

BEHAVIOR OF AMPHIBIANS ON THE ROAD IN RESPONSE TO CAR TRAFFIC

Authors: Mazerolle, Marc J., Huot, Matthieu, and Gravel, Mireille

Source: *Herpetologica*, 61(4) : 380-388

Published By: The Herpetologists' League

URL: <https://doi.org/10.1655/04-79.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

BEHAVIOR OF AMPHIBIANS ON THE ROAD IN RESPONSE TO CAR TRAFFIC

MARC J. MAZEROLLE^{1,3,5}, MATTHIEU HUOT^{1,4}, AND MIREILLE GRAVEL²

¹*Centre de Recherche en Biologie Forestière, Université Laval, Québec, QC G1K 7P4, Canada*

²*Département de Biologie, Université de Moncton, Moncton, NB E1A 3E9, Canada*

ABSTRACT: Nocturnal car traffic often results in amphibian casualties, especially during rainy nights. The behavior of amphibians presumably influences their vulnerability to mortality on the road, but this hypothesis remains untested. We investigated the behavioral response of individuals of six species of amphibians on roads when confronted by an approaching vehicle. We first conducted a field study consisting of 50 night-driving surveys over 4 yr during which we recorded the behavior (i.e., moving or immobile) of frogs, toads, tree frogs, and salamanders encountered on a 20-km stretch of road. In an effort to tease apart the effects of headlights and the sound of motors on amphibian behavior, we carried out a field experiment on a test road where we exposed individuals to different car-associated stimuli. Here, we tested the hypothesis that simultaneous exposure to headlights and the sound of a car motor would elicit a stronger response than exposure to a single stimulus or a control. Based on the observations of the 2767 individuals in the field survey, immobility was the most common response to the approach of a car (mean probability of 0.82 of remaining immobile); the response differed across species but depended on the season of the survey (May–June vs. July–September). Similarly, the 91 individuals included in the field experiment were more likely to move during the control treatment than during any of the car-associated treatments. The combined stimuli elicited the strongest response, followed by the headlights-only and the motor-only treatments. Spring peepers (*Pseudacris crucifer*) tended to move more often than the other species we tested in the field experiment, which suggests they spend less time on the road and are less vulnerable to traffic mortality than other species. Both the field survey and field experiment consistently indicated that amphibians tend to remain immobile at the approach of a vehicle. This behavior highlights the vulnerability of amphibians to road traffic and should be considered in measures to mitigate road impacts.

Key words: Automobile; Field experiment; Frogs; Headlights; Highway mortality; Movement; Salamanders

ROADS have deleterious impacts on animal and plant communities (reviewed in Forman and Alexander, 1998; Forman et al., 2003) by contributing to habitat loss and fragmentation (Forman et al., 2003; Semlitsch, 2000), which can lead to isolation of populations through reduced movements and gene flow (Baur and Baur, 1990; Gibbs, 1998; St. Clair, 2003; Wyman, 1991). These negative effects of roads on amphibian populations may result from an avoidance of roadside areas (deMaynadier and Hunter, 2000; Reijnen et al., 1995; Jaeger et al., 2005), a reluctance to cross roads (Baur and Baur, 1990; Swihart and Slade, 1984), or more directly, from mortality on roads.

Roads can be especially deadly for small-sized animals such as small mammals, reptiles, and amphibians (Adams and Geis, 1983; Ashley and Robinson, 1996; Fahrig et al., 1995; Hodson, 1966). Pond-breeding amphibians, which migrate in large numbers to and from breeding sites, are particularly vulnerable to “collisions” with vehicles (Fahrig et al., 1995; Hels and Buchwald, 2001; Palis, 1994). These collisions may be associated with specific behaviors of amphibians (e.g., staying immobile, adopting threat displays, fleeing) in response to intense light or sound associated with vehicles. Differences in such responses across species could reveal which species are particularly vulnerable to mortality on the road.

The behavioral mechanisms responsible for amphibian mortality on the road have typically been overlooked in investigations of road traffic on amphibians (but for snakes see Andrews and Gibbons, in press; Shine et al., 2004). This omission is rather surprising, as behavior relative to an oncoming vehicle

³ PRESENT ADDRESS: USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708-4017, USA.

⁴ PRESENT ADDRESS: Département des sciences fondamentales, Université du Québec à Chicoutimi, 555, boulevard de l'Université, Chicoutimi, Québec G7H 2B1, Canada.

⁵ CORRESPONDENCE: e-mail, mmazerolle@usgs.gov

presumably influences the fate of an amphibian on the road. With the assumption that remaining immobile on the road should be a worse strategy than leaving the road, we quantified, through a field survey and a controlled experiment, the behavior of amphibians on the road relative to different stimuli associated with car traffic. Because individuals of several species of amphibians become immobile at the sight of a predator (Brodie et al., 1979; Formanowicz and Brodie, 1979; Heinen, 1994; Heinen and Hammond, 1997; Marchisin and Anderson, 1978), we tested the hypothesis that amphibians on the road stop moving at the approach of a vehicle. Then, we postulated that amphibians on the road respond more strongly to the simultaneous exposure to light and sound than to either stimuli taken singly or to a control.

METHODS

Study Area

We conducted the research within Kouchibouguac National Park, in eastern New Brunswick, Canada. The area is characterized by mixed forest dominated by black spruce (*Picea mariana*), white pine (*Pinus strobus*), red pine (*P. resinosa*), balsam fir (*Abies balsamea*), maple (*Acer* spp.), and birch (*Betula* spp.). Wetlands are prominent in the park, in the form of peatlands, rivers, brooks, ditches, and permanent and temporary ponds.

Field Survey

The field study consisted of night-driving surveys (sensu Shaffer and Juterbock, 1994) on a 20-km road segment of Route 117 going through the park. The two-laned road is ca. 8-m wide, and has an average nocturnal traffic load of approximately 13.6 vehicles/h during spring and summer (Mazerolle, 2003). We conducted the surveys from May to September 2001–2004 after dark when the road surface was humid (during or following rain) between 2000 and 0400 h. A single 20-km survey was conducted on any given night. Driving along the road at 10–20 km/h, we stopped each time an amphibian was seen on the road. At each stop, we identified the individual to species and noted its behavior (i.e., moving or immobile) when it was first seen on the road from inside the moving car. Because we were

limited by suitable weather conditions (i.e., rainy nights), we only conducted five surveys in 2001 and four in 2002. However, wetter conditions prevailed in 2003 and 2004, during which we realized 27 and 14 surveys, respectively. For each species, we computed the proportion of live individuals encountered on the road that had moved at the approach of the vehicle during each survey night and used these proportions as the basis for our analyses (see “Statistical Analyses” below).

Field Experiment

We selected the six amphibian species most common in the study area for the field experiment: spring peeper (*Pseudacris crucifer*), spotted salamander (*Ambystoma maculatum*), blue-spotted salamander (*Ambystoma laterale*), American toad (*Bufo americanus*), green frog (*Rana clamitans*), and wood frog (*Rana sylvatica*). A total of 91 adult and juvenile amphibians were captured during night-driving surveys on the same stretch of road described above or at a nearby pond. These consisted of (mean snout–vent length \pm 1 SD): 20 mole salamanders (4.3 ± 1.4 cm), 11 American toads (3.8 ± 1.7 cm), 18 spring peepers (2.7 ± 0.8 cm), and 42 ranid frogs (4.3 ± 1.6 cm). Each animal was kept in captivity in an individual, moist container in a dark cool room (ca. 14 C) for no more than 24 h before the trials.

All treatments were conducted on a 62-m stretch of single-lane paved road (4.8 m in width) leading to the parking lot of Kelly’s Bog (46° 58′ 59″ N, 64° 57′ 12″ W) within Kouchibouguac National Park. We selected this road mainly because the very low traffic allowed us to safely conduct the experiment. Furthermore, because the road was unlit (i.e., no street lights), we were able to control all artificial light sources. During the experiment, we poured well water over the road surface to maintain its humidity and simulate wet road conditions such as those encountered during rainy nights.

We conducted the experiment under similar weather conditions on the nights of 31 May, 30 June, 11 July, 10 August, and 13 August 2001. We noted the air temperature before starting a set of trials for a given individual. We conducted all observations between 2200 h and 0430 h, at least 1 h after sunset. On a given

night, we randomly selected each amphibian from the group of individuals captured less than 24 h earlier. We submitted each individual to four treatments in a random sequence. We determined the response (i.e., moving vs. immobile) of each individual following exposure to the sound of the car, the headlights, or a combination of both, relative to a control. Standing at least 5 m from the individuals, the observer used a headlamp fitted with a red filter to monitor amphibians during the trials.

The first treatment (i.e., headlight and motor treatment) simulated the encounter of a car and the individual on the road surface. For the second treatment (i.e., motor-only treatment), we assessed the response of amphibians to the sound associated with a car. We completely covered the headlights of the car with a thick opaque fabric to prevent any light from being emitted. The third treatment consisted of measuring the behavior of amphibians relative to headlights without the sound of the motor (i.e., headlights-only treatment). Because it would have been impossible to move the car during the headlights-only treatment (i.e., no motor), we used a car surrogate. To do so, we fastened two strong flashlights (Mag Lite™ with 3-D cells) at a height and width identical to that of the car onto a children's wagon (Radio Flyer™). The intensity of the flashlights was ca. 39 lux at 5 m (Corben and Fellers, 2001) and equates to that of car headlights at approximately 50 m. This treatment provided a means to isolate the effect of light and the sound of the motor on amphibian behavior. The wagon was pushed from behind to simulate the approach of a car. The fourth treatment (i.e., control) consisted of watching the behavior of individuals under the red light for 30 s without any other disturbance.

Every treatment was preceded by a 2-min habituation period during which the individual was placed in the middle of the road under a 500 ml container to minimize disturbance. At the start of a given trial, the container was removed. The car or wagon then started 62 m from the position of the individual and approached at a speed of 5–10 km/h, coming to a stop 1 m in front of the animal. The observation period began as soon as the vehicle started its approach and was terminated

when the vehicle was 1 m from the individual (ca. 30 s later). We recorded the behavior of the individual during the observation period as moving (i.e., moving/resuming activity) or immobile (i.e., remains in same place). At the end of each of the four trials, we rinsed, with water, the surface on which each individual was placed to minimize the possible effect of secretions on the next individual's behavior. All individuals were measured to snout–vent length (SVL) and released at their point of capture the day following their use in the experiment.

Statistical Analyses

In both the field survey and the field experiment, we recorded whether each amphibian moved (i.e., a binary variable reflecting the probability of fleeing from an approaching car). This type of data is best suited for logistic regression analysis and is analogous to linear regression in its structure and interpretation (Hosmer and Lemeshow, 1989). Because each individual in the field experiment was submitted to four treatments, we used an extension of logistic regression for repeated measures (i.e., generalized estimating equations) to account for repetitive observations on the same individual (Diggle et al., 1994; Horton and Lipsitz, 1999; Stokes et al., 2000). Due to low numbers of certain species and to facilitate comparisons between the survey and the experiment, we pooled the mole salamanders together (*A. laterale* and *A. maculatum*), and the ranid frogs (*R. clamitans*, *R. pipiens*, and *R. sylvatica*).

We chose a modelling approach based on the second-order Akaike Information Criterion (AIC_c), as it prioritizes estimation of the effect, its associated precision, and confidence intervals instead of relying on hypothesis testing and *P*-values (Burnham and Anderson, 2002; Mazerolle, in press). It is especially well-suited for model selection (i.e., finding the best model or variables) because it is not subject to the problems of the more typical model-building procedures such as stepwise, backward, or forward elimination (Burnham and Anderson, 2002). For the field survey data, we considered a set of six models differing in complexity to explain the behavior (i.e., moving or immobile) of amphibians on the road at the approach of a vehicle. We included

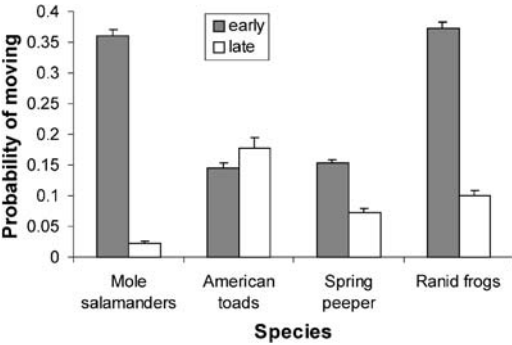


FIG. 1.—Probability of amphibians moving at the approach of a car, based on the predicted values of the logistic regression, across species and period of the season (i.e., early: May–June, late: July–September). Error bars denote 1 SE (obtained from 10,000 bootstrapped samples) around each mean. We included 2767 individuals in the study: 307 mole salamanders, 65 American toads, 1391 spring peepers, and 1004 ranid frogs.

the categorical variable species (i.e., with ranid frogs as the reference level), as well as the categorical covariates year and period of survey (i.e., May–June vs. July–September) to account for potential temporal variation in amphibian behavior. We also considered the species \times period interaction, as the behavior of certain groups might differ with changing weather conditions (e.g., air temperature) across seasons.

For the field experiment, we considered a total of 14 different models. Some of these involved the continuous variables snout–vent length (SVL), air temperature, and time at which the trials of each individual were conducted (log of min after sunset). Other models included the categorical variables car treatment (i.e., with the control as the reference level), species group (i.e., with ranids as the reference level), as well as previous car treatment. The latter was to test whether the effect of a given treatment influenced the response of individuals later during the experiment (i.e., carry-over effects, see Diggle et al., 1994). Finally, some models included interactions (i.e., species \times treatment, species \times previous treatment), or combinations of the variables mentioned earlier (e.g., air temperature, SVL).

All analyses were conducted with SAS 8.02, using the LOGISTIC and GENMOD procedures. The Hosmer–Lemeshow goodness-of-fit statistic suggested the logistic regression mod-

TABLE 1.—Ranking of logistic regression models corrected for overdispersion ($c\text{-hat} = 1.77$) assessing the probability of an amphibian to flee from an approaching vehicle on the road during night driving surveys in summers 2001–2004. We included 2767 individuals in the analyses: 307 mole salamanders, 65 American toads, 1391 spring peepers, and 1004 ranid frogs.

Set of candidate models	Number of parameters ¹	Delta QAIC _c	Akaike weight
Intercept year period			
species period*species	12	0	0.997
Intercept year period			
species	9	12.07	0.002
Intercept period species			
period*species	9	13.86	0.00
Intercept year period	6	30.65	0.00
Intercept species	5	91.17	0.00
Intercept only	2	94.68	0.00
Model-averaged estimates (\pm unconditional SE) ²			
Species \times period interaction ³			
Mole salamanders \times early			
American toads \times early			
Spring peepers \times early			
1.569	–1.885		–0.802
(0.765)	(1.014)		(0.376)

¹ Count of parameters includes the overdispersion parameter, $c\text{-hat}$.
² Characters in bold indicate that 90% confidence interval excludes 0 and that response of a given species varies across period.
³ Species: ranid frogs used as reference level; period: early (May–June) vs late (July–September).

els were appropriate for the data. We computed the AIC_c (or where there was evidence of overdispersion, the QAIC_c) and measures derived from it (i.e., delta AIC_c and Akaike weights) to assess the strength of each model and the effect of each explanatory variable in the models (Anderson et al., 2000; Burnham and Anderson, 2002; Pan, 2001). We obtained the estimates and standard errors for each variable with model-averaging techniques, as described in detail in Burnham and Anderson (2001, 2002) and Mazerolle (in press).

RESULTS

Field Survey

Most of the 2767 live amphibians observed during night-driving surveys remained immobile during encounters with the car (Fig. 1). The model which included the species \times period interaction had the most support, being more than 400 times better (i.e., based on evidence ratio of Akaike weights: 0.9966/0.0024) than the model ranked in second place (Table 1). Indeed, the behavior of amphibians differed considerably across species and period. Spring peepers, mole salamanders, and ranid

TABLE 2.—Highest-ranked logistic regression models for repeated measures (i.e., $\Delta AIC_c < 5$) and estimates assessing the probability of amphibians to flee in response to light and noise associated with car traffic. We used 91 amphibians in the experiment: 20 mole salamanders, 11 American toads, 18 spring peepers, and 42 ranid frogs.

Models			Number of parameters	Delta AIC _c	Akaike weight	
Intercept treatment species svl			8	0	0.54	
Intercept treatment species svl airtemp time			10	2.32	0.17	
Intercept treatment species			7	3.21	0.11	
Intercept treatment species airtemp			8	3.32	0.10	
Intercept treatment species time			8	4.84	0.05	
Model-averaged estimates (\pm unconditional SE) ¹						
Treatment ²			Species ³			
Headlights and motor	Motor only	Headlights only	Mole salamander	American toad	Spring peeper	SVL
−2.561 (0.416)	−1.670 (0.361)	−1.752 (0.361)	0.373 (0.437)	0.886 (0.511)	1.037 (0.529)	−0.226 (0.125)

¹ Characters in bold indicate that the 90% confidence intervals exclude 0 and that the variable influences amphibian behavior.

² Control treatment used as reference level.

³ Ranid frogs used as reference level.

frogs on the road were less likely to remain immobile at the approach of the vehicle early in the season (May–June) than later (July–September), but the response was weaker in spring peepers than in ranid frogs, whereas it was stronger in mole salamanders than in ranid frogs (Table 1). Based on the data for the amphibians observed on the road, the mean predicted probability \pm 1 SE of amphibians remaining immobile when encountering a car on the road (i.e., probability calculated from the logistic regression equation; SE obtained from 10,000 bootstrapped samples) was 0.82 ± 0.01 : individuals had, on average, an 82% chance of remaining immobile at the approach of a car.

Field Experiment

Overall, the 91 individuals used in the experiment tended to remain immobile in the presence of car-associated stimuli (Table 2, Fig. 2). The mean predicted probability \pm 1 SE (calculated as above) of amphibians to remain immobile when faced with the motor and headlights treatment, the motor only, the headlights only, or the control treatments was 0.92 ± 0.01 , 0.80 ± 0.01 , 0.84 ± 0.01 , and 0.48 ± 0.02 , respectively. The response of individuals of different species did not vary across the four treatments (i.e., no effect of species \times treatment interaction). The car treatment (combination of headlights and sound of motor) elicited the strongest response for all amphibians, with very few individuals

moving on the road, followed by the headlights-only treatment, and the motor-only treatment. Amphibians moved more often under the control than any of the car-associated stimuli. Spring peepers were more likely to flee during trials than the other species tested, but behaved similarly relative to the four treatments.

Large individuals were less likely to move at the approach of a car (Table 2). The other covariables did not influence the behavior of individuals. Air temperature and time after

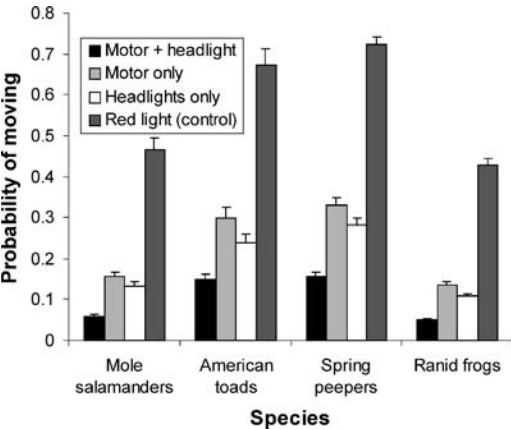


FIG. 2.—Probability of amphibians moving, based on the predicted values of the logistic regression for repeated measures, when exposed to car-associated stimuli during a controlled field experiment. Error bars denote 1 SE (obtained from 10,000 bootstrapped samples) around each mean. We used 91 individuals in the experiment: 20 mole salamanders, 11 American toads, 18 spring peepers, and 42 ranid frogs.

sunset were not good predictors of the response of amphibians. Finally, preceding treatments did not alter individuals' behavior later during the experiment (i.e., no carry-over effect).

DISCUSSION

The results from both the field survey and the field experiment suggest car-associated stimuli disrupt amphibian activity on roads. Indeed, the individuals of all species tended to remain immobile at the approach of the car during the field survey. Similarly, individuals were likely to remain immobile during treatments involving either headlights or the sound of the motor. The response to light was not surprising, as anuran activity can be disturbed under certain light intensities (Buchanan, 1993; Cornell and Hailman, 1984), and amphibians can take from several minutes to hours before regaining normal vision, depending on the species (Cornell and Hailman, 1984). On the road, amphibian vision may be disturbed, leading to a cessation in activity, without a chance for reacclimation of the visual apparatus before the arrival of the vehicle. However, the absence of a carry-over effect in our experiment suggests that the individuals rapidly regained their activity after disturbance.

It is unknown whether the high light intensity associated with car traffic attracts or repels individuals at the edge of the road. Hailman and Jaeger (1974) and Jaeger and Hailman (1971), using a maximum light intensity of ca. 89.9 lux, found that the phototactic response to light on anuran amphibians varied according to species. They observed that a light source elicited a negative phototactic response if it was greater than the preferred light intensity (i.e., the degree of light intensity to which it is exposed during foraging) and a positive phototactic response if it was lower than the preferred light intensity. Car headlights have an intensity of ca. 500 lux at 10 m, which is lower than what diurnal amphibians are exposed to, sunlight having an intensity of 50,000–10,000 lux. Thus, it is possible that certain amphibians are attracted to the light on the road, increasing the risk of mortality, but this requires further investigation.

Frogs and salamanders both responded to the motor-only treatment. The response of

frogs is not surprising because frogs use auditory cues in communication (Schwartz, 2001), and some can discriminate calls with variations in frequency as small as 5–10% (Bee and Gerhardt, 2001). At 60–80 km/h, vehicles can produce noise levels reaching 65 dB at frequencies between 0 and 4 kHz (Gołębiewski et al., 2003). Such noise is within the range audible to several anuran species (Bee and Gerhardt, 2001; Wollerman and Wiley, 2002). We expected salamanders to be less sensitive to the sound of the car alone, as they do not typically use sound in communication (Pough et al., 2001). Salamanders and frogs may have been responding to vibrations on the road surface rather than the sound of the motor, *per se*. The exact sensory mechanism involved needs further study.

One might argue that the motivation of individuals in the field survey differed from that of individuals in the experiment. We acknowledge that individuals placed on the road may not have the same “drive” as those moving across the road during migrations or foraging excursions. However, the result was consistently the same for individuals in the survey and the experiment: the approach of a vehicle caused a cessation in activity.

Behavioral Patterns Across Species

Though our field experiment revealed that spring peepers are more likely to move than other amphibians regardless of the treatment, the data from the field survey indicate that this behavior can change across the season. Indeed, differences may stem from a shift in the motivation of the individuals across the season, as well as body size. During the breeding season, most individuals encountered on the road were undergoing migrations, whereas later in the summer, some individuals may have been either migrating or foraging. Andrews and Gibbons (in press) observed that the motivation of snakes to cross or avoid roads varied across species, and that smaller individuals had a greater tendency to avoid roads. They also reported that the probability of remaining immobile at the approach of a car and time spent on the road varied greatly across snake species.

All else being equal, we would expect the probability of mortality to decrease as the individual spends less time on the road.

Mazerolle (2004) found a decreasing number of spring peepers dead on the road with increasing traffic intensity. He attributed this effect to either an avoidance of busy roads by individuals or a sampling artefact (i.e., small-sized hybrid carcasses repeatedly crushed by traffic are difficult to detect, see also Dodd et al., 2004). The behavior of spring peepers we report here may partly explain Mazerolle's (2004) results. This suggests that during certain periods, the species is less susceptible to road mortality than ranid frogs and slow-moving species such as toads and mole salamanders (Hels and Buchwald, 2001).

Road Traffic and Amphibians

Hels and Buchwald (2001) estimated that the probability of amphibians getting killed while crossing a secondary road ranged between 0.34 and 0.61, but increased to 0.89 and 0.98 while crossing a motorway. Amphibian mortality on roads will depend on the traffic intensity (Fahrig et al., 1995; Mazerolle, 2004; Palis, 1994), but also, as our study indicates, on the behavior of individuals relative to car-associated stimuli. This is especially relevant as the probability of amphibians remaining immobile when faced with an approaching vehicle is 0.82–0.92, based on our field experiment and 4-yr survey.

The avoidance or attraction of amphibians towards roads undeniably requires further investigation. Though recent efforts have been deployed to study road-crossing in snakes (Andrews and Gibbons, in press; Shine et al., 2004), birds (St. Clair, 2003), and mammals (Clevenger et al., 2001), comparable data for amphibians remain scarce. For animals already on the road, the pause in activity at the approach of a vehicle will increase the time spent on the road, thus increasing the chance of mortality. In some cases, however, staying on the road could be a better strategy than fleeing at the approach of a car, depending on where the amphibian stops on the road. For instance, a hopping frog might be hit by the bumper or hot exhaust pipe of a passing car.

CONCLUSION

Based on our results, amphibian forays across roads are disturbed by car traffic. Indeed, both the field survey and formal field

experiment suggest the six groups of amphibians we tested tend not to move when confronted to any of the car-associated stimuli, either taken alone or in combination, relative to the control. This cessation in activity in response to the approach of a vehicle presumably increases the mortality rate on the road for the six species of amphibians in this study (e.g., Ashley and Robinson, 1996; Fahrig et al., 1995; Palis, 1994; Smith and Dodd, 2003). Our field experiment indicated that regardless of the treatment, spring peepers were more likely to flee at the approach of a car than the other species, which suggests they are less vulnerable to traffic mortality, at least during certain periods of the season of activity. Indeed, during our 4-yr field study, we observed a shift across the season in the probability of individuals of some species to remain immobile at the approach of a vehicle. Mortality on roads is not only due to external factors such as traffic intensity, or road width, but depends on the behavior of the individuals on the road in response to vehicles. Thus, behavior should be considered in efforts of mitigating road impacts on amphibians.

RÉSUMÉ

La circulation des véhicules sur les routes résulte souvent en mortalités d'amphibiens, particulièrement pendant les soirées pluvieuses. Afin de tester l'hypothèse que le comportement des amphibiens influence leur susceptibilité à être écrasés sur la route, nous avons quantifié la réponse chez des individus de six espèces d'amphibiens face à l'approche d'un véhicule. Pour ce faire, nous avons effectué une série de 50 suivis nocturnes de 2001–2004 pendant lesquels nous avons noté le comportement (i.e., mobile ou immobile) des grenouilles, crapauds, rainettes et salamandres sur un segment de route de 20-km. Afin de séparer les effets des phares et du son du moteur, nous avons réalisé une expérience de terrain contrôlée, sur un segment de route expérimental, où nous avons soumis des individus des groupes ci-mentionnés à différents stimuli associés aux automobiles. Nous avons prédit que le traitement combinant les stimuli (phares et moteur) éliciterait une réponse plus marquée chez les amphibiens que l'exposition à un seul stimulus ou au

traitement témoin. Nos observations de 2767 amphibiens pendant l'étude de terrain ont révélé que les individus ont une probabilité moyenne de 0.82 de demeurer immobile sur la route à l'approche d'un véhicule. La réponse des individus différait selon les espèces, mais dépendait de la période de la saison (mai-juin vs juillet-septembre). Les 91 amphibiens inclus dans l'expérience de terrain étaient plus mobiles lors du traitement témoin que lors des traitements associés aux stimuli automobiles. L'exposition aux stimuli combinés a provoqué la plus forte réponse, suivie de l'exposition aux phares seuls et au moteur seul. De plus, les rainettes crucifères (*Pseudacris crucifer*) bougeaient plus souvent que les autres amphibiens de l'expérience de terrain, ce qui suggère qu'elles passent moins de temps sur les routes et sont moins susceptibles d'être écrasées que d'autres amphibiens. Nos travaux indiquent que les amphibiens tendent à s'immobiliser à l'approche d'un véhicule. Ceci souligne la fragilité des amphibiens à la circulation automobile et l'importance de tenir compte du comportement dans les efforts d'atténuation des effets des routes.

Acknowledgments.—We thank É. Tremblay of Kouchibouguac National Park for logistical support of this project. M. Bélisle, A. Desrochers, C. Girard, R. Hébert, L. Imbeau, S. Brugerolle, A. Mathis, and two anonymous reviewers provided valuable comments on the manuscript. This work was conducted with the financial support of the NSERC and FCAR graduate fellowships to MJM. Additional funding was provided by the Wildlife Trust Fund of New Brunswick. Research and collecting permits were obtained from the appropriate provincial and federal agencies.

LITERATURE CITED

- ADAMS, L. W., AND A. D. GEIS. 1983. Effects of roads on small mammals. *Journal of Applied Ecology* 20:403–415.
- ANDERSON, D. R., K. P. BURNHAM, AND W. L. THOMPSON. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- ANDREWS, K. M., AND J. W. GIBBONS. In press. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia*.
- 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.
- BEE, M. A., AND H. C. GERHARDT. 2001. Habituation as a mechanism of reduced aggression between neighboring territorial male bullfrogs (*Rana catesbeiana*). *Journal of Comparative Psychology* 115:68–82.
- BRODIE, E. D., JR., R. T. NOWAK, AND W. R. HARVEY. 1979. The effectiveness of antipredator secretions and behavior of selected salamanders against shrews. *Copeia* 1979:270–274.
- BUCHANAN, B. W. 1993. Effects of enhanced lighting on the behaviour of nocturnal frogs. *Animal Behaviour* 45:893–899.
- BURNHAM, K. P., AND D. R. ANDERSON. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* 28:111–119.
- . 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, 2nd ed. Springer-Verlag, New York, New York, U.S.A.
- CLEVINGER, A. P., B. CHRUSZCZ, AND K. GUNSON. 2001. Drainage culverts as habitat linkages and factors affecting passage by mammals. *Journal of Applied Ecology* 38:1340–1349.
- CORBEN, C., AND G. M. FELLERS. 2001. A technique for detecting eyeshine of amphibians and reptiles. *Herpetological Review* 32:89–91.
- CORNELL, E., AND J. P. HAILMAN. 1984. Pupillary responses of two *Rana pipiens*-complex anuran species. *Herpetologica* 40:356–366.
- DE MAYNADIER, P. G., AND M. L. HUNTER, JR. 2000. Road effects on amphibian movements in a forested landscape. *Natural Areas Journal* 20:56–65.
- DIGGLE, P. J., K.-Y. LIANG, AND S. L. ZEGER. 1994. *Analysis of Longitudinal Data*. Oxford University Press, Oxford, U.K.
- DODD, C. K., JR., W. J. BARICHIVICH, AND L. L. SMITH. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. *Biological Conservation* 118:619–631.
- FAHRIG, L., J. H. PEDLAR, S. E. POPE, P. D. TAYLOR, AND J. F. WEGNER. 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73:177–182.
- FORMAN, R. T. T., AND L. E. ALEXANDER. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- FORMAN, R. T. T., D. SPERLING, J. A. BISSONETTE, A. P. CLEVINGER, C. D. CUTSHALL, V. H. DALE, L. FAHRIG, R. FRANCE, C. R. GOLDMAN, K. HEANUE, J. A. JONES, F. J. SWANSON, T. TURRENTINE, AND T. C. WINTER. 2003. *Road Ecology: Science and Solutions*. Island Press, Washington, D.C., U.S.A.
- FORMANOWICZ, D. R., JR., AND E. D. BRODIE, JR. 1979. Palatability and antipredator behavior of selected *Rana* to the shrew *Blarina*. *American Midland Naturalist* 101:456–458.
- GIBBS, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62:584–589.
- GOŁEBIEWSKI, R., R. MAKAREWICZ, M. NOWAK, AND A. PREIS. 2003. Traffic noise reduction due to the porous road surface. *Applied Acoustics* 64:481–494.
- HAILMAN, J. P., AND R. G. JAEGER. 1974. Phototactic responses to spectrally dominant stimuli and use of colour vision by adult anuran amphibians: a comparative survey. *Animal Behaviour* 22:757–795.
- HEINEN, J. T. 1994. Antipredator behavior of newly metamorphosed American toads (*Bufo a. americanus*),

- and mechanisms of hunting by eastern garter snakes (*Thamnophis s. sirtalis*). *Herpetologica* 50:137–145.
- HEINEN, J. T., AND G. HAMMOND. 1997. Antipredator behaviors of newly metamorphosed green frogs (*Rana clamitans*) and leopard frogs (*R. pipiens*) in encounters with eastern garter snakes (*Thamnophis s. sirtalis*). *American Midland Naturalist* 137:136–144.
- HELS, T., AND E. BUCHWALD. 2001. The effect of road kills on amphibian populations. *Biological Conservation* 99: 331–340.
- HODSON, N. L. 1966. A survey of road mortality in mammals (and including data for the grass snake and common frog). *Journal of Zoology* 148:576–579.
- HORTON, N. J., AND S. R. LIPSITZ. 1999. Review of software to fit generalized estimating equation regression models. *American Statistician* 53:160–169.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied Logistic Regression*. John Wiley and Sons, New York, New York, U.S.A.
- JAEGER, J. A. G., J. BOWMAN, J. BRENNAN, L. FAHRIG, D. BERT, J. BOUCHARD, N. CHARBONNEAU, K. FRANK, B. GRUBER, AND K. T. VON TOSCHANOWITZ. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185:329–348.
- JAEGER, R. G., AND J. P. HAILMAN. 1971. Two types of phototactic behaviour in anuran amphibians. *Nature* 230: 189–190.
- MARCHISIN, A., AND J. D. ANDERSON. 1978. Strategies employed by frogs and toads (Amphibia, Anura) to avoid predation by snakes (Reptilia, Serpentes). *Journal of Herpetology* 12:151–155.
- MAZEROLLE, M. J. 2003. Night driving surveys as an amphibian monitoring technique in Kouchibouguac National Park, 1995–2002. Parks Canada—Ecosystem Monitoring and Data Reports 9, Parks Canada, Halifax, Nova Scotia, Canada.
- . 2004. Amphibian road mortality in response to nightly variations in traffic intensity. *Herpetologica* 60:45–53.
- . In press. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia*.
- PALIS, J. G. 1994. *Rana utricularia* (southern leopard frog). Road mortality. *Herpetological Review* 25:119.
- PAN, W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics* 57:120–125.
- POUGH, F. H., R. M. ANDREWS, J. E. CADLE, M. L. CRUMP, A. H. SAVITZKY, AND K. D. WELLS. 2001. *Herpetology*, 2nd ed. Prentice-Hall, Upper Saddle River, New Jersey, U.S.A.
- REIJNEN, R., R. FOPPEN, C. J. F. TER BRAAK, AND J. THISSEN. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology* 32:187–202.
- SCHWARTZ, J. J. 2001. Call monitoring and interactive playback systems in the study of acoustic interactions among male anurans. Pp. 183–204. In M. J. Ryan (Ed.), *Anuran Communication*. Smithsonian Institution Press, Washington, D.C., U.S.A.
- SEMLITSCH, R. D. 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615–631.
- SHAFFER, H. B., AND J. E. JUTERBOCK. 1994. Night driving. Pp. 163–166. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. -A. C. Hayek, and M. S. Foster (Eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, D.C., U.S.A.
- SHINE, R., M. LEMASTER, M. WALL, T. LANGKILDE, AND R. MASON. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). *Ecology and Society* 9:9 [online]. Available at: <http://www.ecologyandsociety.org/vol9/iss1/art9>.
- SMITH, L. L., AND C. K. DODD, JR. 2003. Wildlife mortality on U. S. Highway 441 across Paynes Prairie, Alachua County, Florida. *Florida Scientist* 66:128–140.
- ST. CLAIR, C. C. 2003. Comparative permeability of roads, rivers, and meadows to songbirds of Banff National Park. *Conservation Biology* 17:1151–1160.
- STOKES, M. E., C. S. DAVIS, AND G. G. KOCH. 2000. *Categorical Data Analysis Using the SAS System*, 2nd ed. SAS Institute, Inc., Cary, North Carolina, U.S.A.
- SWIHART, R. K., AND N. A. SLADE. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. *Journal of Mammalogy* 65:357–360.
- WOLLERMAN, L., AND R. H. WILEY. 2002. Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* 52:465–473.
- WYMAN, R. L. 1991. Multiple threats to wildlife: climate change, acid precipitation, and habitat fragmentation. Pp. 134–155. In R. L. Wyman (Ed.), *Global Climate Change and Life on Earth*. Chapman and Hall, New York, New York, U.S.A.

Accepted: 2 August 2005

Associate Editor: Alicia Mathis