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NOTE

Factors affecting the permeability of road mitigation measures to the movement of small mammals

Adam T. Ford and Anthony P. Clevenger

Abstract: Mitigation measures, such as wildlife-exclusion fencing and crossing structures (overpasses, underpasses, culverts), have been widely demonstrated to reduce the negative effects of roads on medium-sized and large animals. It is unclear how these mitigation measures influence the movement of small mammals (<5 kg). Our study has three objectives: (1) to test whether culverts improve highway permeability; (2) to determine factors associated with culvert use, such as culvert obstruction by snow; (3) to evaluate factors contributing towards fence permeability, such as the presence of a culvert, snow depth, and fence mesh size. We used snow tracking to assess the movement for four small-mammal taxa along the Trans-Canada Highway corridor in Banff National Park, Alberta, Canada. We found that the presence of a culvert within 100 m of transects significantly improved fence and highway permeability. Obstruction of the culvert entrance by snow was negatively correlated with the probability of use, and therefore, of highway permeability. Furthermore, the mesh size of the fencing did not affect fence or highway permeability. We recommend that culvert entrances be located on the outside of fenced right-of-ways to reduce obstruction by highway maintenance activities such as snowplowing.

Key words: connectivity, conservation, fence, red squirrel, *Tamiasciurus hudsonicus*, snowshoe hare, *Lepus americanus*, *Martes* sp., *Mustela* sp., road ecology, wildlife.

Résumé : Il a été amplement démontré que les mesures d'atténuation comme les clôtures d'exclusion des animaux sauvages et les ouvrages de franchissement (passages supérieurs, passages inférieurs, ponceaux) réduisent les effets négatifs des routes sur les animaux de moyenne et grande taille. L'influence de ces mesures d'atténuation sur les déplacements des petits mammifères (<5 kg) n'est toutefois pas bien établie. L'étude a trois objectifs, à savoir : (1) vérifier si les ponceaux améliorent la perméabilité des routes, (2) déterminer quels facteurs sont associés à l'utilisation des ponceaux, comme l'obstruction des ponceaux par la neige, et (3) évaluer les facteurs qui jouent un rôle dans la perméabilité des clôtures, comme la présence d'un ponceau, l'épaisseur de la neige ou la taille des mailles de la clôture. Nous avons utilisé l'observation d'empreintes dans la neige pour évaluer les déplacements de quatre taxons de petits mammifères le long du corridor de la route transcanadienne dans le Parc national Banff (Alberta, Canada). Nous avons constaté que la présence d'un ponceau dans un rayon de 100 m d'franchissements améliorait significativement la perméabilité de la clôture et de la route. L'obstruction de l'entrée d'un ponceau par la neige était négativement corrélée à la probabilité d'utilisation et, donc, à la perméabilité de la route. En outre, la taille des mailles de la clôture n'avait pas d'effet sur la perméabilité de la clôture ou de la route. Nous recommandons de situer les entrées de ponceau à l'extérieur des emprises clôturées afin de réduire les obstructions causées par les activités d'entretien des routes, comme le déneigement. [Traduit par la Rédaction]

Mots-clés : connectivité, conservation, clôture, écureuil roux, *Tamiasciurus hudsonicus*, lièvre d'Amérique, *Lepus americanus*, *Martes* sp., *Mustela* sp., écologie routière, animaux sauvages.

Introduction

Small animals (<5 kg) comprise the most abundant and rich taxa in many temperate ecosystems. The fecundity of many small animals should make their populations resistant to disturbance; however, their limited dispersal ability and habitat specificity can make these species vulnerable to the impacts of habitat modification, such as roads (Fahrig 2007). Roads are a barrier to the movement of many small animals and can increase mortality rates from collisions with vehicles (Ford and Fahrig 2007; Fahrig and Rytwinski 2009; Baxter-Gilbert et al. 2015). The combined barrier and mortality effects of roads influence population sizes and persistence of small animals, with potential cascading effects through the food web (Fahrig and Merriam 1994; Jaeger et al. 2005; Bissonette and Rosa 2009).

In a growing number of jurisdictions, wildlife and transportation managers are implementing mitigation measures to both reduce wildlife–vehicle collisions and facilitate the safe passage of animals across highways (Rytwinski et al. 2016). Mitigation measures have been designed for a variety of taxa, including ungulates (Sawyer et al. 2016), reptiles (Woltz et al. 2008), salamanders (Pagnucco et al. 2012), and other small fauna (van der Grift et al. 2013). For example, drainage culverts have been used alongside larger structures to help encourage road crossings by small mammals (Clevenger et al. 2001*a*; McDonald and St. Clair 2004*a*; Rytwinski et al. 2016). The majority of mitigation projects in North America are targeted at large mammals (i.e., ungulates) where road permeability is both a conservation and a human safety concern (Forman et al. 2002). It is not clear if and how these mitiga-

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A.T. Ford. Department of Biology, The University of British Columbia, Okanagan Campus, #109 Science Building, 1177 Research Road, Kelowna, BC V1V 1V7, Canada.
A.P. Clevenger. Western Transportation Institute, Montana State University, P.O. Box 174250, Bozeman, MT 59717, USA.
Corresponding author: Adam T. Ford (email: adam.ford@ubc.ca).

tions, such as exclusion fencing and crossing structures, influence the movement of nontarget species like small mammals. Exclusion fencing designed for large mammals, for example, could also interfere with the movement of smaller taxa like rodents and birds. As such, there is a need to understand the impacts of road mitigation on the broader ecological community.

Among the growing number of road mitigation projects globally, the Trans-Canada Highway (TCH) in Banff National Park (hereafter referred to as Banff), Alberta, Canada, is one of the most intensively managed and studied in the world (Ford et al. 2010). The TCH has over 80 km of wildlife-exclusion fencing and over 40 dedicated, large-mammal wildlife crossing structures (Ford et al. 2009). Banff has attempted to reduce road effects on small-mammal populations by installing hundreds of smaller (<1 m diameter) drainage culverts and by using variable-dimension mesh fencing. Variable-dimension mesh fencing has a smaller mesh height (ca. 8 cm × 16 cm) near the bottom of the fence and a taller mesh height (ca. 16 cm × 16 cm) at ≥0.75 m from the ground. In addition, the TCH fencing in Banff has a "dig-apron" of chain-link fencing that is buried below ground by 1 m and extends vertically up the main fence by ~0.75 m. This apron was designed to reduce the intrusion of species of the genera *Ursus* Linnaeus, 1758 and *Canis* Linnaeus, 1758 onto the highway, but it also reduces the mesh size of the bottom portion of the fence to 3 cm × 3 cm. Studies along the TCH showed that drainage culverts built under the highway serve as habitat linkages for small mammals (Clevenger et al. 2001*a*; McDonald and St. Clair 2004*a*).

In spite of the efforts taken to facilitate the safe movement of small mammals across the TCH, there is little evidence to show how animals interact with the fence, road, and culverts together. Intuitively, if an animal is small enough to fit through fence mesh, then the fence should not pose a barrier to movement. Likewise, if a culvert is present, and we know that culverts are used by small mammals (Clevenger et al. 2001*a*), then road crossings should be more prevalent in areas near culverts. However, these assumptions assume that animals are not averse to anthropogenic structures like fences or the roadside verge (i.e., the right-of-way; Ford and Fahrig 2008). Many of the culverts along the TCH have entrances inside the right-of-way (i.e., located between the road surface and the fence), which means that animals crossing the road must also cross the fence, venture into the treeless right-of-way, and then access the culvert entrance. Once an animal encounters a fence, and is unlikely to cross it, then it diminishes the conservation value of culverts. On the other hand, if animals pass through the fence, but do not use culverts or cross roads, it suggests that culvert entrances need to be located on the habitat side of the fence. Moreover, during the winter conditions that dominate about half the year in Banff, snow may either facilitate or hinder small-mammal movement. Deep snow could enhance movement by providing access to the larger mesh sizes (that are higher off the ground) along the fence for species travelling on the snow surface. At the same time, snow may block entrances to culverts, making their use less likely for species that use the snow surface. To our knowledge, an evaluation of these design features — fencing mesh size and the accessibility of culvert entrances — has never been performed, so it is unclear if conservation goals are being met for the small-mammal community in Banff.

Using noninvasive snow-tracking methods, we measured small-mammal movement at fences near and away from culverts. We assessed if and how snow depth, age of fence, species, presence of a culvert, and track location influence permeability of both fences and roads. In addition, culvert entrances at some sites were inside the right-of-way and some were on the "habitat side" of the fence. We tested the prediction that culverts improve highway permeability, given that the fence is permeable. Second, we evaluated factors associated with culvert use, such as obstruction of the culvert entrance by snow.

Materials and methods

Study area

Our study took place along the TCH in Banff National Park, Alberta, Canada. The TCH is the major transportation corridor across western Canada and traverses approximately 82 km of Banff, from the eastern park boundary to the western boundary at the Alberta – British Columbia border. Traffic volume was estimated at 19 000 vehicles per day in 2016 and is increasing at a rate of 2.5% per year (Ford et al. 2009). In the 1970s, safety issues compelled planners to upgrade the TCH within Banff from two to four lanes (i.e., twinning), beginning from the eastern boundary of Banff and working west (McGuire and Morrall 2000). Large animals were excluded from the road with a 2.4 m high fence erected on both sides of the highway. Underpasses were also built to allow wildlife to cross the road. The first 27 km of highway twinning included 11 wildlife underpasses and was completed by 1988 (mitigation Phase I and Phase II). This stretch of highway also contains 104 drainage culverts. The next 18 km section was completed in late 1997 with 11 additional wildlife underpasses and 2 wildlife overpasses (Phase IIIA; see Ford et al. 2010). The final 30 km of twinning to the western park boundary was completed in 2014 and consists of 21 wildlife crossing structures, including four 60 m wide wildlife overpasses (Phase IIIB). The Phase IIIA and Phase IIIB sections have 85 drainage culverts.

Data collection

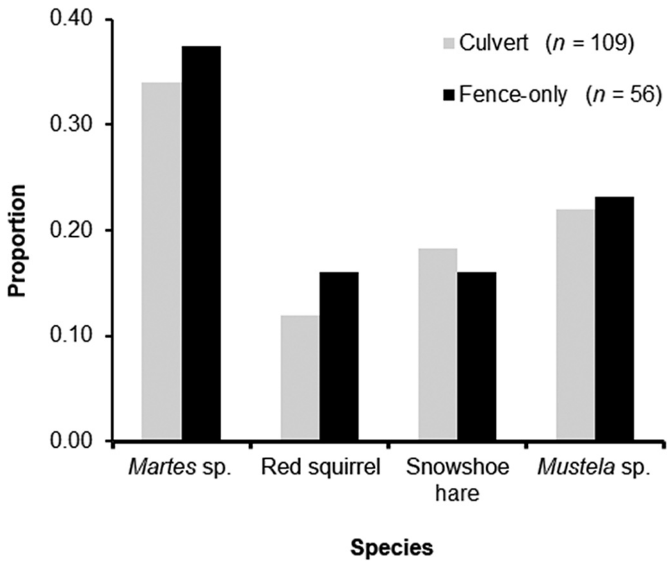
We checked both ends of 9 culverts and one end of 4 culverts for a total of 22 culvert sites. We checked only one side of the four culverts because the opposite end of the culvert opened on the habitat side of the fence and our interest was on the combined effects of fence and culverts on road permeability. On each occasion that the 13 culverts were checked, we also monitored six control sites (hereafter referred to as fence-only sites) that were located along the fence but were >200 m from the nearest culvert, bridge, or wildlife crossing. At each control, we visited both sides of the highway, for a total of 12 fence-only sites per sampling period. We visited culvert and fence-only sites five times each between 4 January and 20 February 2008. Sites were visited when ~4 days had passed since the last track-clearing snowfall, which was typically an accumulation >1 cm of new snow. Culvert and fence-only sites occurred in areas where the fence was constructed recently (<2 years old) or was well established (>10 years old).

At each site, we set up a 50 m long transect, centered on the culvert entrance at culvert-only sites (Fig. 1). Transects were 2 m wide on the habitat side and 1 m wide on the highway side of the fence. We documented species presence and track orientation based on impressions left in the snow. We documented track orientation as either (*i*) towards the highway, (*ii*) towards the habitat, (*iii*) parallel to the highway, or (*iv*) undirected (Supplementary Figs. 1–4).[1] Undirected tracks did not persist in any one of the other orientations for >5 m within the transect. We noted which tracks crossed the fencing, the highway, and which tracks indicated use of the culvert if one was present. At the center of each transect, we measured snow depth and fence mesh dimension for the lowest portion of the fence that was completely above the snowline. At culvert sites, we visually estimated the proportion of the culvert entrance that was obstructed by snow.

We focused on four species that were commonly detected: martens (genus *Martes* Pinel, 1792), red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)), snowshoe hares (*Lepus americanus* Erxleben,

[1]Supplementary figures are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2018-0165.

Fig. 1. Proportion of site visits in which at least one track was detected for the four focal taxa of small mammals (martens, *Martes* sp.; red squirrels, *Tamiasciurus hudsonicus*; snowshoe hares, *Lepus americanus*; weasels, *Mustela* sp.) near culvert (gray bars; n = 13) and fence-only (black bars; n = 6) locations along the Trans-Canada Highway in Banff National Park, Alberta, Canada. Culvert sites were visited a total of 109 times and fence-only sites were visited a total of 56 times.



1777), and weasels (genus *Mustela* sp.). Due to overlap in track sizes among conspecifics, we separately pooled *Martes* sp. (which are most likely dominated by tracks from American martens (*Martes americana* (Turton, 1806))) and *Mustela* sp. (which include ermine (*Mustela erminea* Linnaeus, 1758), least weasel (*Mustela nivalis* Linnaeus, 1766), and long-tailed weasel (*Mustela frenata* Lichtenstein, 1831)). Rarer species included deer mice (*Peromyscus maniculatus* (Wagner, 1845)), voles (genera *Microtus* Schrank, 1798 and *Clethrionomys* Tilesius, 1850), and shrews (genus *Crocidura* Wagler, 1832). Rare species were excluded from further analysis because sample sizes were too low. We note that some species in our study may use subnivean habitat for travel. We have no data on the frequency or occurrence of this behaviour.

Data analyses

We performed three statistical analyses to assess the combined permeability of the road, fence, and culvert. We used a mixed-effect logistic regression to determine significant factors affecting fence permeability (cross or did not cross) for small mammals. We included treatment (culvert or fence-only sites), species, snow depth, fence age, and the side of the fence in which the track occurred when it first entered the transect. We included a random effect for site.

Next, we performed a second mixed-effects logistic regression to determine significant factors affecting road permeability (cross or did not cross). Again, we included treatment (culvert or fence-only sites), species, snow depth, fence age, and the side of the fence in which the track occurred when it first entered the transect. We included a random effect for site. Third, we again analyzed road permeability, but only used data from the culvert-only sites. In this case, we assessed the effects of "culvert obstruction by snow" on probability of road crossing.

We used model selection procedures to determine the best-fitting model. We present model-averaged coefficients for the top-performing models (i.e., $\Delta AIC_c < 4.0$, where AIC is Akaike's information criterion corrected for small sample size). All analyses were performed using the R (version 3.51) statistical environment (R Core Team 2018) and packages lme4 (Bates et al. 2015) and MuMIn (Barton 2018). We excluded records where we could not determine if the animals crossed the highway because of poor tracking conditions. We based track identification on descriptions in Elbroch (2003).

Results

We visited 13 culverts five times each and visited another 57 fence-only transects for a total sample effort of 8450 m. We detected 94 track sequences from the four focal species at culverts and 42 track sequences from four species at fence-only locations (Fig. 1). For each taxa, there was a similar proportion of the total number of track sequences detected at culvert and control sites (Fig. 1).

The fence was highly permeable for all taxa. When pooled among culvert and fence-only locations, the fence was highly permeable, with the majority of tracks crossing for *Martes* sp. (83%), red squirrels (77%), snowshoe hares (58%), and *Mustela* sp. (78%). The road was far less permeable, with 38%, 10%, 32%, and 23% of tracks crossing for *Martes* sp., red squirrels, snowshoe hares, and *Mustela* sp., respectively. We could not determine if 7%–22% of tracks (by species) crossed the road.

The top-performing model for fence permeability included side of fence at track origin, species, presence of culvert, snow depth, and age of fence (Table 1). Tracks were significantly (P = 0.002) more likely to cross the fence if they began on the highway side of the fence than if they began on the habitat side, suggesting motivation to cross is anisometric. There was a species effect that was driven primarily by differences between snowshoe hares and *Martes* sp.

The top-performing model for road permeability included the same terms as the fence permeability model (Table 1). However, unlike the fence permeability model, snow depth had a significant negative effect (deeper snow was a greater barrier), whereas fence age had a significant positive effect (older fences were more permeable) on road permeability. The species effect was driven primarily by differences between red squirrels and *Martes* sp. Tracks were more likely to cross the road if they originated on the highway side of the fence, suggesting directional persistence in movement behaviour.

When examining just the subset of data at the culvert-only sites and terms from the best-fitting model in the road permeability analyses, we found a significant negative effect of culvert obstruction by snow on road permeability (Fig. 2; $\beta = -0.021 \pm 0.007$, P = 0.003).

Discussion

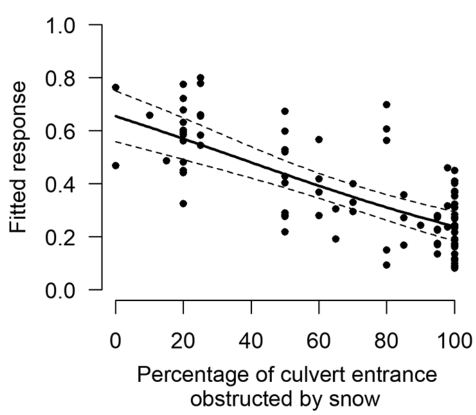
Fencing designed for large mammals was ineffective at reducing small-mammal intrusions into the right-of-way, as we found that 58%–83% of tracks crossed the fence. We detected no effect of fence mesh size on fence permeability, suggesting that variable-dimension mesh designed for ungulates and other large mammals is not an effective deterrent for small-mammal movement onto the right-of-way. Fence and road permeability were predicted by the same variables (i.e., culvert presence, fence age, side of origin, and snow depth), suggesting general influences on movement.

Snow depth had a significant negative effect on fence and road permeability. We found this surprising, given that the animals we tracked travelled on the surface of the snow and that greater snow depth meant that the size of the fence mesh at the snow surface was larger and presumably more permeable. For larger animals, snow depth increases the energetic costs of travel and reduces vagility (Parker et al. 1984; Crête and Larivière 2003), but we do not anticipate that this would influence movement patterns for the species in our study. We speculate that increasing snow depth reduces the availability of understory vegetation cover, which

Table 1. Model-averaged ($\Delta AIC_c < 4.0$, where AIC is Akaike's information criterion corrected for small sample size) coefficients for factors influencing fence and highway permeability for small mammals (martens, *Martes* sp.; red squirrels, *Tamiasciurus hudsonicus*; snowshoe hares, *Lepus americanus*; weasels, *Mustela* sp.) in Banff National Park, Alberta, Canada.

Model	Term	β	SE	Z	P
Fence permeability	Intercept	1.452	0.976	1.482	0.138
	Culvert absent	−0.579	0.378	1.520	0.129
	Fence age (relative to new)	−0.134	0.441	0.303	0.762
	Side of origin (relative to habitat side)	1.169	0.379	3.063	0.002
	Snow depth	−0.020	0.021	0.949	0.342
	Red squirrel (relative to *Martes* sp.)	−0.086	0.502	0.171	0.864
	Snowshoe hare (relative to *Martes* sp.)	−1.095	0.441	2.468	0.014
	Mustela sp. (relative to *Martes* sp.)	0.148	0.539	0.273	0.784
Road permeability	Intercept	1.771	1.843	0.958	0.338
	Culvert absent	−0.660	0.480	1.366	0.172
	Fence age (relative to new)	−1.386	0.595	2.318	0.020
	Side of origin (relative to habitat side)	0.688	0.357	1.913	0.056
	Snow depth	−0.050	0.024	2.042	0.041
	Red squirrel (relative to *Martes* sp.)	−1.649	0.632	2.589	0.010
	Snowshoe hare (relative to *Martes* sp.)	−0.066	0.493	0.134	0.893
	Mustela sp. (relative to *Martes* sp.)	−0.59	0.584	1.002	0.316

Fig. 2. The effect of culvert obstruction (percent obstructed by snow) on the predicted road permeability of small mammals (martens, *Martes* sp.; red squirrels, *Tamiasciurus hudsonicus*; snowshoe hares, *Lepus americanus*; weasels, *Mustela* sp.) in Banff National Park, Alberta, Canada. To clarify presentation of this multivariate, mixed-effects model, we show the fitted effects without culvert obstruction included in the model on the *y* axis. The solid line shows the predicted effects of the logistic regression in a model with only culvert obstruction as a predictor variable. The broken lines show the SE of the estimate.



may then deter animals from using the right-of-way (McDonald and St. Clair 2004*b*). Other small mammals appear averse to changes in roadside vegetation in the absence of fencing, leading to a barrier effect (Ford and Fahrig 2008). Our focal species are all forest- and cover-associated, and their habitat use is largely dependent upon forest and vegetative structure. As such, we speculate that snow depth may be less of an issue for road permeability in species associated with more open habitat types.

Fence age had a significant positive effect on road permeability (i.e., older fences are more permeable than newer fences). Nonlethal disturbance stimuli, such as human activities or novel objects, are hypothesized to trigger predator avoidance responses in prey animals (Kavaliers and Choleris 2001; Stankowich and Blumstein 2005; Gavin and Komers 2006). In this way, more established fences are less novel and are therefore less likely to trigger an aversive response. The positive effect of fence age may also be explained by animals having adapted to the altered habitat in the highway corridor that occurred at the time of mitigation. While many of the culverts in our study have been in place for several decades prior to mitigation, the wildlife exclusion fencing along Phase IIIB is entirely new within the year the study was conducted. This result suggests that the species in our study have a neophobic response to the fence. Providing cover (e.g., brush piles) at new fences could mitigate these temporary losses in permeability for small mammals (McDonald and St. Clair 2004*b*). The age-of-fence effect also suggests that long-term monitoring is appropriate to determine effectiveness of highway mitigation projects. A similar adaptive response to road mitigation was detected for grizzly bears (*Ursus arctos* Linnaeus, 1758) in our study area (Ford et al. 2017).

There was a species effect on road permeability, but it was driven primarily by differences between red squirrels and *Martes* sp., the smallest and largest of the four species in our study, respectively. We also found a species effect on fence permeability, driven primarily by differences between snowshoe hares and *Martes* sp. Life-history characteristics such as body size, diet, and home-range size may explain the likelihood of mammal species interacting with roads (Ford and Fahrig 2007; Fahrig and Rytwinski 2009; Barthelmess and Brooks 2010). The permeability of the highway (i.e., 10%–38% of tracks) in our study was higher than that observed in studies conducted on small mammals (<200 g), in which 2%–7% of animals cross the road (Ford and Fahrig 2008; McGregor et al. 2008). Though we only examined four species in detail, our results are consistent with life-history theory (Fahrig 2007) in that the larger bodied, more vagile species tended to make more highway and fence crossings than smaller species.

Our results have important implications for the design and engineering of road mitigation. For drainage culverts to be more effective as wildlife passages, we recommend culvert openings be on the habitat side of the fence, rather than the right-of-way side of the fence for two reasons. First, there are some species that use culverts (Clevenger et al. 2001*a*), but they are too large to pass through the fence, such as coyotes (*Canis latrans* Say, 1823), Canada lynx (*Lynx canadensis* Kerr, 1792), bobcats (*Lynx rufus* (Schreber, 1777)), red foxes (*Vulpes vulpes* (Linnaeus, 1758)), and wolverines (*Gulo gulo* (Linnaeus, 1758)). A culvert opening on the habitat side would add connectivity value for these species. Second, extending the culvert opening farther away from the highway will also reduce snow accumulation deposited from snowplows at culvert entrances. We found that when culverts were blocked, animals were not only less likely to use the culvert, they were less likely to cross the highway altogether. We recommend that culvert entrances be extended beyond the "snow-throw" radius of snowplows in areas expected to receive >1 m of snowpack.

People and the roads that they travel on continue to expand farther into pristine habitats (Laurance et al. 2014; Venter et al. 2016), causing a global decline in animal vagility (Tucker et al. 2018). The need to counter these effects has generated a great deal of research and policy on connectivity (Hodgson et al. 2009). Part of this research focuses on understanding how fencing can benefit or hinder conservation (Packer et al. 2013; Woodroffe et al. 2014; Pfeifer et al. 2014). Past work has found that fencing is essential for impeding the movement of large animals onto roads and reducing wildlife–vehicle collisions (Clevenger et al. 2001*b*; Ford et al. 2011); very little work has examined the effect of roadside fencing on small animals. Our study is a step towards filling this knowledge gap by focusing on the factors contributing to animal movement through fences and culverts. Future work could provide additional insights on landscape-scale connectivity through a before-after-control-impact design that would compare animal movement and population dynamics near roadside fencing with areas that are near fences but are road-free (Rytwinski et al. 2015). Indeed, there is a pressing need to understand if and how fencing can be an effective conservation tool, including research on species size, the disturbance type, fence design, environmental seasonality, and other contextual factors.

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