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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 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.


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## 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

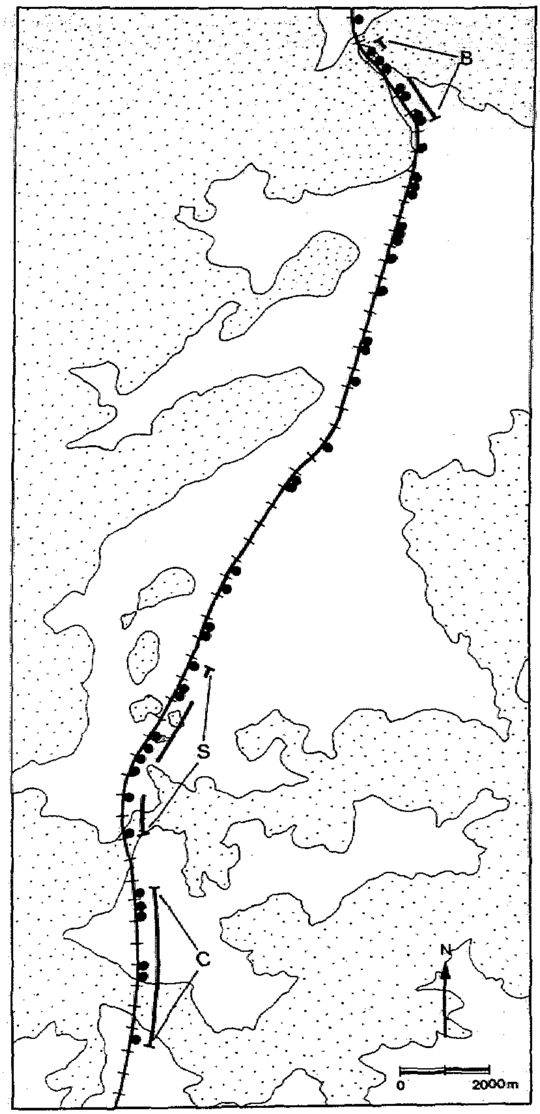


**Fig. 1.** Sketch of the study area, showing the approximate distribution of farmland (white) and scrubland (dotted). Circles indicate the location of transverse passages across the high speed railway (thick line). Sampled passages in scrubland (S), farmland (C) and border (B) habitats are marked with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

**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)

**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).

**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, $P < 0·05$), 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, $F = 19·47$, d.f. = 1,88, $P < 0·001$; Analysis 2, $F = 10·73$, d.f. = 1,58, $P < 0·005$). 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

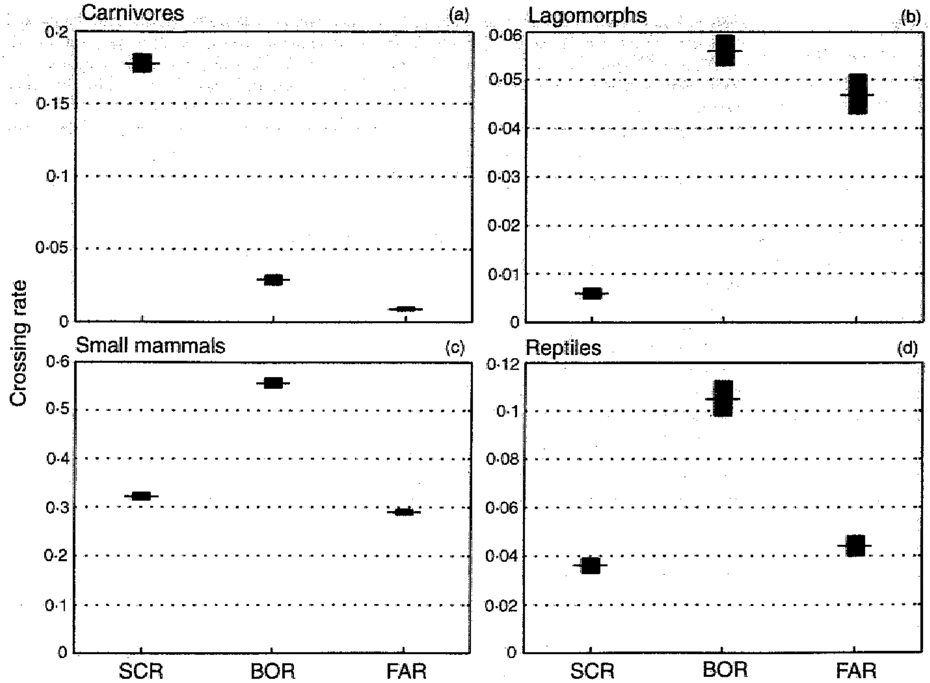


**Fig. 2.** Mean (and SE) monthly crossing rates (number of days with visits divided by the number of operative days for each passage) of terrestrial vertebrates as a function of the habitat location of passages: scrubland (SCR), border (BOR) and farmland (FAR). For each level, $n = 20$.

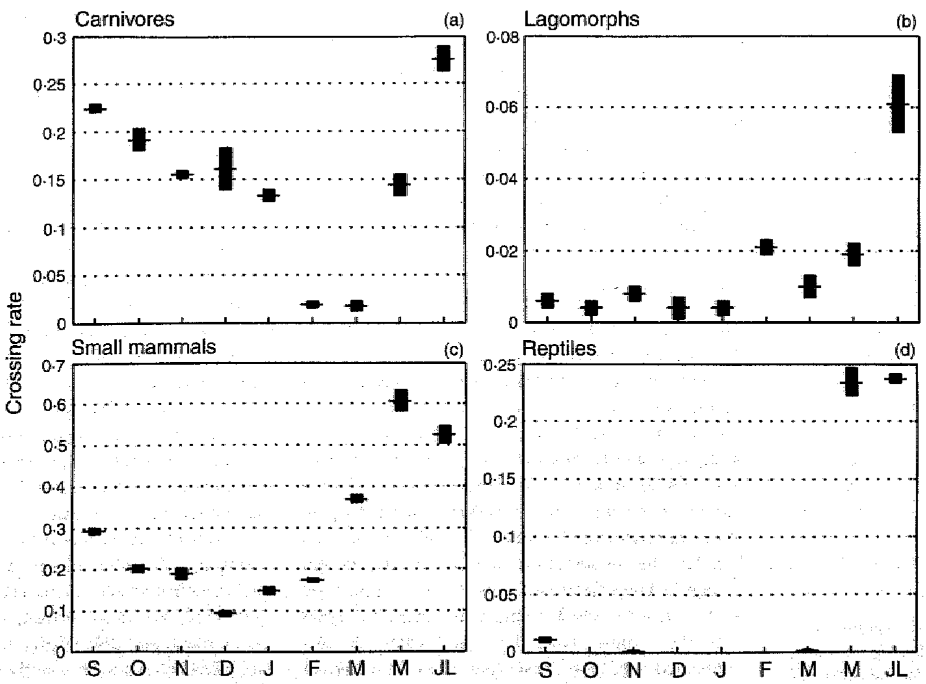


**Fig. 3.** Mean (and SE) monthly crossing rates (number of days with visits divided by the number of operative days for each passage) of terrestrial vertebrates as a function of the time of year (pooled habitats). For each level, $n = 10$.

**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


*Journal of Applied Ecology*, **33**, 1527–1540

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

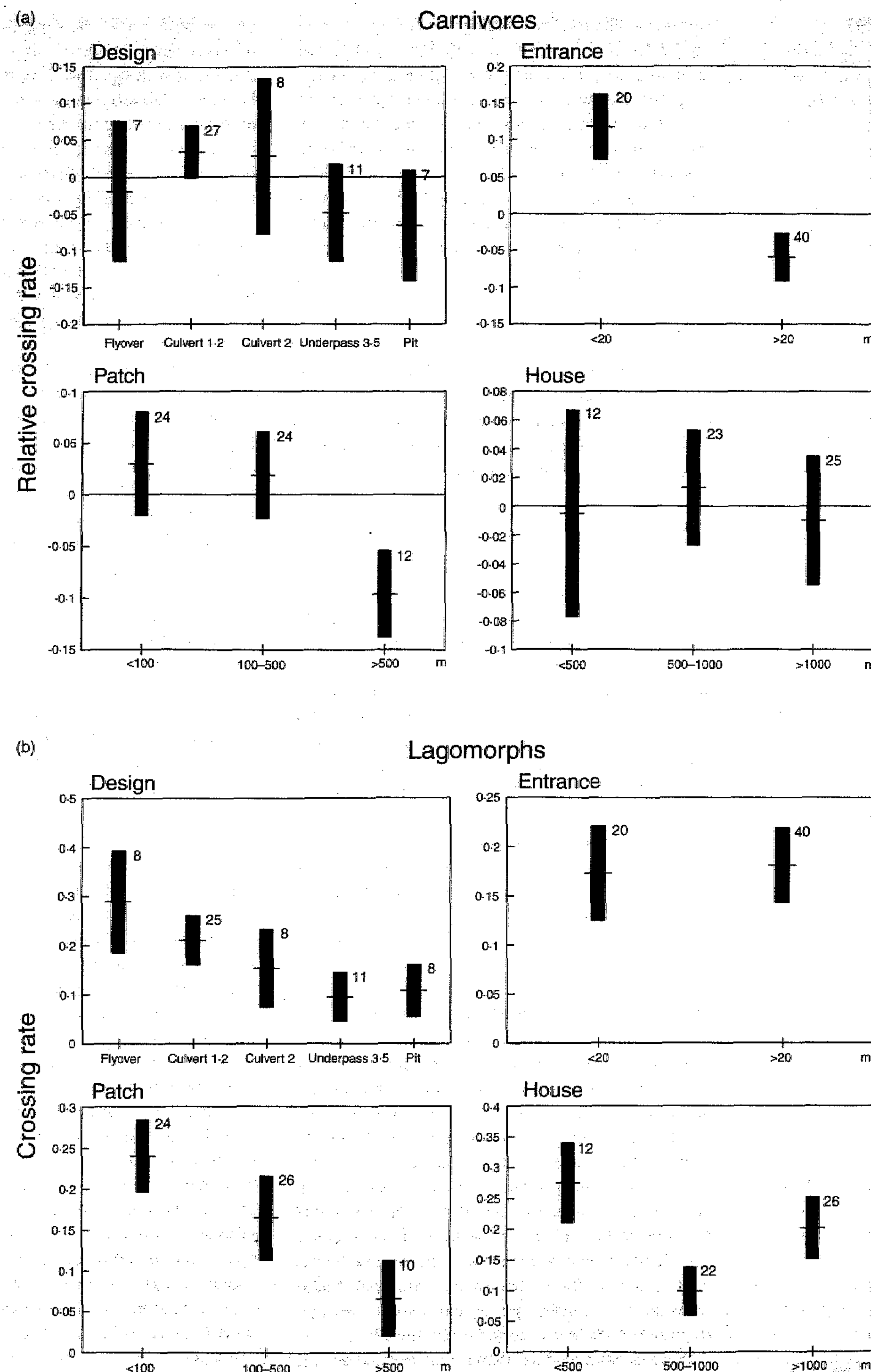


**Fig. 4.** Mean (and SE) vertebrate relative crossing rates (i.e. residuals) for different levels of factors indicating non-wildlife passage characteristics. For lagomorphs, original crossing rates are shown. Design: categories of passage structure and dimensions. Entrance: presence/absence of cover 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.

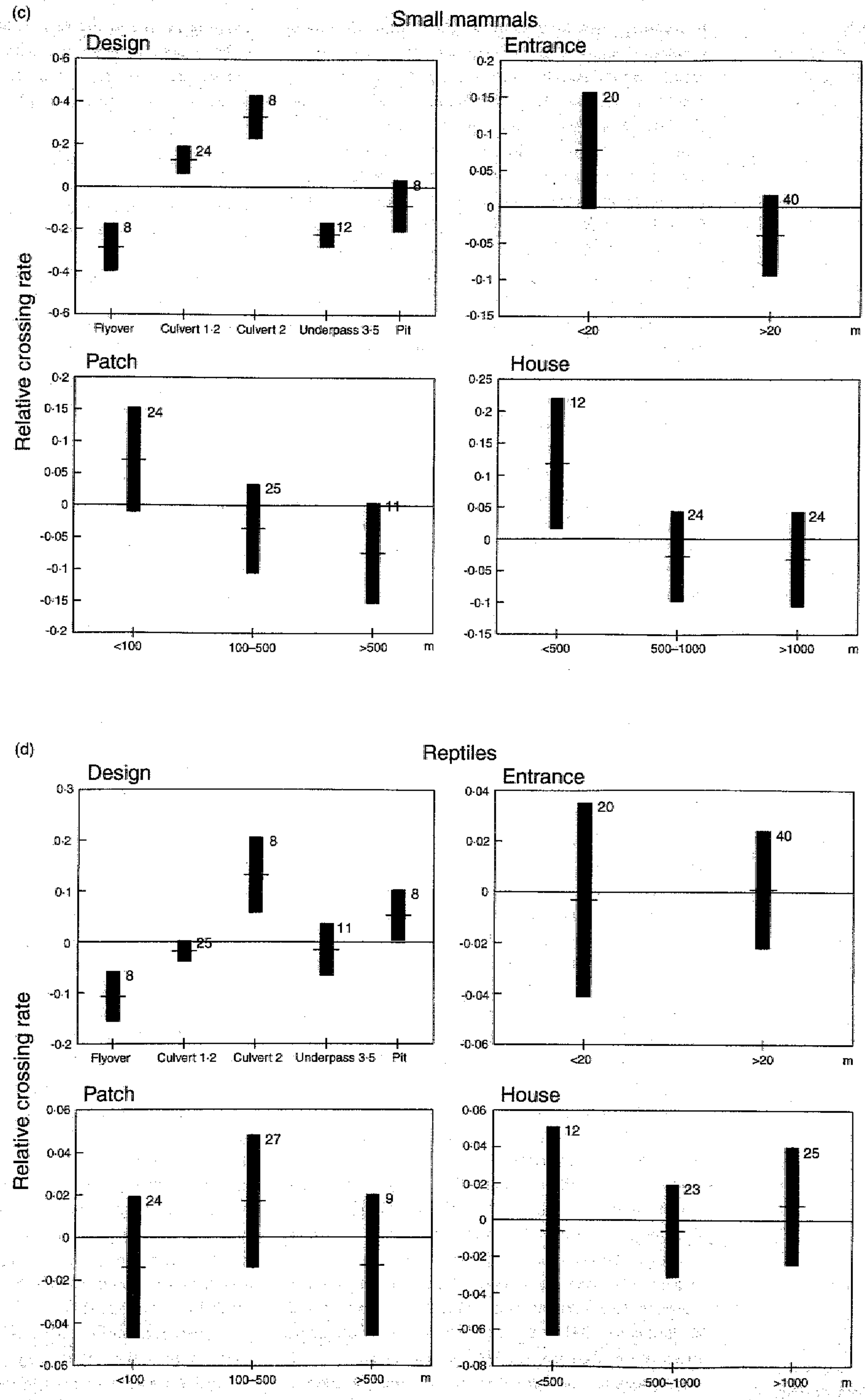
(c)
Small mammals
Design
Entrance
Patch
House
Relative crossing rate
Flyover
Culvert 1·2
Culvert 2
Underpass 3·5
Pit
<20
>20
m
<100
100–500
>500
<500
500–1000
>1000
(d)
Reptiles
Design
Entrance
Patch
House
Relative crossing rate




**Fig. 4.** *(cont.)*

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-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 as 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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