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Anuran carcass persistence on roads: causes and implications for conservation

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Abstract

Roads are pervasive and ubiquitous landscape features that have substantial and predominantly negative effects on wildlife. Conducting road surveys to count animals that have been struck and killed by vehicles is a common method for estimating the impact of roads on wildlife, especially for species at risk and animals with low road avoidance (i.e., herpetofauna). For road surveys to provide accurate animal mortality data, information about carcass persistence in different environmental contexts and in relation to survey frequency is necessary, but few studies have implemented these data into evaluations of road effects. Using road survey data collected in Ontario, Canada, in 2015 and survival analysis, we quantified anuran carcass ($n = 91$) persistence and determined the effects of carcass characteristics (size, species, condition), road characteristics (lane position, traffic volume), and environmental characteristics (precipitation, temperature) on carcass persistence on the road. Contrary to previous findings, we found that anuran carcasses persisted on roads longer than expected (5.5 ± 4.4 days, mean $\pm$ SD), with some carcasses persisting for up to 30 days. Temperature and precipitation had the greatest influence on the duration of anuran carcass persistence. Carcass condition, (i.e., intact versus partially intact carcasses), species, location on the road, and traffic volume had little to no effect on persistence. We recommend incorporating carcass persistence into road ecology studies, especially in the context of evaluating population-level impacts of road mortality. Failure to do so could alter estimates of population viability and misinform management decisions.

KEYWORDS
amphibian, monitoring effectiveness, proportional hazard, road ecology, survey design, survival analysis

Roads have been identified as a serious global threat to wildlife (Laurance and Balmford 2013) and have been shown to affect a wide array of vertebrates (Trombulak and Frissell 2000, Kociolek et al. 2011, Teixeira et al. 2013), invertebrates (Muñoz et al. 2014, Baxter-Gilbert et al. 2015*b*, Skórka 2016), and plants (Angold 1997, Tikka 2001, Brisson et al. 2010). One of the key impacts of roads on animals is mortality via wildlife–vehicle collisions (Fahrig and Rytwinski 2009). Road mortality can impair population persistence, especially for species with slow life histories or low road-avoidance behaviors (Jaeger and Fahrig 2004, Jaeger et al. 2005, Keevil et al. 2023). Carcass counts from road surveys are often used as the response variable to study road effects (Baxter-Gilbert et al. 2017, Piczak et al. 2019), design road-effect mitigation (Langen et al. 2009, Teixeira et al. 2013, Boyle et al. 2017), or evaluate mitigation success (Baxter-Gilbert et al. 2015*a*, Markle et al. 2017, Dillon et al. 2020, Boyle et al. 2021). However, the value and accuracy of road survey data is contingent upon the ability to account for systematic biases during data collection. Variable carcass persistence and detectability thus mean that carcass counts may not completely represent the mortality associated with roads (Santos et al. 2015, Barrientos et al. 2018) and can yield misleading results to the detriment of management efforts (Lesbarrères and Fahrig 2012, Santos et al. 2015). If carcass counts are being used to make population-level inferences, or if relative counts are being used to estimate the efficacy of a conservation intervention (2 common applications of carcass data), then it is critical to ensure that the number of carcasses detected is representative of the population and that the conditions under which data are collected are representative of the study system over time. While detectability is primarily related to body size and survey methodology (Baxter-Gilbert et al. 2017, Barrientos et al. 2018), carcass persistence remains poorly understood and consequently often remains unaddressed in transportation ecology research (Barrientos et al. 2018, Dasoler et al. 2020, Bénard et al. 2024).

Carcass persistence on roads can be highly variable (Teixeira et al. 2013, Barrientos et al. 2018). Generally, carcasses are removed in 2 ways: 1) when animals are struck by vehicles, the carcasses can bounce off the road surface or adhere to vehicle tires (thus being missed during road surveys), deteriorate, or be smeared into asphalt (Baker et al. 2004, Beckmann and Shine 2015, Santos et al. 2016), and smaller carcasses are typically removed more quickly (Teixeira et al. 2013); or 2) carcasses are removed from the road by scavengers (Slater 2002). Over time, decomposition likely plays a role in both removal processes.

The impact of decomposition on carcass persistence remains largely unexplored and is likely driven by several physical characteristics of the carcass. Carcass size influences how likely a scavenger is to remove an entire carcass; large carcasses may be removed piece by piece (Ponce et al. 2010, Schutgens et al. 2014), while smaller carcasses can be removed all at once (Smallwood 2010). Body size has been shown to affect carcass persistence when comparing taxa of drastically different sizes (9–4,000 g; Barrientos et al. 2018) but has not been studied within smaller size ranges, such as within an anuran community. Body mass also influences how long a carcass will take to naturally decompose (Flint et al. 2010, Ponce et al. 2010, Smallwood 2010), which may alter persistence. Taxon has been shown to influence persistence, likely because of a combination of scavenger preferences (Paula et al. 2015, Henrich et al. 2017) and differences in body structure such as the thin skin of amphibians (Hels and Buchwald 2001). Smaller species are more likely to be bumped off the road or to adhere to the asphalt (Santos et al. 2011, Beckmann and Shine 2015) than larger species because motorists would be more likely to avoid hitting larger carcasses.

Environmental conditions also play a role in carcass persistence, especially temperature. For example, Selva et al. (2005) demonstrated that mammalian carcasses persisted on roads longer in freezing conditions, while Santos et al. (2011) found that on days that are hot and dry, carcasses may desiccate, increasing persistence. Further, warm and humid conditions have been associated with reduced persistence (Bénard et al. 2024). There is also evidence that carcass persistence of most taxa varies seasonally (Prosser et al. 2008, Urquhart et al. 2015). Many North American anurans are active predominantly during spring and summer months, when temperatures may fluctuate substantially but generally remain within a range in which there is no risk of freezing (e.g., 10–40°C). Given the thin permeable nature of amphibian skin, temperature and precipitation within seasons also likely have a strong influence on the dynamics of carcass persistence on roads; anurans can desiccate rapidly on roads (Boyle et al. 2019), potentially changing the way they adhere to the road surface, or how appealing they are to scavengers. Despite higher road mortality rates than other taxa, herpetofauna have received less attention than larger fauna in road ecology studies (Andrews et al. 2015, Popp and Boyle 2017). Yet accounting for carcass persistence is especially important for these taxa, which face substantial mortality threats associated with roads (Böhm et al. 2013, Ottburg and van der Grift 2019). Amphibian carcasses persist for shorter durations compared to mammals and birds (Barrientos et al. 2018), making it even more important that the factors affecting anuran carcass persistence are understood, and that wildlife managers have tools to account for anuran carcass persistence in assessments of road effects.

Developing and implementing generalizable guidelines to account for the impact of carcass persistence on road mortality estimates remains a challenge in road ecology. Some tools exist to estimate simple correction rates (carcass, Korner-Nievergelt et al. 2015, 2023; icenReg, Anderson-Bergman 2017; GenEst, Simonis et al. 2018). To further this line of research, we investigated the factors that modulate anuran carcass persistence on roads during summer by assessing the impacts of individual characteristics (i.e., species and body size) and environmental and anthropogenic factors (i.e., temperature, rainfall, and traffic volume) on carcass persistence in southeastern Ontario, Canada, in 2015. We predicted that because the carcasses of larger individuals (i.e., greater snout–vent length [SVL]; Santos et al. 2015, Henry et al. 2021) and species with thicker skin (i.e., American toads [*Anaxyrus americanus*]; Hels and Buchwald 2001) are less prone to deterioration and scavenging, they would persist longer on roads. We predicted that warmer summer temperatures would increase carcass persistence as carcasses desiccated and adhered to the road surface. Although the impact of precipitation on carcass persistence is poorly studied, some evidence suggests that humid conditions may decrease persistence times by mitigating mummification and adherence to the road and promoting decomposition (Santos et al. 2011, Bénard et al. 2024); thus, we predicted that increased precipitation would decrease persistence. Lastly, corresponding to previous research (Gonçlaves et al. 2023, Bénard et al. 2024), we predicted that increased traffic volume would reduce carcass persistence on the road because fewer cars would imply fewer chances that the carcass could be damaged or bumped off the road entirely.

STUDY AREA

Our study took place near Brighton, Ontario, Canada, in Presqu'ile Provincial Park (PQP; 43°59′33.6″ N 77°43′33.9″ W). During July and August 2015, we surveyed sections of 2 roads daily (1.25 km each). One road was located inside PQP, and the other was located at PQP's periphery. Both roads had similar traffic volume, speed limits (40–50 km/hr), and surrounding habitat composition (marsh, fen, mixed wood forest). For additional details about the study site, see Boyle et al. (2021). Total rainfall during the monitoring period was 319.9 mm (single day max. = 62.2 mm), and the average temperature during the monitoring period was 19.2°C (range = 11.7–25.3°C).

METHODS

Data collection

As a part of a larger road mortality study (Boyle et al. 2017, 2021), 2 people performed road surveys for anurans simultaneously on both roads daily at ~1000 via walking and at 0900, 1800, and 2200 via bicycle. Each day, which surveyor was at each site was randomized between SPB and MKCB to reduce observer bias. Upon identifying an anuran carcass, we recorded the species, the length between the tip of the snout and the most posterior point of the cloaca (SVL), and the initial carcass condition. We estimated carcass condition categorically, defining carcasses as either half (carcasses that had sustained substantial damage but were still readily identifiable and retained at least 2 limbs) or full (carcasses that had minimal damage and retained all species-specific traits; Figure 1). To avoid interfering with natural deterioration rates, we excluded all individuals for which we were unable to identify species or measure SVL without disturbing the carcass (Prosser et al. 2008, Urquhart et al. 2015). We then marked carcasses with flags stuck into the soil such that the line from the flag to the carcass was perpendicular to the road and labeled each carcass with the initial

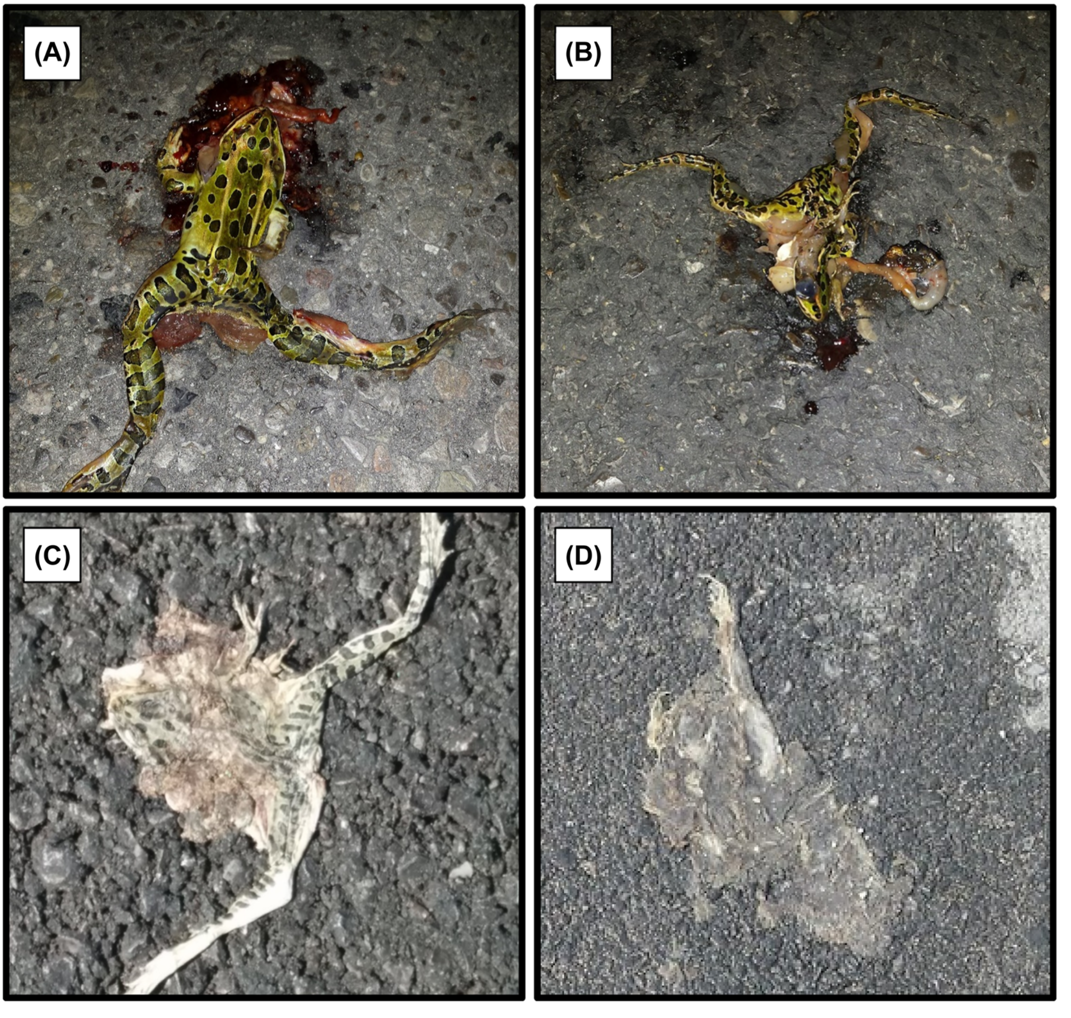

FIGURE 1 Anuran carcasses found in various conditions during surveys in Presqu'ile Provincial Park in Ontario, Canada, in 2015. In this figure, all 4 panels are adult northern leopard frogs (*Lithobates pipiens*) of approximately the same size. We included only carcasses that were classified as full (i.e., 3–4 limbs and the body mostly intact; A) or half (i.e., at least 2 limbs intact, the body somewhat intact to mostly destroyed; B). There was minor variation in the freshness of carcasses such as the difference between an anuran struck immediately before a survey versus a carcass struck 6 hours before a survey (C). We excluded heavily desiccated or degraded carcasses from the study (D); however, we monitored intact carcasses, even if their condition became heavily degraded, until there was no trace of the carcass remaining. Photos by Sean P. Boyle.

detection date, species, and an individual carcass ID. The carcasses left on the road were a subset of carcasses from a larger road mortality study that involved daily surveys. We collected all other carcasses and placed them in forests away from the road so that we could be confident in the identity of the carcasses we were monitoring for persistence. We checked each flagged carcass daily at 1000 during walking surveys, noting changes in the appearance of carcasses to make general inferences about the deterioration process. Once a carcass was absent from the road (i.e., no soft or bony tissue remained), we removed the flag from the side of the road. We noted the time and date the flag was removed. We calculated carcass persistence as the number of days between its initial detection and the date the carcass was absent from the road. If we detected the carcass during the 1800 or 2200 surveys, this counted as 0.5 days.

In addition to physical carcass characteristics, we considered the potential impacts of mean daily precipitation (mm), mean daily maximum air temperature (°C), and traffic volume on carcass persistence. We collected mean precipitation and temperature data from a weather station approximately 20 km from the study site (Trenton A; Environment and Natural Resources 2015). We averaged mean precipitation and temperature values over the number of days a carcass persisted on the road. We estimated traffic volume by counting cars at each location 3 times per month (once each on a Wednesday, Friday, and Saturday from 1400–1600) in June-August, and assumed that our counts were representative of other similar days (i.e., weekday or weekend) within those months. Because we could not collect traffic count data continuously throughout our study, we extrapolated our 2-hour traffic counts to the period during the day with most traffic, 0800–2000 (i.e., multiplied our 2-hour counts by 6). We extrapolated traffic data to weekdays using month-specific Wednesday counts. We extrapolated weekend traffic data using the mean of month-specific Friday and Saturday counts because our study area has higher weekend traffic associated with camping within PQP (e.g., if we discovered a carcass the morning of Wednesday, 5 August and noted it was absent the morning of Monday, 10 August, we assigned traffic for 2 weekdays and 3 weekend days). We calculated the relative mean daily traffic volume (relative MDTV) for each carcass based on its persistence measured in days.

Data analyses

We conducted a survival analysis to test the following physical and environmental characteristics on anuran carcass persistence: species, SVL (proxy for size), initial carcass condition (full or half), mean daily precipitation (mm), mean daily temperature (°C), relative MDTV (vehicles/day), lane position (i.e., middle of road, north or southbound), and Julian date (Table A1). Survival analyses have more statistical power for analyzing time-to-event data over more basic linear regression because they include events that might not have been observed, like the removal of a carcass from the road (Kaplan and Meier 1958). Cox proportional hazards models are a type of survival analysis for testing how the relative risk of an event, carcass disappearance in our case, changes over values of a covariate in comparison to average conditions (Cox and Snell 1968). To determine the effect that each of our covariates (SVL, species, relative MDTV, lane position, Julian date, initial carcass condition, precipitation, and temperature) had on carcass persistence, we first fit a global Cox proportional hazards model including all covariates using the coxph function from the survival package v3.5-8 in R (Therneau 2020), along with survminer (Kassambara et al. 2021), and coxme (Therneau 2024). We also fit a weather model including only temperature and precipitation to tease apart their impacts (Table A1).

Kaplan-Meier curves illustrate how survival probability, or carcass persistence in our case, changes over time when accounting for the effect of important covariates (Kaplan and Meier 1958). We fit Kaplan-Meier curves for the null model with no environmental characteristics and 2 curves for the upper percentiles of temperature and precipitation. We identified the time required for carcasses to have a 50%, 75%, and 90% probability of remaining on the road, which is relevant information for designing robust road mortality studies. We also assessed how these cut-offs shifted with changes in temperature and precipitation by comparing between the null and temperature and precipitation models.

We performed 2 simulations to demonstrate the effects of the most influential physical and environmental characteristics on the length of carcass persistence under varying conditions and the number of carcasses a study would capture depending on survey frequency. In our first simulation, we fit a survival regression model to predict the expected number of days a carcass would persist on the road under the 5th, 50th, and 95th percentile values of the covariates from the best Cox proportional hazards model (Tables A1 and A2). In our second simulation, we fit a logistic regression model to demonstrate how the probability of encountering a carcass would change with a survey frequency from 1–30 days, under varying conditions. We performed all analyses and created all graphs using R v. 4.0.3 (R Development Core Team 2021) and ggplot2 (Wickham 2016).

RESULTS

We detected 1,308 anuran carcasses during the study period; of these, 1,217 did not meet our inclusion criteria. We monitored the remaining 91 anuran carcasses that met our inclusion criteria (measurable SVL, species ID, 2 or more limbs); these consisted of 6 species (Table 1). Anuran carcass persistence varied substantially, with over half of all carcasses (50/91; 55%) disappearing within the first five days since death, but some remained on the road for over two weeks. One grey treefrog (*Dryophytes versicolor*) carcass (47 mm SVL) persisted for 30 days on the road but was heavily degraded and desiccated for most of this persistence period. Mean carcass persistence was 5.4 ± 4.4 (SE) days. We observed carcass deterioration in both soft and boney tissues. The softest tissues (i.e., viscera) were the fastest to deteriorate, while bones and skin deteriorated more slowly (Figure 1).

The number of carcasses that remained on the road declined sharply within the first 5 days following being struck by a vehicle (Figure 2A). Surveys completed every other day captured approximately 85% of carcass data and surveys every 5 days captured only 50% of carcass data. Our global model (Table A2) indicated that carcass persistence was reduced by increases in both mean daily maximum air temperature (β = 0.37, 95% CI = 0.13–0.61, $P = 0.003$; Table A2) and mean daily precipitation (β = 0.71, 95% CI = 0.27–1.16, $P = 0.002$; Table A2). Upon further inspection of how temperature and precipitation modulated carcass persistence, we found that when temperatures exceeded approximately 22°C, the likelihood of carcass removal sharply increased, doubling between 24–28°C (Figure 3). Precipitation exceeding approximately 4 mm was indicative of an even steeper increase in which the probability of carcass removal increased by roughly 300% between 4–15 mm of precipitation, and by roughly 800% between 4–30 mm of precipitation (Figure 4). In the upper percentiles of temperature (22.15–24.7°C) and precipitation (3.7–23.2 mm), carcass removal occurred earlier than predicted by the null model at multiple thresholds

TABLE 1 Anuran carcass counts and mean values for morphometrics, environmental covariates, and persistence rates for carcasses found during road surveys in Brighton, Ontario, Canada, 2015.

Species	Count	SVL (mm)	Precipitation (mm)	Temperature (°C)	Relative MDTV (vehicles/day)	Persistence (days)
Northern leopard frog (*Lithobates pipiens*)	45	60.7	26.0	20.9	2,089.1	6.0
Green frog (*Lithobates clamitans*)	19	55.8	11.4	21.5	2,459.3	4.1
Grey treefrog (*Dryophytes versicolor*)	13	45.1	16.6	21.4	2,217.0	5.0
American toad (*Anaxyrus americanus*)	7	51.7	15.9	21.7	2,092.0	5.9
Wood frog (*Lithobates sylvaticus*)	5	45.6	12.9	22.6	2,519.5	4.0
American bullfrog (*Lithobates catesbeianus*)	2	94.0	42.4	19.6	1,755.3	11.5

Abbreviations: MDTV, relative mean daily traffic volume; SVL, snout–vent length relative.

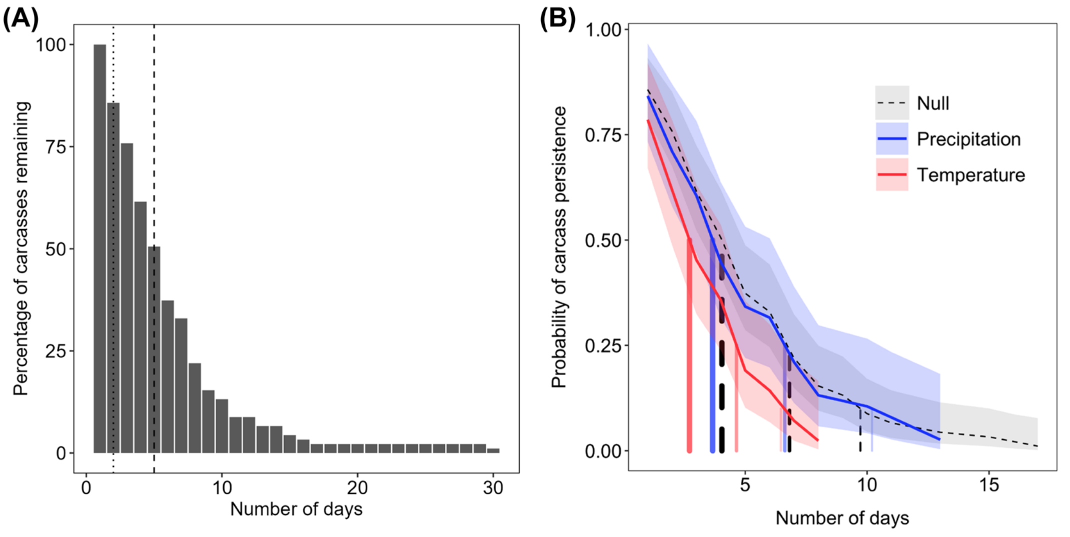

FIGURE 2 A) Percentage of anuran carcasses that would have been detected given the corresponding frequency of surveys in southeastern Ontario, 2015. Surveying every other day would result in a detection rate of 85% relative to daily surveys (dotted line). Surveying every 5 days, would result in a loss of 50% of the possible data collected relative to daily surveys (dashed line). B) Probability of carcass persistence based on the upper percentile observations over the study period for precipitation (blue; 3.7–23.2 mm) and temperature (red; 22.15–24.7°C) compared to the null model without the effect of either variable on carcass persistence (black, dashed line). Both precipitation and temperature negatively affected persistence, although the probability of persistence declined faster in the temperature model. Vertical lines represent the number of days after which 50% (largest, darkest lines), 75% (medium-weight lines), and 90% (smallest, lightest lines) of carcasses would likely be removed for the high temperature (red) and high precipitation (blue) models and the null model (black).

(Figure 2B), indicating the consistent negative effect of precipitation and temperature on carcass persistence. Our simulations demonstrated that carcasses remain on roads for shorter durations during warmer periods and cooler periods with more precipitation (Figure 5A), and that higher temperatures and more precipitation would be expected to bias mortality estimates lower than the true mortality (Figure 5B).

Overall, species was not significant in our global Cox proportional hazards model, but grey treefrogs were more likely to be removed from the road than northern leopard frogs (*Lithobates pipiens*; $\beta = 4.98$, 95% CI = 0.62–9.34, $P = 0.025$; Table A2). Initial carcass condition, SVL (56.7 ± 18.6 mm), relative MDTV (2,185.3 ± 537.2 vehicles/day), lane position, and Julian day did not affect carcass persistence ($P > 0.05$ in all cases; Table A2).

DISCUSSION

Environmental conditions had a major influence on the persistence dynamics of anuran carcasses. Specifically, warm and wet conditions increased how quickly carcasses were removed from the road surface, whereas cooler temperatures and minimal precipitation were associated with longer carcass persistence. Limited prior research has focused on the effect of environmental covariates on carcass persistence (Bénard et al. 2024), yet our work shows that temperature and precipitation have substantial implications for data collection and interpretation in road ecology studies.

We found that carcasses persisted longer when precipitation was below about 4 mm. This is in agreement with recent research describing how humid environments (rain vs. no rain) are associated with reduced carcass

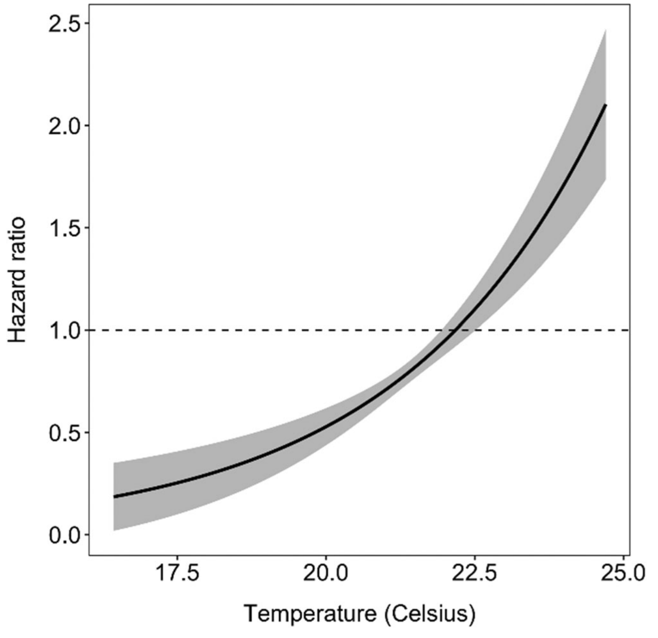

FIGURE 3 Effect of temperature on the relative risk that an anuran carcass would be removed from the road surface. Hazard ratios <1 (dashed black line; shaded area is 95% CI) indicate that the relative risk of removal is lower (i.e., carcasses would persist for longer or would be more likely to persist) than under average conditions, and hazard ratios >1 indicate that the carcass would be removed more quickly or be less likely to persist. The hazard ratio of carcass persistence increases on days with a mean temperature above roughly 22°C. The change from 22–25°C depicts an approximately 100% increase in the likelihood of anuran carcasses disappearing from the road surface. Data collected in Presqu'ile Provincial Park, Ontario, Canada, during summer 2015.

persistence (Bénard et al. 2024). Anecdotally, we observed that it was much easier for researchers to remove or peel carcasses from the road after rain (Boyle et al. 2021). Thus, we interpreted 4 mm of precipitation as an approximate threshold relating to the minimum amount of precipitation that reduces carcasses adherence by increasing the ability of scavengers or contact with tires to remove carcasses from the road surface. The effect of precipitation was strong; the 800% increase in the rate of carcass removal above the 4 mm of precipitation threshold indicates how neglecting to account for precipitation-associated variation could impair inferences. When measuring road mortality, observers could miss up to 87.5% of carcasses because of precipitation effects.

Temperature was also correlated with anuran carcass persistence, with carcasses persisting longer at cooler temperatures, below about 22°C (Figure 3). The effect size of temperature on carcass persistence was also considerable, displaying a 100% increase in likelihood of removal from the road. When measuring road mortality, observers could miss up to 50% of carcasses because of temperature effects. This is in contrast to our prediction that warmer temperatures would be associated with increased desiccation, and thus increased carcass persistence (Boyle et al. 2019). Evidence from carcass persistence experiments in open fields (i.e., without asphalt) indicate that decomposition and scavenging is highest in summer months when temperature is the highest (Prosser et al. 2008). We argue that the dynamics of temperature and carcass adherence to the road surface are complicated given that we observed carcasses remaining on the road for up to 30 days. There are also likely interactions with other drivers of carcass persistence and removal such as the combined effects of precipitation and scavengers, and these interactions merit additional research.

Carcass size (i.e., SVL) had little effect on carcass persistence. Carcass size has been proposed as an important factor in persistence for other small-bodied species, either through scavenging, or being removed from the road by

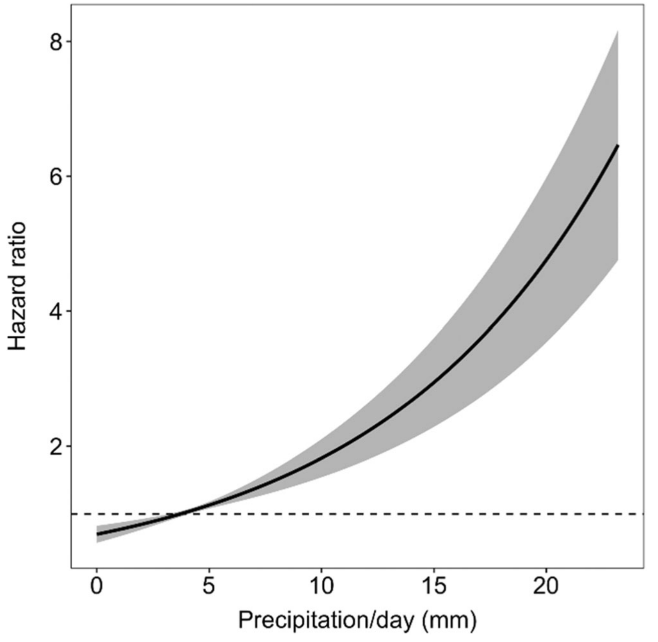

FIGURE 4 Effect of precipitation on the relative risk that an anuran carcass would disappear from the road surface. Hazard ratios <1 (dashed black line; shaded area is 95% CI) indicate that the relative risk of removal is lower (i.e., carcasses would persist for longer or would be more likely to persist) than under average conditions, and hazard ratios >1 indicate that the carcass would be removed more quickly or be less likely to persist. The hazard ratio of carcass persistence quickly increased on days with more than roughly 4 mm of rain and depicts an approximately 800% increase in anuran carcass removal from the road between 4–25 mm of precipitation. Data collected in Presqu'ile Provincial Park, Ontario, Canada, during summer 2015.

vehicles (i.e., birds and amphibians; Barrientos et al. 2018). For example, some data suggest that carcass removal from roads will occur within one day for birds (Flint et al. 2010, Barrientos et al. 2018), amphibians (Beckmann and Shine 2014, Barrientos et al. 2018), and mammals (Barrientos et al. 2018). In contrast, Santos et al. (2016) demonstrated that animals >100 g were approximately 50% more likely to persist for 3 days compared to animals <100 g, and that 20% of carcasses persist >5 days. Body size also influences carcass removal of large-bodied species (Barrientos et al. 2018); however, a large carcass may be removed slowly in pieces, whereas a small carcass is typically removed all at once (Ponce et al. 2010, Schutgens et al. 2014).

Similarly, we found little to no evidence of an effect of species on persistence, except for a small difference between grey treefrog and northern leopard frog. We predicted that bufonid carcass persistence would be the highest but found no evidence to support our prediction; thus, we suspect skin thickness does not adequality explain the variation between grey treefrog and northern leopard frog persistence rates. Slight variation in integument structure could explain the difference between grey treefrog and northern leopard frog persistence rates; however, additional research to discern those differences is required. In other studies where persistence rapidly approached zero (Flint et al. 2010, Beckmann and Shine 2014, Barrientos et al. 2018, Bénard et al. 2024), or even those where carcasses persisted for 5-6 days (Santos et al. 2011, 2016), individuals might have been missed or excluded because their adherence to the road made them unidentifiable. However, when we lifted carcasses from the road surface in our study, sometimes after several weeks, it was typically possible to observe species-specific, or at least family-specific, characteristics for identification.

We did not find an effect of carcass condition (i.e., half or full) on carcass persistence. Carcass condition could contribute to persistence in 2 related ways. First, the level of damage the animal sustained upon initial impact could

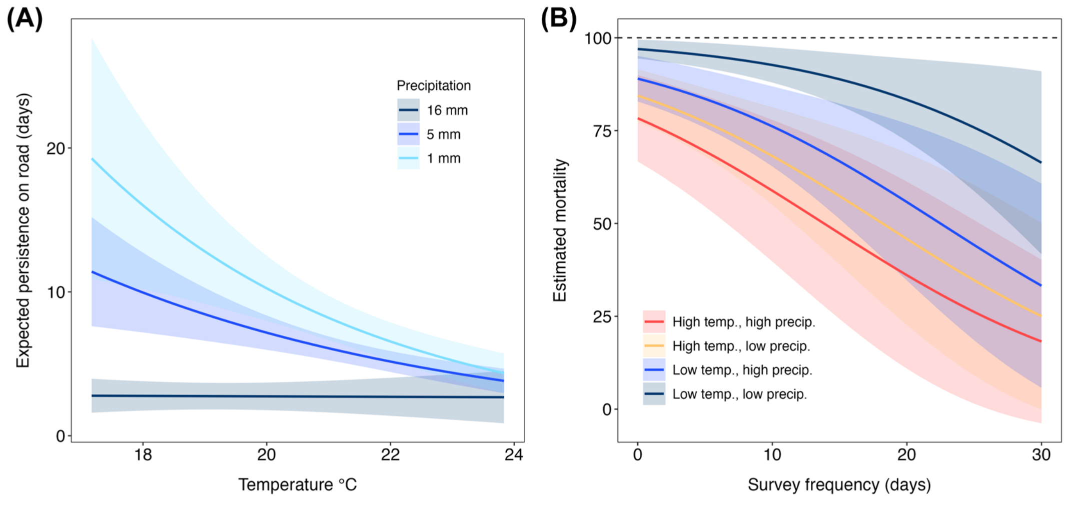

FIGURE 5 A) Predicted anuran carcass persistence on roads in southeastern Ontario, 2015, under varying temperature and precipitation conditions, simulated from a survival regression model testing the interactive effects of these variables on days to carcass removal. Predictions are shown for 3 precipitation levels: mean (5 mm) and the 5th and 95th percentiles (1 and 16 mm, respectively) across the range of temperatures in our study. Each line shows the mean predicted persistence with 95% confidence intervals (shading). Carcasses are expected to remain on roads for shorter durations during warmer periods and cooler periods with more precipitation. B) Simulated road mortality estimates (i.e., number of carcasses) for different survey frequencies under varying environmental conditions. The predictions were generated from a logistic regression model testing the interactive effects of temperature (temp.) and precipitation (precip.) on carcass presence by day. Each line shows the mean number of carcasses a study would capture, assuming a true count of 100 carcasses on the road, with 95% confidence intervals (shading). Functionally, this can be interpreted directly as the proportion of carcasses on the road that are observed during the survey. Low and high temperature and precipitation (1 mm, 16 mm) levels correspond to the 5th and 95th quantiles recorded during the study.

affect the degree to which its carcass binds to the road surface (e.g., viscera often adhered strongly to the asphalt). Second, carcasses that are more heavily damaged may have different levels of attractiveness to scavengers, but this second reason is likely somewhat case- and context-specific. We included the initial carcass condition as an independent variable in our study to control for any influence that it may have on scavenging or rates of deterioration; however, given no difference between full and half carcasses, our data suggest that the impact of scavenging was minimal. Further evaluation of carcass condition from the perspective of carcass scavenging is warranted, as we did not formally evaluate the impact of scavengers. Though scavenger assemblages may differ among landscapes (Ward et al. 2006, Henrich et al. 2017), land cover type per se has been shown to have little to no effect on carcass persistence (Barrientos et al. 2018). Robust methods of monitoring carcass scavenging, including remote camera traps or predator exclusion cages, would help elucidate the role of scavenging in carcass persistence (Paula et al. 2015).

We did not observe an effect of traffic volume on carcass persistence. This result was contrary to our expectations and the results presented in other studies that demonstrate increased traffic volume leading to decreased carcass persistence (Ruiz-Capillas et al. 2015, Gonçlaves et al. 2023, Bénard et al. 2024). Despite apparent variation in our relative MDTV data (range = 1,008–3,808 vehicles/day, mean = 2,185 ± 537 vehicles/day), it is difficult to tease apart the impact of traffic from other factors like temperature and precipitation because traffic in a public park depends partially on the weather (i.e., more vehicles access the park on warmer, less rainy days). Unfortunately, the temporal grain at which we collected traffic data is insufficient to tease out this effect. Further, our method of extrapolating traffic counts represents a coarse estimate rather than true MDTV. Although it is common to extrapolate traffic volume, this is typically performed when data are collected over a longer period of time to reduce sampling bias. Our findings thus should be interpreted with some caution as traffic volume could vary more day to day, or more substantially within a day than our sampling method assumed.

In contrast to previous studies in which a large majority of anuran carcasses were removed from the road within about 5 days (Santos et al. 2011, 2016), we observed highly variable durations in carcass persistence. While many carcasses in our study were removed within 5 days, several were removed as quickly as overnight (2200 to 1000 the next day; $n = 10/91$, 11%). Overall, carcasses persisted on the road for longer than predicted by our null model, taking 2 days for 15% of carcasses to be removed, 5 days for 50% of carcasses to be removed, 7 days for 75% of carcasses to be removed, and 10 days for 90% of carcasses to be removed (Figure 2A). Our simulations reinforce this finding, indicating that under ideal conditions for carcass persistence (dry and cool), surveys can take place less frequently without major data loss, but in warm and wet conditions, carcass persistence has serious implications for mortality estimates (Figure 5B). Our study highlights the importance of considering how search methodology may affect the inclusion or omission of certain individuals (Baxter-Gilbert et al. 2017). Carcasses may be ejected from the road surface; however, during surveys, we found many individuals still on the road that could not be included in our assessment because carcass condition was poor (1,217 carcasses were excluded). This includes carcasses that had been flattened by vehicle traffic or suffered large lacerations to their skin, causing their viscera to be ejected. The substantial number of carcasses that we observed that were already heavily degraded strongly supports our position that frequent surveys is the best way to ensure the data collected are representative of actual mortality rates.

MANAGEMENT IMPLICATIONS

Our study demonstrates large variability in rates of anuran carcass persistence on roads, thus providing a critical perspective to researchers and managers interested in using carcass counts to make inferences about population-level effects. Environmental conditions should explicitly inform correction factors used to account for imperfect detection. Specifically, carcasses are removed more rapidly during hot weather and high rainfall events, especially within the first 1–2 days following road mortality as opposed to slower removal during cool and dry weather. We acknowledge that we are presenting an ideal scenario where carcasses are not heavily damaged upon impact with a vehicle, and thus the substantial loss of carcass data that we present between increasingly disparate surveys is likely conservative.

Daily surveys, especially in diverse weather conditions, should be used to more accurately estimate persistence and mortality rates. However, logistical constraints may limit survey frequency, necessitating careful consideration of survey type and frequency in study design (Ruiz-Capillas et al. 2015, Santos et al. 2016, Baxter-Gilbert et al. 2017) and the non-linear impacts of environmental variation on carcass persistence. While it may be appealing from a financial or logistical perspective, caution should also be taken when extrapolating correction factors between sites with different environmental regimes, as the variation we observed was non-linear and strongly influenced carcass persistence dynamics. When correction rates must be used, site-specific correction rates for persistence can be determined using our methods, or by using one of several statistical tools available such as the R packages carcass (Korner-Nievergelt et al. 2015, 2023) and icenReg (Anderson-Bergman 2017) or the independent program GenEst (Simonis et al. 2018). While our study focused on a low-use road with specific environmental conditions, variation between systems underscores the need for context-specific approaches. Furthermore, the importance of accounting for missed carcasses and environmental influences on carcass detection emphasizes the need for thorough survey planning to accurately assess road impacts on wildlife populations.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This research was carried out under a Laurentian University animal use permit (# 2013-04-01) held by DL and provincial permits (WSCA # 1076845, ESA # SEZ-B-001-13, Ontario Parks #BOYLEHERPSPQ14-16) held by SPB, JDL, DL.

DATA AVAILABILITY STATEMENT

Data available in Laurentian University data repository.

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APPENDIX A: COX PROPORTIONAL HAZARD MODEL RESULTS

TABLE A1 Models of risk of anuran carcasses being removed from the roadway in Ontario, Canada, 2015, compared with corrected Akaike's Information Criterion (AIC_c) values.

Model (with covariates)	AIC_c
Weather	623.05
Mean daily precipitation (mm)	
Mean daily temperature (°C)	
Global	628.37
Mean daily precipitation (mm)	
Mean daily temperature (°C)	
Initial carcass condition (full/half)	
Snout-vent length (mm)	
Species	
Lane position (northbound, middle, southbound)	
Relative mean daily traffic volume (vehicles/day)	
Julian day	
Condition	645.16
Initial carcass condition (full/half)	
Julian day	
Null	645.33
Traffic	645.55
Lane position (northbound, middle, southbound)	
Relative mean daily traffic volume (vehicles/day)	
Carcass	646.61
Snout-vent length (mm)	
Species	

TABLE A2 Global model output from Cox proportional hazard analysis of anuran carcasses being removed from the roadway in Ontario, Canada, 2015. Bolded values represent evidence of an effect on carcass persistence.

Covariate	coefficient	conf.low	conf.high	z	Pr(>|z|)
Carcass condition (reference: full)					
half	−0.41	−0.99	0.17	−1.377	0.168
Julian day	0.00	−0.02	0.02	0.002	0.998
Snout–vent length (SVL; mm)	0.01	−0.01	0.03	0.663	0.508
Species (reference: northern leopard frog)					
American bullfrog	−2.00	−6.30	2.30	−0.912	0.362
Green frog	0.49	−1.50	2.47	0.479	0.632
American toad	0.87	−1.97	3.71	0.603	0.546
Grey treefrog	4.98	0.62	9.34	2.238	**0.025**
Wood frog	−1.99	−8.35	4.36	−0.615	0.539
Precipitation (mm)	0.71	0.27	1.16	3.160	**0.002**
Temperature (°C)	0.37	0.13	0.61	3.008	**0.003**
Lane position (reference: middle of road)					
Carcass in northbound lane	0.04	−0.57	0.65	0.123	0.902
Carcass in southbound lane	0.17	−0.39	0.73	0.599	0.549
Relative mean daily traffic volume (vehicles/day)	0.43	−0.09	0.96	1.607	0.108
SVL (mm)×species interaction (reference: northern leopard frog)					
SVL×American bullfrog	0.01	−0.03	0.06	0.647	0.517
SVL×green frog	0.01	−0.03	0.04	0.509	0.610
SVL×American toad	−0.02	−0.07	0.03	−0.604	0.546
SVL×grey treefrog	−0.09	−0.18	0.01	−1.828	0.068
SVL×wood frog	0.05	−0.08	0.19	0.761	0.446
Precipitation (mm)×temperature (°C)	−0.03	−0.05	0.00	−2.373	0.018