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CONCEPTS & THEORY

A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume

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Abstract. Roads, while central to the function of human society, create barriers to animal movement through collisions and habitat fragmentation. Barriers to animal movement affect the evolution and trajectory of populations. Investigators have attempted to use traffic volume, the number of vehicles passing a point on a road segment, to predict effects to wildlife populations approximately linearly and along taxonomic lines; however, taxonomic groupings cannot provide sound predictions because closely related species often respond differently. We assess the role of wildlife behavioral responses to traffic volume as a tool to predict barrier effects from vehicle-caused mortality and avoidance, to provide an early warning system that recognizes traffic volume as a trigger for mitigation, and to better interpret roadkill data. We propose four categories of behavioral response based on the perceived danger to traffic: Nonresponders, Pausers, Speeders, and Avoiders. Nonresponders attempt to cross highways regardless of traffic volume. Pausers stop in the face of danger so have a low probability of successful crossing when traffic volume increases. Hence, highway barrier effects are primarily due to mortality for Nonresponders and Pausers at high traffic volumes. Speeders run away from danger but are unable to do so successfully as traffic volume increases. At moderate to high volume, Speeders are repelled by traffic danger. Avoiders face lower mortality than other categories because they begin to avoid traffic at relatively low traffic volumes. Hence, avoidance causes barrier effects more than mortality for Speeders and Avoiders even at relatively moderate traffic volumes. By considering a species' risk-avoidance response to traffic, managers can make more appropriate and timely decisions to mitigate effects before populations decline or become locally extinct.

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TRAFFIC VOLUME AS AN INDICATOR OF BARRIER STRENGTH

Roads impede wildlife movement through a combination of direct mortality from collisions and road avoidance behavior by animals (Forman et al. 2003, Fahrig and Rytwinski 2009), yet a comprehensive approach toward identifying animal characteristics that increase effects has not been developed (Lima et al. 2015). The barrier

effect of roads can reduce dispersal rates and so limit demographic rescue and gene flow, increasing the risk of local extinction (Clark et al. 2010). Vehicle-caused mortality and road avoidance behavior can create population-level reductions in a variety of species from freshwater turtles to Florida panthers (*Puma concolor coryi,* Dickson et al. 2005, Patrick and Gibbs 2010). Commonly, transportation planners develop mitigation measures for barrier effects specifically for a given population (Jacobson et al. 2010).

Traffic volume, the number of vehicles passing a point per day, has had mixed results as a predictor of adverse effects to wildlife (Hels and Buchwald 2001, Bissonette and Kassar 2008). Investigators initially predicted that effects to wildlife and the number of carcasses present would increase linearly with increasing traffic volume (Case 1978). The expectation of a similar and linear response by all species, and using a coarse scale to measure traffic volume (i.e., averaging traffic volume over 10s or 100s of miles) has led some investigators to conclude that traffic volume is not a useful indicator (Meek 2012). Colino-Rabanal and Lizana (2012) reviewed the plethora of responses by species of herpetofauna to traffic volume and concluded that animals show specific behaviors in response to traffic that reduce the accuracy of models. However, the effects of traffic volume on some species have been predicted reliably by using the traffic flow model (e.g., Hels and Buchwald 2001, Aresco 2005). The traffic flow model predicts that as traffic volume increases, an animal's probability of a lethal collision with a vehicle increases steeply at first then approaches an asymptote. The traffic flow model illustrates why mortality risk does not increase linearly with traffic volume. However, the model assumes animals will cross with little regard to vehicles, whereas some animals avoid roads or otherwise react to vehicles. Although many factors influence animal responses to roads, this article focuses on how traffic volume can be an effective explanatory variable for the barrier effect of roads on species, provided that animal behavior is also considered. We hypothesize that consideration of species-specific behavioral responses to risk will improve the ability of traffic volume, a readily measured explanatory variable, to predict barrier effects on populations.

Closely related species may exhibit different responses to traffic (Alexander et al. 2005, An-drews et al. 2005, Lee et al. 2010), although several studies have used taxonomic classifications as high as class as their guide (e.g., Clevenger and Huijser 2011). The variables that contribute most to mortality risk in the traffic flow model are the animal's crossing speed and its size relative to the vehicle's killing surface (van Langevel-de and Jaarsma 2004). Slow animals have the greatest mortality risk. Therefore, species with antipredator adaptations that slow them further, such as freezing, have even higher risk of mortality from vehicles if they recognize and respond to approaching vehicles as threats. Using species-specific behavioral responses to risk therefore may improve interpretation of traffic effects on populations.

Perceived Risk as the Foundation of Animal Response

Combining traffic volume with predictable wildlife behavioral responses to perceived risk can improve management efforts to reduce animal–vehicle collisions and the barrier effect of roads and root research about effectiveness of management in established ecological theory. Cook and Blumstein (2013) suggest that species traits affect animal responses to roads, but they focused on life history traits and diet not directly associated with response to vehicles. Rytwinski and Fahrig (2012) found large body size, low reproductive rates and large home ranges to be important predictors of road density effects but did not consider the effects of traffic volume. Food preferences and the need to move to forage and seek unoccupied habitat helps explain lack of response by some owl species to traffic volume (Grilo et al. 2014). The most comprehensive approach to date that directly addresses responses to vehicle traffic, an approach used in European transportation guidance, is based on a conceptual model that suggests vehicle-caused mortality decreases and avoidance increases as traffic volume increases (Müller and Berthoud 1997, Seiler and Helldin 2006).

Our framework is based on the risk-disturbance hypothesis (Frid and Dill 2002) and related research showing that risk assessment changes with the type of animal defense system (Stanko-wich and Blumstein 2005). The risk-disturbance hypothesis suggests that responses elicited from

anthropogenic stimuli that cause deviations in behavior relative to patterns without human influence are analogous to responses to predation risk (Frid and Dill 2002). For some species, the cue that triggers a flight response is not very specific and therefore could include recent agents of disturbance such as vehicles approaching (Frid and Dill 2002). For example, the visual cue of an enlarging shape or rapid approach is enough to trigger antipredator response in a small fish (Dill 1974).

We expect that vehicle traffic is likely to trigger antipredator responses because of the risk of mortality from vehicles (Andrews et al. 2005). Moreover, the main predictions of the risk-disturbance hypothesis seem likely to be met with traffic and roads: risk response increases with a direct and fast approach, larger individual or group size, and distance to refuge (Frid and Dill 2002). Risk response increases with direct and rapid approach because such an approach can convey intent to kill (Stankowich and Blumstein 2005). Second, Frid and Dill (2002) predicted risk responses would increase when the approaching object was bigger or part of a larger group. When traffic volume is higher, vehicles likely appear as part of a larger group and increase perceived risk. Consistent with this hypothesis, Tibetan antelope (*Pantholops hodgsoni*) exhibit more risk-avoidance behavior during times of high traffic than low (Lian et al. 2011). The risk-disturbance hypothesis therefore incorporates ecological and evolutionary implications for animal behavior toward traffic.

We hypothesize that individuals perceive increased traffic as increased threat based on a risk response that is not a function of taxonomy (Alexander et al. 2005, Andrews et al. 2005, Lee et al. 2010, Clevenger and Huijser 2011). Furthermore, we hypothesize that species responses to traffic are reasonably predictable—individuals avoid roads, speed across roads, pause on roads, or fail to respond—based on their behavioral adaptations in response to perceived risk.

FOUR RISK-AVOIDANCE BEHAVIORAL RESPONSES TO TRAFFIC VOLUME

We propose a framework of four categories, primarily based on responses to perceived danger that subsume most observed responses to vehicle traffic: Nonresponders, Pausers, Speeders, and Avoiders. These categories reflect the interplay between avoidance behavior and vehicle-caused mortality that culminate in the overall barrier effect of traffic on wildlife and disruption of habitat connectivity. We propose that the traffic flow model (Hels and Buchwald 2001, van Langevelde and Jaarsma 2004) be modified to incorporate behavior, resulting in four different sets of mortality, avoidance, and total barrier curves (Fig. 1). The responses and the traffic volumes at which these barrier effects manifest are species-specific but the species within a category still will follow general patterns (Fig. 1). The height of the curves and carcass counts decrease over time whenever mortality exceeds reproductive output.

Nonresponders

Nonresponders do not recognize moving vehicles as threats or are unable to detect a moving vehicle in time to avoid mortality regardless of traffic volume. The Nonresponder group includes species that do not respond to traffic either because they have limited sensory abilities or because the hunting styles of their predators are not analogous to approaching vehicles. The shape of the curve of barrier effect vs. traffic volume essentially follows the traffic flow model (Hels and Buchwald 2001, van Langevelde and Jaarsma 2004).

As gaps between vehicles decrease, mortalities increase at an accelerating rate. As traffic volume and therefore the probability of an individual encountering a vehicle increases, the chance of a successful crossing approaches 0 and the road becomes a strong barrier (Fig. 1a). Nonresponder populations near roads would predictably experience strong fragmentation effects and relatively high risk of local extinction. Predictably, Nonresponders are likely to be commonly found as roadkill victims, at least until the mortality rate exceeds recruitment.

Species with the Nonresponder behavior include many invertebrates, some frogs, some snakes, some turtles, and some owls (Grilo et al. 2014). Northern leopard frogs (*Rana pipiens*) were nonresponsive in experiments testing response to traffic in Canada (Bouchard et al. 2009). Western Barn Owls (*Tyto alba)*, common victims of vehicles, were found to cross highways without regard to traffic intensity (Grilo
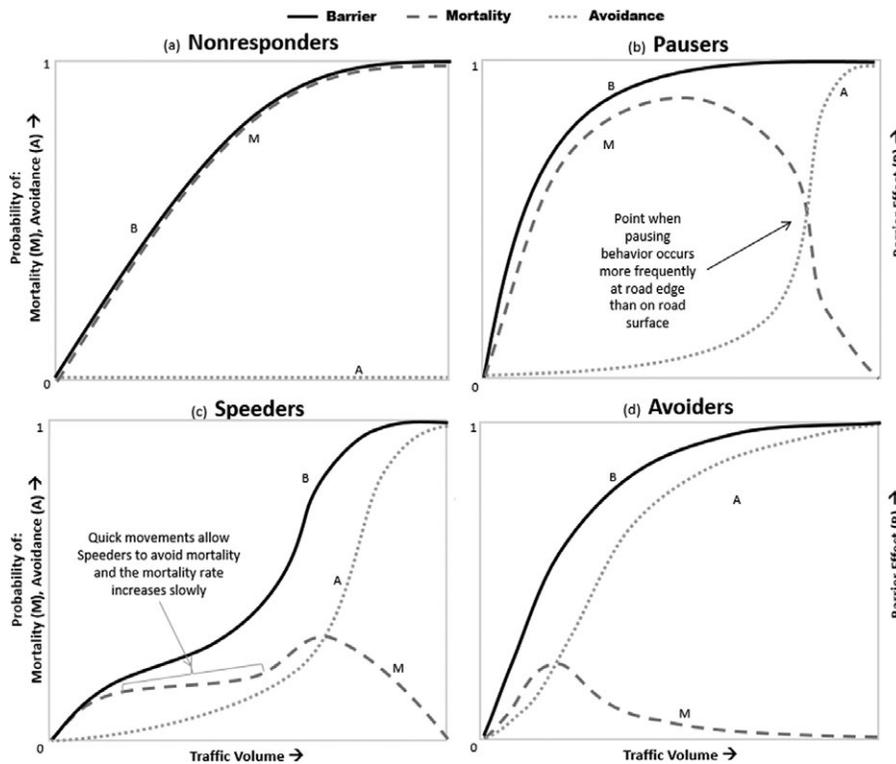
Fig. 1.   The total barrier effect (solid line) from mortality (dashed line) and avoidance (dotted line) for the four response categories. (a) Nonresponders do not recognize moving vehicles as threats or are unable to detect a moving vehicle in time to avoid mortality regardless of traffic volume. (b) Pausers respond to threats with adaptations that slow or stop them. Defenses include crypsis, armoring, or malodorous sprays. (c) Speeders recognize moving vehicles as threats and react with a rapid flight response. (d) Avoiders recognize moving vehicles as threats and respond by avoiding the road at much lower traffic volume than Speeders. The shape of the curves depends on species characteristics, such as animal speed, home range size, seasonality, and motivation to cross. These graphs do not include actual traffic volume values because the response varies across species, but it is not likely that individuals of any species will successfully cross when AADT exceeds 35,000.

et al. 2012), and were locally extirpated when a new highway was constructed (Joveniaux 1985), both results suggesting lack of suitable response to a new "predator" with no natural analog. In the case of Western Barn Owls, a species with few to no natural predators while on the wing, their undivided attention during foraging especially during food shortages (Grilo et al. 2014) predisposes them to fail to respond to potentially lethal, yet novel, sounds such as approaching vehicles. Juvenile bats showed greater mortality at higher traffic volumes (Lesiński 2007). Anecdotally, orange sulfur butterflies (*Colias eurytheme*) and California tortoiseshells (*Nymphalis californica*) during fall migration exhibited no evasive maneuvers as vehicles approached.

Pausers

Pausers respond to a perceived risk of predation by relying on alternatives to fleeing, such as using crypsis, counter-threat, or an armored exterior. Pausers respond to the perceived threat by reducing their speed or freezing, which increases time spent on the roadway and therefore increases mortality risk (van Langevelde and Jaarsma 2004). When traffic has reached sufficient volume for an animal to pause before attempting crossing, the probability of avoidance becomes greater than the probability of mortality. Complete barrier effects are due to the combination of high mortality from pausing in the roadway and avoidance from halting at the roadside (Fig. 1b). Pausers are abundantly

represented as roadkill and include skunks *(Mephitis sp.)*, porcupines (*Erethizon dorsatum)*, opossums (*Didelphis virginiana),* gray kangaroos (*Macropus robustus erubescens*), cryptic snakes, some amphibians, and some turtles (Andrews et al. 2005, Mazerolle et al. 2005, Lee et al. 2010). Armadillos (*Dasypus novemcinctus)* are Pausers whose slow movements and inappropriate responses to danger—jumping then curling into their armored exterior—increase mortality risk as the gaps between vehicles decrease (Inbar and Mayer 1999). The majority of amphibians Mazerolle et al. (2005) studied met our criteria for Pausers although they found the stimuli needed to elicit a pause response varied.

Speeders

Speeders are characterized by anatomical and behavioral adaptations to flee as a primary response to threat. Pausers may also temporarily flee, but unlike Speeders their primary defense is not flight. Speeders may stop to gather information on the threat of oncoming vehicles, but otherwise tend to flee from danger. Speeders can be ungulates, such as mule deer (*Odocoileus hemionus;* Geist 1981) and pronghorn (*Antilocapra americana*; Einarsen 1948), and are also represented by other groups such as rapidly moving snakes (Andrews et al. 2005) and red kangaroos (*Macropus rufus,* Lee et al. 2010). The probability of mortality increases slowly with increased traffic volume for a period when speeding allows them to exploit traffic gaps (Fig. 1c). Eventually as traffic increases to a threshold in which quick fleeing movements are no longer sufficient to exploit gaps between vehicles, the probability of mortality increases steeply until the traffic volume elicits avoidance. Individuals may be hit at lower traffic volumes if they pause as a protective response to young or to update information about the threat. Barrier effects manifest at higher traffic volume more than the previous groups because their speed can reduce mortality risk at relatively low and moderate volumes; barrier effects occur both as a result of mortality and ultimate avoidance of the road. With high traffic volume, barrier effects result primarily from avoidance rather than mortality.

Pronghorn represent the ultimate Speeder, as pronghorn rely on endurance and speed as a predator avoidance strategy. Pronghorn increase their speed to cross highways, occasionally even racing to cross in front of vehicles (Einarsen 1948). As traffic volume increases, however, pronghorn avoid crossing (Dodd et al. 2009). Higher traffic volumes inhibit crossing attempts by deer as well; deer-vehicle collisions are most probable on two-lane highways of moderate traffic volume rather than high volume interstate highways (Huijser et al. 2008). The dragonfly *Tramea lacerata* is a Speeder that moves vertically out of the way of vehicles, but avoids crossing roads with high traffic volume (Soluk et al. 2011).

Avoiders

Avoiders, such as bears (*Ursus spp.)*, cougar (*Puma concolor)*, and some bats are currently known to recognize moving vehicles as threats and respond by avoiding the road at much lower traffic volume and further distances from the road than Pausers and Speeders (Fig. 1d). This response results in relatively low roadkill rates and suggests individuals more consistently recognize vehicles as dangerous and avoid interactions. Barrier effects occur mostly through avoidance instead of mortality as traffic volume increases.

Even moderate traffic volume can restrict movement of Avoiders. For example, grizzly bears (*U. arctos)* avoid roads starting as low as 10 vehicles/d (Mace et al. 1996). While flighted birds are frequently the taxon most killed by traffic despite their ability to fly (Erickson et al. 2005), some passerine birds respond to increasing traffic volume by avoiding roads and adjacent habitat (Reijnen et al. 1996), and therefore presumably face increased fragmentation and loss of habitat use. Woodland and grassland grouse (Tetraonidae) are displaced away from roads, especially when roads are associated with other infrastructure such as oil and gas extraction sites (Hovick et al. 2014), and are infrequently found as roadkill (Räty 1979). When vehicles were present, 60% of endangered Indiana bats (*Myotis sodalis*) avoided crossing roads, whereas only 32% of bats reversed their course when no traffic was present (Zurcher et al. 2010). Orange tip butterflies (*Anthocharis cardamines*) turned around at a motorway and were much

less likely to cross it than an adjacent meadow (Dennis 1986).

Some Avoiders reroute to cross elsewhere or cross roads only when traffic volume is low, which can reduce roadkill when traffic volume is high. Elk-vehicle collisions occurred more frequently on lower traffic volume weekdays than higher traffic volume weekend days in Arizona suggesting more crossings were attempted (Dodd et al. 2005). Forest bats avoid higher volume roads even if it involves a longer journey, but fly straight across similar-width roads with no traffic (Kerth and Melber 2009). Raccoons (*Procyon lotor)* attempt to cross lower volume roads and avoid higher volume roads (Gehrt 2002) or use wildlife crossing structures such as culverts (Ng et al. 2004). Both grizzly and black bears *(U. americanus)* modify their crossing attempts to times of lower traffic volume (Waller and Servheen 2005, McCown et al. 2009). Similarly, moose (*Alces alces*) were found to cross roads at night when traffic volume was 33% lower than during daylight hours (Laurian et al. 2008). These findings are consistent with Seiler's (2005) finding that highway barrier effects to moose change from mortality to avoidance as traffic volume increased, and provide support for the shape of the avoidance curve for Avoiders in our framework.

Considerations and Research Needs

Our framework is meant as a guide to enhance understanding of how and why animals react to vehicles across different traffic volumes. Although behaviors can vary among individuals, basic ecology can be used to predict the primary response of a population, thereby providing increased predictive ability about the barrier effect of roads based on evolved responses to risk. Even with some within-species variation, recognizing the behavior or behaviors typical of a population will help interpret roadkill and avoidance data and determine most appropriate mitigations given those behaviors and local traffic volume (see Application section). Individuals vary based on their motivation, experience, and individual characteristics including gender, age, and body size. At times the response can be situational; thus, we predict that if an animal is highly motivated to cross to meet an urgent survival or reproductive

need, the onset of avoidance behavior would occur at a higher traffic volume for Pausers, Speeders, and Avoiders than otherwise (e.g., turtles; Aresco 2005) but not for Nonresponders. The effects of vehicle speed on animal response and collision risk are complex and require more investigation; for example, vehicle speed may affect mortality risk of Speeders because higher vehicle speeds reduce the response time within traffic gaps, thus decreasing the effectiveness of fleeing strategies. Within-species variation resulting from habituation to human disturbance may also cause considerable variation in response to perceived risk. For example, black bears appear less wary of vehicles in Florida than Idaho (McCown et al. 2009, Lewis et al. 2011). Some species conform closely to one type of response, whereas others have multiple-response strategies as a function of individual variation (Fig. 2). Sometimes the variation will be predictable, as with immature individuals exhibiting different behavior from adults. For example, moose can be generally classified as Avoiders; however, if encountering traffic, inexperienced young moose tend to run and older male moose may stand their ground and challenge vehicles in a confrontational form of Pausing (Child et al. 1991, Laurian et al. 2008).

A few species straddle more than one category (Fig. 2). Bobcats (*Felis rufus*) may exhibit a gradation in the Speeder to Avoider categories because they flee from danger and also show avoidance behavior at relatively low traffic volumes. Lovallo and Anderson (1996) found bobcat patterns of response to various traffic volumes consistent with Speeder response, where they crossed less often than expected on roads with higher traffic volumes. Black racer snakes (*Colubris constrictor*) may represent a gradation between Pausers and Speeders because they use speed to escape predators and move quickly across roads, and also respond to passing traffic with immobilization. Black racers will stop and wait several minutes after a vehicle passes, indicating a barrier effect with traffic volume as low as 10 vehicles/h (less than 240 AADT; Andrews et al. 2005).

This framework will be most helpful for practitioners once a variety of traffic volume–species combinations are tested across the four behavioral categories. Testing for each response type
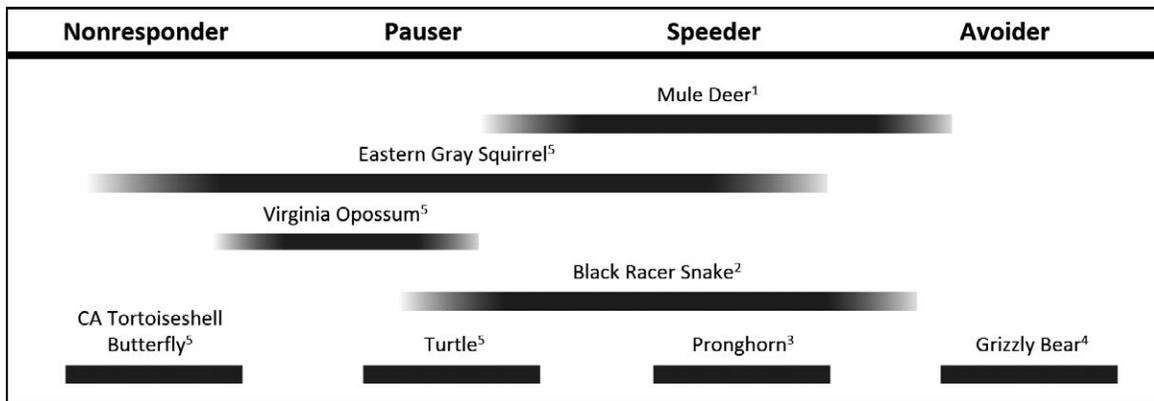
Fig. 2. Conformity of response conceptual model. Individual species vary in how tightly they conform to a given categorical response. While behavior between these categories is not continuous, a species can exhibit multiple categories of these behaviors. California tortoiseshell butterfly, turtles, pronghorn antelope, and grizzly bears all tightly conform to one category. The eastern gray squirrel, for example, spans a wider range of responses centered in the Pauser category. The species examples given here illustrate the potential variability within a species' range of response to a given traffic volume response category. Saturation of bars approximate the span of response categories for the labeled species. Notes: [1]Huijser et al. (2008). [2]Andrews et al. (2005). [3]Dodd et al. (2009). [4]Mace et al. (1996). [5]Position based on observed behaviors: thanatosis in Virginia opossum, contractive behavior in turtles, erratic behavior in eastern gray squirrel (*Sciurus carolinensis*), and nonresponsive behavior in California tortoiseshell butterfly.

would allow researchers to create more exact functional relationships between organisms and traffic volume and therefore better predictions and management. Results are already available showing the effect of traffic volume for a few Speeders (Gagnon et al. 2007) and Avoiders (Mace et al. 1996). Data are also needed to verify that Pausers consistently stop at the edge of a road once traffic volume reaches a certain level. It is important to note that the basic shape will stay the same across organisms within a category but the traffic volume trigger points of switching from crossing to avoidance and of the cumulative barrier effect will differ across species within the group. It would be extremely useful for researchers to determine species-specific relationships of the effects of traffic volume that could be used to identify traffic volume thresholds above which mortality or barrier effects are unacceptably high. Threshold models have been used in Europe (Iuell et al. 2003, Helldin et al. 2010) and have been most useful for large ungulates that in our classification are Speeders. Caution in such generalizations is needed because of the variance in response of many animals even to the individual level.

We recommend several important characteristics of traffic volume to consider in studies of barrier effects on wildlife, based partly on the deficiencies shown in most existing studies that could be improved with more accurate and precise traffic volume data (Appendix S1). We further recommend the use of standardized traffic volume categories, used by the Federal Highway Administration, to make better comparisons across studies. Currently, most studies use terms relative only to the roads within a study area.

Traffic volume along with the risk response categories does not explain all variation in mortality and avoidance. Some roadkill at low traffic volume is due to intentional hits by drivers (Langley et al. 1989). Vehicle speed and road width also likely affect relative barrier strength to wildlife, though these are correlated with traffic volume because planners often increase road width to meet increased traffic volume demands; the increased capacity in turn results in increased speed limits (Falcocchio and Levinson 2015). Vehicle speed may affect animal behavior as well, interacting with traffic volume in complex ways that have had little investigation to date. Variation in mortality within a response category,

including among individuals of a species, can also be due to variations in their experience, speed, or processing ability, or in the terrain, that allows them to differentially perceive risk at longer distances, for instance. Our framework does not apply to species that avoid the road surface due to lack of cover or inhospitable surface conditions, or those that are attracted to the road for food or other reasons. These groups face a barrier effect independent of traffic volume. Research examining such nuances will also be useful for management.

APPLICATION

This framework helps to accurately identify barrier effect type (mortality or avoidance), helps interpret roadkill data, facilitates predictions that indicate the urgency of management responses given the category of the affected species and the current or predicted traffic volume (Table 1), and helps to identify mitigation options (Table 2). Without such a framework that more carefully describes generalized patterns than has been available currently, transportation planners may miss important indications of barrier effects. Low traffic volume roads have been considered benign, but they likely limit populations of some species, especially Nonresponders. The framework presented here suggests mitigation will be needed at lower traffic volumes for Pausers and Nonresponders than most Speeders. Also, if Speeder mortality is unacceptably high, it may be more important to mitigate effects on moderate traffic volume highways than higher traffic roads (Jaeger and Fahrig 2004). If an Avoider species cannot access key habitats, barrier effects can be as lethal as vehicle collisions, yet less obvious.

Table 1. Summary of population-level impacts from traffic based on species' risk response characteristics.

Risk response category	Species characteristics	Key barrier effects of traffic volume (TV)† across risk response categories	Population-level impacts due to animal–vehicle collisions and avoidance‡	
			Initial impacts	Advanced impacts
Nonresponder	Little sensory capacity to detect vehicles OR failure to interpret vehicles as threats OR high motivation to move despite risk	Mortality risk and therefore barrier effect increases as a saturating hyperbola with increasing TV until the barrier is complete	Reduced population size due to direct mortality	Reduced population size, low genetic diversity, inbreeding depression, and eventual extirpation§
Pauser	Primary predator avoidance strategy involves slowing or immobilization, e.g., due to armature or crypsis	Mortality peaks at moderate TV while avoidance increases sigmoidally, together creating a barrier effect that quickly increases with TV and levels off at moderately high TV	Reduced population size due to direct mortality; effects manifest at low TV	
Speeder	Primary predator avoidance strategy is fleeing, evading predator using greater speed	High levels of mortality at moderate TV when Speeders can no longer outpace vehicles; barrier effect is due mainly to avoidance at higher TV regardless of speed	Reduced population size due to direct mortality at low to moderate TVs; at high TV, lowered fecundity, poor condition, or mortality due to lack of access to key resources	
Avoider	Sensory capacity to detect predators at a distance and highly wary of anthropogenic features	Mortality relatively low and peaks at low TV; avoidance causes barrier effect across traffic volumes	Lowered fecundity, poor condition, or mortality due to lack of access to critical resources	

† The TV at which mortality, avoidance, and the barrier effect peaks differs across populations, but within a category, all populations follow the same basic shapes and trends.

‡ Population-level effects will vary with quality of habitat, size of the source population, and the degree to which the barrier effect is due to mortality vs. avoidance.

§ Saccheri et al. 1998.

Table 2. Interpretation of carcass evidence and priority mitigation approaches across traffic volume levels and risk response categories.

Risk response category	Relative carcass evidence expected across traffic volumes (TV)[†][‡]			Priority mitigation approach		
	Relative traffic volume§					
	Low	Moderate	High	Low	Moderate	High¶
Nonresponder	Moderate carcasses due to few vehicles; impacts may be sustained over time when reproductive rate exceeds mortality	More carcasses than at low TV	Many carcasses over short time until population size reduces, then few to no carcasses	Reduce mortality by fencing then reestablish connectivity with Wildlife Crossing Structures (WCS); reducing speed limit# may be effective	Where high mortality is greater concern than connectivity, install fencing; where access to key habitats limits population, fencing and WCS	Fencing and WCS‖
Pauser	Carcasses increase rapidly with TV, starting at low TV as Pausers exploit traffic gaps	Carcasses peak at moderate TV as animal pauses in traffic thus maximizes risk	Fewer carcasses than at moderate TV because pausing begins prior to entering road	Fencing reduces mortality until connectivity can be reestablished with WCS	Fencing keeps species off road during occasional traffic gaps to reduce mortality, and WCS restore connectivity	WCS restore access to key habitats
Speeder	Few to moderate carcasses as Speeders exploit traffic gaps	Most carcasses as speed no longer suffices to cross as gaps decrease	Fewer carcasses as avoidance reduces mortality	Rare species may need fencing; reducing speed limit to the animal's speed may be effective	WCS restore connectivity; simultaneously install fencing	Fencing less necessary; WCS maintain access to key habitats
Avoider	Few to moderate carcasses before avoidance response begins	Carcasses reduce as avoidance begins	Carcasses remain few as avoidance continues	WCS imperative for small populations and ones blocked from key habitats; fencing minimizes mortality††	Fencing less necessary; WCS maintain access to key habitats	Fencing less necessary; WCS maintain access to key habitats

† Carcass quantities will vary with quality of habitat, size of the source population, and other factors (see main text). Large populations will produce relatively more carcasses than small populations relative to risk. Carcass quantities will vary for categories until local extirpation occurs.

‡ Assuming sufficient population size (see Table 1).

§ Values in table are relative. See Appendix S1 for standardized traffic volume terms (Low Traffic Volume LT 500 AADT (Average Annual Daily Traffic); Moderate Traffic Volume = AADT between 500 and 4999; High Traffic Volume = AADT between 5000 and 9999).

¶ For Very High or Extreme Traffic Volume roads (above 10,000 AADT), fencing is most likely to reduce mortality for terrestrial Nonresponders, and crossing structures are most likely to reduce barrier effects from both mortality and avoidance for all four response categories.

Speed limit reductions are unlikely to be effective unless they are lowered to be approximately equal to the animal's speed.

‖ Ascensão et al. 2013.

†† Fences may not be advisable, or may need to be marked, where grouse are vulnerable to fence collisions (Wolfe et al. 2009).

Management options to mitigate effects are suggested by understanding the primary barrier effect of each category (Table 2). For Nonresponders and Pausers, mortality is the primary barrier effect, whereas for Speeders and Avoiders avoidance is the primary barrier effect.

While the management options for all behavior categories mainly include fences and crossing structures, they vary in three key components: priority, siting, and design. Pausers and Nonresponders suffer high levels of mortality across many traffic volumes, so installing fencing is a priority to immediately reduce population-level impacts of vehicles on these species (Jackson and Fahrig 2011). Populations of Speeders in areas of high traffic volumes, and Avoiders at relatively moderate to high traffic volume, conversely have a greater need for reestablishing connectivity because they are limited mostly by the avoidance barrier effect. With regard to siting, passages for Nonresponders and for Pausers will likely be the most effective when located in places of relatively high traffic and good habitat, and more frequently for animals with smaller home ranges (Bissonette and Adair 2008). Avoiders may need passages to be sited where topography decreases the reach of traffic effects, and may need passages installed at sites even with low traffic volume. In real-life applications of these mitigation measures, some solutions for one group or species can increase adverse effects on others. For example, fences may reduce mortality for some species while restricting movement for others. Response to predation risk can also inform design and barrier effects of structures and fences as is discussed in Kintsch et al. (2015).

Our framework is valuable not only for determining appropriate mitigation measures but also for diagnosing the problem accurately. Considering risk response along with traffic volume helps reduce the chance of missing or misinterpreting data about barrier effects from mortality and avoidance, and helps identify the type of risk a population is experiencing given current traffic volume (Tables 1 and 2). The nature of the increasing barrier varies across the categories, with Nonresponders experiencing direct mortality across traffic volumes, and the other categories switching from mortality-induced to avoidance-induced barriers (Fig. 1, Table 2). Behavioral responses to risk can be used to determine effects of traffic on wildlife populations rather than attempting to interpret the problem from roadkill data. Interpreting roadkill data can be misleading because few carcasses can indicate either no problem or an advanced barrier effect resulting from near extirpation (Eberhardt et al.

2013), strong avoidance, or displacement. Genetic differentiation may provide evidence of an advanced barrier effect from avoidance when carcasses are rare, and such evidence may support or refute our framework.

Few mortalities will occur independent of traffic volume after the onset of avoidance behavior in Pausers, Speeders, and Avoiders, or if population abundance is low for all categories (Fahrig et al. 1995). For example, Rudolph et al. (1999) noted that some snake species may be so susceptible to vehicle-caused mortality that roads can remove nearly all individuals in an area. Such extirpation, consistent with the expected result of the behavior of Nonresponders or Pausers, prevents evidence of a correlation between traffic volume and mortality. In response to TV increasing beyond a daily average of 8000 vehicles, mule deer, a Speeder, rerouted their migration, locally reducing collisions with vehicles but causing the deer to parallel the highway for 45 km until they reach an area with lower TV (Coe et al. 2015).

Resource managers could fail to foresee an imminent threshold of population risk if risk response behavior is not used, or if the range of traffic volume investigated is too narrow, or traffic volume categories too broad to detect responses. For investigations on Nonresponder, Pauser and Avoider response categories, precise traffic volume is needed because small numbers of vehicles per day can affect these species (see Appendix S1). For example, European toads (*Bufo bufo*) experienced a 30% mortality rate at an equivalent of 240 ADT (van Gelder 1973). Our conceptual model suggests that the range of traffic volume that needs to be measured is species-specific; therefore, the point at which the road becomes a complete barrier varies even within one response category. For rare species, research to indicate the exact shape of the response curves as well as likely thresholds could be of critical importance in developing mitigation measures to reduce barrier effects. To determine the road threats to a species and how to best mitigate them, both the risk response category and the animal's speed are needed as they both affect the shape of the animal's response to traffic volume (Fig. 1, Hels and Buchwald 2001, van Langevelde and Jaarsma 2004). In fact, 1000 to 12,000 ADT must be measured to detect changes in the behavioral response to traffic of most large Speeders (Seiler

Taxon	Non-Responders	Pausers	Speeders	Avoiders
Invertebrates	California tortoiseshell (*Nymphalis californica*)		Hine's emerald dragonfly (*Somatochlora hineana*)	Oregon silverspot butterfly (*Speyeria zerene hippolyta*)
Snakes		Timber Rattlesnake (*Crotalus horridus*)	Ring-necked Snake (*Diadophis punctatus*)	
Birds	Western barn owl (*Tyto alba*)			Meadow pipit (*Anthus pratensis*)
Marsupials		Grey kangaroo (*Macropus robustus erubescens*)	Red kangaroo (*Macropus rufus*)	
Carnivores			Bobcat (*Lynx rufus*)	Grizzly bear *Ursus arctos*)
Ungulates			Pronghorn (*Antilocapra americana*)	Moose (*Alces alces*)

Fig. 3. Diverse behavioral response to traffic by closely related taxa. Species response to traffic is driven behaviorally rather than taxonomically, and closely related species can fall into different behavioral response categories. Photo sources: ring-necked snake, timber rattlesnake, western barn owl, bobcat, moose from USDA Forest Service. Meadow pipit courtesy of Ruud Foppen, taken by Menno Hornman. Gray and red kangaroos courtesy Enhua Lee. Grizzly bear taken by K. Mueller and Hine's emerald dragonfly from U.S. Fish and Wildlife Service. Pronghorn and silverspot butterfly taken by Steve Hillebrand.

and Helldin 2006, Gagnon et al. 2007). Pooling data for even closely related species in different response categories may mask traffic volume effects.

This framework encompasses many species and highlights the important concepts that species do not respond to traffic volume linearly or along taxonomic lines (Fig. 3). Child et al. (1991)

argued that biologists may not discover appropriate solutions to vehicle-caused mortality to moose without a research focus on avoidance-flight responses. As in most ecological investigations, behavioral responses in the real world are complex and a framework that includes animal behavior, such as the one presented here, is therefore crucial to understanding the effects of highways on wildlife. Fortunately, effective mitigation measures such as wildlife crossing structures are becoming available to reduce barrier effects across highways (Gagnon et al. 2007). Our proposed framework can advance the understanding of wildlife and road interactions. We encourage nuanced investigations that evaluate how traffic volume affects behavior and connectivity, and evaluate the effectiveness of management options given the combination of traffic volume and the response of local populations to traffic.

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