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Use of non-wildlife passages across a high speed railway by terrestrial vertebrates

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Summary

1. Seventeen culverts and pathway passages across a high speed railway were monitored for one year in order to determine factors influencing their use by terrestrial vertebrates.
2. Carnivores, lagomorphs, small mammals and reptiles used the passages. Crossing rates generally reflected the spatiotemporal variation in vertebrate abundance and activity, suggesting that the passages could be valuable in allowing movement across the railway.
3. Wild ungulates known to be present did not use the passages, probably due to a combination of unsuitable dimensions and placement, a lack of cover near their entrances and human disturbance. Ungulates probably need specifically designed passages.
4. The presence of cover in the passage entrances favoured their use by carnivores, while small mammals preferred narrow passages where, presumably, predation risk was lower. Reptiles preferred passages of intermediate size, in which they moved between sun-warmed and shaded vertical surfaces for thermoregulation.
5. The main factor determining the use of passages by vertebrates was their location with respect to habitat.
6. Minor modifications to non-wildlife passages and to the management of surrounding areas may further improve the efficacy of these passages for allowing wildlife to cross linear barriers and, therefore, potentially reduce the effects of habitat fragmentation.

Key-words: barrier effect, crossing facilities, fragmentation, vertebrate conservation.

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Introduction

The isolation of animal populations as a result of habitat fragmentation has become common. Barriers may be defined as any area where animal mobility is reduced, and result from the combination of quantitative (barrier width) and qualitative (species tolerance to the barrier) components (Buechner 1987; Stamps, Buechner & Krishnan 1987; Fahrig & Merriam 1994). Population isolation is recognized as a common cause of local extinction (Saunders, Hobbs & Margules 1991; Fahrig & Merriam 1994) and it is therefore important for conservationists to determine and, where possible, mitigate potential barriers to animal movements.

Linear infrastructures (roads, railways, canals and pipelines) are known to be powerful inhibitors of movement in several groups of terrestrial vertebrates (Oxley, Fenton & Carmody 1974; Mader 1984; Camby & Maizeret 1985; Curatolo & Murphy 1986). Specific transverse passages, designed to increase barrier permeability, have been constructed for some vertebrate groups (Singer & Doherty 1985; Mansergh & Scotts 1989; Foster & Humphrey 1995), but target species are often reluctant to use them (Reed 1981; Vassant, Brandt & Jullien 1993). Consequently, determining the features of wildlife passages that favour their use by vertebrates is of considerable interest. Previous studies indicate that the use of passages by vertebrates, especially large ones, may be influenced by passage dimensions and placement, as well as the presence of nearby cover, the presence of leading fences, and the extent and type of human activities (Reed & Ward 1985; Singer, Langlitz & Samuelson 1985; Ballon 1986; Désiré & Mallet 1991; Foster & Humphrey 1995).

Wildlife passages, especially those for large animals, are expensive (Camut 1985; Gounot 1985) and this may limit their use as a conservation tool. As an alternative, non-wildlife passages (i.e. placed and

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designed for purposes other than to allow wildlife crossing), such as culverts, common in every linear infrastructure, have proved practical for several vertebrate species (Camby & Maizeret 1985; Hunt, Dickens & Whelan 1987; Yanes, Velasco & Suárez 1995).

Thus far, the permeability of linear structures to vertebrates has been investigated mainly in relation to roads (reviewed by Bennett 1991). In roads, however, factors other than their physical structure, such as traffic or general human activity, may have an overriding influence on the behaviour of approaching animals (Elgmork 1978; Rost & Bailey 1979). Thus, railways are particularly suitable sites to study passage use by vertebrates, since the low volume of traffic and the lack of associated development avoid the non-physical (confounding) effects on crossing rates.

In this study we first sought to determine which groups of terrestrial vertebrates used non-wildlife passages across a high speed railway (HSR). Secondly, we examined whether non-wildlife passage use by vertebrates was an ordinary or an occasional phenomenon, as these alternatives have different conservation implications. If non-wildlife passages are suitable for use by vertebrates we would expect the rates of crossing for each group to be higher in preferred habitats, and at times of high numbers or activity, than in suboptimal habitats and times of low abundance or activity. Conversely, if animals are reluctant to cross through passages we would predict low crossing rates regardless of variation in abundance or in activity. It is assumed that there are no significant differences in resource availability (for the group considered) on either side of the HSR in the same habitat type at a given time.

Thirdly, we determined the effect of several passage features on crossing rates. We specifically tested the following predictions:

1. for carnivores, the frequency of use was expected to be higher in passages located near scrubland patches and with cover near their entrances, as cover is selected by species living in the study area;
2. since carnivores avoid sources of human disturbance (e.g. McLellan & Shackleton 1988; Beier 1995), lower crossing rates were expected in passages used for human activities;
3. small mammal crossing rates were expected to be higher in passages with small cross-sections which may reduce their predation risk;
4. also related to antipredatory behaviour, a negative relationship between crossing rates and distance to scrubland was predicted for lagomorphs.

Finally, if crossings were not confined to passages before fencing and if fences were an effective deterrent to vertebrate movements (Reed & Ward 1985; Foster & Humphrey 1995), we would expect a significant increase in crossing rates after the fencing of the railway was completed.

Materials and methods

THE RAILWAY AND THE STUDY AREA

The HSR Madrid-Seville was constructed between 1987 and 1992. It crosses mainly farmland, but also bisects two mountainous areas, Montes de Toledo and Sierra Morena, both of which are of conservation importance (de Juana 1988; Blanco 1989). In the rugged Sierra Morena the HSR goes mostly through tunnels and viaducts. In the Montes de Toledo, however, hill slopes are gentler, and the railway line passes through embankments and cuttings; in this area animals must cross the actual HSR structure to go from one side to the other.

The study was conducted along a stretch of HSR, 24·7 km in length, which crosses the whole breadth of the eastern Montes de Toledo (Fig. 1). The valleys and foothills are cultivated with cereals, whereas the slopes and top of the hills (up to 1300 m) are covered with scrub (mainly *Cistus ladanifer*), scattered trees (mainly *Quercus rotundifolia*), pine stands (*Pinus pinaster*) and pasture. Land use is predominantly agricultural, including cereals, livestock grazing and timber plantations. The climate is continental, and rainfall is about 700 mm per annum.

Along the stretch studied, the HSR width (i.e. two tracks, two lateral ditches, plus the width of embankments or cuttings) varies between 13 and 46 m. There are 42 transverse passages, all of concrete construction, including bridges (large underpasses for rivers; 4·7%), culverts (61·9%), underpasses (16·7%) and flyovers (16·7%). Most culverts remain dry for most of the year. No special passages designed for wildlife use were constructed. One busy road and 13 smaller roads with low traffic (two of them paved) cross the HSR via underpasses and flyovers. Between July 1991 and March 1992, both sides of the railway were fenced with wire netting 2 m in height, topped with two strands of barbed wire.

FIELD PROCEDURES

A layer of dry, fine sand, 3 cm thick and 1 m wide, was put on the ground inside each sampled passage, and spread evenly across its entire width near one entrance. Trails and other signs of animal activity on the sand layer were recorded daily and then the surface was smoothed with a brush. If necessary, extra sand was added, and the sand sifted or replaced.

Between September 1991 and July 1992 passages were monitored for 15–22 days each month. At each visit the sand surface was declared 'operative' when it allowed a correct printing of animal signs which could be read clearly. Disturbance by weather, livestock or human activity on the substrate prevented tracks being read.

Presence–absence data, independent of the number of trails found, were used as estimates of crossing

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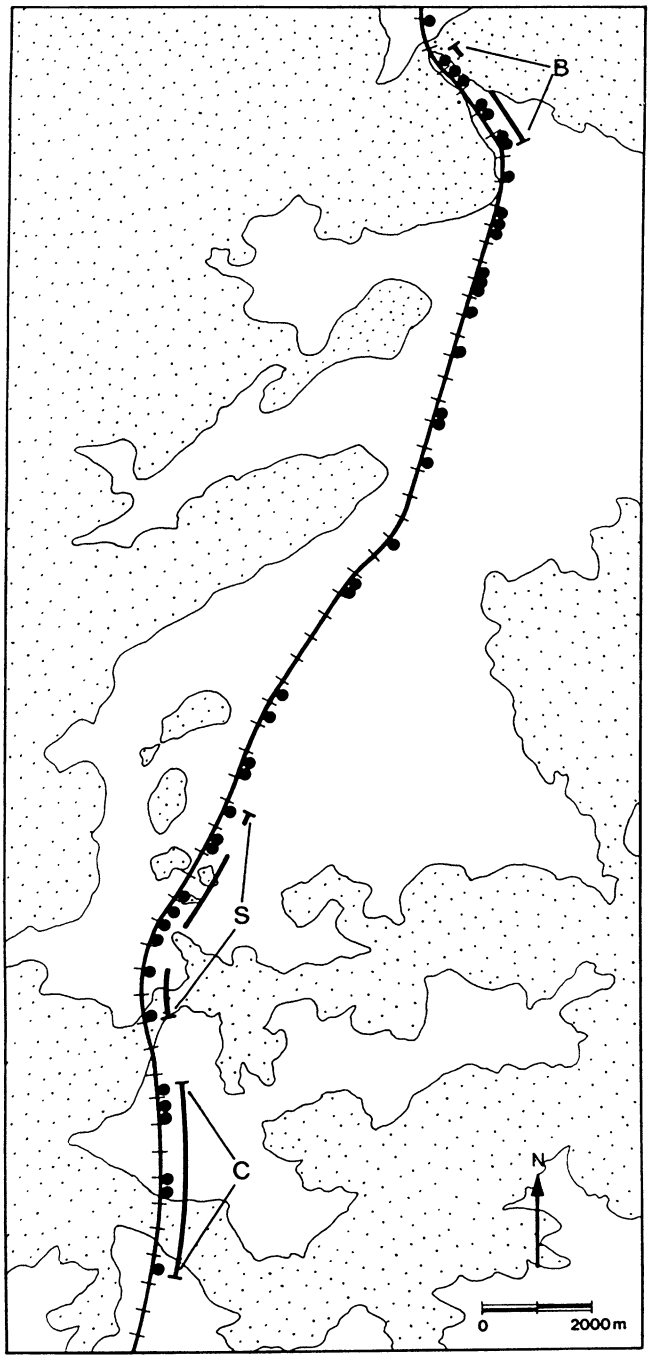

Fig. 1. Sketch of the study area, showing the approximate distribution of farmland (white) and scrubland (dotted). Circles indicate the location of transverse passages across the high speed railway (thick line). Sampled passages in scrubland (S), farmland (C) and border (B) habitats are marked with parallel lines.

rates. For each passage the monthly crossing rate was calculated as the ratio between the number of days per month in which the animal tracks were recorded and the number of operative days. Crossing rates were calculated only if the number of operative days was five or more per month. Ninety-one per cent of the rates were calculated using 10 or more operative days each month (mean = 13·5; SD = 3·8; n = 110).

For each sampled passage, three types of variables were recorded (Table 1): physical characteristics, distribution of cover and degree of human disturbance. Physical variables included:

1. *Length*, passage length;
2. *Width*, passage width;
3. *Height*, height of underpasses or of lateral structures along flyovers;
4. *Pit*, presence or absence of pits at culvert entrances (pits with vertical walls up to 1·5 m deep were designed to prevent culverts becoming blocked with materials carried by water).

Passage dimensions were combined in two indices: Openness, for culverts and underpasses, defined as width × height/length; and Bridge, for flyovers,

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Table 1. Features of sampled passages. Columns 2–4 show passage dimensions. Pit: presence of pits at culvert entrances. The index Openness is defined for culverts and underpasses as width × height/length; the index Bridge (for flyovers) is defined as (width × $\sqrt{\text{height}}$)/length (Reed & Ward, 1985). Passages 11 and 16 were flyovers, the other were culverts or underpasses. Entrance: presence of cover within 20 m of passage entrance. Patch: distance to the nearest scrubland patch. House: distance to the nearest inhabited house or farm. Human use: average (and SE) monthly rate of use by human activities

	Physical characteristics					Cover distribution		Human disturbance		
									Human use	
Passage code	Length (m)	Width (m)	Height (m)	Pit	Openness (Bridge)	Entrance	Patch (km)	House (km)	Mean	SE
1	16	2·0	2·0	No	0·25	Yes	0·02	0·35	0·36	0·10
2	16	1·2	1·2	No	0·09	Yes	0·01	0·95	0·06	0·04
3	14	2·0	2·0	Yes	0·28	No	0·20	0·91	0·05	0·05
4	17	1·2	1·2	No	0·08	No	0·04	0·35	0·03	0·03
5	13	3·5	3·5	No	0·94	Yes	0·02	0·34	0·39	0·09
6	16	2·0	2·0	Yes	0·25	No	0·78	1·40	0·12	0·08
7	28	2·0	2·0	No	0·14	No	0·35	1·87	0·41	0·07
8	44	1·2	1·2	No	0·03	Yes	0·02	1·26	0·10	0·05
9	42	1·2	1·2	No	0·03	Yes	0·24	0·99	0·07	0·05
10	26	3·5	3·5	No	0·47	No	0·12	0·67	0·62	0·03
11	64	6·0	2·0	No	(0·13)	No	0·07	1·53	0·53	0·14
12	20	1·2	1·2	No	0·07	No	0·52	1·03	0	0
13	14	3·5	3·5	No	0·88	No	0·56	1·00	0·31	0·14
14	22	1·2	1·2	No	0·07	No	0·61	0·97	0·17	0·17
15	17	1·2	1·2	No	0·08	No	0·37	1·29	0	0
16	50	6·0	2·0	No	(0·17)	No	0·35	1·38	0·28	0·10
17	40	2·0	2·0	No	0·10	No	0·32	1·45	0·58	0·09

defined as (width × $\sqrt{\text{height}}$)/length (Reed & Ward, 1985). Cover variables were:

1. *Entrance*, presence or absence of trees or scrub within 20 m of one or both entrances;
2. *Patch*, the distance to the nearest scrubland patch.

Human disturbance variables were defined as:

1. *House*, the distance to the nearest inhabited house or farm;
2. *Human use*, the monthly rate of use by human activities.

This rate was calculated as the number of days in which any track of persons, livestock, domestic animals or vehicles was recorded divided by the number of operative days each month.

DESIGN AND ANALYSES

Separate data sets were used for ungulates, carnivores, lagomorphs, small mammals, reptiles and amphibians. Among mammals this division was based on differences between groups in behaviour and range of movements (related to body size). Monthly crossing rates were calculated for samples of passages located in three different habitat types:

1. 'Scrubland', in which large areas of scrubland in a matrix of farmland connected two forested regions; human activity in this habitat type was low.
2. 'Border', where scrubland and farmland were clearly separated by the railway line; a busy road ran within 200 m, and three farms were nearby.
3. 'Farmland', an area with low human disturbance, where the HSR ran through cereal crops.

Distances between consecutive passages along the railway were randomly distributed (fitting a Poisson distribution; chi-square = 0·977, d.f. = 3, $P > 0{\cdot}75$; mean distance between passages = 602 m), so that there was considered to be independence between crossing rates from consecutive passages in the same month for each group. There were six consecutive passages in the scrubland and farmland habitat types, and five in the border habitat type (Fig. 1).

Crossing rates were approximated to a normal distribution using the arcsine transformation and a two factor ANOVA was employed to analyse the effects of 'habitat' (three levels: farmland, border and scrubland) and 'month' (11 levels; all months but August) on crossing rates. Unfortunately, two problems arose in the field. First, some data were unobtainable because of adverse weather (flooding of passages in April and June) or because of access difficulties (from September to January in the wholly farmland segment). Second, equal replication, as intended in the initial design, was not possible because weather and/or human activity caused a decrease in the number of operative days under the fixed threshold of five in some passage-month combinations. Consequently, we performed two separate analyses, In Analysis 1, the factor 'habitat' had two levels (scrubland and border)

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Table 2. Total number of crossings through non-wildlife passages, preferred habitats, and intra-annual population peak in abundance and/or activity of terrestrial vertebrates in eastern Toledo Mountains during an 11-month period

Vertebrate group	Records	Preferred habitat	Seasonal peak	Source
Ungulates	0	Scrubland/border	Early summer	Tellería & Sáez-Royuela (1984)
Carnivores	264	Scrubland/border	Early summer/autumn	Delibes (1983)
Lagomorphs	89	Border	Early summer	Soriguer & Rogers (1981)
Small mammals	582	All	Summer	Stoddart (1979)
Reptiles	112	Scrubland/border	Summer	Salvador (1974)
Amphibians	0	All	Spring & autumn	Salvador (1974)

and the factor 'month' had nine. In Analysis 2, the factor 'habitat' had all three levels, while the factor 'month' had only four (February, March, May and July). Five replicates per cell were considered; equal replication was achieved by deleting one datum at random in the samples having six data points (Zar 1984), and by estimating missing data in the two samples which had four data points (Shearer's procedure; Zar 1984).

Estimated spatiotemporal variations in abundance for groups which used the passages were taken from the literature (Table 2).

To investigate the additional effects of passage characteristics on crossing rates, the effects of abundance had to be removed. Thus, we used the residual crossing rate as the response variable, calculated from the minimum adequate model (that having only significant terms) which captured spatiotemporal influences for each vertebrate group. This response variable was called 'relative crossing rate'. All variables except 'Human use' were combined and/or transformed on factors (Table 3), and their effects on the relative crossing rate for each data set were analysed with ANCOVA, using 'Human use' as a covariate. The maximal model was fitted and then simplified by inspecting increases in deviance after sequentially removing each explanatory variable. This process was repeated until only significant terms remained in the model (Crawley 1993).

Table 3. Definition of levels for factors used in the analyses of covariance

Factor	Level	Definition
Design	1	Flyover
	2	Culvert of 1·2 m in width
	3	Culvert of 2·0 m in width
	4	Culvert or underpass of 3·5 m in width
	5	Culvert having a deposition pit
Entrance	1	Cover within 20 m of passage entrances
	2	Cover beyond 20 m of passage entrances
Patch	1	Nearest scrubland patch within 100 m
	2	Nearest scrubland patch between 100 and 500 m
	3	Nearest scrubland patch beyond 500 m
House	1	Nearest inhabited house within 500 m
	2	Nearest inhabited house between 500 and 1000 m
	3	Nearest inhabited house beyond 1000 m

In the northern section of the study area, fences were erected after several months of monitoring and we could compare average relative crossing rates before and after fencing.

Results

We monitored vertebrates crossing on 167 days. A total of 1851 passage-days were sampled, 1571 of which were operative. We recorded vertebrate tracks on 1047 occasions, an average of 66 crossings per 100 operative passage-days. Small mammals accounted for 55·6% of records, followed by carnivores (25·2%), reptiles (10·7%) and lagomorphs (8·5%) (see Table 2). All passages were used by at least two different groups of vertebrates and thirteen passages (76%) were visited by all four groups of vertebrates.

Crossing rates varied greatly with the habitat type and the season. As results of both analyses were consistent (Tables 4 and 5), we show average values of crossing rates only for the analyses which use the higher number of levels in each factor (Figs 2 and 3).

Crossing rates were influenced also by some passage features, but the amount of variance explained by physical design, cover and human disturbance was generally lower than that explained by fluctuations in spatiotemporal abundance or activity of vertebrates (Table 6). The proportion of variance explained by the whole model was higher than 44% for carnivores, small mammals and reptiles. The pattern of relative crossing rates was consistent in Analyses 1 and 2. Thus, we illustrate results only for Analysis 2 (Fig. 4).

Fencing did not result in a significant change in relative crossing rates in the five suitable passages for any vertebrate groups (t-tests, $P > 0{\cdot}05$). There was little disturbance within the passages: we found, on average, less than one sign of human activities per passage-day, mainly in flyovers and underpasses (Table 1).

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Table 4. ANOVA table showing the effects of habitat type and season on vertebrate crossing rates through HSR passages. Factor habitat has two levels (scrubland and border). Factor month has nine levels (all months excepting April, June and August)

	SS	df	MS	*F*	*P*
Carnivores					
Habitat	1·131	1	1·131	15·392	0·000
Month	1·678	8	0·211	2·869	0·008
Habitat × month	0·703	8	0·088	1·196	0·313
Error	5·291	72	0·074		
Lagomorphs					
Habitat	0·025	1	0·025	0·902	0·356
Month	0·305	8	0·038	1·366	0·226
Habitat × month	0·420	8	0·053	1·883	0·076
Error	2·007	72	0·028		
Small mammals					
Habitat	0·799	1	0·779	6·974	0·010
Month	3·120	8	0·390	3·492	0·002
Habitat × month	0·472	8	0·059	0·528	0·831
Error	8·043	72	0·112		
Reptiles					
Habitat	0·158	1	0·158	8·977	0·004
Month	3·702	8	0·463	26·305	0·000
Habitat × month	0·375	8	0·047	2·662	0·013
Error	1·267	72	0·018		

Table 5. ANOVA table showing the effects of habitat type and season on vertebrate crossing rates through HSR passages. Factor habitat has three levels (scrubland, farmland and border). Factor month has four levels (February, March, May and July)

	SS	df	MS	*F*	*P*
Carnivores					
Habitat	1·282	2	0·641	12·919	0·000
Month	1·221	3	0·407	8·201	0·000
Habitat × month	0·313	6	0·052	1·051	0·405
Error	2·382	48	0·050		
Lagomorphs					
Habitat	0·314	2	0·157	3·102	0·054
Month	0·036	3	0·012	0·238	0·870
Habitat × month	0·375	6	0·062	1·236	0·305
Error	2·426	48	0·051		
Small mammals					
Habitat	0·878	2	0·439	3·508	0·038
Month	1·613	3	0·538	4·294	0·009
Habitat × month	0·435	6	0·073	0·580	0·745
Error	6·009	48	0·125		
Reptiles					
Habitat	0·229	2	0·114	4·036	0·024
Month	3·440	3	1·147	40·488	0·000
Habitat × month	0·572	6	0·095	3·368	0·008
Error	1·360	48	0·028		

UNGULATES

Although wild ungulate species (roe deer, *Capreolus capreolus*; red deer, *Cervus elaphus*; wild boar, *Sus scrofa*) were common in the study area, no sign of them was detected in the passages and few sightings of ungulates within 500 m of the HSR (none of wild boar) were made in 463 h of observation. However, we saw roe deer and red deer within the railway enclosure four times, and a red deer was once observed trying to jump over the fence.

CARNIVORES

Tracks of four species were detected in the passages: red fox, *Vulpes vulpes*; wild cat, *Felis silvestris*; common genet, *Genetta genetta*; and Iberian lynx, *Lynx pardinus*. The stone marten, *Martes foina*, a common species in the study area (Rodríguez, Barrios & Delibes 1992), and other scarcer carnivore species were not recorded.

There was a significant effect of habitat on carnivore crossing rates (Tables 4 and 5). Rates in the scrubland were six times higher than in the border and 20 times higher than in the farmland (Fig. 2a), as was expected from the known habitat preferences of carnivores (Table 2). Although carnivores prefer the border habitat type to farmland, differences between pairs of means were all significant (Tukey test, $P < 0{\cdot}05$), except for the border-farmland pair.

Crossing rates were highest in the summer and lowest in late winter (Fig. 3a), with crossing rates in July on average 15 times higher than in March. This temporal crossing pattern was also as predicted from expected changes in abundance (litters start to leave the den in early summer) and mobility (both dispersal and mating take place mainly in autumn and winter; Table 2).

Carnivores used culverts more than the other passage types and preferred passages within 500 m of scrubland (Fig. 4a). Passage use was unaffected by the distance to inhabited buildings. Culverts with pits had the lowest usage rates (6% of records) among all monitored designs.

There were no significant effects of Design, Patch, House and Human use. In contrast, relative crossing rates were significantly lower in passages without cover near their entrances compared to those having cover nearby (Analysis 1, $F = 19{\cdot}47$, d.f. = 1,88, $P < 0{\cdot}001$; Analysis 2, $F = 10{\cdot}73$, d.f. = 1,58, $P < 0{\cdot}005$). The five passages with cover in their entrances comprised 64% of carnivores crossings. One of these passages (number 9) was relatively distant from the scrubland (560 and 240 m to each entrance) and yet 15·6% of all carnivore crossings were recorded in it.

LAGOMORPHS

The two species present in the area, the brown hare, *Lepus granatensis*, and the European rabbit, *Oryctolagus cuniculus*, used the passages infrequently (an average of 5 crossings per 100 passage-days). Records of hares were especially scarce (13% of lagomorphs).

Percentages of records were 16, 45 and 39% for the scrubland, border and farmland, respectively (Fig. 2b), but there were no significant differences between

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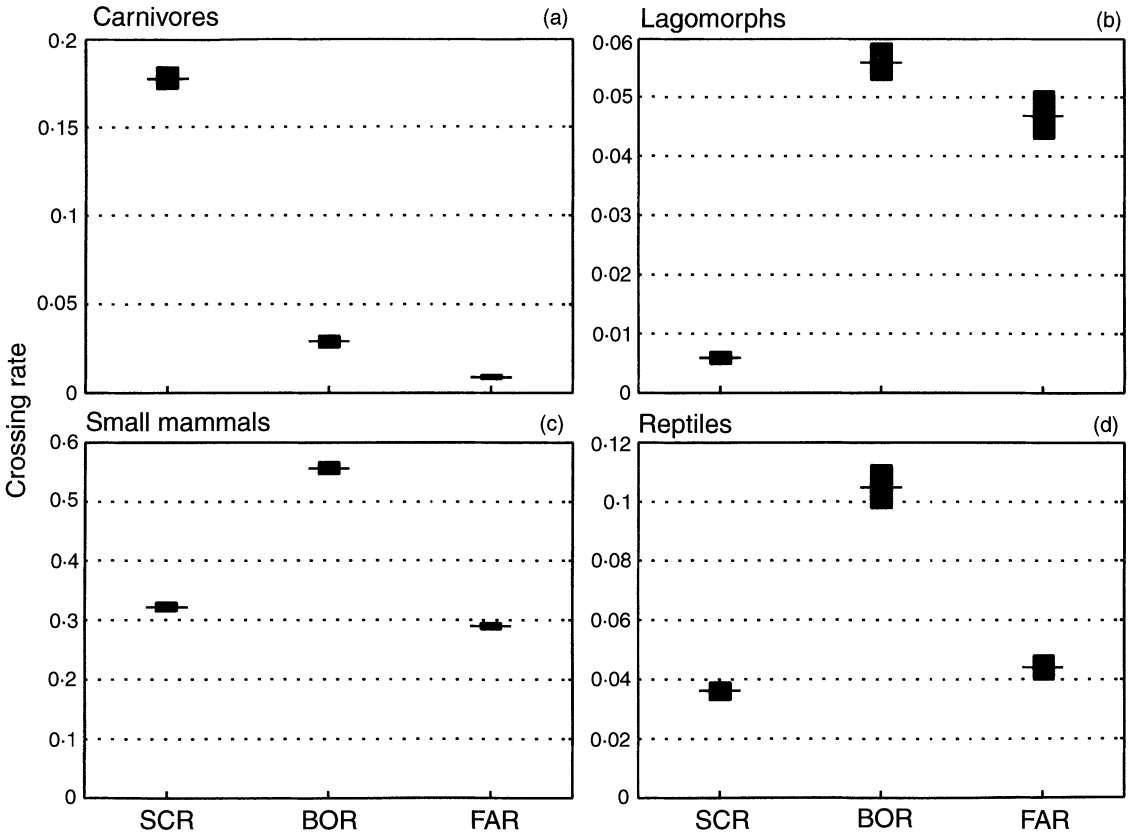

Fig. 2. Mean (and SE) monthly crossing rates (number of days with visits divided by the number of operative days for each passage) of terrestrial vertebrates as a function of the habitat location of passages: scrubland (SCR), border (BOR) and farmland (FAR). For each level, $n = 20$.

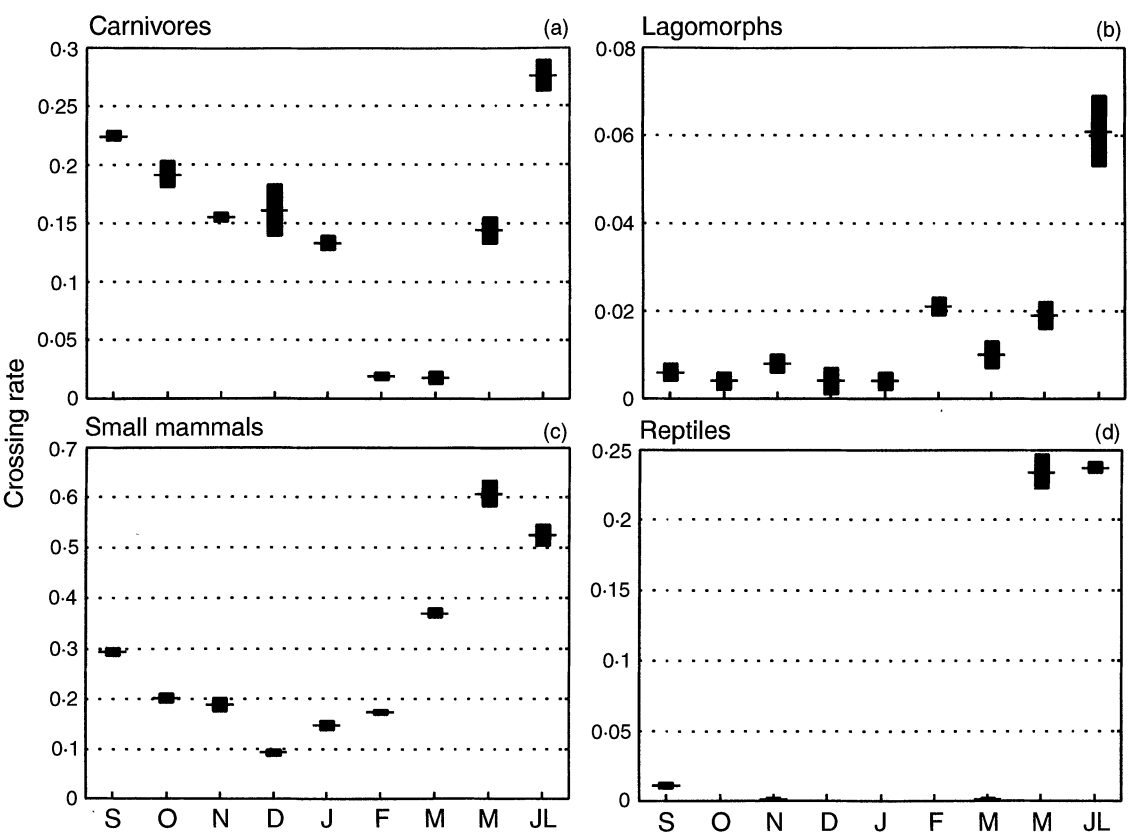

Fig. 3. Mean (and SE) monthly crossing rates (number of days with visits divided by the number of operative days for each passage) of terrestrial vertebrates as a function of the time of year (pooled habitats). For each level, $n = 10$.

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Table 6. The amount of deviance (sum of squares) in crossing rates explained by (1) spatiotemporal fluctuations in vertebrate abundance or activity (H: habitat, M: month, H × M: interaction term), and (2) passage features (D: design, E: cover at the entrances, HU: monthly rate of use by human activities). Only significant terms are considered. SST: total sum of squares. Coefficients of determination for each group of factors (STA and PF, respectively) and for the whole model (last column) are shown

		Spatiotemporal abundance/activity				Passage characteristics				
	SST	H	M	H × M	STA r^2 (× 100)	D	E	HU	PF r^2 (× 100)	TOTAL r^2 (× 100)
Analysis 1										
Carnivores	8·813	1·131	1·687		31·98		1·086		12·32	44·30
Lagomorphs	2·757									
Small mammals	12·414	0·779	3·120		31·41	2·210			17·80	49·21
Reptiles	5·501	0·158	3·702	0·375	76·97					76·97
Analysis 2										
Carnivores	5·199	1·282	1·221		48·15		0·421		8·10	56·25
Lagomorphs	3·150									
Small mammals	8·935	0·878	1·613		27·88	2·570			28·76	56·64
Reptiles	5·601	0·229	3·440	0·572	75·73	0·283		0·107	6·96	82·69

habitats for crossing rates (Tables 4 and 5). Monthly variation in crossing rates followed the trend of seasonal abundance (Fig. 3b, Table 2), but differences were not significant (Tables 4 and 5).

There was considerable variation in the number of records per passage (79% of crossings occurred in only seven passages). Crossing rates were higher in flyovers than in underpasses (Fig. 4b). Within underpasses relative rates differed between Analyses 1 and 2, and no clear pattern emerged with regard to passage design. Culverts with pits had the lowest rate of use (only three records in all). Passages with and without cover at their entrances were used almost equally. Crossing rates were highest in passages within 100 m of and lowest in passages beyond 500 m of the scrubland. The relationship between the response variable and House did not follow any clear trend. The analyses of covariance showed no significant effects of any explanatory variable on lagomorph crossing rates.

SMALL MAMMALS

This group had the highest crossing rate (a mean of 37 crossings per 100 passage-days). Common species in the study area included insectivores (*Erinaceus europaeus*, *Crocidura russula*) and rodents (*Apodemus sylvaticus*, *Mus spretus*, *Pitymys duodecimcostatus*). Analyses showed significant effects of habitat and time of year on the crossing rates of small mammals (Tables 4 and 5). Crossing rates were higher in the border than in the scrubland and farmland ($P < 0{\cdot}05$; Tukey test; Fig. 2c). The temporal pattern of passage use showed a peak in late spring and summer, decreasing until winter when the trend changed, and increased again until the summer (Fig. 3c). The Tukey test discriminated only the extreme values, that is, the crossing rates of December and January from those of May and July ($P < 0{\cdot}05$).

More visits were recorded in passages with cover in their entrances than in passages without it; in passages within 100 m from the scrubland than in the other categories, and in passages within 500 m of inhabited houses than elsewhere (Fig. 4c). However, no significant effects of Entrance, Patch, House, and Human use on relative crossing rates were found. On the other hand, both ANCOVAs showed a significant influence of the physical design of passages on the relative crossing rates of small mammals (Analysis 1: $F = 7{\cdot}62$, d.f. = 4,85, $P < 0{\cdot}001$; Analysis 2: $F = 7{\cdot}44$, d.f. = 4,55, $P < 0{\cdot}001$). Lowest values were recorded in the flyovers and highest values in culverts with small cross-sections (less or equal to 2 m in width; Fig. 4c).

REPTILES

Common species of lizards in this study area were *Lacerta lepida*, *Podarcis hispanica* and *Psammodromus algirus*. Common snake species included *Elaphe scalaris*, *Malpolon monspessulanus* and *Vipera latasti*. The average crossing rate for reptiles was 7 records per 100 passage-days. Both analyses indicated significant effects of the type of habitat, the time of year and the interaction between these two factors on the crossing rates of reptiles (Tables 4 and 5). Crossing rates were on average 2–3 times higher in the border habitat than in the other habitat types (Fig. 2d), but significant differences (Tukey test, $P < 0{\cdot}05$) were found only for the border-scrubland pair.

Frequent records occurred in late spring and summer, followed by a large decrease in crossing rates in September which was maintained for the rest of the year (Fig. 3d). Mean crossing rates in May and July were equal, and differed significantly from the other months (Tukey test, $P < 0{\cdot}05$).

Lizards and snakes were often observed basking both on passage walls and in the sand we put near

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entrances. The relative crossing rates of reptiles were similar for all levels of factors Entrance and House, whereas there was no clear trend with regard to Patch (Fig. 4d). Relative crossing rates were higher in culverts and underpasses than in flyovers. Among the former, higher values were found in culverts of intermediate width (with or without pits) than in the other types (Fig. 4d; Analysis 2, $F = 3{\cdot}87$, d.f. = 4,54, $P < 0{\cdot}02$). Moreover, relative crossing rates had a positive relationship with Human use ($F = 5{\cdot}84$, d.f. = 1,54, $P < 0{\cdot}05$).

AMPHIBIANS

Due to the relative dryness of the study area, the most abundant species of amphibians were the toads, *Bufo bufo* and *Bufo calamita*. No sign of adult amphibians was found, but tadpoles of these species were observed in spring in the flooded passages.

Discussion

UNGULATES

Wild ungulates generally seemed to avoid the HSR, although there was evidence that they sometimes tried to cross the railway. They did not, however, use the available non-wildlife passages, probably because of narrow passage size (Reed 1981; Ballon 1986), the lack of cover near the entrances of most passages (Singer & Doherty 1985; Désiré & Mallet 1991) and human disturbance. In the study area, all passages greater than 3 m in width were used almost daily by vehicles, livestock, persons or dogs (Table 1). This use of passages was slight, but even low levels of human activity have been related to low ungulate crossing rates (Ballon 1984).

CARNIVORES

Most carnivore species used the passages. Stone martens were not recorded at all, but we do not attribute this result to passage avoidance. This species may not need the passages to cross the HSR, as martens are physically capable of passing over or under the fence, and they show little avoidance of the HSR. For example, a radiotagged resident stone marten included a stretch of railway within its home range and was never found using a passage (authors, unpublished). Crossing rates of carnivores followed fluctuations in abundance. Low crossing rates in the suitable border habitat may be due to disturbance from road traffic, to which carnivores appear particularly sensitive (Elgmork 1978; McLellan & Shackleton 1989).

Previous studies have shown that carnivores tend to avoid artificial structures, such as small roads or underpasses similar to those studied here (e.g. McLellan & Shackleton 1988; Beier 1995). Relative crossing rates were highest in the few passages with cover near one or both entrances, suggesting that the presence of cover near entrances may reduce the carnivore's distrust of such structures. No relationship was found between relative crossing rates and Patch, but the effect of the distance to the nearest patch of scrubland on carnivore crossing rate was probably largely included in the effect of habitat (Table 6), which was removed by calculating residuals.

Carnivores used the whole range of passage dimensions available in the sample, in agreement with published information. Badgers *Meles meles* can use underpasses as narrow as 0.25 m in diameter (Van Haaften 1985), several mustelid and viverrid species used both culverts of 0.53 m in diameter and game passages (cross-section of 3×3 m; Camby & Maizeret 1985), and large underpasses (>20 m in width and >3 m in height) were visited by species ranging in size from the raccoon, *Procyon lotor*, to the black bear, *Ursus americanus* (Foster & Humphrey 1995). Carnivores were able to negotiate pits up to 1.5 m in height. The absolute pit avoidance reported by Yanes *et al.* (1995) may be due to their lower temporal sampling effort (336 passage-days). No relationship was found between relative crossing rates and disturbance rates. Although carnivores avoid human activities (e.g. Elgmork 1978; Van Dyke *et al.* 1986), disturbance levels in the passages are probably low enough to allow normal carnivore behaviour. In addition, there is a temporal segregation of human (mainly diurnal) and carnivore (mainly nocturnal) use of passages that may further reduce the potential effects of disturbance.

LAGOMORPHS

Hares rarely visited the passages. They prefer open land and may avoid entering sites with low visibility such as the underpasses. Rabbits select border habitats (Soriguer & Rogers 1981) and consistently most trails were recorded in passages located in this habitat type. However, spatiotemporal differences in crossing rates were not significant. Rabbits had a scattered local distribution after a recent population crash due to viral haemorrhagic disease (Rodríguez *et al.* 1992). Thus, rabbits were still absent in some patches of scrubland near passages but, on the other hand, were established in some rock piles on the HSR embankments and used nearby passages in open farmland. This pattern of use (most records concentrated in a few passages) probably reflects a patchy distribution of rabbits, resulting from the slow recolonization of areas near the HSR, rather than the distribution of scrubland near passages. When suitable refuge (not only scrubland) was nearby, rabbits used all passage designs, except culverts with pits which may be serious obstacles.

SMALL MAMMALS

As small mammals cannot be reliably identified to species from their tracks, spatiotemporal differences

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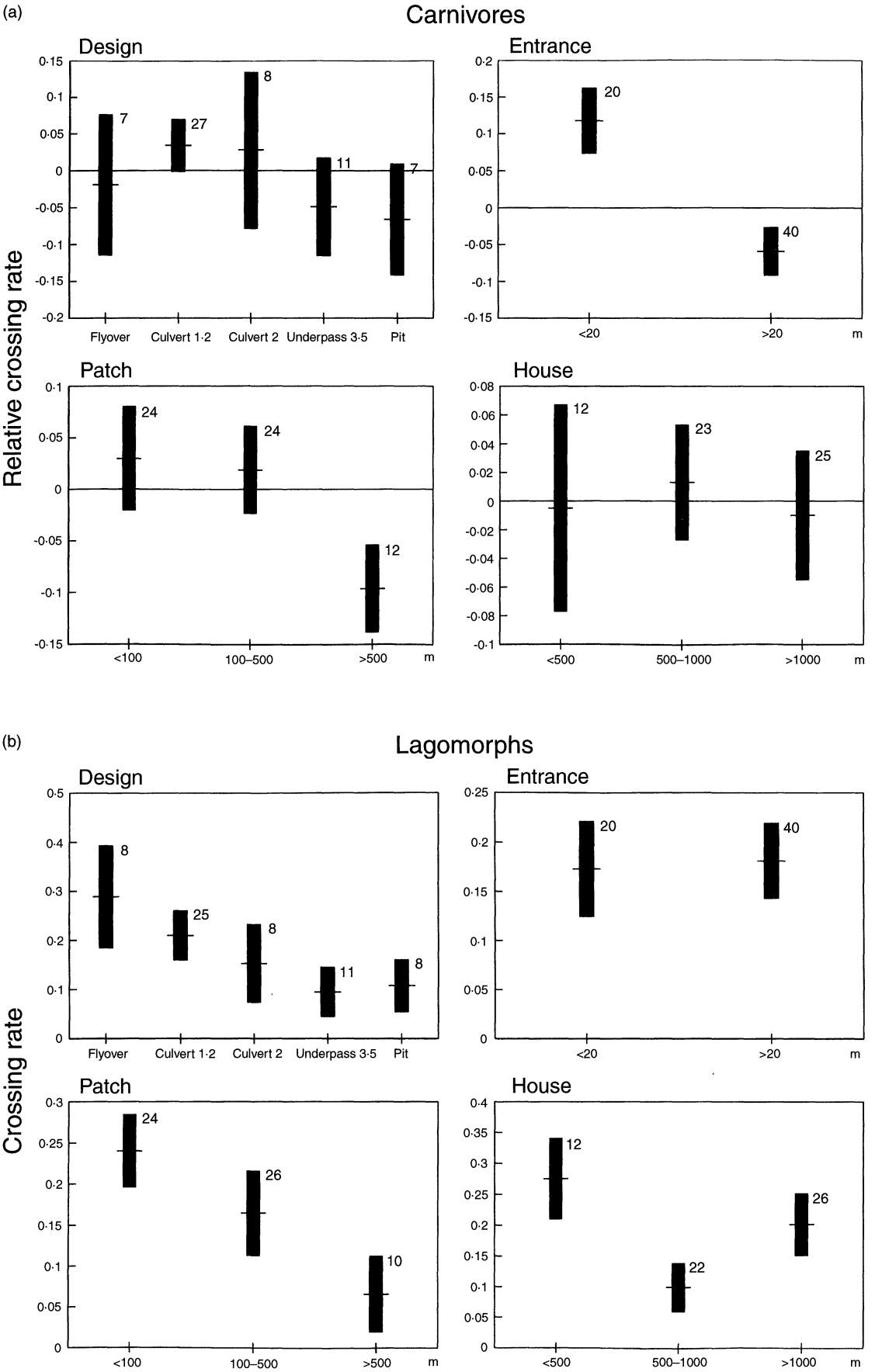

Fig. 4. Mean (and SE) vertebrate relative crossing rates (i.e. residuals) for different levels of factors indicating non-wildlife passage characteristics. For lagomorphs, original crossing rates are shown. Design: categories of passage structure and dimensions. Entrance: presence/absence of cover within 20 m of some passage entrance. Patch: distance to the nearest patch of scrubland. House: distance to the nearest inhabited building. The sample size is given beside each error bar.

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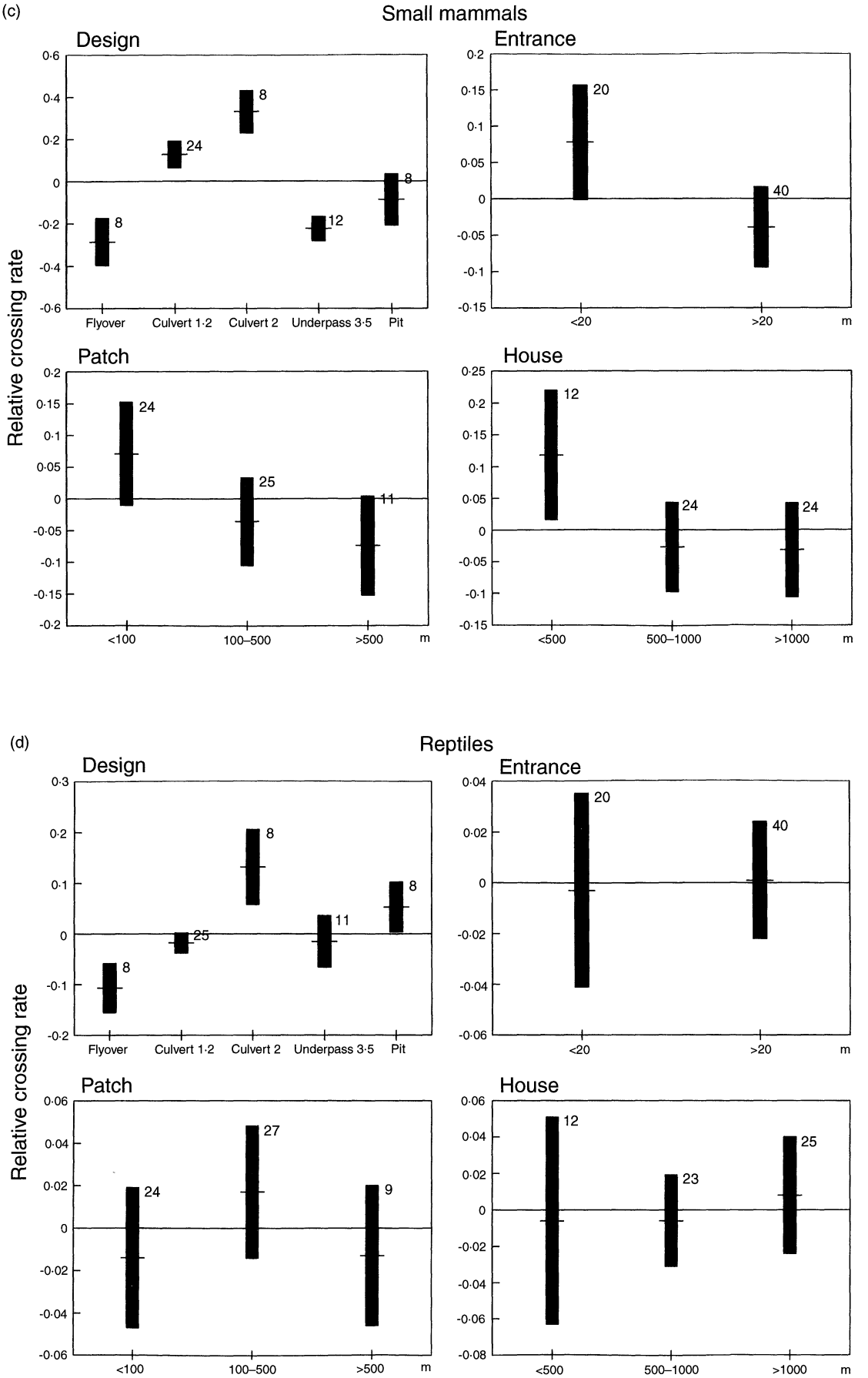

Fig. 4. (*cont.*)

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in crossing rates are difficult to disentangle. Common species of small mammals in the study area differ greatly in preferred habitats, e.g. *Apodemus sylvaticus* selects shrub cover (Kufner & Moreno 1989), whereas *Pitymys duodecimcostatus* and *Mus spretus* inhabit more open habitats (Stoddart 1979). The peak in crossing rate found in the border might be related to the higher species richness which would be expected in such a heterogeneous habitat (Begon, Harper & Townsend 1990). Intra-annual fluctuations in small mammal abundance are variable, but for most species living in the temperate zone, births generally occur in spring, and mortality generally increases through autumn and winter (Pimm 1991). The temporal variation in small mammal crossing rates roughly agrees with this pattern (Fig. 3c).

We observed frequent crossing of small mammals through HSR passages, even those up to 64 m long. This result contrasts with the widely reported reluctance of small mammals to cross any type of cleared habitat (Oxley *et al.* 1974; Mader 1984; Swihart & Slade 1984), but culverts might differ from other cleared habitat strips in that they provide shelter from aerial predators. The cost of exploring or exploiting resources at the other side of the HSR, in terms of predation risk, might thus actually be lower at the culverts, especially those having small cross-sections, than at less protected points along the railway. Results support this hypothesis, as crossing rates were highest in culverts with small cross-sections.

REPTILES

As with small mammals, the high crossing rates of reptiles in the border habitat could reflect a higher species diversity. The temporal pattern of passage use by reptiles is in agreement with expected seasonal fluctuations in their activity, with very low rates of crossing from autumn to early spring, when reptiles are inactive. During the active season, habitat differences were found in crossing rates (Fig. 2d), probably due to differences between microhabitat preferences of common species (Castilla & Bauwens 1991; Díaz & Carrascal 1991).

Passage design and the rate of human use had significant effects on reptile crossing rates. Culverts 2 m in width and underpasses had higher relative crossing rates than the other designs. We suggest that these results may be explained by the thermoregulatory behaviour of reptiles. In order to maintain body temperature within their preferred range, some lizard species select microhabitats which allow them to shuttle between sun-warmed and shaded surfaces (Castilla & Bauwens 1991). As the HSR has a north–south orientation, flyovers are not shaded for most of the day, whereas small culverts receive only sunlight at dawn and dusk. On the other hand, large culverts and underpasses offer more hours of suitable microhabitat. The positive relationship between reptile crossing rates and the rate of human use may be an indirect sign of the same selection of thermal conditions because most records of human activities occurred in underpasses and large culverts (Table 1).

AMPHIBIANS

There were no records of amphibians, for which there are two alternative explanations:

1. the main toad activity period (i.e. toad migration in the wet season) coincided with passage flooding;
2. the possibility that amphibians can cross the HSR without using passages.

Some roads and highways do not stop toad migrations, even where there are no transverse passages (Langton 1989).

Conclusions

Our results indicate that non-wildlife passages allow several vertebrate groups to cross the HSR, and consequently culverts and pathway passages could be important in the conservation management of these groups. Moreover, carnivores, lagomorphs, small mammals and reptiles used the passages frequently rather than occasionally, suggesting that possible isolation effects exerted by the HSR (demographic and genetic) might be highly reduced.

Non-wildlife passages can be improved as crossing facilities for wildlife with relative minor modifications. Cover near passages and over corridors between scrubland patches and passages may favour passage use by carnivores and other groups. Culverts with small sections may attract small mammals, while large culverts and underpasses would be attractive for reptiles, especially in open habitats without vertical substrates. Ungulates clearly need specifically designed passages, taking into account required dimensions, distribution of cover, placement and human disturbance levels. Obstacles such as pits can be overcome by some carnivore species. However, records of smaller species in passages with pits did not prove actual complete crossing, and therefore our data are inconclusive about pit suitability. Human disturbance was generally low in the studied railway and did not influence the use of passages by terrestrial vertebrates. However, disturbance from a close busy road might be responsible for reduced carnivore crossing and, therefore, passages near sources of permanent disturbance should be established, when possible, in open or degraded areas.

Fence fitting did not alter vertebrate crossing rates, suggesting either that vertebrates used passages exclusively as crossing points before fencing, which is unlikely, or alternatively, the HSR was not an effective deterrent to vertebrate movement. If the latter is true, crossing rates through the passages will be under-

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estimates of actual rates of vertebrate movement across the HSR.

Passage features explained a smaller amount of variance in crossing rates than spatiotemporal fluctuations in vertebrate abundance. Thus, it can be concluded that the most important factor in wildlife passage design is placement. Success of passages às vertebrate crossing facilities depends, first, upon their location in suitable habitat of the target species and, secondly, upon the suitable design of passages and management of surrounding areas.

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Factors Affecting Crossing of Red Foxes and Wildcats through Non-Wildlife Passages across a High-Speed Railway

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Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway

Alejandro Rodríguez, Giulia Crema and Miguel Delibes

Rodríguez, A., Crema, G. and Delibes, M. 1997. Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway. – Ecography 20: 287–294.

We used trail records on sand surface within non-wildlife passages to test whether foxes and wildcats used them regularly, and to identify passage features which may favour crossing across a railway and, therefore, may alleviate possible barrier effects. Both species crossed more in places and periods corresponding with assumed peaks in abundance and mobility, thus supporting the regular use hypothesis. The vicinity of cover favoured crossing, but both species used infrequently passages near permanent sources of human perturbation (especially intense traffic) even in suitable habitats with abundant cover. The presence of cover in the passage entrances further favoured fox and wildcat crossing. Cover near entrances may be particularly important to improve carnivore crossing chances in open habitats and when human activity levels are high. Passage design and dimensions had little effect on crossing rates. Location of passages within or close to suitable habitats explained a greater amount of variance in crossing rates than favourable passage features. There was a remarkable similarity in the behaviour of foxes and wildcats, possibly representing the rule for other carnivore species.

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The mechanisms by which linear infrastructures produce a barrier effect on mammal populations can be physical and/or behavioural (Klein 1971). The physical mechanism seems to have a limited influence in carnivore species, irrespective of their body size (Oxley et al. 1974, Burke and Sherburne 1982, Davies et al. 1987, Trewhella and Harris 1990). On the other hand, carnivores often avoid human manifestations associated to infrastructures (e.g. buildings, noise, lights, machinery; van Dyke et al. 1986, McLellan and Shackleton 1989a, b, Beier 1995), even in small roads with little traffic (McLellan and Shackleton 1988). Some species can accustom themselves to some degree of human activity (Tietje and Ruff 1983, Follmann and Hechtel 1990), but intense disturbance following road network development may result in both strong avoidance and a decrease in carnivore population density (Elgmork 1978, Thiel 1985, Mech et al. 1988).

Recently, culverts and pathway passages (i.e. non-wildlife passages) have been suggested as valuable alternatives to scarce and expensive wildlife passages (Yanes et al. 1995, Rodríguez et al. 1996) for restoring vertebrate free movement across infrastructures. In particular, we concluded that non-wildlife passages can be useful to reduce potential isolation in carnivores (Rodríguez et al. 1996). In this paper we further analyse the use of non-wildlife passages by two carnivore species, the red fox *Vulpes vulpes* L. and the wildcat *Felis silvestris* Schreber, which are of management and conservation concern in Europe. Following the method of Rodríguez et al. (1996), we test firstly whether these species use regularly non-wildlife passages or, on the contrary, they

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show a consistent avoidance. Under the hypothesis of a regular use, we expect the pattern of crossings to reflect the spatiotemporal pattern of animal abundance and activity. This hypothesis has two predictions: 1) crossing rates will be highest at passages located within or close to wood and scrub patches (i.e. preferred habitats; Delibes 1983, Blanco 1988); 2) crossing rates will be highest in the yearly peak of abundance (summer and autumn; Rau 1986, Stahl and Léger 1992) and mobility (autumn, when dispersal takes place; Blanco 1988, Stahl and Léger 1992). Under the alternative hypothesis of consistent passage avoidance, low crossing rates would be expected regardless of variations in habitat and season.

Secondly, we analyse the influence of passage features on the frequency of crossing. We expect higher crossing rates in passages close to cover and with low disturbance than in those far from cover and close to sources of human activity. We have not found any published criteria to establish specific predictions about the relationship between crossing rates and passage dimensions.

Fences can increase the barrier effect of infrastructures on carnivores (e.g. Foster and Humphrey 1995). The studied railway has side fences all along. Assuming that 1) fences preclude transverse movement of foxes and wildcats, and 2) before fencing, animals crossed both through passages and elsewhere, we expect a higher passage use after fencing.

Material and methods

Study area

The study was carried out in eastern Montes de Toledo, central Spain (39°10′–39°30′N, 3°45′–3°55′W). It is a hilly area with gentle slopes and continental climate. Cereal crops occupy valleys while hills are covered with Mediterranean scrubland. Human habitation is very low and sparse even in farmland, and there is no village within 10 km. Foxes and wildcats are common.

The railway crosses the study area through cuttings and embankments. Neither tunnels nor viaducts are available, and terrestrial animals cannot cross the railway without taking its structure into account. The study stretch (24.7 km) contains 42 non-wildlife passages through which animals can move across the railway. Most pathway passages are for low traffic, unpaved rural paths. Culverts remain dry most of the year. Fencing (wire netting 2 m high) was completed during the study period. There was little train traffic: always <10 trains per day, limited to the daylight hours.

Crossing rates

Between September 1991 and July 1992, 15–22 days a month, we sought fox and wildcat tracks on a layer of sand placed inside each monitored passage, near one of its ends. For each species, we recorded presence or absence of tracks, as well as the direction of every trail. When the sand surface did not show recognizable prints because of wind, rain, vehicles, domestic animals, or persons, the passage-day was considered non-operative. For each combination passage-month, we defined crossing rate as the number of days with tracks of the species under consideration divided by the number of operative days (i.e. those days in which sand conditions allowed clear track printing). Monthly crossing rates were calculated on an average of 13 operative days per month. We did not use rates when operative days were <5 per month.

Passage characteristics

We assigned each passage to one of three types of habitat having different land use and degree of human disturbance: 1) scrubland, a mosaic of scrubland and farmland with low human activity, 2) border, the interface between scrubland and farmland, with high human activity due to the vicinity of several inhabited farms and a road with intense traffic, and 3) open farmland, i.e. pastures and cereal crops with low degree of human disturbance.

We recorded the following data for each passage (Table 1): 1) Type of passage; all passages were made of concrete and belonged to five different simple designs: overpasses 6 m wide with wooded walls 2 m high all along, big culverts and pathway underpasses of square section (3.5 × 3.5 m), culverts of square (2 × 2 m) or circular (2 m in diameter) section, culverts of 1.2 m in diameter, and culverts 2 m wide (squared or circular section) having deposition pits at one of their entrances. These pits were box-like, and had their floor at the ground level and concrete walls 1.5 m in heigth. Pits store wood, stones and other objects carried by water. Passage length varied between 13 and 46 m, as did the railway width. 2) Presence or absence of cover (trees or shrubs) within 20 m of at least one of the entrances. 3) Distance to the nearest scrubland patch, categorized in <100 m, 100–500 m, and >500 m. 4) Distance to the nearest inhabited farm, categorized in <500 m, 500–1000 m, and >1000 m. 5) The monthly rate of use by human activities (persons, domestic animals, and vehicles), calculated in the same way as monthly crossing rates of foxes and wildcats.

Analyses

For each habitat type we calculated monthly crossing rates in five randomly sampled passages. Spatiotemporal variations in species abundance were analysed with factorial ANOVA on arcsin transformed crossing rates.

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Table 1. The number of operative days (days in which sand conditions allowed clear footprinting), the number of fox and wildcat records, and the overall crossing rate per passage. Design: C1.2, C2: culverts of 1.2 m and 2 m in diameter, respectively; CP: culvert with deposition pit; U: underpass 3.5 m wide; O: overpass. Cover: E: presence (+) of cover within 20 m; S: the distance to the nearest patch of scrubland (A: <100 m, B: 100–500 m, C: >500 m). Human disturbance: F: the distance to the nearest inhabited farm (A: <500 m, B: 500–1000 m, C: >1000 m).

Habitat passage	Passage	Design	Cover			Operative passage-days	Records		Crossing rate	
			E	S	F		*Vulpes*	*Felis*	*Vulpes*	*Felis*
Border	1	C2	+	A	A	138	11	17	0.080	0.123
Border	2	C1.2	+	B	B	143	9	6	0.063	0.042
Border	3	CP	–	B	B	130	0	3	0.000	0.023
Border	4	C1.2	–	A	A	136	1	5	0.007	0.037
Border	5	U	+	A	A	73	2	7	0.027	0.096
Scrubland	6	CP	–	C	C	64	3	7	0.047	0.109
Scrubland	7	C2	–	B	C	118	12	9	0.102	0.076
Scrubland	8	C1.2	+	A	C	144	30	32	0.208	0.222
Scrubland	9	C1.2	+	B	B	143	21	17	0.147	0.119
Scrubland	10	U	–	B	B	131	26	5	0.199	0.038
Scrubland	11	O	–	A	C	56	1	4	0.018	0.071
Farmland	12	C1.2	–	C	C	40	0	0	0.000	0.000
Farmland	13	U	–	C	B	52	0	0	0.000	0.000
Farmland	14	C1.2	–	C	B	52	0	1	0.000	0.019
Farmland	15	C1.2	–	B	C	51	3	1	0.059	0.020
Farmland	16	O	–	B	C	47	0	3	0.000	0.064
Farmland	17	CP	–	B	C	53	1	1	0.019	0.019
Total						1571	120	118	0.076	0.075

Sampling problems (general floodings, impossible access to some passages during long periods, < 5 operative passages-day per month) forced us to split the analysis in two ANOVAs. Analysis 1 lacked data in the farmland habitat and also in April and July in all habitat types. Thus the factor habitat had two levels and the factor month had nine. In Analysis 2 the factor habitat had all three levels, but the factor month had only four (February, March, May, and July). We used Tukey tests for examining contrasts between level means.

In order to analyse the influence of passage features, we removed the effect of spatiotemporal fluctuations in animal abundance taking residuals from the simplest significant model. We called these residuals the relative crossing rate, which was the response variable in an ANCOVA with passage characteristics (variables 1–5; see above) as independent variables. Again, we calculated the simplest significant model following Crawley (1993).

In a subsample of five passages located in the border habitat type, we compared monthly crossing rates before and after fencing (t-test).

Results

The number of operative days per passage varied between 40 and 144. Highest total rates were recorded in the same passage for the fox (20.8%) and the wildcat (22.2%; Table 1). Trail direction indicated that foxes and wildcats crossed the whole railway width in at least 87% and 89% of the visits, respectively.

The factors habitat and month had a strong effect on crossing rates in both species. The results were largely consistent in ANOVAs 1 and 2 (Table 2). For this reason, we show only descriptive statistics from the analysis in which the number of levels of each factor was highest (Figs 1 and 2). Among variables representing passage features, only those related to the distribution of cover in the railway surroundings had a significant effect on fox and wildcat crossing rates. There was a considerable amount of variance explained by the whole model (37–59% for the fox, 39% for the wildcat; Table 3). The proportion of variance explained by passage characteristics was much lower than that explained by the pattern of abundance and activity (Table 3). Average monthly crossing rates did not significantly differ before and after fencing in every passage and for both species.

Four passages with cover near their entrances (all but passage 5 in which the direction of trails was not always recorded) allowed a comparison between the number of trails recorded in each direction of travel (both species pooled data). One passage had cover at both entrances and, accordingly, the number of trails in each direction was not significantly different. In two passages the number of trails coming from the entrance with cover was higher than the number of trails in the opposite direction, but only in one instance was this difference significant (goodness of fit $\chi^2 = 5.40$, DF = 1, p = 0.020). In the remaining passage differences in the direction of travel were not significant.

Whereas overall fox crossings were similar in both directions (58 vs 54 records), wildcat crossings from

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Table 2. ANOVA results showing the effects of the type of habitat and month on crossing rates of foxes and wildcats. In Analysis 1, habitat type has 2 levels (scrubland and border) and the factor month has 9 (all but April, July and August). In Analysis 2, habitat type has all 3 levels, while month has 4 (February, March, May and July).

	DF	MS	F	p
Fox				
Analysis 1				
Habitat	1	0.756	21.05	0.000
Month	8	0.172	4.78	0.000
Habitat × Month	8	0.098	2.74	0.011
Error	72	0.036		
Analysis 2				
Habitat	2	0.205	6.54	0.003
Month	3	0.239	7.62	0.000
Habitat × Month	6	0.065	2.07	0.074
Error	48	0.031		
Wildcat				
Analysis 1				
Habitat	1	0.254	5.43	0.023
Month	8	0.102	2.19	0.038
Habitat × Month	8	0.038	0.81	0.593
Error	72	0.047		
Analysis 2				
Habitat	2	0.225	7.45	0.002
Month	3	0.157	5.20	0.003
Habitat × Month	6	0.060	1.98	0.087
Error	48	0.030		

west to east (63) were more than twice the number of crossings from east to west (28), which caused carnivore crossing to be biased towards the west to east direction ($\chi^2 = 4.74$, DF = 1, $p < 0.05$). Although cover is present in the western entrance in four out five passages having cover, wilcats tend to enter also uncovered passages mainly from the west side. This pattern in the direction of travel of wildcats may hide a stronger than observed association between the side in which cover is present and the side by which animals enter the passage.

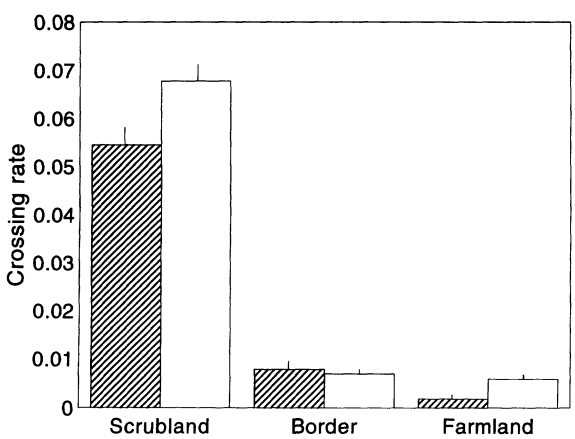

Fig. 1. The average crossing rate for each habitat type (+SE). Hatched bars: fox. Open bars: wildcat. N = 20 for every habitat type.

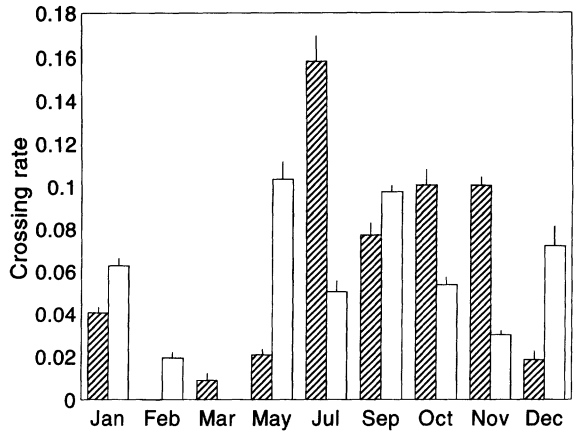

Fig. 2. The average crossing rate for each month (+SE). Hatched bars: fox. Open bars: wildcat. N = 10 for every month.

Fox

There were significant differences between fox crossing rates in passages placed in different habitats (Table 2). The average monthly crossing rate in the scrubland was 7 times higher than in the border, and 30 times higher than in farmland (Fig. 1, Tukey test, $q = 3.72$ and $q = 4.90$, respectively, DF = 48, $p < 0.05$). Crossing rates in the border and farmland were not significantly different.

There were also significant temporal differences in the use of passages (Table 2). Crossing rates in February were significantly lower than in the period July-November ($q > 4.68$ in all cases, DF = 72, $p < 0.05$), and rates in July were 18 and 8 times higher than in March ($q = 5.26$, DF = 72, $p < 0.02$) and December ($q = 4.56$, DF = 72, $p < 0.05$), respectively (Fig. 2). Temporal differences in the scrubland were more pronounced than in the border (significant interaction term in analysis 1, Table 2).

Regarding passage features, the average relative crossing rate in passages with cover within 20 m of some entrance was higher than in other passages (analysis 1: $F_{1,88} = 13.4$, $p < 0.001$; analysis 2: $F_{1,58} = 4.0$, $p < 0.1$; Fig. 3b). The effects of the remaining variables were not significant. However, relative rates tended to be lower 1) in overpasses and culverts with pits than in other designs, 2) in passages far from the cover than in those close to it, and 3) in passages far from inhabited farms than in closer ones (Fig. 3).

Wildcat

There were significant effects of habitat and month on wildcat crossing rates (Table 2). Rates in the scrubland were 10 and 11 times higher than in the border ($q = 4.40$, DF = 54, $p < 0.05$) and farmland ($q = 4.56$, DF = 54, $p < 0.05$), respectively (Fig. 1). Temporal variations in

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Table 3. The amount of variation in crossing rates explained by animal abundance and passage features. SST: sum of squares. H: habitat. M: month. E: cover at the entrances. F: distance to the nearest inhabited farm. r^2: coefficient of determination.

	Analysis	SST	Abundance and mobility				Passage features			TOTAL r^2
			H	M	H × M	r^2	E	F	r^2	
Fox										
	1	5.501	0.756	1.372	0.786	0.53	0.342		0.06	0.592
	2	3.018	0.409	0.716		0.37				0.373
Wildcat										
	1	4.746	0.254	0.818		0.23	0.488	0.268	0.16	0.385
	2	2.730	0.450	0.471		0.34	0.166		0.06	0.398

crossing rates were similar to, but less marked than, the ones for fox (Fig. 2). The Tukey test resulted in significant differences between the March-May ($q = 4.82$, $DF = 80$, $p < 0.05$) and March-September ($q = 4.68$, $DF = 80$, $p < 0.05$) pairs of months.

Relative crossing rates in passages with cover in their entrances were significantly higher than in passages without cover (Fig. 4; analysis 1: $F_{1,86} = 14.2$, $p < 0.001$; analysis 2: $F_{1,58} = 5.8$, $p < 0.05$). We did not detect clear trends for other passage features (Fig. 4), but relative rates were significantly lower in passages located at intermediate distances from inhabited farms than elsewhere (analysis 1: $F_{2,86} = 3.9$, $p < 0.05$; Fig. 4d).

Discussion

According to the predictions of the regular use hypothesis, foxes and wildcats preferably used passages located in habitats with cover and low degree of human disturbance. Both factors seem to be important, as in scrubland areas with permanent human activity (i.e. the border habitat) crossing rates were almost as low as in the unsuitable farmland habitat. Results also fitted predictions concerning temporal fluctuations in abundance and activity. Many fox crossings occurred from July to November, a period including the end of the breeding season and the dispersal season in the Iberian peninsula (Rau et al. 1986, Blanco 1988, Travaini 1994). Although the biology of the wildcat is largely unknown in Mediterranean environments, existing evidence indicates that kittens abandon dens in late spring and natal dispersal occurs mainly in autumn, at least for males (Stahl et al. 1984, Stahl and Léger 1992). In these periods we found the highest overall frequency of wildcat crossings through passages. In both species, a second peak of crossings appeared in winter (January for the fox; December-January for the wildcat) which might be related to the increase in mobility during the mating period (Artois 1989, Stahl and Léger 1992).

Seasonal differences in the use of passages by the fox in the scrubland were more marked than in other habitat types. Apart from the fox preference of scrubland for bedding (Blanco 1988, Cavallini and Lovari 1994), these differences might reflect a higher fox productivity in wooded areas, where they tend to place their dens (Meia and Weber 1992).

The presence of cover by the passage entrances was the only passage feature which was significantly associated to high crossing rates in both species. Foxes and wildcats tended also to enter passages by the entrance with cover. Cover would contribute to masking passage structure, so reducing vertebrate reluctance to approach and cross through them. Moreover, cover in entrances may function as landmarks, especially for transient individuals that do not know the railway surroundings. The high rate of use in the passage 9 (where the distance to the nearest scrubland patch is 240 m; Table 1) suggests that foxes and wildcats may be attracted by this cover especially in open environments. On the other hand, the predicted inverse relationship between crossing rates and distance to the nearest cover patch was not significant, probably because most of the effect of distance to cover was already included in the factor habitat, removed after the calculation of residuals.

We found no effect of passage length on crossing rates. This result contrasts with those of Yanes et al. (1995), who found an inverse relationship between a crossing index of carnivores (mainly foxes and wildcats) and the infrastructure width, this width being a measure equivalent to passage length in our study. There was no special preference or avoidance of passages with a particular physical design, in agreement with most of the scarce published information. The range of section sizes able to be used by carnivores seems to be wide, from 0.2 m to >20 m in width (Camby and Maizeret 1985, van Haaften 1985, Foster and Humphrey 1995). However, Beier (1995) points out that mountain lions *Felis concolor* L. strongly avoided culverts across highways of different widths, and only crossed under large vegetated bridges. Our data, taken from an infrastructure with little traffic, indicate that dimensions alone do

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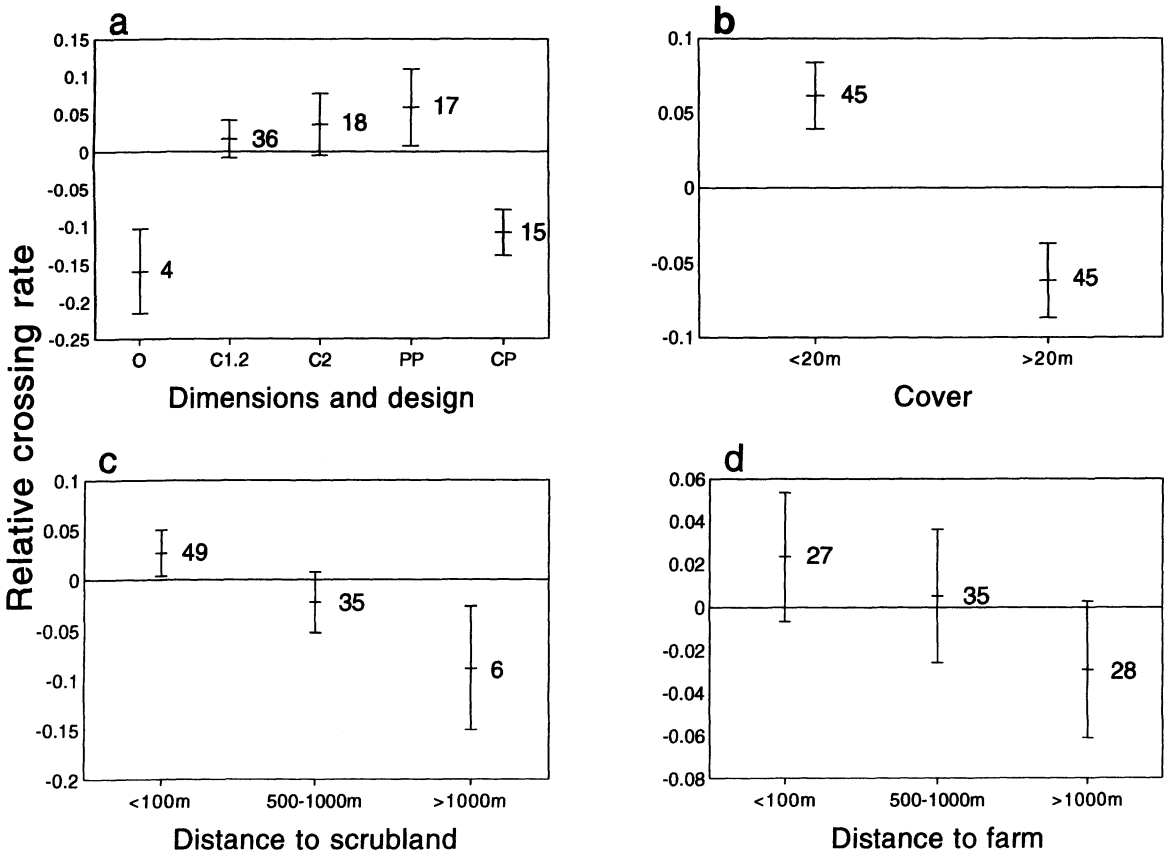

Fig. 3. The influence of passage features on the average relative crossing rate ($\pm$ SE) of foxes. Relative crossing rates are the residuals from the simplest significant model which takes into account the effect of spatiotemporal fluctuations in fox abundance and mobility. Sample size noted at each error bar. O: overpass. C: culverts (width is indicated). PP: pathway passage. CP: culvert with pit.

not affect the usage of non-wildlife passages by the two studied species. Therefore, other factors, as traffic disturbance, might account for culvert avoidance by mountain lions (Beier 1995), and lions, as well as other carnivores, might indirectly prefer big passages by active selection of protective cover. Riparian vegetation offers cover continuity under bridges, whereas it is absent inside concrete culverts. Cover would be particularly valuable in infrastructures where carnivores may perceive threat from intense traffic.

Traffic near the passages belonging to the border habitat probably lowered crossing rates of foxes and wildcats below the expected values from a good quality habitat. On the other hand, we did not find a negative relationship between crossing rates and the frequency of use of passages by human activities (on average <1 sign per passage-day; Rodríguez et al. 1996). The effect of the distance to the nearest inhabited farm was not significant either. In fact, for the fox, the trend we found was the opposite to that expected (Fig. 3d). In the wildcat the distribution of crossing rates did not indicate positive or negative selection of passages near houses and farms (Fig. 4d). However, we found significant differences, which might suggest a possible contamination of the sample by domestic cats. These are common in farms and their tracks are in practice difficult to distinguish from tracks of small sized wildcats. Nevertheless, during the last 6 months of study we performed intensive trapping (baited traps) around passages close to farms and we only captured wildcats (Rodríguez et al. 1993). Apart from intense traffic near a subsample of passages, human disturbance levels were low and probably not enough to influence carnivore crossing rates. Foster and Humphrey (1995) also found the use of passages by species as the mountain lion and the bobcat *Lynx rufus* Schreber compatible with moderate use by humans (on average <1 person/day).

We found fox faeces on the railway tracks before fencing, suggesting that foxes crossed the railway not only through passages. As fencing did not result in an increase of crossing rates through passages, we suggest that fences might not be efficient for channelling fox movement into passages as well as for preclude it elsewhere. Our data support the same conclusion for the wildcat. The observed pattern of crossing from west to east can hardly be related to a higher density of cats

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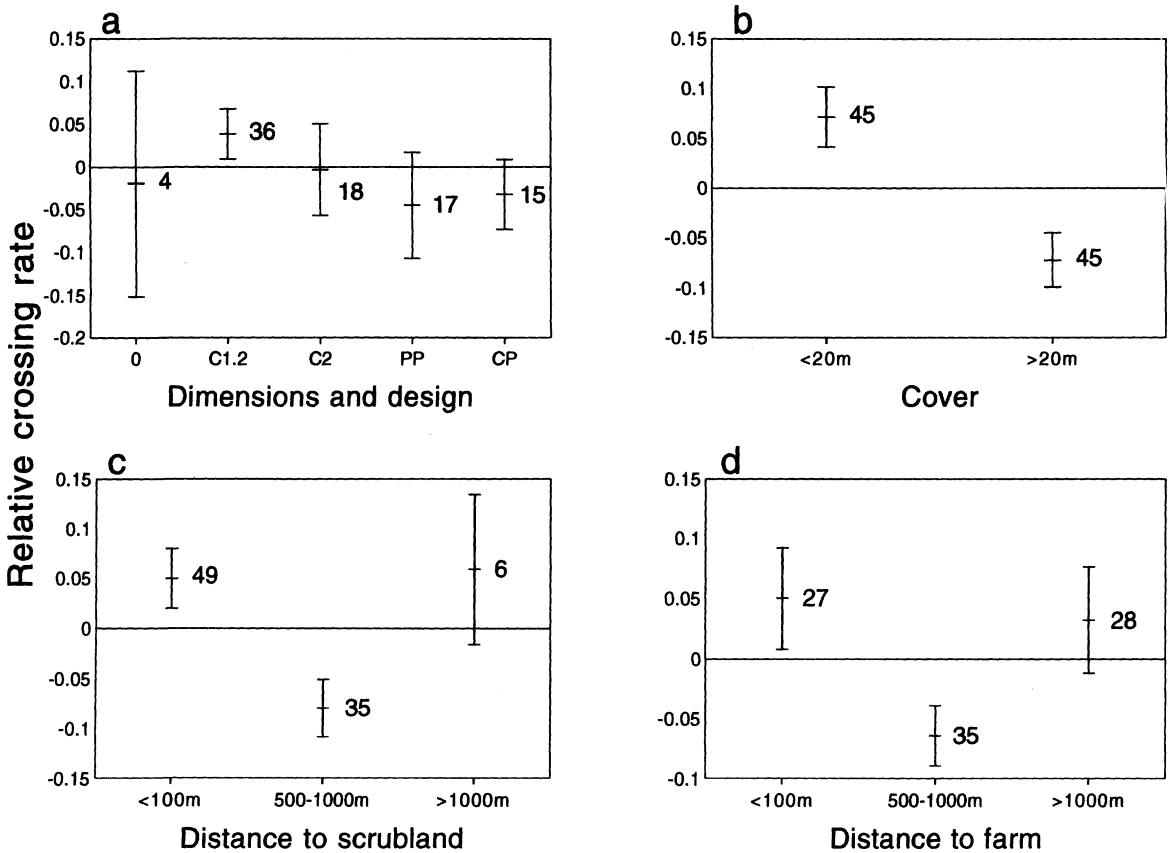

Fig. 4. The influence of passage features on the average relative crossing rate (± SE) of wildcats. Relative crossing rates are the residuals from the simplest significant model which takes into account the effect of spatiotemporal fluctuations in wildcat abundance and mobility. Sample size noted at each error bar. O: overpass. C: culverts (width is indicated). PP: pathway passage. CP: culvert with pit.

in the west side of the railway because, under such hypothesis, one would expect differences in crossing rate mainly in the dispersal season. As wildcats enter passages mainly from the west throughout the year, resident cats (with home ranges that include the railway line) have also to contribute to the biased pattern of travel direction, suggesting that return trips across the railway take place not always through passages, as observed in the stone marten (Rodríguez et al. 1996).

Our results do support a regular use of non-wildlife passages by foxes and wildcats. Crossing rates seem to be density dependent, as suggested by Camby and Maizeret (1985) for several mustelid and viverrid species. Fluctuations in abundance and activity explain a greater amount of variance than passage features do. As a result, two management recommendations arise: 1) suitable placement of culverts and pathway passages near (and preferably within) forested tracts is the main determining factor for passage usefulness as conservation facilities, and 2) in open areas with low human activity, cover near passage entrances would increase crossing by foxes and wildcats, while, when possible, artificial cover connections between passages and vegetated patches would also improve crossing chances and reduce potential barrier effects. The observed behaviour of both species was largely consistent, and possibly representative of many wild carnivores.

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Experimental study designs to improve the evaluation of road mitigation measures for wildlife

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ABSTRACT

An experimental approach to road mitigation that maximizes inferential power is essential to ensure that mitigation is both ecologically-effective and cost-effective. Here, we set out the need for and standards of using an experimental approach to road mitigation, in order to improve knowledge of the influence of mitigation measures on wildlife populations. We point out two key areas that need to be considered when conducting mitigation experiments. First, researchers need to get involved at the earliest stage of the road or mitigation project to ensure the necessary planning and funds are available for conducting a high quality experiment. Second, experimentation will generate new knowledge about the parameters that influence mitigation effectiveness, which ultimately allows better prediction for future road mitigation projects. We identify seven key questions about mitigation structures (i.e., wildlife crossing structures and fencing) that remain largely or entirely unanswered at the population-level: (1) Does a given crossing structure work? What type and size of crossing structures should we use? (2) How many crossing structures should we build? (3) Is it more effective to install a small number of large-sized crossing structures or a large number of small-sized crossing structures? (4) How much barrier fencing is needed for a given length of road? (5) Do we need funnel fencing to lead animals to crossing structures, and how long does such fencing have to be? (6) How should we manage/manipulate the environment in the area around the crossing structures and fencing? (7) Where should we place crossing structures and barrier fencing? We provide experimental approaches to answering each of them using example Before-After-Control-Impact (BACI) study designs for two stages in the road/mitigation project where researchers may become involved: (1) at the beginning of a road/mitigation project, and (2) after the mitigation has been constructed; highlighting real case studies when available.

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1. Introduction

Roads and traffic have negative impacts on a wide range of animals (reviewed in Trombulak and Frissell, 2000; Spellerberg, 2002; Fahrig and Rytwinski, 2009; Benítez-López et al., 2010; Rytwinski and Fahrig, 2012; van der Ree et al., 2015a). The main focus of road ecology research is to quantify these negative impacts, with the aim of avoiding, minimizing, mitigating, or offsetting negative impacts on individuals, populations, communities, and ecosystems (van der Ree et al., 2011). Options to avoid or mitigate these negative impacts are numerous and have been widely and increasingly implemented around the world (van der Ree et al., 2015b). Examples of mitigation measures include: animal

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detection systems, wildlife warning signs, changes in road-verge management, measures to reduce traffic volume, speed and/or noise, temporary road closures, wildlife crossing structures, wildlife fences [e.g., barrier fencing (or exclusion fencing) that prevents wildlife from accessing the road, or funnel fencing that primarily funnels animals to wildlife crossing structures but can also prevent wildlife from accessing the road], wildlife reflectors, wildlife repellents, and modified road designs/viaducts/bridges/lighting (Clevenger and Ford, 2010; Huijser and McGowen, 2010). Wildlife crossing structures (e.g., under- or over-passes: amphibian tunnels, badger pipes, ledges in culverts, land bridges, rope bridges, glider poles), combined with fencing to prevent mortality and funnel wildlife towards crossing structures, have gained considerable recent attention by transportation agencies because they enhance landscape connectivity without affecting traffic flow (van der Grift et al., 2013).

There is compelling evidence that many wildlife species regularly and frequently use crossing structures (reviewed in van der Ree et al., 2007), and that well-designed and maintained fencing greatly reduce rates of wildlife mortality and funnels animals towards the crossing structures (reviewed in Glista et al., 2009). Unfortunately, documenting use of a crossing structure (i.e., 'success' at the individual level) is so far removed from higher level quantities of interest (i.e., population size and persistence), that such studies provide little information as to whether the structure actually mitigates the effect of the road enough to ensure a viable population (van der Grift et al., 2013). Consequently, the influence of these mitigation structures on population viability is unclear for most road-affected species.

Ultimately, we want to be confident that the predicted impact of a road on a wildlife population will be at least partially mitigated by the proposed road design and that the investment in crossing structures and/or fencing is justified. For example, if the mitigation for an endangered species is ineffective such that the population of the target species declines, the road agency must respond and retrofit the road or modify the mitigation structures. In such cases, it is essential that road agencies have reliable evidence to make informed decisions about which feature of the road or mitigation should be implemented or modified and by how much.

Here we identify seven key questions road planners commonly have about crossing structures and/or fencing that for many species and structure types remain largely unanswered at the level of ultimate concern (e.g., population or community) and at the required level of certainty by existing research (Box 1). These questions must be answered not only so that resources for road mitigation are allocated in the most effective manner, but that they indeed have the predicted (desired) effect.

Box 1
Seven key questions road planners commonly have about crossing structures and fencing.

Questions road planners have about mitigation structures:

Question 1
Does a given crossing structure work? What type and size (width, height and length) of crossing structures should we use?

Question 2
How many crossing structures should we build?

Question 3
Is it more effective to install a small number of large-sized crossing structures or a large number of small-sized crossing structures?

Question 4
How much barrier fencing is needed for a given length of road?

Question 5
Do we need funnel fencing to lead animals to crossing structures, and how long does such fencing have to be?

Question 6
How should we manage/manipulate the environment in the area around the crossing structures and fencing?

Question 7
Where should we place crossing structures and barrier fencing?

There are two main reasons why these questions have remained unanswered. First, the existing approach to road mitigation is to simply adopt current best-practice in terms of the type, number, and location of mitigation. While this approach identifies the best known mitigation for installation, it does not explicitly facilitate learning about the effectiveness of mitigation because the mitigation was installed to solve a problem, not generate new information. Second, studies evaluating the effectiveness of mitigation structures have low inferential strength, and, as such, comparatively low predictive power. For example, studies often lack: (1) comparisons between treatment sites (also referred to as 'impact' sites in Before-After-Control-Impact (BACI) study designs (Roedenbeck et al., 2007; van der Ree et al., 2015b)) and control sites (i.e., sites that have not been affected by the treatment – these will vary depending on the question and goals of the road mitigation, but may include e.g., road-free areas, areas with narrow or low-traffic volume roads, unmitigated roads, and/or unmanipulated mitigation measures; see section 5 on experimental designs for more detail); (2) data on population sizes or trends prior to mitigation; (3) replication in both space and time; and (4) randomization of treatment and control sites across the pool of potential study sites. Moreover, many study designs confound mitigation variables (e.g., overpass width, density of shrubs at culvert entrance) such that their independent effects cannot be evaluated (reviewed in van der Ree et al., 2007; Glista et al., 2009). For road agencies to make informed and reliable decisions, we need to improve the rigor of studies that evaluate the effectiveness of mitigation measures.

Ways to improve the quality and impact of road ecology research and monitoring have been previously discussed. Roedenbeck et al. (2007) provided a research agenda for road ecology, identifying relevant questions (e.g., Under what circumstances do roads affect population persistence?, and Under what circumstances can road effects be mitigated?), and specifying a hierarchy of study designs for answering these questions. van der Grift et al. (2013) used the principles outlined in Roedenbeck et al. (2007) to propose a methodological framework for increasing the inferential strength of mitigation monitoring schemes. Lesbarrères and Fahrig (2012) proposed the use of such monitoring schemes as a type of experiment, but they did not suggest associated experimental protocols. van der Ree et al. (2015b) summarises these papers into an accessible format for practitioners. Here, we set out the need and standards for using experimental approaches to road mitigation to improve knowledge on the influence of mitigation structures on wildlife populations. We first demonstrate the need for an experimental (manipulative) approach to road mitigation projects. We then outline the road/mitigation project stages and describe how flexibility in experimental design depends on the stage in the road project at which researchers become involved. We provide experimental approaches to answering each of the questions in Box 1, highlighting real case studies when possible, and we conclude with a discussion of potential issues in using experimentation to evaluate the effectiveness of crossing structures and fencing.

2. Why we need an experimental approach to road mitigation

Most road agencies currently evaluate the effectiveness of

mitigation efforts through post-implementation monitoring (van der Ree et al., 2015b). Questions commonly asked with monitoring include: Will a particular species use an underpass to cross the road? and/or Which factors are correlated with the number of crossings? However, the state of road ecology has matured since mitigation structures were first developed, and while monitoring rate of crossing is an important first step, and likely appropriate in certain circumstances, it is no longer enough to simply document the use of a structure by the target animal(s) (van der Grift et al., 2013). In addition, we need to answer questions such as: Is the rate of road mortality sufficiently low and/or the rate of crossing sufficiently high to ensure a viable population? or Which parameter of the road, traffic, or mitigation structure should we modify to improve population viability to an acceptable level? These questions are best addressed with an experimental approach.

The advantage of experimentation is that it can yield stronger inference (if done correctly) and often more efficiently than a non-experimental approach. For example, suppose that to inform future wildlife overpass designs, one wanted to know the relative importance of certain overpass attributes (say, vegetation cover, x_1) compared to others (say, overpass width, x_2). If one had a sample of overpasses that varied in these attributes at which one monitored crossing rates (y), one could address this question by fitting models $y = f(x_1, x_2)$ and estimating the corresponding partial regression coefficients. Doing so, however, would require a comparatively large number of overpasses to get robust estimates of model parameters [e.g., if x_1 and x_2 are both ratio/interval valued, the simplest model with a multiplicative interaction would have $p = 4$ parameters, and assuming one wants $N/p \geq 10$ (the usual rule of thumb), this means $N \geq 40$ overpasses are required]. And parameter robustness notwithstanding, one still has comparatively weak inference because of the correlative study design. By contrast, employing a BACI experimental approach (see Appendix A for a description of general study designs for road mitigation), one could design the study with half the required sample size (e.g., 2 levels for each of x_1 and x_2, with 5 replicates each – yielding $N = 20$ overpasses for a fully factorial design). The result? Stronger inference at lower cost, i.e., greater informational efficiency.

Another reason that an experimental approach is required is that road mitigation can be expensive, particularly when it is retrofitted to existing roads. Transportation agencies often have limited funds to implement and evaluate mitigation measures. For example, under the Provincial Highways Management Division Strategic Plan for the Ontario Ministry of Transportation (MTO), Canada, the report states that at least 75 cents of every construction dollar should be invested directly in bridges and pavements, leaving only 25 cents for all other aspects, including mitigation (B. Carruthers, MTO, pers. comm). The cost of mitigation demands that effective solutions are deployed, and where an effective but cheaper solution is available, it should be adopted. An experiment is the best way to compare possible solutions and determine their relative effectiveness.

The most powerful aspect of experiments is that they efficiently produce new knowledge. For example, if the route of a proposed road project were to intersect a number of approximately equal-sized streams, the current approach to road mitigation is typically to install similar underpasses at each stream crossing. An evaluation of crossing rates may indicate that species X uses the underpasses, but we are unable to say whether larger or smaller underpasses or a different type of mitigation structure would increase the rate of use compared to those installed. Alternatively, if the mitigation were designed as an experiment where, for example, underpasses were installed at a random selection of half of the stream crossings and the remainder installed with extended bridges, we could then explicitly test how structure type affects the rate of use (or better yet, population size). Installation of mitigation measures explicitly in accordance with an experimental protocol, which when possible includes a replicated BACI study design, will increase the understanding of their effectiveness and accumulate new knowledge (Fig. 1). Furthermore, to build mitigation knowledge that can be applied in a variety of situations, we need to move beyond asking whether species X crosses the road at location Z, to broader questions relevant to different species, landscapes, roads and/or road projects (Fig. 2). In this way, each new mitigation experiment will build on the insights obtained from existing knowledge and previous experiment(s), thus continually improving understanding of mitigation effectiveness and increasing predictive power for extrapolating results from one location to another and/or from one species to another. Specifically, if experiments are designed well, information gained in one location or for a particular species can be applied to other locations or species helping to provide ecologically-effective and cost-effective solutions.

3. Road project stages and experimentation

There is a direct relationship between the road/mitigation project stage at which researchers become involved, the ease of experiment implementation, and the knowledge gain at the end of the experiment. If the experiment is designed early in the planning process, a wider range of experiments are possible with some at least having comparatively high inferential strength, broader implications, and greater potential to extrapolate to other locations/species. On the other hand, such experiments will typically require more funds, a longer evaluation time-frame, more political/stakeholder support, and more organization and planning than simpler (and likely less valuable) studies designed late in the planning process. Even when researchers become involved in the early planning stages, there will be limitations on the kind of study that can be implemented; a conceptually feasible experiment is not necessarily practically feasible. For example, the length of a proposed road may be too short for the number of treatment and control sites needed to adequately address the research question. This reinforces the need for researchers and road planners to be in communication at the earliest stages, so that the researcher can identify a set of feasible experiments and select the one that will be the most informative, given the constraints of the road project.

There are typically six stages in the road planning process (Ontario Ministry of Transportation, 2010; U.S. Department of Transportation, 2012; Roberts and Sjölund, 2015). Although their names and scale often vary across agencies and with the size of the project, they are: (1) strategic planning, (2) project development (preliminary design), (3) detailed design, (4) property acquisition, (5) construction, and (6) operation and maintenance. While there are many different process models for building, upgrading, and/or improving a road, here we provide a general description of each stage. In strategic planning, route options are developed and key project goals established. The strategic planning stage usually concludes with the preparation of an investment plan identifying targets for cost, traffic access, safety, and design, but rarely provides targets for environmental or ecological issues (Roberts and Sjölund, 2015). In the project development stage, the transportation project is more clearly defined. This stage includes studies of the environmental impacts of broad transportation alternatives and specific highway improvement options. By the end of the project development stage, there is generally a description of the location and major design features of the project (U.S. Department of Transportation, 2012). In the detailed design stage, engineers undertake surveys, test for soil conditions, determine construction material requirements, and design interchanges, bridges, and

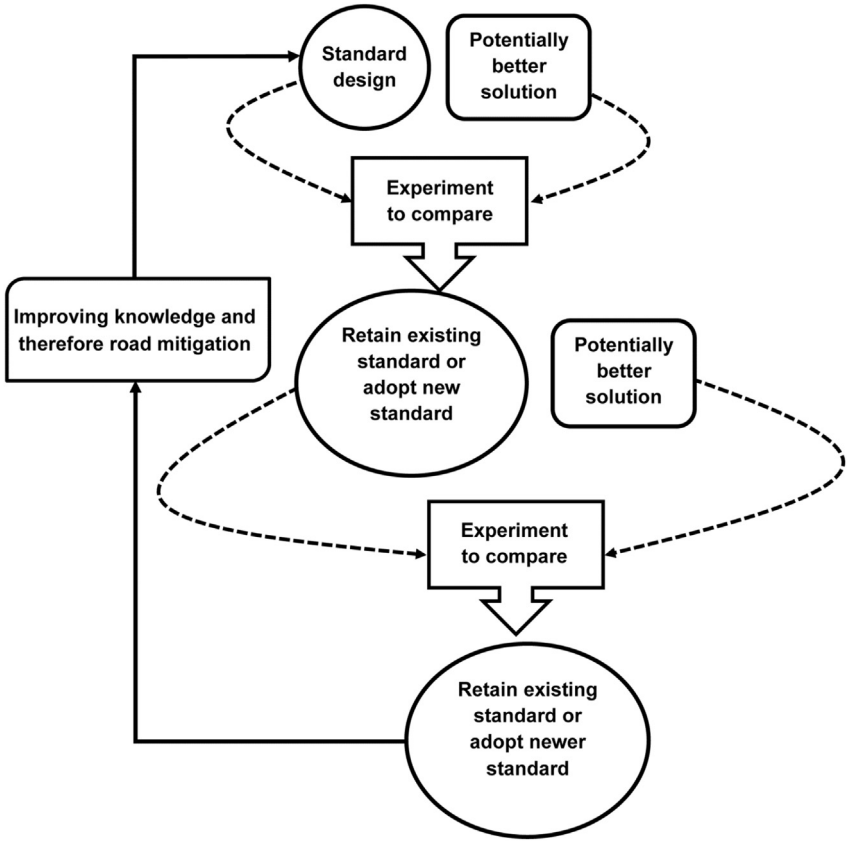

Fig. 1. Flow diagram illustrating the iterative process of improving knowledge through experimentation and, as a result, improving mitigation on the next road project, which is then used as another experiment to further improve mitigation on the next road, and so on. Where possible, a BACI experimental approach should be used in the experiment to compare the current standard with the potentially better solution.

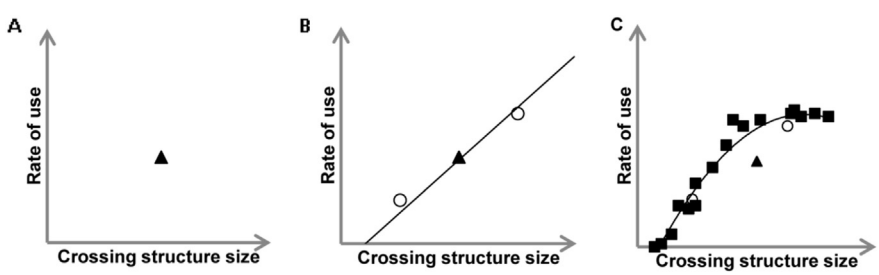

Fig. 2. In this hypothetical example, the rate of use of a crossing structure by wildlife has been monitored over time. In (A) the question was "how often does species X use the structure?" (a normal road agency question), and a single data point has been collected which cannot be extrapolated or generalised to other locations. In (B), the question is slightly broader, and three crossing structures have been monitored, but because the sample size is still insufficient, one might conclude that very large crossing structures will always perform better than smaller ones. With sufficient replication (C), the data show that there is a threshold in the benefit of increasing the size of a crossing structure, beyond which the increasing cost of larger structures would not be justified.

culverts; a comprehensive set of plans is produced during this stage (Ontario Ministry of Transportation, 2010). Once environmental reviews have been approved by government(s), acquisition of land needed for the project can begin. In the final stages, the project is constructed, followed by operation and maintenance activities.

The duration of the road project will depend on many factors, including the jurisdiction(s) involved and complexity of the project, funding availability, property availability, and timing of environmental clearances with permits. The planning, design, and construction of a highway expansion in Canada for example can typically take up to eight or more years, and 10 years or more to build a new highway (Ontario Ministry of Transportation, 2010). To break this down further, the duration of the planning and design stages can take up to 5 years, up to 3 years for environmental assessments, 1.5–5 years for property acquisition, and 5–8 years for construction (Ontario Ministry of Transportation, 2010). Furthermore, these stages may not always happen sequentially.

4. Opportunity for improved experimental design

The flexibility to change components of the experimental design will be influenced by the stage within the road/mitigation project when researchers begin collaborating with road planners (Fig. 3). For a description of general study designs for road mitigation see Appendix A. Here, we define treatment sites as sites where mitigation measures are to be installed or manipulated, and there can

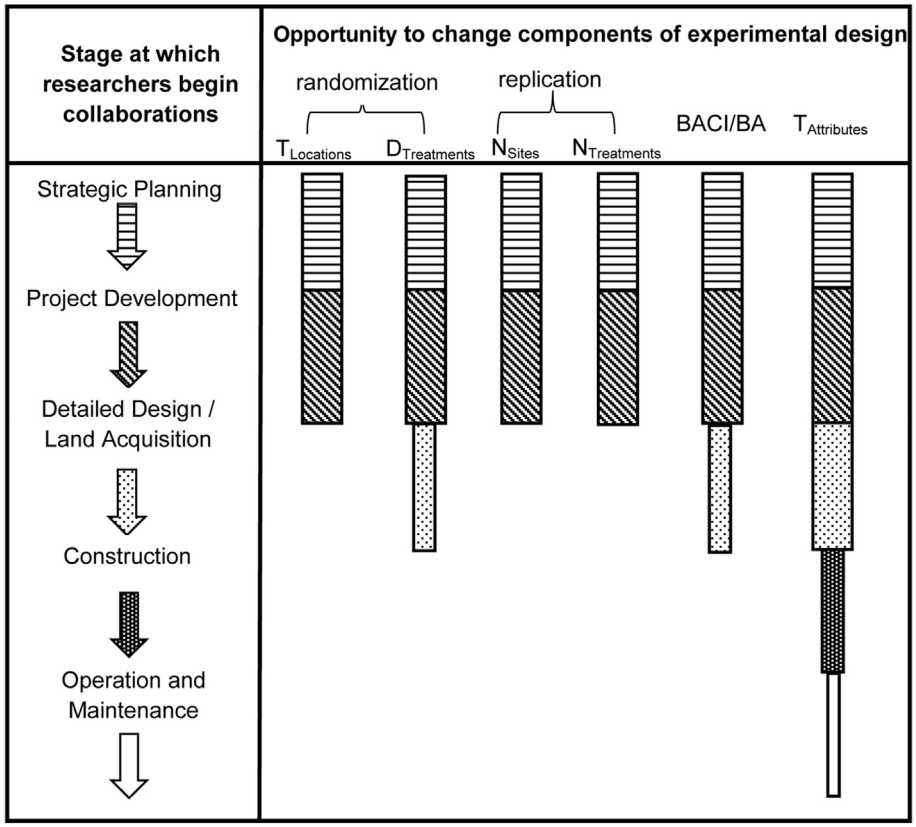

Fig. 3. The flexibility of researchers to change components of the mitigation experimental design depends on the stage of the road/mitigation project in which they become involved. The width of the bars represents the amount of flexibility researchers have in changing components of the experimental design, with wider bars indicating greater flexibility than more narrow bars. Bar design (i.e., dotted, striped etc.) corresponds to the road/mitigation project stage at which researchers begin collaborating with road planners. $T_{Locations}$ = location of treatments (mitigation structures); $D_{Treatments}$ = type of treatment (e.g., barrier fencing, land-bridge, underpass, extended stream crossing); N_{Sites} = number of treatment sites; $N_{Treatments}$ = number of different mitigation treatments; BACI = before-after-control-impact experiment design; BA = before-after experiment design; $T_{Attributes}$ = treatment attributes (e.g., type and height of barrier fencing, type and size of furniture added to land-bridge (trees, boulders), substrate type and size of underpasses and extended stream crossings).

be different types of treatments used in an experiment e.g., barrier fencing, land-bridges, culverts, extended stream crossings (i.e., allowing for terrestrial passage alongside the stream bed), etc. At the strategic planning stage, researchers have a nearly blank canvas to design a mitigation experiment with, potentially, high inferential strength. At this point, within the physical constraints of the project, there is still high flexibility in: (1) randomizing the locations of treatments (mitigation structures) and the types of treatments, and controls among sites; (2) selecting the number of treatment and control sites, and the number of different treatments to be installed; and (3) collecting before data for the measurement of interest (Fig. 3). If researchers begin collaboration with road planners at the beginning of the project development stage, they retain the same level of flexibility for all components of the experimental design as if they begin at the strategic planning stage; however, they likely have lost up to three years of time for collecting 'before' data (Fig. 3).

The length of time required to evaluate mitigation effectiveness before (and after) construction will depend on the ecological outcome of interest (e.g., population abundance, number of road-kills, movement, etc.) and the characteristics of the focal species. In general, for a long-lived, highly mobile species, the collection of before data would be required over a longer period to assess a change in population abundance than that required to detect a change in movement (see van der Grift et al., 2013 for further details on appropriate sampling schemes and possible ecological outcomes of interest). At the end of the project development stage, however, the road/mitigation project is more clearly defined with the location and major design features already selected. Researchers entering into the planning process at the beginning of the detailed design stage no longer have flexibility in randomizing the locations of the treatments, but they may have some flexibility in randomizing treatments among the selected mitigation locations. Furthermore, researchers no longer have the ability to select the number of treatment sites as well as the number of different mitigation treatments (i.e., replication) since the number of treatment locations will have been selected prior to the detailed design stage (Fig. 3). For example, if ten locations have been pre-selected for the installation of mitigation structures (during the project development stage), researchers cannot select five different treatment types to evaluate mitigation effectiveness since the number of replicates per treatment (i.e., 2 replicates) would not be sufficient to provide robust conclusions. Flexibility in collecting 'before' data for BACI or BA (Before-After) experimental designs (see Appendix A) may also be very limited at this stage because if construction is imminent it will be difficult to obtain a sufficiently long time sequence of before data, to make robust comparisons with the 'after data' (Fig. 3). However, if the time between the start of the detailed design stage and construction is long enough (e.g., if land acquisition is expected to take longer than normal), it may still be possible to obtain adequate before data even if the researcher only becomes involved at the beginning of the detailed design stage. Once construction begins, the attributes of the mitigation structures (e.g., type and/or height of fencing, substrate type and size of

underpasses) of the pre-selected mitigation treatments (e.g., fencing, underpasses), become highly constrained (Fig. 3). For example, only minor attributes such as reducing the size of a wildlife underpass or changing the substrate type can potentially be modified. After construction, only mitigation attributes can be experimentally manipulated (e.g., mowing, addition of coarse woody debris, manipulating (reducing) underpass width).

5. Experimental designs

In this section, we describe potential experimental approaches for each of the research questions in Box 1 and provide, when possible, case studies highlighting mitigation experiments that have been conducted or are proposed. More specifically, we provide example BACI study designs for two stages in the road/mitigation project where researchers may become involved: (1) at the beginning of a road/mitigation project i.e., project development stage, and (2) after the mitigation has been constructed i.e., operation and maintenance stage (post-mitigation). We chose these two project stages as they represent the extremes in terms of the amount of opportunity and/or flexibility in designing high-inference studies, with experiments conducted at the project development stage having more flexibility and therefore higher potential inferential strength than post-construction experiments. To reiterate, to conduct mitigation experiments, a high level of collaboration among researchers and transportation agencies will be required at all stages in the road project. Furthermore, researchers will need to design the experiments within the constraints of the road project.

BACI mitigation experiments at the project development stage can be carried out on both new and existing roads, resulting in two design situations: (1) the road and mitigation are to be constructed simultaneously; or (2) the mitigation is to be constructed on an existing road. For new roads, researchers collect data on an outcome of interest before and after the road and mitigation are installed at treatment and control sites. For existing roads, researchers collect data on a measurement of interest before and after the mitigation is installed on an existing road at treatment and control sites. In the case of mitigation retrofits of an existing road, usually only a limited range of BACI experiments are possible, such as evaluation of fencing, or manipulation or modification of existing mitigations (e.g., reducing underpass width or height, reducing fence permeability, addition of coarse woody debris to underpasses, or temporarily closing/opening existing crossing structures). New crossing structures are only occasionally constructed on existing roads, primarily due to the higher costs associated with retrofitting an existing road compared to the costs of building new roads and mitigation simultaneously. However, this is likely to change in North America and Europe as the rate of construction of new roads slows and shifts to a greater focus on expanding the capacity of the existing network and repair of failing infrastructure providing an opportunity for a wide range of BACI mitigation experiments on existing roads. For all mitigation experiments, two sets of replicated sites are required: (1) treatment sites where mitigation measures are to be installed or manipulated, and (2) control sites where sites are not affected by the treatment. To evaluate mitigation effectiveness, treatment sites are compared to control sites. The type of control site will vary depending on the question and goals of the road mitigation, and may include road-free areas, areas with narrow or low-traffic volume roads, unmitigated roads, and/or unmanipulated mitigation measures (Fig. 4) (also see van der Grift et al., 2013).

5.1. Question 1: Does a given crossing structure work? What type and size (width, height and length) of crossing structures should we use?

This question is frequently posed by road planners. However, to design an experiment to answer it, we first need to define 'work'. The general question has to be translated into goals that are highly specified, or SMART: Specific, Measurable, Achievable, Relevant and Time-framed (van der Ree et al., 2007). There are generally two potential objectives in road mitigation goals: (1) no net loss (i.e., road impacts will be fully mitigated), and (2) limited net loss (i.e., a limited road impact will be accepted) (van der Grift et al., 2013). Proper evaluations of the extent to which the full effect of roads have been mitigated (i.e., no net loss/full mitigation) can only be made by comparing treatment sites to road-free control sites (Fig. 4).

Proper evaluations of the extent to which population size improves (i.e., limited net loss/partial mitigation) can only be made by comparing treatment sites to mitigation-free control sites (i.e., how much better (or worse) is the mitigation treatment than having no mitigation at all?) (Fig. 4). Proper evaluations of the extent to which a modification to an existing mitigation improves population size in comparison to the existing unmodified mitigation can only be made if modification-free control sites are included (i.e., how much better (or worse) is the modified mitigation than the existing mitigation?). Road planners and researchers need to decide on mitigation targets early in the planning process to ensure the study design (e.g., type of control sites) and data collected can rigorously address the questions of interest.

In practice, question 1 needs to be rephrased to include the specific objectives of the particular mitigation. For example, if it was feared that a proposed road would impact species X by reducing connectivity between its breeding and foraging habitat, the researcher and road planner may ask "Do crossing structures allow sufficient movement of species X such that the population level after construction remains similar to road-free conditions (i.e., no net loss)?" Furthermore, if we suspect that crossing structure type and/or size will affect use by species X, we should explicitly attempt to incorporate these factors into the design so that the mitigation experiment tests how structure size and type affect the rate of use. Question 1 can be most effectively answered using a BACI experiment designed at the project development stage. The goal would be to maximize the information derived by having as many different mitigation treatments as possible (i.e., types and sizes of crossing structures), while still ensuring sufficient replication of each treatment (Fig. 5). For example, if many potential mitigation sites are available, the researcher could include wildlife underpasses and overpasses in a range of sizes and shapes (e.g., narrow overpasses vs. wider land bridges, box culverts vs. arched culverts etc.), yet maintaining the required degree of replication. To address the broader question as to whether a given mitigation structure works at all, a second control type will need to be added to this study design at unmitigated road sites (mitigation-free). This would allow researchers to determine the relative effect of each treatment on population size compared to roads that are built without crossing structures (i.e., how much better are different types and sizes of crossing structures at restoring or maintaining populations than roads with no crossing structures at all?). In the example figures (Figs. 5, 7–10, 12, 13, and Appendix B–E), we include three or four replicates of each mitigation treatment. Note we are not suggesting this level of replication is sufficient for all experiments. The number of required replicates will vary depending on the measurement of interest, the species of concern, and the location (e.g., habitat type, topography) (see van der Grift et al., 2013). Furthermore, in these same example figures, we provide

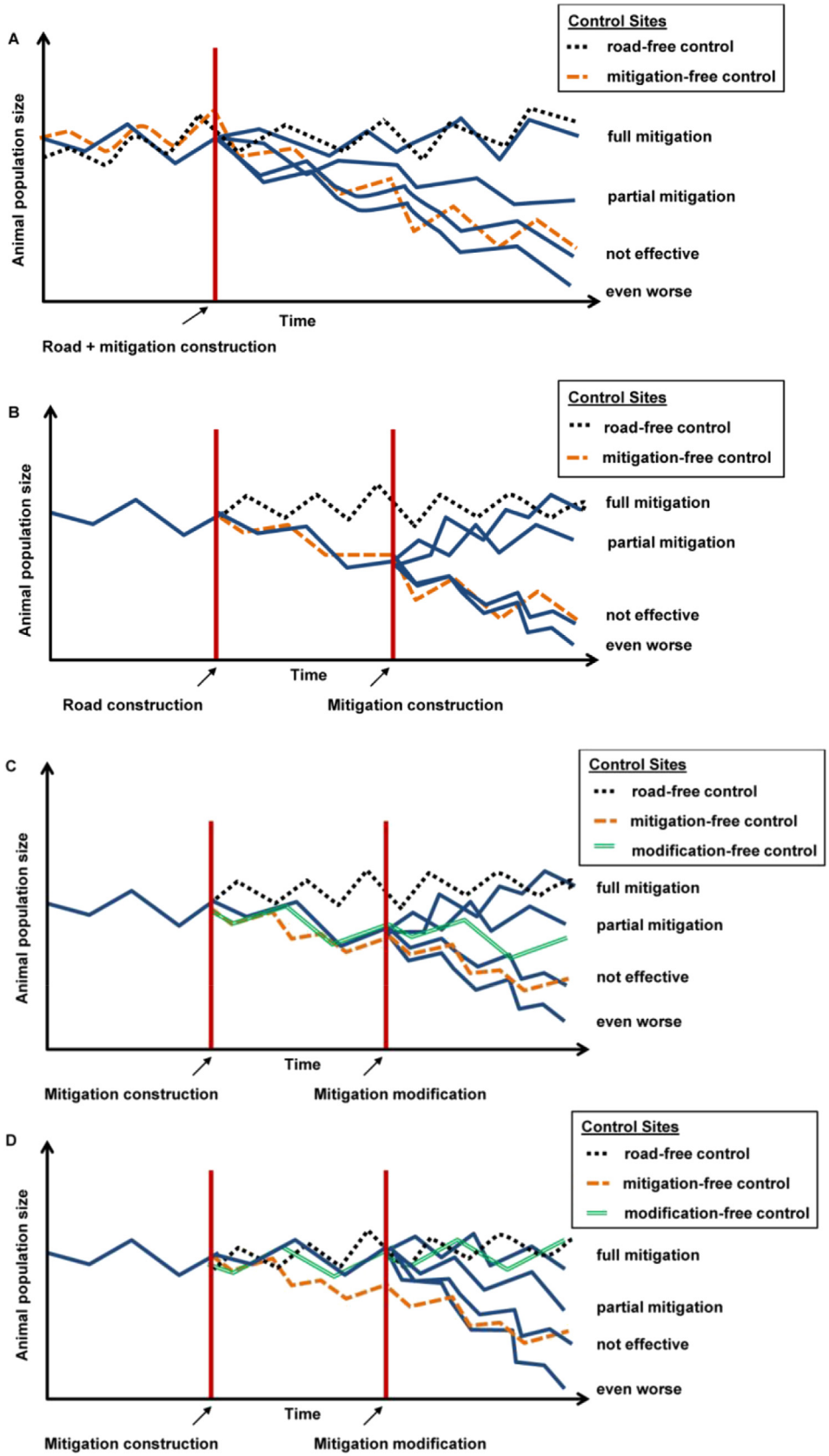

Fig. 4. Illustration of changes in animal population size over time (blue solid lines) when evaluating the effectiveness of road mitigation measures where (A) the construction of the road and mitigation take place simultaneously, (B) there is mitigation of an existing road, and (C and D) there is modification (or manipulation) to existing mitigation. In all panels, it

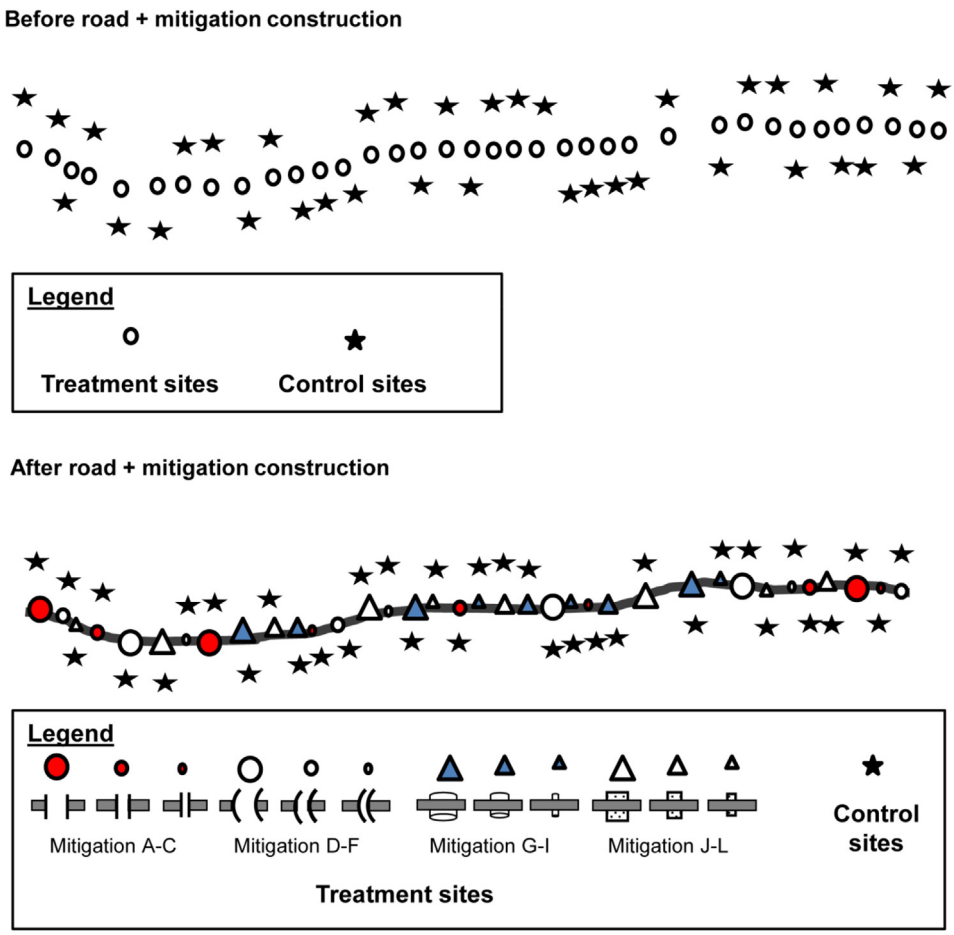

Fig. 5. BACI experimental design at the project development stage for Question 1: Does a given crossing structure work, and if so, what type and size (width, height and length) of crossing structures should we use? Specific question: What type and size of crossing structure allows sufficient movement of species X such that the population size remains the most similar to conditions at road-free areas? In this example, the road and mitigation structures are constructed simultaneously. Data (e.g., relative population size) are collected at treatment and control sites before and after the road and mitigation structures are constructed. Two different overpass types (mitigation A–F) and two different underpass types (mitigation G–L), each of three different sizes are constructed. For each mitigation type, there are three replicates and all treatment sites are randomly located along the road segment while control sites are in road-free areas outside of the road effect zone.

an example measurement of interest i.e., relative population size, to be collected at treatment and control sites before and after the road and mitigation structures are constructed/modified. As suggested by van der Grift et al. (2013), the most informative measurement of interest is the trend over time in the size (or density) of the local population since this is most closely related to the outcome of real concern i.e., population viability. Note we are not suggesting that this is the only measurement of interest that can be collected. The type of data collected will depend on the species of concern, time and budget of the project, and whether or not the road and mitigation are constructed simultaneously. For example, road-kill counts cannot be collected before construction of a project where the road and mitigation are built simultaneously since there is no road for animals to be killed on at this stage. In addition, we do not include a spatial scale to our experimental design figures as these are intended to be example protocols to which modifications can be made. As noted by van der Grift et al. (2013), it is difficult to provide a guideline to determine the spatial scale of a study since the size of the road effect zone varies depending on the road effect being mitigated, the focal species, and the local habitat and topography.

is assumed that the species of interest is negatively impacted by roads. In general, for panels A–C, there are four scenarios after mitigation or modification to mitigation: (1) the mitigation/modification measures are 100% effective at mitigating road impacts and population size remains similar (A) or increases (B and C) to the level of the road-free control sites (i.e., no net loss/full mitigation); (2) the mitigation/modification measures partially mitigate road impacts and population size increases compared to the mitigation-free control sites (i.e., sites where the road is present but without mitigation) but does not reach the level of the road-free control sites (i.e., limited net loss/partial mitigation); (3) the mitigation/modification measures are not effective and population size remains similar to the mitigation-free control sites; and (4) the mitigation/modification measures are not effective and even worsen the situation by reducing population size compared to the mitigation-free control sites. Proper evaluations of the extent to which the full effect of roads have been mitigated (i.e., full mitigation) can only be made if road-free control sites are included (black dotted lines). Proper evaluations of the extent to which population size improves (i.e., partial mitigation/limited net loss) can only be made if mitigation-free control sites are included (orange dashed line) (i.e., how much better (or worse) is the mitigation/modification measures than no mitigation at all?). Proper evaluations of the extent to which a modification to an existing mitigation improves population size in comparison to the existing unmodified mitigation can only be made if modification-free control sites are included (green double lines) (i.e., how much better (or worse) is the modified mitigation than the existing mitigation?). Panel D depicts the situation where the existing mitigation is currently fully mitigating the effects of roads but researchers want to know if modification(s) made to the existing mitigation (i.e., reducing underpass width) could be as effective (and likely cheaper) (e.g., Do we need underpasses as big as they currently are or are more narrow underpasses as effective as the existing wide underpasses?). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For example, for a highly mobile species, the distance between treatment and control sites would likely be greater than for a less mobile species to ensure spatial independence (see van der Grift et al., 2013 for more details on selecting the appropriate spatial scale of the study). Therefore, certain elements of our example study designs may need to be modified to address individual projects.

Post-mitigation BACI experiments (initiated at the operation and maintenance stage) are possible as well if there is sufficient opportunity for replication. For example, existing crossing structures can be monitored before and after experimentally manipulating the sizes of the structures (i.e., narrowing structure width or height) and comparing those manipulated sites with unmanipulated (control) sites (Appendix B; Fig. 4D).

5.1.1. Case study 1

A new transportation corridor (GTA West) is being planned (2014) in southern Ontario, Canada. The planned corridor is a freeway with ≥4 lanes and is currently in Stage 2 of planning and environmental assessment. The Ontario Ministry of Transportation (MTO) has committed to working with members of the Ontario Road Ecology Group (OREG) and regulatory agencies to assess the viability of collaborating on a wildlife passage research project. OREG began communication with MTO in late 2008 for consideration of a BACI mitigation experiment on the GTA West freeway. The proposed experiment includes four treatment types: (1) extended stream crossings (i.e., allowing for terrestrial passage alongside the stream bed) without funnel fencing, (2) culverts without funnel fencing, (3) extended stream crossings with funnel fencing, and (4) culverts with funnel fencing. The mitigation would be installed where streams intersect the highway and each mitigation site would be paired with a randomly allocated control site located outside the road effect zone. Treatment type would be randomly allocated to stream crossings and all treatments would be replicated. This project would be the first of its kind, providing the opportunity to collect population trend data over time both before and after construction, on a range of wildlife species, to determine which, if any, mitigation will be effective at maintaining populations at pre-road conditions.

5.1.2. Case study 2

The Squirrel Glider (*Petaurus norfolcensis*) is an arboreal marsupial from eastern Australia whose primary mode of travel is by gliding between trees. Many populations are at risk of extinction because of extensive clearing of habitat for agriculture and urbanisation. In recent years, numerous road projects have further threatened the species, because treeless gaps >30–40 m in length can restrict glider movement (van der Ree and Bennett, 2003; van der Ree et al., 2003). However, the ability to assess and mitigate the impact of roads and traffic on Squirrel Gliders was hampered by a lack of information (but see van der Ree, 2006). Therefore, researchers from The Australian Research Centre for Urban Ecology, The University of Melbourne and Monash University, in partnership with VicRoads and the Australian Research Council, set up a BACI experiment to evaluate the effect of a freeway and subsequent mitigation on the movement, gene flow and survival rates of Squirrel Gliders. Capture-mark-recapture surveys, radiotracking and genetic analyses were conducted along the existing 4-lane divided Hume Freeway in rural south-eastern Australia, including sites with vegetated medians (treeless gap across the road < 20 m), unmitigated sites (gap > 50 m), and control sites away from the freeway (gaps < 15 m). Treatment and control sites were identical with the exception that the road at treatment sites was large, with higher traffic volumes and larger gaps than the road at control sites. Radiotracked gliders rarely crossed the freeway at unmitigated sites (van der Ree et al., 2010) and the survival of gliders at the freeway was approximately one third of those at control sites (McCall et al., 2010). Three glider poles and two rope bridges (Fig. 6) were then installed at sites where the treeless gap across the freeway exceeded 50 m. After mitigation, Squirrel Glider movement across the freeway at mitigated sites increased and matched sites with vegetated medians, while the unmitigated freeway remained a barrier. However, movement at all treatments – glider poles, rope bridges and vegetated medians – was still lower than across the narrow gap at control sites (Soanes et al., 2013), indicating that mitigation facilitated road-crossing, but did not fully restore it. The benefit of this study design, where poles and rope bridges were retrofitted to an existing road, allow careful measurement of the effectiveness of mitigation without the added complication of dealing with a simultaneous road expansion. The research is continuing, and includes a post-mitigation analysis of survival rates and an assessment of gene flow before and after mitigation.

5.2. Question 2: How many crossing structures should we build? I.e., how far apart should crossing structures be?

This question can be answered using a BACI experiment planned at the project development stage, if the proposed road is long enough to incorporate different road sections with different numbers of crossing structures per section. The proposed road would be divided into equal-sized zones to which researchers allocate different numbers of crossing structures (Fig. 7). Road zones should be far enough apart to ensure spatial independence, which will be influenced by the movement patterns of the target species. Ideally there should be replicate zones containing the same number of structures for each treatment (number of structures). This experimental design would be logistically very difficult to implement because of the length of road required to incorporate multiple segments, each long enough to contain multiple crossing structures, while being as similar as possible.

An alternative study design would be a post-mitigation construction BACI experiment on a road section with a sufficient number of mitigation structures. Random subsets of the structures could be temporarily closed to manipulate the effective number of crossing structures on the road (Appendix C). Data on population size (or other outcomes of interest) would be first collected at control and treatment sites before any structures are temporarily closed. Then, for example, at time 1, half the structures could be randomly selected to be closed and the populations would be measured again at the control and treatment sites. At time 2, an additional 25% of remaining open structures could be then closed, reducing the number of open structures to 25% of the total number of existing structures. The populations would be again measured at both control and treatment sites. The duration of pre-, during- and post-closure monitoring and the duration of the treatment itself will depend on the level of acceptable risk to the species of concern and the likely time for an effect to be observed.

5.3. Question 3: Is it more effective to install a small number of large-sized crossing structures or a large number of small-sized crossing structures?

A BACI experimental approach planned at the project development stage is the only possible option for addressing this question. As with question 2, the proposed road would be divided into equal-sized zones to which researchers allocate different numbers of crossing structures (Fig. 8). The number of replicates possible will depend on the total length of the proposed road. Similar to the previous example, this experiment will be very difficult to implement as it requires a long road, with sites as similar to each other as

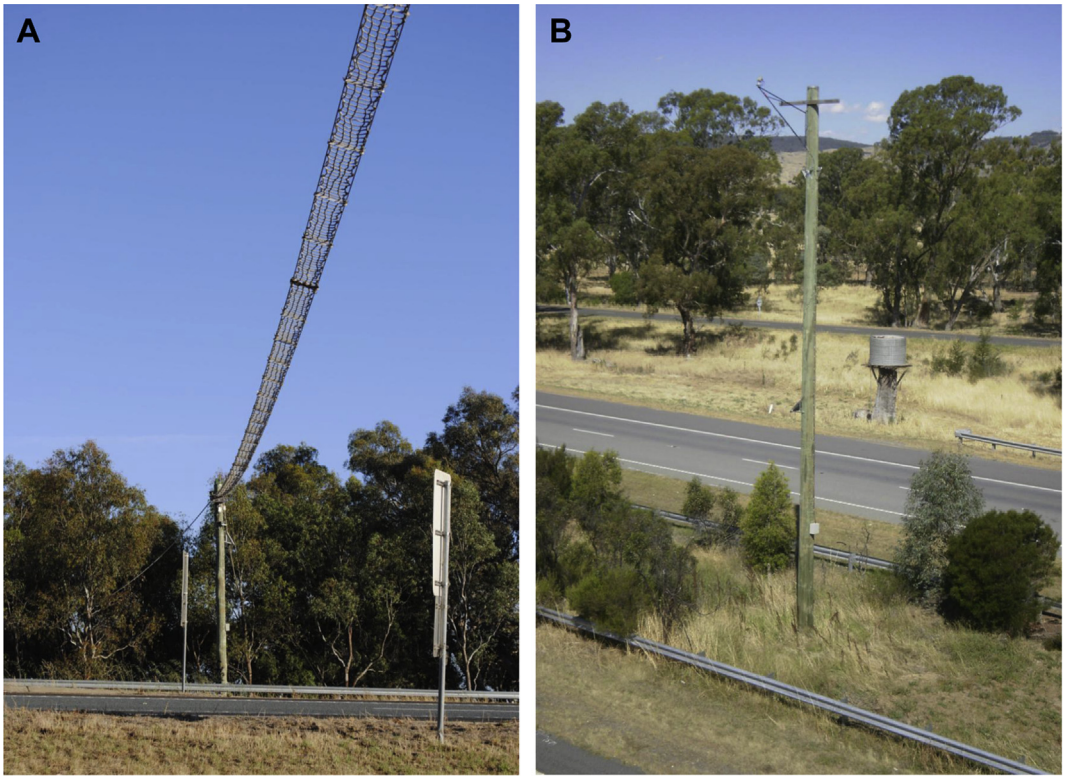

Fig. 6. Mitigation structures installed in a BACI experiment for case study 2. (A) Rope bridges and (B) glider poles installed along the Hume Freeway in south-east Australia to allow Squirrel Gliders to safely cross the freeway. Photos: R. van der Ree.

possible, and the ability to install many mitigation structures.

5.4. Question 4: How much barrier fencing is needed for a given length of road?

Similar to crossing structures, road planners also have questions about the effectiveness of barrier fencing that prevents wildlife from accessing the road, for example, how much fencing should there be for a given length of road. A BACI experiment where the proposed road would be divided into equal-sized zones to which researchers randomly allocate different lengths of fencing would be most effective (Fig. 9). The number of different possible treatments will depend on the total length of road planned and the project budget. Depending on the design of the fence (e.g., for amphibians vs. ungulates) and the terrain, this design is logistically easy to implement as an experiment, and as such is highly recommended. Furthermore, this experiment could be done at any time.

5.5. Question 5: Do we need funnel fencing to lead animals to crossing structures, and how long does such fencing have to be?

This question would be most effectively addressed at the project development stage where the road and mitigation measures are to be constructed simultaneously. A potential study design might, for example, include eight treatments involving combinations of two different crossing structure types (e.g., over- and under-pass), each with three different fencing lengths extending out from the crossing structures (e.g., long, medium, and short) (Fig. 10). Two of these eight treatments should include the two different crossing structure treatments without any fencing to compare with the fenced treatments (Fig. 10).

This question might also be at least partially addressed experimentally using a post-mitigation construction BACI design. For example, existing crossing structures can be monitored before and after installing funnel fencing of varying lengths and comparing those treatment sites with control sites (Appendix D).

5.5.1. Case study 3

Along a 24-km section of the St. Laurence Islands Parkway in eastern Ontario (near Saint Lawrence National Park), Canada, Cunnington et al. (2014) conducted a BACI post-construction experiment by temporarily modifying existing culverts to determine whether underpasses and/or funnel fencing reduce road mortality in anurans (frogs and toads). Study predictions were: (1) if the culverts alone reduce road mortality, than mortality should increase when anurans are not allowed to enter them (culverts with grates blocking their openings), and (2) if fencing is the key to effectiveness, mortality should decrease when fencing is placed on either side of culverts. In 2009, two modifications (treatments) were made to 10 of 20 existing culverts: (1) six culverts were grated preventing anurans from entering the culverts and (2) four culverts were left open but were fenced on either side (Fig. 11). Road kill surveys were conducted before (2008) and after culvert modifications (2009 and 2010). Ten control sites were selected at roaded sites where culverts were present but that had no grates or fencing to compare to treatment sites.

5.6. Question 6: How should we manage/manipulate the environment in the area around the crossing structures and fencing?

This question can be addressed at the operation and maintenance stage. A BACI experiment can be designed wherein different aspects of the crossing structure microhabitat are altered or added (e.g., manipulating tree cover, digging ponds, mowing vegetation

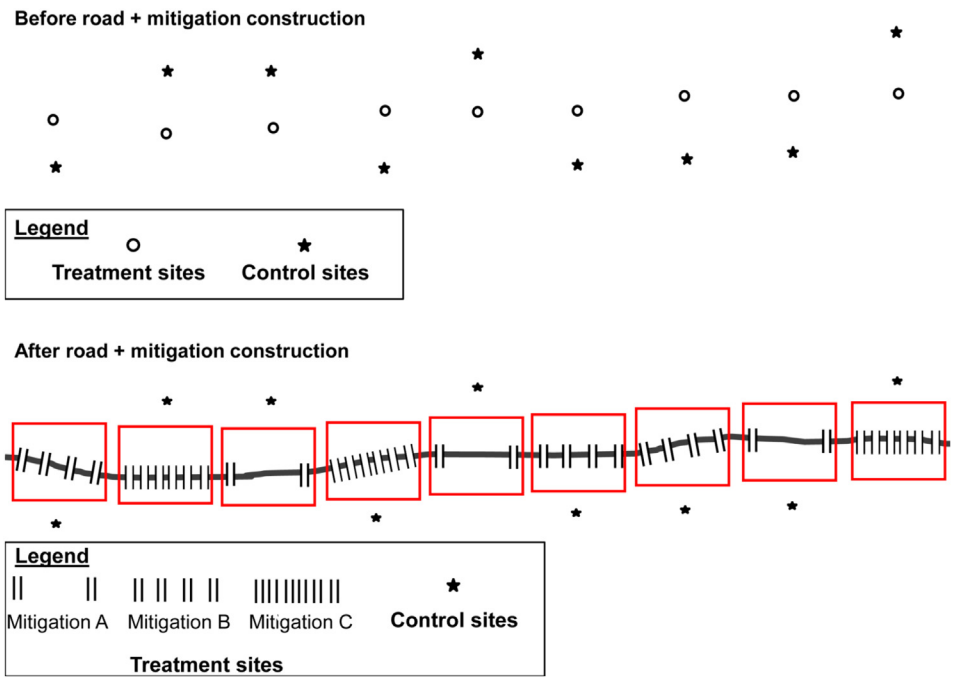

Fig. 7. BACI experimental design at the project development stage for Question 2: How many crossing structures should we build? I.e., how far apart should crossing structures be? Specific question: For a given length of road, what distance between crossing structures allows sufficient movement of species X such that the population size remains most similar to road-free conditions? In this example, the road and mitigation structures are constructed simultaneously. Data (e.g., relative population size) are collected at treatment and control sites before and after the road and mitigation structures are constructed. The proposed road would be divided into equal-sized zones (red boxes) to which researchers randomly allocate different numbers of crossing structures. Here three different road sections with 2, 4, 6 crossing structures (i.e., Mitigation A, B, or C) per section are constructed. For each of the three treatments there are three replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

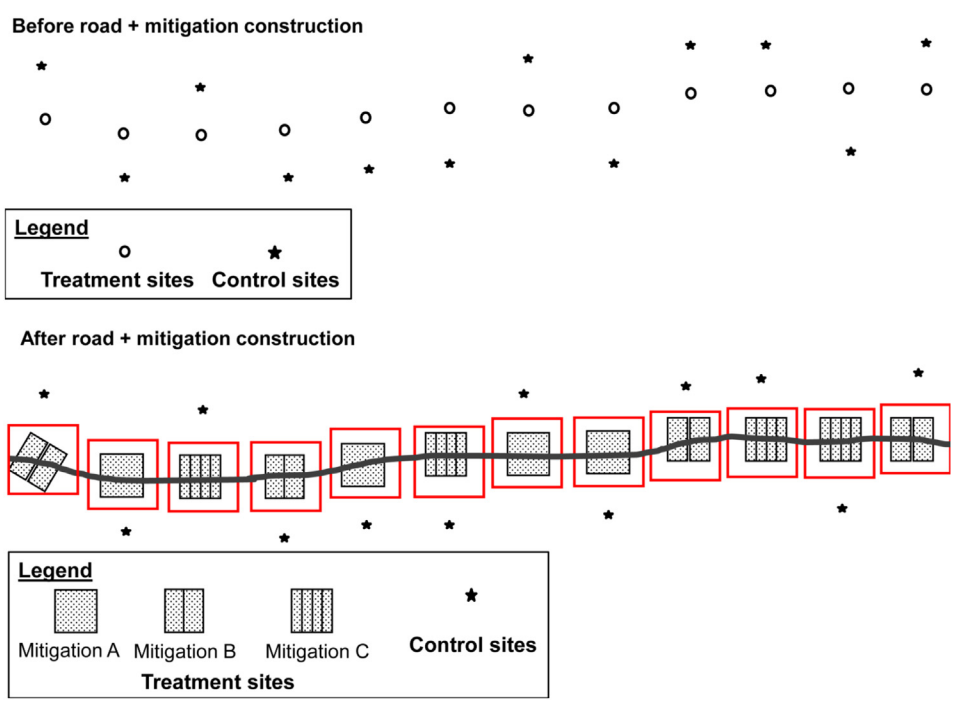

Fig. 8. BACI experimental design at the project development stage for Question 3: Is it more effective to install a small number of large-sized crossing structures or a large number of small-sized crossing structures? Specific question: For a given mitigated road length, what size and number of crossing structures allows sufficient movement of species X such that the population size remains the most similar to road-free conditions? In this example, the road and mitigation structures are constructed simultaneously. Data (e.g., relative population size) are collected at treatment and control sites before and after the road and mitigation structures are constructed. The proposed road would be divided into equal-sized zones (red boxes) to which researchers randomly allocate different numbers of crossing structures. Here three different road sections with different numbers and sizes of crossing structures (i.e., 1 large, 2 medium, 4 small) per section are constructed. For each of the three treatments there are four replicates. Other variants of this design could include also having zones that contain a mixture of different sizes of crossing structures (e.g., 1 large, 2 small). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

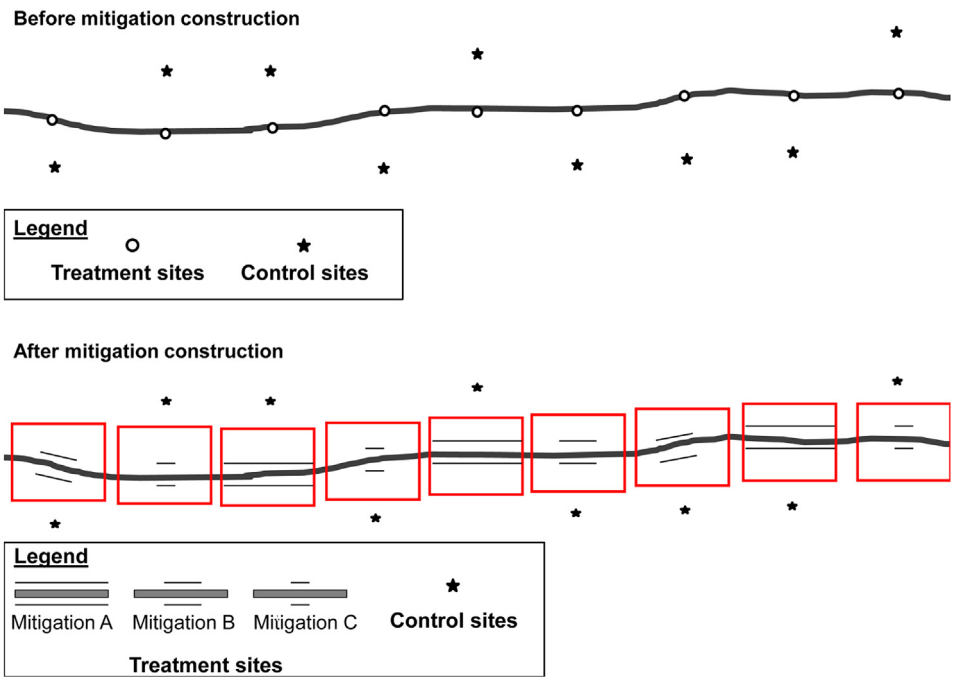

Fig. 9. BACI experimental design at the project development stage for Question 4: How much barrier fencing is needed for a given length of road? Specific question: For a given length of road, what proportion of the road should be fenced to reduce road mortality of species X such that the population size remains the most similar to conditions at road-free areas? In this example, the fences are constructed on an existing road. Data (e.g., relative population size) are collected at treatment and control sites before and after the fences are installed. The proposed road would be divided into equal-sized zones (red boxes) to which researchers randomly allocate different lengths of fencing. Here three different road sections with different proportions of fenced road (i.e., 100%, 50% or 25%) per section are constructed. For each of the three treatments, there are three replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

around underpass openings or along fencing etc.). These types of experiments are relatively easy to implement. For example, coarse woody debris can be added to half of the existing crossing structures and the data before and after the manipulation compared to equivalent data taken at unmanipulated sites (Fig. 12). However, designs using existing crossing structures require that the

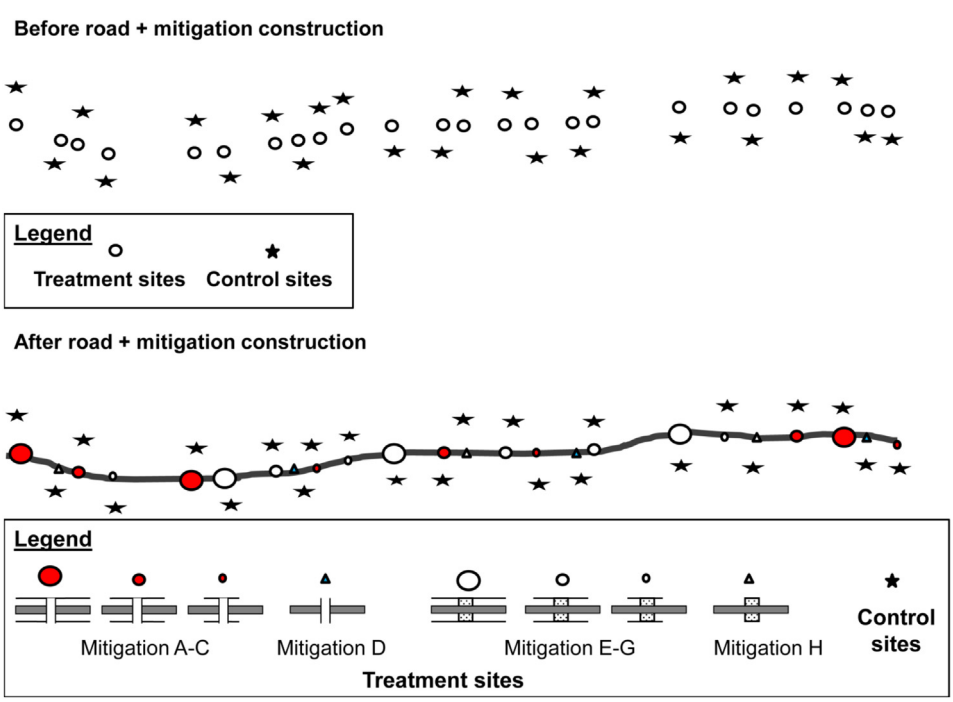

Fig. 10. BACI experimental design at the project development stage for Question 5: Do we need funnel fencing to lead animals to crossing structures, and how long does such fencing have to be? In this example, the road and mitigation structures are constructed simultaneously. Data (e.g., relative population size) are collected at treatment and control sites before and after the road and mitigation structures are constructed. Here two different crossing structure types (e.g., over- and under-pass), each with three different fencing lengths (e.g., long, medium, and short). Two of the eight treatments include an overpass (mitigation D) and underpass (mitigation H) without any fencing. For each treatment, there are three replicates and all treatment sites are randomly located along the road segment while control sites are in road-free areas outside of the road effect zone.

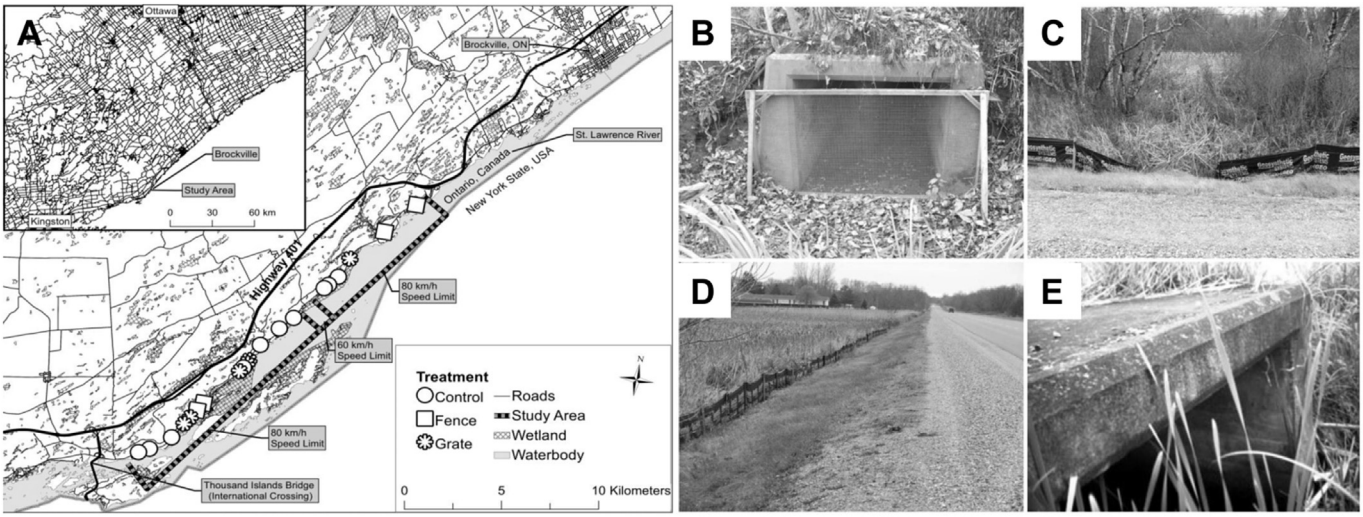

Fig. 11. (A) BACI post-construction experimental design for case study 3 along the St. Laurence Islands Parkway in eastern Ontario, Canada. Two treatment types were randomly allocated to twenty existing culverts along a 24-km road section: (B) grated culverts (n = 6) and (C and D) fenced open culverts (n = 4). Road kill survey data were compared before and after the mitigation modifications were installed at treatment sites and (E) control sites (unmodified culverts n = 10). Modified from Cunnington et al. (2014). Reprinted with permission from © 2014 Ecoscience (ECO-3673).

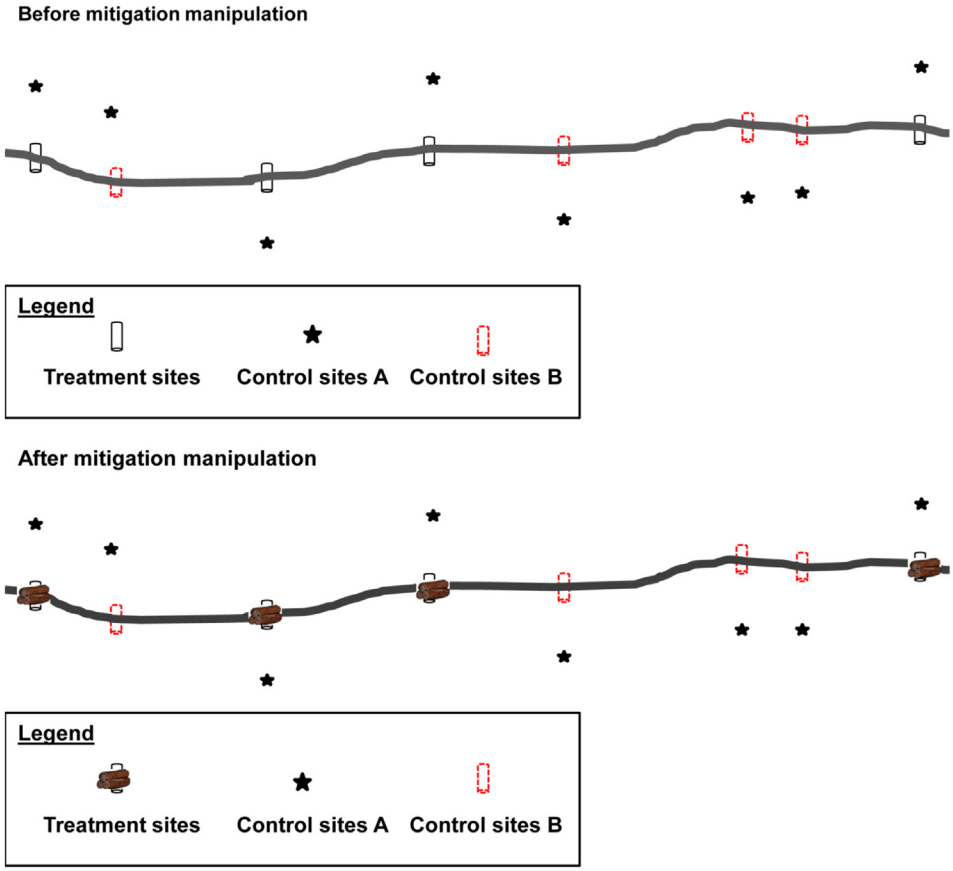

Fig. 12. BACI experimental design post-mitigation construction for Question 6: How should we manage/manipulate the environment in the area around the crossing structures and fencing? Specific question: Does the addition of coarse woody debris in culverts allow movement of species X such that the population size increases after the manipulation in comparison to the unmanipulated culverts? In this example, existing culverts are monitored (e.g., relative population size) before and after adding coarse woody debris to half of the randomly selected culverts. The unmanipulated culverts (control sites B) act as a second control type.

structures are relatively similar to each other or can be grouped into types.

Another common question related to managing the environment is how we should manage co-use of crossing structures (i.e., wildlife, and humans or domestic animals) (van der Ree and van der Grift, 2015). A potential post-construction BACI approach for this question can involve temporarily opening crossing structures to people and/or domestic animals (Appendix E). Another option here

could be to experiment with the rate of use of humans or domestic animals (e.g., 5 vs. 500 vs. 5000 users per day) instead of opening and closing the crossing structures.

5.6.1. Case study 4

It has been previously suggested that some taxa, such as small mammals, amphibians, reptiles, and many insects, often avoid open areas because they require cover (e.g., live vegetation, tree stumps, branches, or rocks) to reduce predation risk and because of the microhabitat it provides (e.g., temperature, moisture). In response to the lack of research on modifying crossing structures with coarse woody debris, Connolly-Newman et al. (2013) investigated the effect of cover on the abundance and movements of small mammals in ten large mammal underpasses along U.S. Hwy 93 North on the Flathead Indian Reservation, Montana, USA. Connolly-Newman et al. placed cover (dead tree limbs) inside five of the ten underpasses, while the remaining five underpasses served as control sites. Small mammal track tubes recorded abundance in and around the ten structures before and after underpass modification, thereby permitting inferences about the effects of the modification. More specifically, with only modification-free control sites, Connolly-Newman et al. (2013) can only address the questions: how much better (or worse) is the modified mitigation than the existing mitigation?

5.7. Question 7: Where should we place crossing structures and barrier fencing?

The placement of crossing structures and barrier fencing is believed to be important to mitigation efficacy (Clevenger and Ford, 2010). Wildlife crossing structures and fencing are typically located where animals naturally encounter roads, e.g., along streams or rivers, within a valley, and/or in areas that are vegetated, or at observed road mortality hotspots or landscape variables associated with the hotspots. For example, if animals tend to move along riparian corridors, placing mitigation measures where watercourses

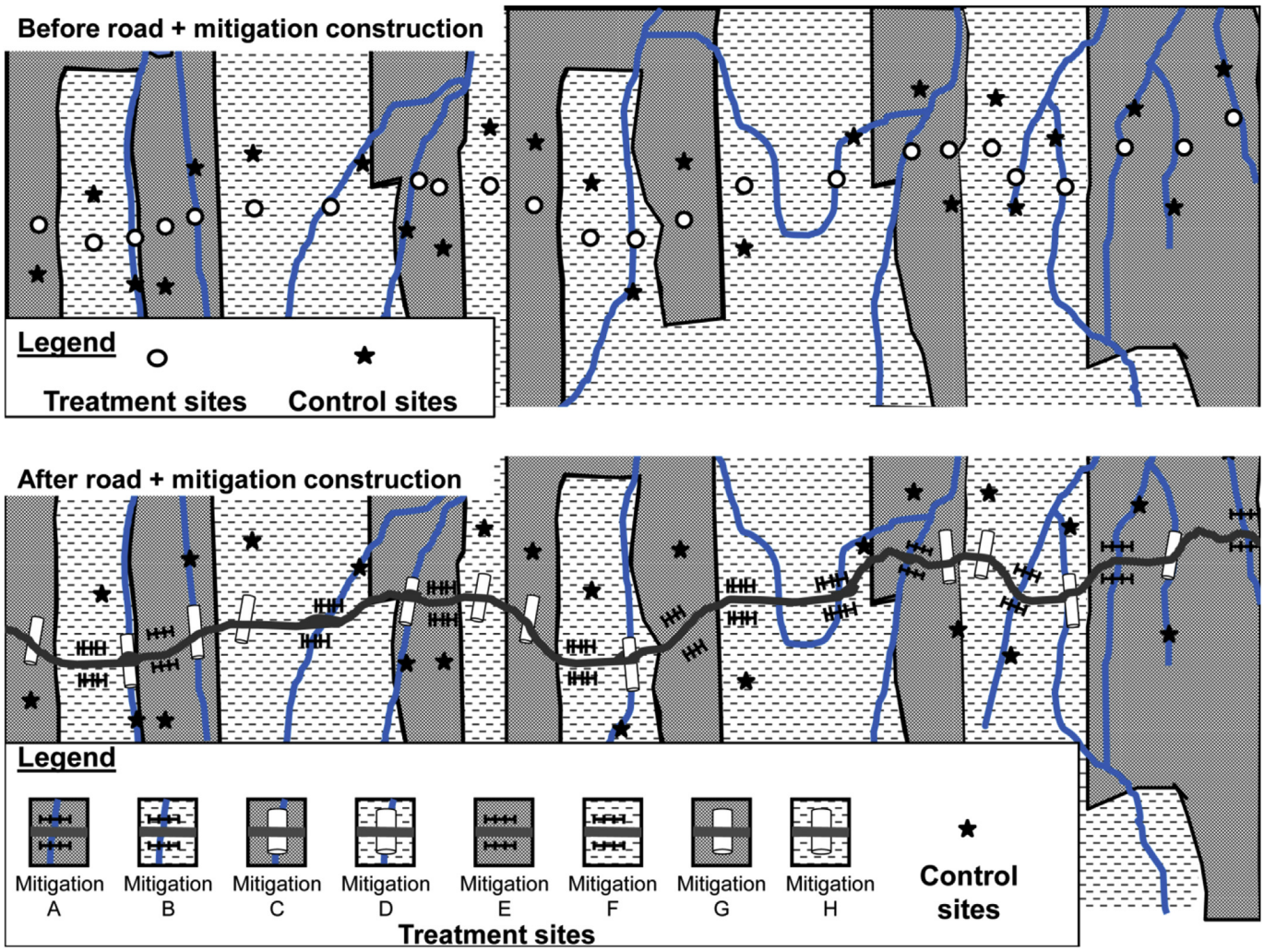

Fig. 13. BACI experimental design at the project development stage for Question 7: Where should we put crossing structures and barrier fencing? Specific questions: (1) Are mitigation structures placed at locations where streams intersect the proposed road (mitigation A - D) more effective at maintaining the population size of species X to levels similar to road-free areas compared to areas with similar mitigation but without streams (mitigation E–H)?, (2) Does mitigation effectiveness at stream vs. no stream locations depend on the type of mitigation structure installed (i.e., barrier fencing vs. culvert) and/or the cover type surrounding the mitigation structures (forest vs. crop fields)? In this example, the road and mitigation structures are constructed simultaneously. Data (e.g., relative population size) are collected at treatment and control sites before and after the road and mitigation structures are constructed. Here there are two different treatment types included (barrier fencing and culverts), each installed at two different locations (stream and no stream), each in two different cover types (forest and crop field). For each treatment, there are three replicates and all treatment sites are randomly located along the road segment while control sites are in road-free areas outside of the road effect zone.

intersect a proposed road should be more effective than in other locations without watercourses. Testing hypotheses about mitigation placement using a BACI experiment requires initiation at the project development stage (Fig. 13). This experiment will be very difficult to implement as it may be difficult for researchers to convince road planners to finance placement of structures in sites where one would *a priori* predict low mitigation effectiveness.

6. Challenges with experimentation

Using experimentation to evaluate road mitigation effectiveness does not come without challenges. First, ethical issues may arise when the experimental design includes mitigation measures that the researcher suspects (but has not yet demonstrated) to be ineffective. A possible solution to this issue might be to build all the structures to the design suspected to be effective, but install reversible modifications in some (randomly selected) that 'downgrade' them to designs that are assumed to be less effective. If it turns out that the researcher's 'gut feeling' was correct, the less effective structures can be readily upgraded (modifications removed) following the experiment. Second, for experiments that address questions requiring several years of data, researchers may need to design experiments such that road agencies do not need to wait several years for findings. For example, an experiment to determine the effectiveness of different types of crossing structures for improving connectivity for species X should be designed to provide useful information to road agencies within the first few years as well as population-level insights over the full duration of the experiment. Designing experiments in this way will help deliver useful information to managers and decisions makers both in the short term and long term of the study. Third, studies addressing questions that require large temporal scales, such as some of those addressed in this paper, are not compatible within most graduate programs (i.e., a single MSc or PhD thesis), post-doctorate fellowships, or short-term research contracts (van der Ree et al., 2011). As a consequence, researchers are often reluctant to carry them out or are unable to find stable funding for the required period. A fourth difficulty in planning mitigation experiments is that road planners may need to be convinced of the need for experimentation. For example, transportation agencies may not like the idea of installing some structures that are predicted to be less effective than others. The most feasible solution to this is for researchers to plan the range of structure types such that the expected 'worst' structure is still a design that is expected to be effective. The question then becomes, is it actually effective, or is another (e.g., taller, wider) design needed. Finally, many road agencies may even argue that this type of work is outside of their remit i.e., they are not research funding agencies. In summary, to help transportation agencies realize the potential gains in knowledge, performance, and cost saving, researchers must become more engaged with those setting policy for funding, planning, designing, building and maintaining the infrastructure (van der Ree et al., 2015b).

In situations where experimentation is not feasible, some information can still be derived from observational and modelling studies. For example, the use of global positioning system (GPS) and satellite-based telemetry to monitor wildlife movements (van Manen et al., 2001; Waller and Servheen, 2005) may be useful for addressing the question: Where should we place crossing structures and barrier fencing? Movement data can be collected from GPS-collared animals monitored before the construction of a new road, and virtual road crossing frequencies can be modelled as a function of cover type (e.g., forest, wetlands, streams, crop fields). This information can then be used to install mitigation structures in locations where animals are most likely to cross the future road. After the road and mitigation structures are constructed, monitoring of GPS-collared animal movements would continue to determine whether crossing locations change.

Modelling studies can be useful for making predictions about mitigation effectiveness, although only empirical studies can test these predictions. For example, van der Ree et al. (2009) used population viability modelling to predict the effectiveness of under-road tunnels installed to restore connectivity for the critically endangered Mountain Pygmy-possum in Australia (*Burramys parvus*; Mansergh and Scotts, 1989). They estimated that the tunnels reduce, but do not completely eliminate the negative effect of the road, with the density of the population affected by the mitigated road 15% lower than a comparable undivided population nearby (van der Ree et al., 2009). While population viability analyses (PVA) are typically strongly limited by lack of accurate population parameters (van der Ree et al., 2009), in the example above, the authors were fortunate to have a 20-year data set with which to parameterize their model. Spatially explicit population models can be used to predict optimal locations and types of mitigation structures, and the crossing rates that are likely to be required to achieve certain population-level outcomes (see van der Grift and Pouwels, 2006; Ascensão et al., 2013) but here, as elsewhere, strong tests of these hypotheses require comparison of modelled predictions with empirical data.

7. Concluding remarks

If road mitigation experiments became a standard part of any new or existing road project, how will the next 20–30 years look? Quite simply, improvements in road mitigation would increase rapidly. Each new mitigation experiment would build on the insights from past experiments (even those in other regions or on other species) and be incorporated in the design of new road mitigation experiments to ensure more effective mitigation. Currently there is simply not enough information on the effectiveness of mitigation measures to know, for example, the degree to which a bigger underpass is more or less effective at the population-level than a smaller underpass. If an experiment was designed to address this question, the next experiment could then compare that new standard with something even better, thus continually improving knowledge about mitigation effectiveness and increasing predictive power. If the information gained from experiments became a standard part of road upgrades, then fairly quickly road projects would improve ecological condition rather than worsen it. This might include the protection of road-less areas by preventing road construction (Selva et al., 2011), when it cannot be shown that road mitigation will be effective for all relevant species in the region.

It should be noted that compromise and trade-offs are inherent in the placement, design and construction of all road projects (Roberts and Sjolund, 2015). Multiple route options are evaluated during planning for their social, environmental and economic costs and benefits, and the final route and road-design is one where as many costs as possible are minimised; however it is inevitable that some specific impacts cannot be avoided. The same trade-offs and compromises are a part of experimentation. We are acutely aware that some of the study designs and recommendations outlined here are difficult to achieve (e.g., Figs. 7, 8 and 13) and while it would be ideal from an experimental or study design perspective to have them fully implemented, we realise that this may not always be possible. However, our thesis is that the science of road ecology will move forward significantly even if our recommendations are only partially implemented on the more logistically difficult designs, especially if adopted on numerous projects globally or fully implemented in a few studies (van der Ree et al., 2015b).

Furthermore, by taking the approach of coordinated distributed experiments (CDEs) to research and monitoring (e.g., Fraser et al., 2013), road agencies can significantly increase the quality of the study designs and boost sample sizes because they can more easily pool money for research across a number of projects and plan more comprehensive monitoring programmes that achieve superior outcomes. CDEs have been successfully used in other fields of ecology (Fraser et al., 2013). Standardized methods and controlled protocols allow for much stronger meta-analyses and hence insights into the effectiveness of road mitigation (van der Ree et al., 2015b).

In any case, for road agencies to make more informed and reliable decisions, we must modify our approach to evaluating the effectiveness of mitigation measures. Road mitigation experiments are the best systematic approach that can explicitly and more reliably reveal the effects of important design and landscape parameters (i.e., characteristics of the structure, road and traffic conditions, or adjacent landscape features) on mitigation effectiveness. By identifying and testing a theory, even simple theories or hypothesized relationships, the results of the experiments can be used to inform future mitigation. The research questions typically addressed about mitigation structures are not necessarily wrong, but with a little extra thought and resources, the same research could provide information relevant to different species, landscapes, roads and/or road projects (van der Ree et al., 2015b). These "laws" of road ecology will provide information that has relevance beyond the immediate question or problem. To do so, researchers need to not shy away from "riskier" research that requires high level collaborations despite the fact that road mitigation experiments may appear less "safe" for their research program (Houlahan, 1998). Experiments investigating mitigation effectiveness are a relevant and necessary way forward in road ecology, and this should be acknowledged by both the transportation agencies and research funding agencies.

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Appendices A–E. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2015.01.048.

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