General Versus Specific Surveys: Estimating the Suitability of Different Road-Crossing Structures for Small Mammals

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ABSTRACT The use of wildlife road-crossing structures (WCS hereafter) is less monitored for small mammals than for more emblematic species. Furthermore, because of the undeniable difficulty of small-mammal track identification, most biologists usually carry out general surveys without species recognition. We hypothesized that general surveys traditionally used for monitoring WRC by small mammals may be biased because the degraded habitats along roads are mainly used by generalist and not specialist species. For this reason, we compared the results of a general small-mammal survey with those from a species-specific one, focusing on 3 study species: 1 habitat generalist (North American deer mouse [Peromyscus maniculatus]), 1 forest specialist (southern red-backed vole [Myodes gapperi]), and 1 prairie specialist (meadow vole [Microtus pennsylvanicus]). We sampled along 4 types of WCS (overpasses, open-span underpasses, and both elliptical and box culverts) in Banff National Park (Canada), by placing footprint track tubes along the WCS, and as a reference in front of their entrances (mainly located in roadside grasslands) and in the surrounding woodlands. Using the traditional general survey, we did not detect significant differences in small-mammal presence among WCS and reference sites. In contrast, species-specific surveys showed that only the deer mice did not show preferences for any WCS type, whereas the specialist species (voles) used only overpasses. Therefore, general surveys used without species identification can underestimate the value of WCS for specialist small mammals, with relevant conservation implications. As a consequence, we recommend species-specific surveys of WCS suitability for small mammals. We also suggest improving the habitat (or at least the cover availability) in the WCS and along the space between them and the surrounding environments to increase WCS suitability for specialist species. © 2015 The Wildlife Society.

KEY WORDS Banff National Park, barrier effect, landscape connectivity, meadow vole Microtus pennsylvanicus, North American deer mouse Peromyscus maniculatus, southern red-backed vole Myodes [Clethrionomys] gapperi, track tubes, traffic mitigation measures, wildlife road-crossing structures.

Several studies in the last decades have shown that motorized traffic can negatively affect animal populations with road-kill mortality and barrier effects being the most often documented impacts (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003). Barrier effects may have especially relevant consequences at a population level, limiting animal movements and in some cases gene flow (Merriam et al. 1989, Gerlach and Musolf 2000, Riley et al. 2006). Wildlife road-crossing structures (WCS) are commonly constructed to reduce road-related mortality and increase landscape connectivity for animal populations (van der Ree et al. 2007, Glista et al. 2009), but their effectiveness may change for different taxa (Rodríguez et al. 1996, Clevenger and Waltho 2005). In most cases, the efficacy of WCS has been explored for large and emblematic species (Foster and Humphrey 1995, Clevenger and Waltho 2005, Grilo et al. 2008), whereas small mammals have received less attention (Porto Peter et al. 2013). Furthermore, the undeniable difficulty in surveying WCS use by small mammals has led many researchers to consider them as a category without species identification (Rodríguez et al. 1996; Mata et al. 2003, 2005, 2007; Ascensão and Mira 2007). Different species often show distinct habitat selection, territory structure, and movement patterns, and all of these factors can influence species-specific WCS effectiveness. A misinterpretation of WCS use patterns might arise where habitat generalist species are sympatric with specialists. Indeed habitat generalists may be more likely to use WCS, because in most cases roadsides are characterized by degraded environments (Umetsu and Pardini 2007, Freitas et al. 2012). As a result, the general survey traditionally used to
sample small-mammal WCS use (i.e., surveys without species identification) might represent mainly generalist species, overestimating the presence of specialists, in some cases with relevant implications for conservation.

The purpose of the present study was to verify whether traditional surveys of WCS use without species identification are a suitable method to sample the whole category of small mammals or if they are only estimating the WCS use by generalist species. To test our hypothesis, we selected a study system where a habitat generalist species (the North American deer mouse \textit{Peromyscus maniculatus}, hereafter referred to as deer mouse; Baker 1968, Wywialowski 1987) is sympatric with a forest specialist species (southern red-backed vole \textit{Myodes gapperi}, hereafter referred to as red-backed vole; Merritt 1981) and a prairie specialist species (meadow vole \textit{Microtus pennsylvanicus}; Reich 1981). In a general survey of WCS suitability without species identification, the presence of the ubiquitous deer mouse could hide the absence of the 2 habitat specialist voles. Indeed previous studies showed that when translocating these 3 species to the other side of a highway only few individuals returned to their own territory, and almost all were deer mice (McDonald and St. Clair 2004a,b). These translocations generated an extreme motivation to move back across the road for territorial adults, but the homing ratios and the WCS efficacy were relatively low, particularly for the 2 specialist species (McDonald and St. Clair 2004a,b). Therefore, we suggest that WCS use in a natural context could be even lower than the rate observed in translocation studies because homing behavior would not be affecting movement. In addition, we predict that WCS use would mainly involve deer mice and would be almost nonexistent for the 2 vole species. We also compared the use of different WCS types to explore which WCS features may be able to improve across-road connectivity for the habitat specialist species.

**STUDY AREA**

We completed fieldwork in Banff National Park (51°15’N, 115°30’W), a Canadian protected area established along the Bow River Valley within the Canadian Rocky Mountains ranging in elevation range from 1,300 m to 3,400 m. The valley floor (<2,000 m) was characterized by the presence of the Trans-Canada Highway (Fig. 1). This was the major transportation corridor through Banff and Yoho National Parks, with a relatively high traffic volume of 17,970 vehicles per day in 2008 and increasing 2.5% per year (Highway Service Center, Parks Canada, unpublished data). The federal government and Parks Canada built WCS along the Trans-Canada Highway in phases. In 1988, the first 27 km of road were provided with WCS (phases 1 and 2), the next 18 km in 1997 (phase 3A), and the final 30 km (phase 3B) were nearly finished during our fieldwork (2010).

The climate of Banff National Park is continental with relatively long winters and short summers (Janz and Storr 1977). The protected area includes montane, subalpine, and alpine ecoregions (Achuff and Corns 1983, Holland and Coen 1983). The Trans-Canada Highway is situated along the montane ecoregion, mostly characterized by coniferous forests (Douglas fir \textit{Pseudotsuga menziesii}, Canadian white spruce \textit{Picea glauca}, lodgepole pine \textit{Pinus contorta}, and American quaking aspen \textit{Populus tremuloides}) and natural grasslands (Achuff and Corns 1983, Holland and Coen 1983). Deer mice and red-backed voles are the most abundant rodents in Banff National Park (Holland and Coen 1983); meadow voles are also present (McDonald and St. Clair 2004a,b).

**METHODS**

**Data Collection**

During September and October 2010, we sampled the presence of the 3 study species along 4 different types of WCS: 2 50-m-wide wildlife overpasses, 2 open-span bridge underpasses (approx. 3 m high, 11 m wide), 3 elliptical metal culverts (approx. 4 m high, 7 m wide), and 5 concrete box culverts (2.6 m high, 3.2 m wide; Fig. 2). All of the WCS types were located along the phases 1, 2, and 3A of the Trans-Canada Highway (Fig. 1). The vegetation of wildlife overpasses consisted of sparse young trees, shrubs and open grassland. Underpasses had no vegetation and their entrances were characterized by roadside grasslands (Fig. 2).

We recorded the presence or absence of the 3 study species by noninvasively sampling their footprints on track plates (Mayer 1957, Zielinski and Truex 1995, Cleverger et al. 2001). Each track plate consisted of a tube of 30 cm in length and 10 cm in diameter, with a sooted metal sheet as a floor. We placed these track tubes along every surveyed WCS establishing 2 parallel sample lines; each of them consisted of 5 track tubes (i.e., 10 track tubes per WCS; Fig. 2). For every surveyed WCS, we placed reference track tubes along 4 sample lines (all of them perpendicular to the WCS and parallel to the highway): 1 for each WCS entrance and 2 in the surrounding woodland (1 for each side of the highway; Fig. 2). Every reference sample line consisted of 4 track tubes (i.e., 16 reference track tubes per WCS). Along each sample line, the distance between 2 adjacent track tubes was 10 m.

The survey period consisted of 2 continuous weeks for every WCS (concentrated during Sep–Oct 2010), which corresponded to the habituation time to the track tubes for our study species (Nams and Gillis 2003). We checked the track tubes only at the end of the survey period. We used characteristics in published track keys to identify species-specific tracks (Murie 1974, Elbroch 2003). We also live-trapped 1 individual for each study species using Sherman live traps and had them pass through sooted track tubes, to obtain a reference collection of footprints on our track tubes (more details in the Supporting Information available online). Our animal live-capture and care procedures were in accordance with the Canada Council on Animal Care Standards.

**Data Analysis**

We performed 2 analyses based on the presence or absence of footprints within the track tubes. In the first analysis, we estimated the small-mammal use of any of the WCS, whereas in the second analysis, we investigated the small-mammal use of specific types of WCS. In both cases, we first
considered the small mammals as a category without species identification and afterwards separated them by species, with the aim to detect possible differences between habitat generalist and specialist species.

We performed the WCS use analysis using generalized linear mixed models (GLMMs; McCullagh and Nelder 1989) with a binomial error distribution and logit link function. In the first model, the response variable was small-mammal presence or absence in a given track tube (without species identification). In the 3 species-specific models of WCS use, the response variables were deer mouse, red-backed vole, and meadow vole presence or absence in a given track tube, respectively. The only explanatory variable in WCS use models was the location of the track tube, with 3 categories: WCS, WCS entrance, or woodland (the latter 2 were reference sites). The random variable was the WCS identification code.

We also performed the WCS type analysis using GLMMs with a binomial error distribution and logit link function. In the general analysis, the response variable was small-mammal

Figure 1. Study area map with locations of the surveyed wildlife road-crossing structures (WCS): overpasses, open-span bridge passes, elliptical culverts, and box culverts.

Figure 2. Surveyed wildlife road-crossing structure (WCS) types: 1) overpass, 2) open-span bridge pass, 3) elliptical culvert, and 4) box culvert. Tree symbols represent woodlands, whereas grass symbols correspond to roadside grasslands. Circles represent WCS track tubes (black circles along the overpass, grey circles within underpasses). Rhombuses represent track tubes of both reference sites (WCS entrances and surrounding woodland).
presence or absence in a given WCS track tube (without species identification). In the species-specific models of WCS type, we only considered the species that used the WCS. The all models, the explanatory variables were WCS type (4 categories: overpass, open-span, elliptical culvert, or box culvert) and track tube distance from the center of the WCS. We used the WCS identification code as a random variable.

RESULTS

In 85% of track tubes within WCS and both reference sites \((n = 310)\), we detected the presence of at least 1 of the 3 study species. In 28 track tubes, we found the simultaneous presence of 2 of the species. The generalist deer mice were the most commonly detected species (56% of track tubes), followed by both specialist species: red-backed vole (23%) and meadow vole (15%).

The general survey (no species identification) showed that small mammals were widely distributed because we detected small-mammal tracks in 86% of WCS track tubes \((n = 119)\). Probability of detecting small-mammal tracks did not vary between WCS and reference sites, with footprints recorded in 83% of WCS entrance track tubes \((n = 95)\) and 84% of woodland track tubes \((n = 96), F = 0.10, P = 0.903; \text{Fig. 3}\) in the species-specific surveys, the generalist deer mouse was detected with a higher probability along WCS, with their presences representing 98% of WCS small-mammal records. Deer mouse footprints were recorded in 84% of WCS track tubes, 76% of WCS entrance track tubes, and 33% of woodland track tubes \((F = 27.33, P < 0.001; \text{Fig. 3})\). The red-backed vole scarcely used the WCS, with their presences representing only 2% of WCS small-mammal records. This species was present only in 6% of WCS entrance track tubes. The occurrence of the red-backed vole was higher along woodland reference sites being found in 66% of track tubes \((F = 42.02, P < 0.001; \text{Fig. 3})\). Finally, the meadow vole was detected only 1 time in WCS track tubes and woodland track tubes, whereas this species was detected in 46% of WCS entrance track tubes \((F = 19.19, P < 0.001; \text{Fig. 3})\).

Concerning use of WCS types, in the general survey we found similar occurrence of small mammals in all types of WCS. Small mammals were recorded in 85% of overpass track tubes, 75% of open-span underpasses, and 90% and 87% of elliptical and box culverts, respectively \((F = 0.89, P = 0.449; \text{Fig. 4})\). The distance from the center of the WCS did not affect small-mammal occurrence \((F = 1.37, P = 0.244)\). In contrast, in the species-specific survey we found the generalist deer mouse was the only species consistently using the WCS and occurrence of deer mouse tracks did not vary between WCS types. Deer mouse tracks were recorded in 75% of track tubes of both overpasses and bridges, 90% of elliptical culverts, and 87% of box culverts \((F = 1.26, P = 0.291; \text{Fig. 4})\). The distance from the center of the WCS did not affect deer mouse presence \((F = 1.29, P = 0.210)\). In 119 WCS tubes, red-backed and meadow vole tracks were found only 3 and 1 times, respectively, and only at overpasses (Fig. 4).

DISCUSSION

Our results showed that general surveys without species identification that are traditionally used could erroneously suggest that all types of small mammals were widely using the WCS. Nevertheless, in the species-specific surveys, we found that the only species using the WCS was the habitat generalist deer mouse. Habitat specialists, such as the red-backed and meadow voles, were virtually absent along the WCS despite their frequency in contiguous woodlands and roadside grasslands. As a consequence, the general survey can produce an overestimation of WCS use by habitat specialists. The present study, therefore, suggests that traditional surveys (i.e., without species identification) of WCS suitability for small mammals may reflect only a portion of the small-mammal species in the area.

The habitat generalist deer mouse commonly used both wildlife overpasses and underpasses, as already described by past studies (Clevenger et al. 2001, McDonald and St. Clair 2004a, Meaney et al. 2007). More generally, this species has been described as relatively indifferent towards road disturbances (Yale-Conrey and Mills 2001, McDonald and St. Clair 2004b) as has also been reported for the similar white-footed mouse (Peromyscus leucopus; McGregor et al. 2008). Plasticity in habitat requirements might be favored by the nocturnal habits of deer mice, because at night both traffic volume and consequent disturbance are usually lower (Goosem 2002, McDonald and St. Clair 2004a, McGregor et al. 2008). Our results also showed that the deer mouse was more likely to be detected on WCS than along reference sites, but this finding could be consequence of interspecific displacement by dominant red-backed and meadow voles (Grant 1971, Bowker and Pearson 1975, Crowell and Pimm 1976), which were widely distributed in surrounding woodlands and roadside grasslands.

As we hypothesized, the WCS use by red-backed and meadow voles under natural conditions was even lower than recorded in previous studies that entailed translocations of individuals (McDonald and St. Clair 2004a). The main cause of such a barrier effect may be the well-known road-associated disturbances (Oxley et al. 1974, Kozel and Fleharty 1979, Mader 1984). The barrier effect may also be amplified in the case of the meadow vole because it is active during daylight hours, which coincides with higher traffic intensity (McDonald and St. Clair 2004a,b). Both vole species tend to avoid the road surfaces, as has also been reported for translocated territorial adults that exhibit extreme motivation for homing behavior (Yale-Conrey and Mills 2001; McDonald and St. Clair 2004a,b). On the other hand, road avoidance could also depend on a more general rejection towards unattractive microhabitats (Witt and Huntly 2001, Russell et al. 2007) that in this case may be related to the absence of vegetation along the underpasses. Our findings also confirm the importance of roadside grasslands as habitat for meadow voles that has already been described (Getz et al. 1978, Kirsch 1997), especially in heavily forested landscapes such as our study area (Clevenger et al. 2001).
The overestimation of WCS use by habitat specialist species may have implications for conservation of endangered or keystone species. For example, some authors consider the red-backed vole as a forest keystone species for its role in dispersing woodland ectomycorrhizal spores (Terwilliger and Pastor 1999, Cook and MacDonald 2001). In this context, the long-term viability of red-backed voles when populations are fragmented could be threatened by the barrier effect caused by roads and associated traffic (Browne and Ferree 2007), with possible repercussions on forest regeneration and consequently on ecosystem health (Cook and MacDonald 2001). Therefore, our results highlight the necessity to improve WCS effectiveness for small mammals that are habitat specialist species especially across heavily fragmented landscapes.

The improvement of WCS efficacy principally depends on the understanding of specific preferences of small mammals regarding these infrastructures. In our study, the only WCS type used by red-backed and meadow voles was the wildlife overpass. McDonald and St. Clair (2004a) showed that our study species preferred underpasses in comparison to overpasses, possibly because the overpasses at that time were recently constructed and scarcely vegetated. These authors suggested that the 3 species selected the smaller underpasses in comparison with larger ones, probably because the former can be perceived as safer from predators (McDonald and St. Clair 2004a, see also Rodríguez et al. 1996). In our study, the wildlife overpasses were already characterized by a mosaic of young woodland and grasslands, which for both habitat specialist voles potentially represents a matrix environment with the suitable vegetative cover to minimize the perception of

Figure 3. General and species-specific small-mammal presence probability (with SE) among wildlife road-crossing structures (WCS) and reference sites in Banff National Park, 2010.

Figure 4. General and species-specific small-mammal presence probability among different wildlife road-crossing structure (WCS) types in Banff National Park, 2010. Columns represent the percentage of used track tubes: white columns correspond to the whole category of small mammals without species identification, lighter grey columns to deer mouse, darker grey columns to red-backed vole, and black columns to meadow vole. Least mean squares with standard error bars represent presence probabilities only for the categories with enough data (i.e., small mammals and deer mice).
predation risk (Merritt 1981, Reich 1981). We suggest that translocated voles probably would return to their territories through the most direct (shorter) route or the perceived safer route (wildlife underpasses in McDonald and St. Clair 2004a), whereas in a more natural context without translocations they would choose to cross the highway only in areas with suitable conditions (vegetated wildlife overpasses in our study).

MANAGEMENT IMPLICATIONS

Our results implicate the importance of species-specific habitat quality in determining the occurrence of habitat specialist rodents along WCS. The first recommendation is that we encourage the establishment of overpasses (i.e., the most suitable WCS in our study) whenever economic resources and local topography (usually the main limiting factors) make this possible because they can be effective for the species we studied as well as other road-sensitive species (Clevenger and Waltho 2005, Bond and Jones 2008). The suitability of overpasses for habitat specialist species may be improved by promoting the development of natural vegetation. However, wildlife underpasses are comparatively much more widespread than overpasses, and a strategy for improving their effectiveness for small mammals, such as providing dead woods and brushes as artificial cover (Clevenger et al. 2001, McDonald and St. Clair 2004a), could considerably improve the landscape connectivity for habitat specialist small mammals. Furthermore, avoiding cutting vegetation at the entrance of the WCS, which may decrease the perception of predation risk while approaching the WCS, may be another complementary way to improve both overpass and underpass attractiveness for small mammals (Rodríguez et al. 1996, Clevenger et al. 2001, McDonald and St. Clair 2004a). Finally, because there is the potential for a bias towards more generalist small–mammal species when tracks are not identified to species, we strongly recommend the application of species-specific surveys.

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