogeneous environments and to maintain spatially separated populations (e.g.: a metapopulation or source-sink dynamics). These populations may lose their advantage

and face overall extinction, if individual populations cannot be maintained or recolonized through dispersal (Opdam 1993).

Leopard and green frogs both have relatively high dispersal capabilities compared to other anurans (Hecnar and M'Closkey 1997) yet they reacted very differently to traffic density in this study. This emphasizes that "dispersal capability" should not be used to predict how an organism would react in a fragmented habitat without a clear understanding of its population dynamics, movement pattern and the quality of the intervening habitat (matrix). A "neutral" matrix, one that does not incur mortality, is a simplifying assumption made in many models that regard the effect of dispersal on species' response to patchy habitats (e.g. With and Christ 1995, Lindenmayer and Possingham 1996). The presumption of a neutral matrix is that a vagile species has a higher tolerance to habitat fragmentation than a less vagile species, a widely held notion (Gibbs 1998). However, the negative impact of traffic mortality on amphibian populations demonstrates that the assumption of a neutral matrix is not valid for some landscapes or species.

Future research

This study has demonstrated that traffic mortality is large enough in the Ottawa-Carleton region to cause population decline of leopard frogs. The next step is to determine the mortality rate from vehicular collisions (extraneous mortality) and to relate this to the base or "natural" mortality rate. This relationship could be simulated over a range of

extraneous and natural mortality rates to answer the question, what level of extraneous mortality will cause population decline? This is an important question for species in fragmented habitats where mortality may be higher in the matrix, or along forest edges (Murcia 1995). Population demographics other than natural mortality rate also play a role in the ability of a population to absorb extraneous sources of mortality. Demographics, such as initial population size and fecundity, should be included in the simulation model to determine the impact of extraneous mortality on different species guilds.

Conclusions

Several conclusions can be drawn from my results. First, disturbance free "buffer zones" should be *at least* 1.5 km to protect amphibian populations. Second, a high dispersal mortality rate could outweigh the benefits of dispersal in a fragmented landscape. Third, dispersal-related mortality in roaded landscapes is sufficient to cause population level decline in some species. Fourth, measures of "dispersal capability" should not be used to predict how an organism would react in a fragmented habitat without a clear understanding of its population dynamics, movement pattern and the quality of the matrix. Finally, transportation and resource officials should be alerted to the widespread threat that roads pose to wildlife.

APPENDIX 1

Data- Total chorus and visual survey counts for each pond

Pond	<i>Rana pipiens</i> surveys		<i>Rana clamitans</i> surveys	
	Total chorus counts	Total visual counts	Total chorus counts	Total visual counts
Bakker	1	2	21	24
Bell	35	35	7	13
Bigkidd	0	17	5	4
Bimini	1	0	0	10
Burke	3	8	9	2
Cemetery	0	2	19	50
Deverell	4	7	25	29
Hope	2	2	5	21
Jock	4	35	10	31
Kelly	18	36	25	11
Macgregor	0	0	9	0
Mccauley	0	0	8	5
McNeely	0	28	2	0
Merriam	3	16	3	8
Nesbitt	23	29	6	0
O'connor	0	10	14	13
Patterson	8	3	46	57
Pillar	0	44	9	26
Pond motel	1	4	9	6
Rec centre	0	4	3	8
Reid	0	0	11	7
Rigby	0	5	15	23
Smallkidd	1	24	0	1
Smyth	13	7	2	1
Spratt	3	2	1	2
Stinson	10	1	5	3
Streit	0	0	10	21
Todd	6	47	21	13
Vandam	4	3	18	34
Zanetti	0	6	11	3
Total	140	377	329	426
Minimum	0	0	0	0
Maximum	35	44	46	57

Data continued- Local variables

Pond	pH	Leopard spawning habitat (m)			Green spawning habitat (m)		
		Optimal	Sub-optimal	Low	Optimal	Sub-optimal	Low
	8.04	25	0	125	25	125	0
Bakker	8.02	182	496	60	182	496	60
Bell	9.90	20	0	30	0	20	30
Bigkidd	10.30	115	23	0	69	69	0
Bimini	8.46	40	60	20	20	100	0
Burke	8.73	0	50	80	0	125	25
Cemetery	7.92	84	57	57	170	28	0
Deverell	9.91	90	60	90	90	150	0
Hope	6.52	18	72	18	0	108	0
Jock	8.73	130	0	0	0	130	0
Kelly	6.67	56	42	0	56	42	0
Macgregor	9.78	32	256	0	0	224	64
Mccauley	10.56	314	52	104	210	260	0
McNeely	11.30	114	19	0	95	38	0
Merriam	7.20	138	0	0	69	69	0
Nesbitt	8.67	64	16	16	32	64	0
O'connor	7.30	17	68	34	0	119	0
Patterson	8.48	28	84	28	28	140	0
Pillar	8.66	194	117	62	194	179	0
Pond motel	8.30	30	30	30	60	30	0
Rec centre	8.16	0	0	120	0	20	100
Reid	8.93	90	150	0	150	90	0
Rigby	6.80	0	10	30	0	40	0
Smallkidd	8.71	120	60	30	120	90	0
Smyth	7.33	0	42	85	0	63	64
Spratt	6.94	136	102	0	170	68	0
Stinson	7.90	68	34	136	34	204	0
Streit	9.53	122	49	49	0	220	0
Todd	8.51	160	0	0	140	20	0
Vandam	8.76	110	20	0	110	20	0
Zanetti							
Mean	8.50	83	66	40	67	111	11
Minimum	6.52	0	0	0	0	20	0
Maximum	11.30	314	496	136	210	496	100

Data continued- Landscape habitat variables

Pond	Forest (km²)	Water (km²)	Built-up (km²)	Wetland (km²)	Agriculture (km²)	Stream (km)
Bakker	0.61	0.08	0.13	0.00	6.25	6.36
Bell	2.65	0.01	0.07	0.00	4.31	2.69
Bigkidd	3.00	0.00	0.00	0.56	3.51	0.00
Bimini	1.81	0.01	0.05	0.03	5.18	7.78
Burke	0.96	0.00	0.00	0.19	5.92	6.49
Cemetery	0.48	0.57	0.70	0.00	5.32	4.46
Deverell	2.49	0.00	0.11	0.13	4.35	3.93
Hope	0.81	0.02	0.00	0.00	6.23	7.18
Jock	0.43	0.17	0.62	0.00	5.86	6.10
Kelly	0.95	0.00	0.00	0.00	6.12	9.37
Macgregor	2.91	0.01	0.03	0.10	4.03	0.00
Mccauley	1.12	0.00	0.27	0.00	5.68	10.55
McNeely	3.47	0.00	0.13	0.22	3.24	1.80
Merriam	0.44	0.51	0.41	0.01	5.70	6.69
Nesbitt	1.44	0.01	0.00	2.72	2.90	3.97
O'connor	3.73	0.00	0.00	0.21	3.13	2.54
Patterson	1.31	0.00	0.00	0.00	5.75	12.86
Pillar	3.41	0.00	0.02	0.61	3.03	9.39
Pond motel	1.39	0.00	0.13	1.53	3.06	5.70
Rec centre	1.40	0.01	0.00	2.66	3.00	4.73
Reid	3.85	0.02	0.22	0.33	2.65	3.56
Rigby	2.33	0.08	0.29	0.33	4.04	4.60
Smallkidd	2.41	0.00	0.16	2.56	1.95	0.00
Smyth	2.08	0.00	0.15	0.09	4.75	4.70
Spratt	0.55	0.04	0.02	0.00	6.45	3.81
Stinson	1.05	0.01	0.06	0.00	5.94	4.95
Streit	0.73	0.09	0.00	0.00	6.25	4.29
Todd	1.46	0.00	0.09	0.15	5.37	4.37
Vandam	2.93	0.00	0.00	0.00	4.14	3.23
Zanetti	1.90	0.08	0.27	0.03	4.78	5.42
Mean	1.80	0.06	0.13	0.42	4.63	5.05
Minimum	0.43	0.00	0.00	0.00	1.95	0.00
Maximum	3.85	0.57	0.70	2.72	6.45	12.86

Data continued- Traffic density variables 0.25-1.75 km

Pond	Radius of concentric circle (km)						
	0.25	0.50	0.75	1.0	1.25	1.5	1.75
Bakker	409	724	884	1097	1290	1851	2947
Bell	219	319	373	572	2263	3483	4303
Bigkidd	143	250	305	343	533	828	1043
Bimini	0	1173	9430	14800	17895	20353	22382
Burke	872	1354	1636	4481	6085	7053	7887
Cemetery	4325	5918	14812	31473	43131	52556	59737
Deverell	26121	35853	41514	45559	48665	51254	53586
Hope	12314	16434	18915	20710	22085	25338	28154
Jock	14308	19653	23051	35120	40653	49476	63116
Kelly	306	588	743	852	932	1031	1463
Macgregor	0	1003	1618	21725	34889	49817	60795
Mccauley	0	616	1575	2488	3416	15168	18370
McNeely	1249	1881	11956	16175	18954	21401	23227
Merriam	8836	16596	20456	30311	35481	39025	42398
Nesbitt	1791	2924	3521	3938	4242	4747	5109
O'connor	579	772	886	998	1308	1478	2983
Patterson	167	227	263	461	919	1480	1824
Pillar	297	399	604	1143	1416	1597	3461
Pond motel	26626	36077	41694	45699	48811	56790	62185
Rec centre	0	80	1319	1792	2165	2468	2696
Reid	6502	14315	18268	20928	22931	24537	25889
Rigby	0	0	2869	4318	5349	6075	7681
Smallkidd	813	1144	1323	1446	1613	1741	1841
Smyth	9790	14606	17266	19131	20543	21693	22677
Spratt	1183	1892	2563	2956	3186	3466	3877
Stinson	0	21765	38587	49728	58397	65404	73314
Streit	0	410	9676	13914	17138	19663	22855
Todd	0	346	508	3420	4813	6082	7706
Vandam	1335	2186	2611	2942	6262	8548	10041
Zanetti	406	554	642	2465	4828	6679	7837
Mean	3953	6669	9662	13366	16006	19036	21713
Minimum	0	0	263	343	533	828	1043
Maximum	26626	36077	41694	49728	58397	65404	73314

Data continued- Traffic density variables 2.0-5.0 km

Pond	Radius of concentric circle (km)						
	2.0	2.5	3.0	3.5	4.0	4.5	5.0
Bakker	3572	4148	6244	7397	8497	9679	15754
Bell	4860	5308	5914	7168	7959	8760	10342
Bigkidd	1188	1282	1488	4004	5657	6842	7652
Bimini	24287	25998	27744	29463	32651	36033	42127
Burke	9225	9824	10334	10843	11269	11697	12101
Cemetery	65954	75074	81727	86896	93151	100976	106211
Deverell	55611	57536	59171	60966	62249	63350	64419
Hope	29850	31685	32973	33926	34753	35558	36364
Jock	71190	80645	89324	97125	108688	116520	121492
Kelly	1952	3211	3979	4543	5080	6567	7630
Macgregor	65480	69478	72806	75750	79693	82650	85297
Mccauley	20871	22766	27329	29526	31715	33556	35282
McNeely	24745	26002	27720	29255	30301	31362	33570
Merriam	45452	48370	50789	55029	58110	60536	62670
Nesbitt	5398	5702	8357	13455	16489	18378	20033
O'connor	4175	5051	5552	6018	6415	6815	7172
Patterson	2098	2793	3642	4316	5647	7854	9320
Pillar	4726	5483	5958	6434	6834	7242	7581
Pond motel	66246	70524	73980	77266	80145	82499	84932
Rec centre	6273	9362	10951	13493	17075	19366	20815
Reid	27770	29149	30261	31149	32452	34171	35621
Rigby	9205	10146	10870	11439	12904	14609	18694
Smallkidd	1977	2219	2352	2682	3446	5470	6632
Smyth	23541	24617	25490	26166	27372	28899	29879
Spratt	4319	6076	10516	12807	15089	18387	22307
Stinson	80093	86509	93210	99802	107326	113352	117908
Streit	26098	29663	32759	35504	38601	41389	45745
Todd	8997	9910	10854	12016	12795	13454	14796
Vandam	11337	12334	13189	13977	14590	15146	15632
Zanetti	8843	11028	12137	13055	13892	14605	16839
Mean	23844	26063	28254	30382	32695	56397	58700
Minimum	1188	1282	1488	2682	3446	5470	6632
Maximum	80093	86509	93210	99802	108688	759547	764103

REFERENCES

- 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(3):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.
- Beauregard, N., and R. Leclair. 1988. Multivariate analysis of the summer habitat structure of *Rana pipiens* Schreber (leopard frog) in Lake St. Pierre (Québec, Canada). In *Management of Amphibians, Reptiles, and Small Mammals*, pp. 129-143. U.S. Forestry Service General Technical Report RM-166.
- Behler, J.L., and F.W. King. 1995. *National Audubon Society Field Guide to North American Reptiles and Amphibians*. Alfred A. Knopf: New York.
- Blaustein, A.R., D.B. Wake, W.P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinction. *Conservation Biology* 8(1):60-71.
- Blaustein, A.R., and D.B. Wake. 1995. The puzzle of declining amphibian populations. *Scientific American* 272(4):52-57.
- Berven, K.A., and T.A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 22(8):2047-2056.
- 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.
- Burrough, P.A. 1995. Spatial aspects of ecological data. In *Data Analysis in Community and Landscape Ecology*, eds. R.H.G. Jongman, C.J.R. Ter Braak, and O.F. R. Van Tongeren, pp. 213-251. Cambridge University Press: New York.
- Collins, J.P., and H.M. Wilbur. 1979. *Breeding habits and habitats of the amphibians of the Edwin S. George Reserve, Michigan, with notes on the local distribution of fishes*. Occasional Papers of the Museum of Zoology No. 686. University of Michigan: Michigan.

- COSEWIC. 1999. *Canadian Species At Risk*. Committee On the Status of Endangerend Wildlife In Canada: Canada.
- Courtois, D., R. Leclair jr., S. Lacasse, and P. Magnan. 1995. Habitats préférentiels d'amphibiens ranidés dans des lacs oligotrophes du Bouclier laurentien, Québec. *Canadian Journal of Zoology* 73:1744-1753.
- DeMaynardier, P.G., and M.L. Hunter Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Review* 3:230-261.
- Dole, J.W. 1965. Summer movements of adult leopard frogs *Rana pipiens* Schreber, in northern Michigan. *Ecology* 46(3):236-254.
- Dole, J.W. 1967. Spring movements of leopard frogs, *Rana pipiens* Schreber, in Northern Michigan. *The American Midland Naturalist* 78(1):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. In *Biology of Australasian Frogs and Reptiles*, eds. G. Grigg, R. Shine, and H. Ehmann, pp. 435-47. Surrey Beatty & Sons and Royal Zoological Society of New South Wales: Sydney.
- 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.
- Fahrig, L., and A. Grez. 1996. Population spatial structure, human-caused landscape changes and species survival. *Revista Chilena de Historia Natural* 69:5-13.
- Findlay, C. S., and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* 11(4):1000-1009.
- Findlay, C.S., J. Lenton, and L. Zheng. Effects of adjacent land use on anuran communities of southeastern Ontario wetlands. *In press*.
- Forman, R.T.T. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-31.
- 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(4):465-470.
- Gilhen, J. 1984. *Amphibians and reptiles of Nova Scotia*. Nova Scotia Musuem: Halifax, Nova Scotia.
- Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48:145-166.
- Gustafson, E.J. 1998. Quantifying Landscape Spatial Pattern: What is the State of the Art? *Ecosystems* 1:143-156.
- Hecnar, S.J., and R.T. M'Closkey. 1997. Patterns of nestedness and species association in a pond-dwelling amphibian fauna. *Oikos* 80(2):1-10.
- Heine, G. 1987. Einfache Meß- und Rechenmethode zur Ermittlung der Überlebenschance wandernder Amphibien beim Überqueren von Straßen. *Beih. Veröff. Naturschutz und Landschaftspflege in Baden-Württemberg* 41:473-9.
- Hinch, S.G., K.M. Somers, and N.C. Collins. 1994. Spatial autocorrelation and assessment of habitat-abundance relationships in littoral zone fish. *Canadian Journal of Aquatic Science* 51:701-712.
- Hine, R.L., B.L. Les, and B.F. Hellmich. 1981. *Leopard frog populations and mortality in Wisconsin, 1974-1976*. Technical bulletin No. 122. Department of Natural Resources: Madison, Wisconsin.
- Houlahan, J. Temporal, spatial and taxonomic trends in 891 amphibian populations. *In press*.
- Jackson, S.D., and C.R Griffin. 1998. Toward a practical strategy for mitigating highway impacts on wildlife. In *Proceedings of the International Conference on Wildlife Ecology and Transportation*, eds. G. L. Evink, P. Garret, D. Zeigler, and J. Berry, pp. 17-22. FL-ER-69-98. Florida Department of Transportation: Tallahassee, Florida.
- Koonz, W. 1992. Amphibians in Manitoba. In *Declines in Canadian Amphibian Populations: Designing a National Strategy*, eds. C.A. Bishop, and K.E. Pettit, pp.19-20. Occasional Paper No. 76. Canadian Wildlife Service and Environment Canada: Ottawa, Canada.

- Kuhn, J. 1987. Straßentod der Erdkröte (*bufo bufo* L.): Verlustquoten und Verkehrsaufkommen, Verhalten auf der Straße. *Beih. Veröff. Naturschutz und Landschaftspflege in Baden- Württemberg* 41:175-86.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Langton, T.E.S., ed. 1989. *Amphibians and Roads*. ACO Polymer Products Ltd: Shefford, Bedfordshire, UK.
- Legendre, P., and M.J. Fortin. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80:107-138.
- 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 south-eastern Australia. *Landscape Ecology* 11(2):79-105.
- Linck, M.H. 1998. Reduction in road mortality in a northern leopard frog population. Abstract. *A Joint Meeting of the Great Lakes & Central Division Working Groups of the Declining Amphibian Populations Task Force*. Milwaukee Public Museum: Milwaukee, Wisconsin.
- Loman, J. 1988. Breeding by *Rana temporaria*: the importance of pond size and isolation. *Memoranda Soc. Fauna Flora Fennica* 64:113-115.
- 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.
- MapInfo Corporation. 1997. *MapInfo Pro, version 4.5*. MapInfo Corporation, Troy, New York.
- Martof, B.S. 1953a. Territoriality in the green frog, *Rana clamitans*. *Ecology* 34:165-174.
- Martof, B.S. 1953b. Home range and movements of the green frog, *Rana clamitans*. *Ecology* 34(3):529-543.
- Martof, B.S. 1956. Factors influencing size and composition of populations of *Rana clamitans*. *The American Midland Naturalist* 56(1):224-243.
- McAlpine, D.F., and T.G. Dilworth. 1989. Microhabitat and prey size among three species of *Rana* (Anura: Ranidae) sympatric in eastern Canada. *Canadian Journal of Zoology* 67:2244-2252.

- Merrell, D.J., and C.F. Rodell. 1967. Seasonal selection in the leopard frog, *Rana pipiens*. *Evolution* 22:284-288.
- Merrell, D.J. 1968. A comparison of the estimated and the "effective size" of breeding populations of the leopard frog, *Rana pipiens*. *Evolution* 22(2):274-83.
- Merrell, D.J. 1977. *Life history of the leopard Frog, Rana pipiens, in Minnesota*. Occasional paper No. 15. Bell Museum of Natural History and University of Minnesota: Minnesota.
- 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(4):227-235.
- Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *TREE* 10(2):58-62.
- Oldham, R.S. 1967. Orienting mechanisms of the green frog, *Rana clamitans*. *Ecology* 48(3):477-491.
- Olsen, D.H., W.P. Leonard, and R.B. Bury. 1997. *Sampling Amphibians in Lentic Habitats*. Northwest Fauna No. 4. Society for Northwestern Vertebrate Biology: Washington.
- Opdam, P., R. Van Apeldoorn, A. Schotman, and J. Kalkhoven. 1993. Population responses to landscape fragmentation. In *Landscape ecology of a stressed environment*, eds. C.C.Vos and P. Opdam, pp.147-171. Chapman and Hall: London.
- Orchard, S.A. 1992. Amphibian population declines in British Columbia. In *Declines in Canadian Amphibian Populations: Designing a National Strategy*, eds. C.A. Bishop and K.E. Pettit, pp.10-13. Occasional Paper No. 76. Canadian Wildlife Service and Environment Canada: Ottawa: Ottawa, Canada.
- 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.
- Pechmann, J.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt, and J.W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892-895.
- 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.Sc. thesis. Carleton University: Ottawa.

- Pounds, J.A., and M.L. Crump. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. *Conservation Biology* 8(1):72-85.
- 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: Michigan.
- SAS Institute. 1996. *SAS user's guide: statistics, Version 6.12*. SAS institute Inc., Cary, North Carolina.
- Schroeder, E.E. 1976. Dispersal and movement of newly transformed green frogs, *Rana clamitans*. *The American Midland Naturalist* 95(2):471-474.
- Seburn, C.N.L., D.C. Seburn, and C.A. Paskowski. 1997. Northern leopard frog (*Rana pipiens*) dispersal in relation to habitat. In *Amphibians in Decline: Canadian Studies of a Global Problem*, ed. D.M. Green, pp.64-72. *Herpetological Conservation* 1. Society for the Study of amphibians and Reptiles: Missouri.
- Shirose, L.J., C.A. Bishop, D.M. Green, C.J. MacDonald, R.J. Brooks, and N.J. Helferty. 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. *Herpetologica* 53(3):312-320.
- 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.
- Snell, A. 1987. *Wetland distribution and conversion in southern Ontario*. Working Paper No. 48. Canada Land Use Monitoring Program, Inland Waters and Lands Directorate, Environment Canada: Ottawa, Canada.
- Straker, A. 1998. Management of roads as biolinks and habitat zones in Australia. In *Proceedings of the International Conference on Wildlife Ecology and Transportation*, eds. G. L. Evink, P. Garret, D. Zeigler, and J. Berry, pp. 181-88. FL-ER-69-98. Florida Department of Transportation: Tallahassee, Florida.
- Taylor, P.D., L.Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68(3):571-573.
- Turner, S.J., R.V. O'Neill, W. Conley, M.R. Conley, and H.C. Humphries. 1991. Pattern and Scale: Statistics for Landscape Ecology. In *Quantitative Methods in Landscape Ecology*, eds. M.G. Turner and R.H. Gardner, pp.17-50. Springer-Verlag:London.
- 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.
- Wilcox, B.A., and Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* 125:879-887.
- With, K.A., and T.O. Christ. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76(8):2246-2459.