EFFECTIVENESS OF WILDLIFE CROSSING STRUCTURES AND ADAPTED CULVERTS IN A HIGHWAY IN NORTHWEST SPAIN

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Abstract: An intensive monitoring was carried out between June and September 2002 in different passage types across a highway in NW Spain in order to determine their use by terrestrial vertebrates. We used marble dust-beds to get footprints and a complementary photographic system to identify species which cannot be distinguished by tracks. Footprint data (820 passage-days) were collected from 82 passage structures (33 circular culverts, 10 adapted culverts, 14 wide underpasses, 7 wildlife underpasses, 16 overpasses and 2 ecoducts). The number of recorded vertebrates was high (1,424 tracks, 78.8% wildlife, and 21.2% related to human activity; and 490 photographic contacts, 54.3% and 45.7% respectively). Small mammals (mice, voles and shrews) used the passageways most frequently (414 tracks), followed by lagomorphs (Iberian hare, *Lepus granatensis,* and rabbit, *Oryctolagus cuniculus,* N= 158), canids (*Canis familiaris* and *C. lupus*, N = 142), fox (*Vulpes vulpes*, N= 137) and lacertids (*Lacerta* spp. and *Podarcis* spp., N= 73). Underpasses and non-wildlife-engineered overpasses were the most used structures. Differences were found in the selection of crossing structures by the two lagomorphs, hares selecting wildlife underpasses while rabbits did not show a significative preference. Anurans and ophidians (Fam. *Colubridae* and *Viperidae*) showed a clear preference for adapted culverts, avoiding overpasses. Lacertids and small mammals crossed most frequently through circular culverts, but generally used all passage types. Hedgehog (*Erinaceus europaeus*) and Badger (*Meles meles*) always selected highway underpasses while small mustelids (*Mustela nivalis* plus *M. erminea*) used culverts exclusively. Finally, foxes used all types of crossing structures, showing a preference for wide underpasses. Red deer (*Cervus elaphus*) were found to use wide passages under or above the road, and more frequently ecoducts, but roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa)* were never detected in crossing structures though very abundant in the area.

Four recommendations arise from the study: (1) as a differential use among animal species has been found, it is necessary to keep several crossing structure types; (2) functional structures of the motorway (non-wildlife-engineered) play an important role in the permeability of the road, and their adaptation for wildlife enhances their use by some taxa. Thus, the adaptation of structures related to human activity plays a key role in the achievement of the best solution from a benefit-to-cost point of view. (3) The set of passageways necessary to mitigate the barrier effect suffered by a known mammal community can be established taking into account the animal sizes and the wideness and relative position of crossing structures to the road (over *vs.* under); however ,(4) it seems that some species may not cross through structures up to 20m wide, and thus some of the passageways should be wider (in the form of tunnels and/or viaducts).

Introduction

Most European countries have extensive transportation networks. However, in comparison with countries in Central Europe, the road and railway networks are poorly developed in Spain, though they are expanding quickly (i.e., 1,300km/year in 1987-2002), and they comprised 177,000km by the year 2000 (0.35km by km^2, Mº Fomento 2000). Since the European Environmental Impact Assessment Directive (85/337/EEC) was passed, the Spanish administration has increasingly forced the establishment of mitigation measures for the barrier effect to the road and railway projects to be approved. However, because of the high costs imposed on such projects by fauna passes, little effort has been devoted to assess of their effectivity. Thus, the improvement of their design and even the justification of their need are restricted by the lack of information on effectiveness.

Wildlife passes should help the preservation of local animal populations thanks to their capacity to connect habitats, a function that contributes to the restoration of home ranges and migratory routes as well as to the diminution of road kills (Keller and Pfister 1997). Therefore, the correct functionality of fauna passes should be assessed in terms of their effectiveness in the re-establishment of vertebrate movements with a special focus on the species that are to be promoted (Saunders *et al.* 1991, Beier and Loe 1992, Clergeau 1993, De Santo and Smith 1993, Velasco *et al*. 1995, Rodríguez *et al*. 1996). Though the number of studies and recommendations on the subject is high (see the review by Forman *et al.* 2002), we are still far from having a definitive design to alleviate the barrier effect suffered by a vertebrate community. In this respect, it is important to stress the relevance of two facts: the potential complementarity among passageway types and the final cost of the whole permeability system.

Given the necessity of the transportation infrastructure, several trades-offs arise regarding how to best mitigate the negative effect of the road or railway on animal populations. The first one is its cost in relation to effectiveness. The relevance of pass wideness as a recognized as determinant for the use by big as well as small vertebrates and the construction of wide crossing structures, therefore, are recommended (Reed *et al.* 1975; Reed 1981; Veenbass and Brandjes 1999). However, the cost of fauna passes increases as its size does, and the number of feasible wide crossing structures will be always restricted. Assuming the normal situation of a limited budget and a reasonable knowledge of the vertebrate community in one area, technicians face the question of what is the best solution from a vertebrate community connectivity point of view to maximize the size of fauna passes or to maximize their number?

The second trade-off is related to the potential selective nature of different passageway types. A differential use of crossing structures has been found in several studies (Reed 1981; Singer & Doherty 1985; Vassant *et al.* 1993a,b; Foster and Humphrey 1995; Rosell and Velasco 1999), and it potentially has community-scale effects. Thus, the investment on any type of crossing structure improves the connectivity for a species, but what will be the effect on other species? Is it best to reach a suboptimal solution for the majority of the species even though it may play against some of them? Other trade-offs in the detailed design of fauna passes exist and have potential implications for their effectiveness (Oxley *et al.* 1974; Madder 1984; Camby and Maizeret, 1987), though they are linked to those already mentioned and/or have a secondary relevance.

Within such a framework, our study focuses on a modest but interesting point: the evaluation of the use by fauna of crossing structures in a motorway of Northwest Spain. We compare the use by vertebrates of crossing structures specifically designed for them as well as "functional" (non-wildlife-engineered) structures of the motorway and some modifications of the latter to enhance their use by animals. The results should be applicable not only for Spain but for vast regions of Europe, as most vertebrates in the area have large, geographic distributions (Bang and Dahlström 1995; Blanco 1998).

Methods

Study Area

The study has been conducted along 71.5km of the Rías Baixas motorway (A-52), between the kilometric posts 2,75 and 74,25. The motorway runs across NW Spain, and it was built in 1993-2000. Climate is mild mediterranean with an average temperature of 11ºC and ca. 700mm precipitation (Castillo and Ruiz Beltrán 1977). Cereal dry-crops dominate the first 20km of the study area and are substituted by suboceanic holm oak (*Quercus rotundifolia*) woods and scrubs in the following 30km. The rest of the road runs across *Quercus pyrenaica* forests, tall scrubs dominated by species of *Cytisus* and *Erica*, low scrubs (*Genista tridentata, Halimium ocymoides, and H. lasianthum*) and wet meadows.

Types of Crossing Structures

The six types of crossing structures monitored in the motorway (N=82) and their main characteristics are presented in table 1.

Table 1
Main characteristics of the crossing structures analyzed in the study.

Structure type	Section	Size	Openness index	Specificity	N
Circular culverts	Circular	D: 1.80	0.04-0.09	F	33 (16)
Adapted culvert	Rectangular	W: 2- 3; H: 2	0.05-0.19	M	10 (5)
Wide underpasses	Rectangular	W: 4-9; H: 4-6	0.37-3.31	M	14 (9)
Wildlife underpasses	Rectangular	W: 20; H: 5-7	1.17-4.04	S	7 (6)
Overpasses	-	W: 7- 8	-	F	16 (9)
Wildlife overpasses	-	W: 16 (center) 20 (ends)	-	S	2 (2)

The structures are grouped in the types used along the paper and the total number of them monitored for footprints presented together with that of those provided with the photographic system (in brackets). Sizes are presented in meters for diameter (D), width (W) and/or height (H) and openness as the section to length ratio. The three specificity levels differentiated are functional or non-wildlife engineered (F), modified (M) and specifically designed for fauna (S).

Culverts are concrete pipes that collect running water from the roadsides as well as from creeks. We distinguish between the traditional circular culverts and adapted culverts (rectangular), as these represent the vertebrate-adapted sort of structures thanks to their flat-enlarged base. Underpasses also have rectangular sections and they are built to restore the connection of rural tracks and small roads. Wide underpasses are non-wildlife-engineered passages with square or rectangular sections designed for vehicle traffic. Wildlife underpasses are not crossed by tracks and have a gap in the ceiling between lanes that allows some natural illumination to reach the ground to promote plant growth. Overpasses are bridges that restore road or track connections over the motorway. They are designed for traffic, but they can be used by animals as well. Wildlife overpasses (hourglass-shape overpasses in our case) are exclusive for fauna, and they have been planted with grass and low stature scrubs (*Spartium junceum*). Though none of the wildlife overpasses connected tracks, they were used by vehicles in some occasions.

Five sections of the motorway (ca. 7km each) were selected to conduct the monitoring. The selection was aimed at having a representation of the three traversed landscapes with an over-representation of the two forest-dominated habitats due to their higher abundance and diversity of vertebrates. Thus, one study section was located within the crop-dominated area and two in each of the more forested landscapes. The selection of structures to monitor within each section was carried out with two premises: (1) the inclusion of all specific designs in the section, and (2) the inclusion of representatives from all crossing structure types.

Passageway Monitoring

Monitoring was carried out between the last week of June and the first of September 2002. Detection of crossing structure use by animals was based on track analysis and supplemented by the use of a photographic system specifically designed for the occasion. Marble dust was selected as an experimental tracking ground due to its odorless nature and the high quality of footprints it renders due to its density (Yanes *et al*. 1995). Control marble dust beds 1m wide and 3-10mm depth were laid down covering the whole passageway width near its mid-point (fig. 1). Footprint monitoring lasted in each crossing structure until 10 valid control-days were obtained, as those days in which weather conditions did not allow correct footprinting were not taken into account. Daily monitoring consisted of the identification of the number of tracks, species and crossing direction, following Bang and Dahlström (1995), Strachan (1995), Sanz (1996) and Blanco (1998) for track identification.

Fig. 1. Marble dust beds used for footprint monitoring in a wildlife underpass and a circular culvert. In both cases dust beds are 1m wide.

Some tracks could not be identified at the species level, and identification had to be carried out for species groups in the following taxa:

- Anurans: includes all frog and toad species
- Small mustelids: may include tracks from weasel (*Mustela nivalis*) and stoat (*Mustela erminea*)
- Cats: encompasses domestic cat (*Felis catus*) and european wildcat (*Felis silvestris*)
- Lacertids: several species of lizards and small lizards (*Lacerta* spp. and *Podarcis* spp.)
- Lagomorphs: combines the tracks of rabbit (*Oryctolagus cuniculus*) and Iberian hare (*Lepus granatensis*)
- Ophidians: several species belonging to the Fam. *Colubridae* and *Viperidae*
- Canids: include dog (*Canis familiaris*) as well as wolf (*Canis lupus*) tracks
- Rats: include *Rattus* spp
- Water vole: include a *Arvicola sapidus* and maybe *A. terrestris*
- Small mammals: mice, shrew and vole species

In 47 crossing structures (57% of total, see their distribution among types in table 1) a photographic system was used simultaneously. The photographic system resembles those evaluated by Hernández et al. (1997) and is composed of three elements: an infra-red barrier with active sensors at ground level, a digital camera (Sanyo VPC R1) and an electronic control connecting both. The photographic system allowed the distinction between rabbits and hares, domestic and wild cats, dogs and wolves, and weasels from stoats.

Data Analysis

The basic data handled to analyze the use of crossing structures by different animal species have been the frequency obtained from the 10-day track monitoring (defined as the number of days the species was detected in each passageway). Only data from wild and potentially feral animals (dogs and cats) were taken into account. Data from photomonitoring are used only as complementary information for the species that could not be distinguished by tracks.

The differential use of structure types has been analyzed with a Kruskal-Wallis test due to the lack of normality in datasets. Infrequent species (in less than 10% of passageways) and the two wildlife overpasses have not been introduced in these analyses as the low sample size preclude the unravelling of significant differences. The results of tests are presented with the chi-squared value due to the large sample size.

A use index (UI) has been computed to facilitate the comparison of relative use without bias linked to sample size. The use index has been defined as:

eqn.1 $$UI = (n_{ij}/N_j)/(n_{Ti}/N_T)$$

in which n_{ij} is the number of day-detections of the i-species at structures of j-type, N_j is the number of j-type structures monitored, n_{Ti} is the number of day-detections of the i-species in all structures, and N_T is the total number of monitored structures.

This index compares the number of records in any structure type with the expected one based in the whole dataset, one being the reference value. This index has been applied to structure types independently as well as for the comparison of overpasses vs. underpasses, fauna-specific vs. mixed use, and narrow (<2m) vs. wide (>2m) as these are comparisons frequently found in literature (Foster and Humphrey 1995, Yanes et al. 1995, Rodríguez et al. 1997, Veenbaas and Brandjes 1999).

Results

Species Using Passageways

The total number of tracks recorded was 1,424 and 78.8 percent of them (1,122) belonged to wild and feral animals. Evidences of human use were found in all structure types, with non-wildlife-engineered over- and underpasses totaling 92 percent of their tracks. The photographic system detected 490 crossings, 54.3 percent of which corresponded to wild animals.

The 82 monitored passageways (820 control-days) thus registered an average daily use of 1.37 tracks/structure-day. Small mammals (mice, voles and shrews) are the animals most frequently found using the crossing structures with a total of 414 records (36.9%). Lagomorphs were the second most frequent group, with 158 records (14.1%), followed by canids and red fox with 142 (12.7%) and 137 records (12.2%), respectively. Lacertids were detected in 73 occasions (6.5%), and the rest of the species did not reach 5 percent of records.

Crossing Structure Selection

Underpasses were the most frequently used crossing structure type (UI=1.10), followed by culverts and overpasses. Figure 2 also shows a more intensive use of non-wildlife engineered over and under passes. However, the use of all structure types but ecoducts (wildlife-engineered overpasses, with a UI=0.62) is close to expectation.

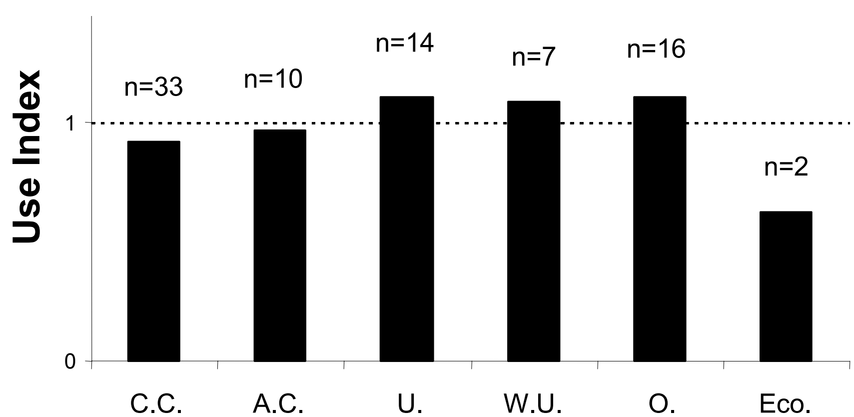

Fig. 2. Use index recorded in the five types of crossing structures differentiated in the study. CC: circular culverts, AC: adapted culverts, U: wide underpasses; WU, wildlife underpasses, O: overpasses and Eco: ecoducts. n: number of monitored structures.

Structure Type Selection by Species

Lagomorphs

Lagomorphs showed a differential use of crossing structure types (Fig. 2, Chi=31.61; 4 d.f.; P<0.001). The pass width seems to be the determinant factor for rabbits and hares, as the use index in wide structures (UI=1.89) is ten times bigger than in narrow structures. Open span and wildlife underpasses rank highest in use, though overpasses are also used.

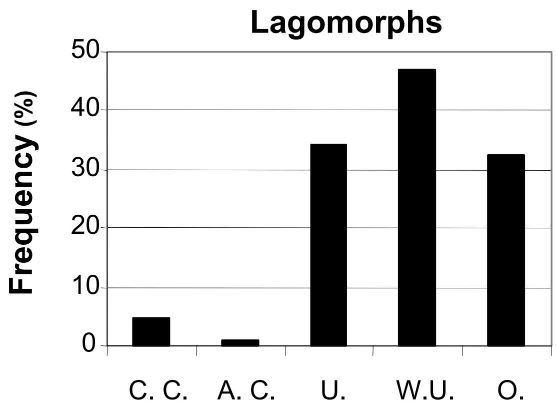

Fig. 3. Use frequency of different structure types by lagomorphs. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

The photographic system allowed the recognition of hares and rabbits (fig. 4). Thus, 60% percent of pictures (N=50) were from Iberian hares that showed a differential use among structure types (Chi=9.97; 4 d.f.; P=0.041). Hares use overpasses (UI=1.18) more frequently than underpasses (UI=0.87) and non-wildlife-engineered (UI=1.11) more than wildlife-specific structures (UI=0.76). Rabbits did not show significantly different use of structure types (chi = 7.852, 1 d.f., P = 0.097), but data suggest a slight selection of underpasses (UI= 1.47) faced to overpasses (UI= 0.35), and wildlife-engineered structures in general (UI= 2.28).

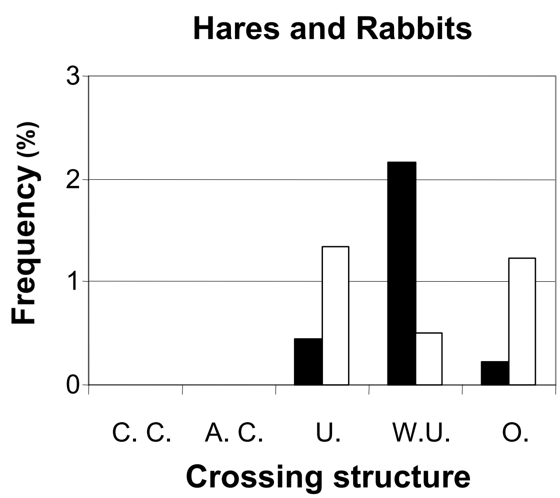

Fig. 4. Use frequency of different structure types by rabbits (empty bars) and hares (solid). CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Anurans, lacertids and Ophidians

Amphibians used all types of crossing structures, and no significant differences were found in their use (fig. 5.; Chi= 4.48; 4 d.f.; P = 0.344). Adapted culverts were slightly more used (UI=3.51) followed by wide underpasses (UI= 1.05) and circular culverts (UI= 0.71). Therefore, there is also a tendency for amphibians to use underpasses (UI=1.39) more than structures over the motorway (UI=0.54).

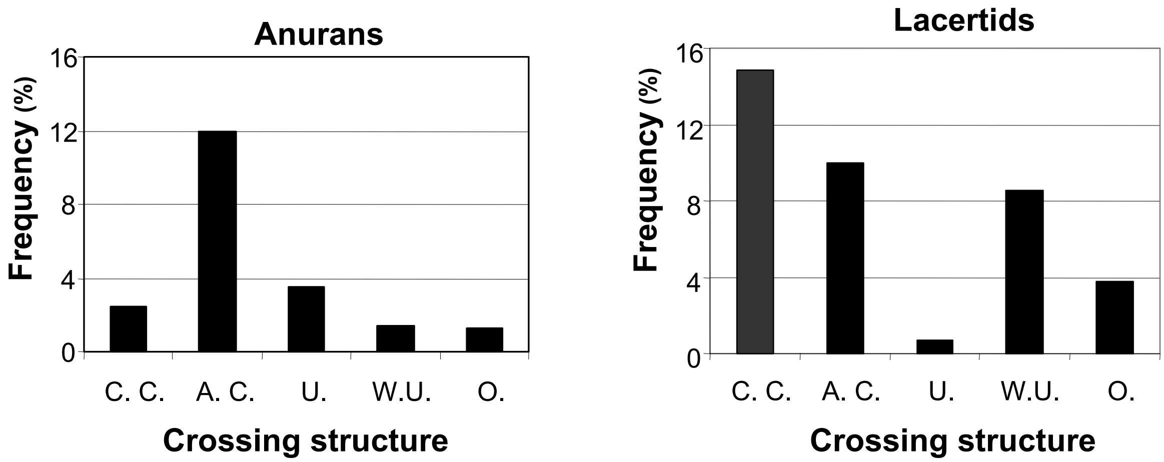

Fig. 5. Use frequency of different structure types by anurans and lacertids. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Lacertids (73 records) also used all structure types with significant differences among them (Chi=13.15; 4 d.f.; P = 0.011). The highest crossing frequency was found in circular culverts (UI= 1.67) and a preference for narrow structures (UI=1.54) over wider ones (UI= 0.40) is noticeable. Similarily, lacertids were found to cross more frequently through wildlife engineered structures (UI= 2.17) than through the multi-purpose ones (UI= 0.65). No selection seem to occur between over and underpasses.

Ophidians were detected in only nine cases, precluding the formal test for preferences. Their tracks were found in all but wildlife-engineered passes, and adapted culverts had the highest use index (UI= 4.56).

Small Mammals and Rats

Small mammals (mice, voles and shrews) were found in all structure types but show relevant differences among them (fig.6.;Chi=30.94; 4 d.f.; P<0.001). Thus circular culverts (UI=1.34) and non-wildlife engineered overpasses (UI=1.28) rank highest, and wide passageways are selected over narrower ones (UI=1.24 and 0.74 respectively). The low use of wildlife engineered structures (UI<0.20) is noteworthy.

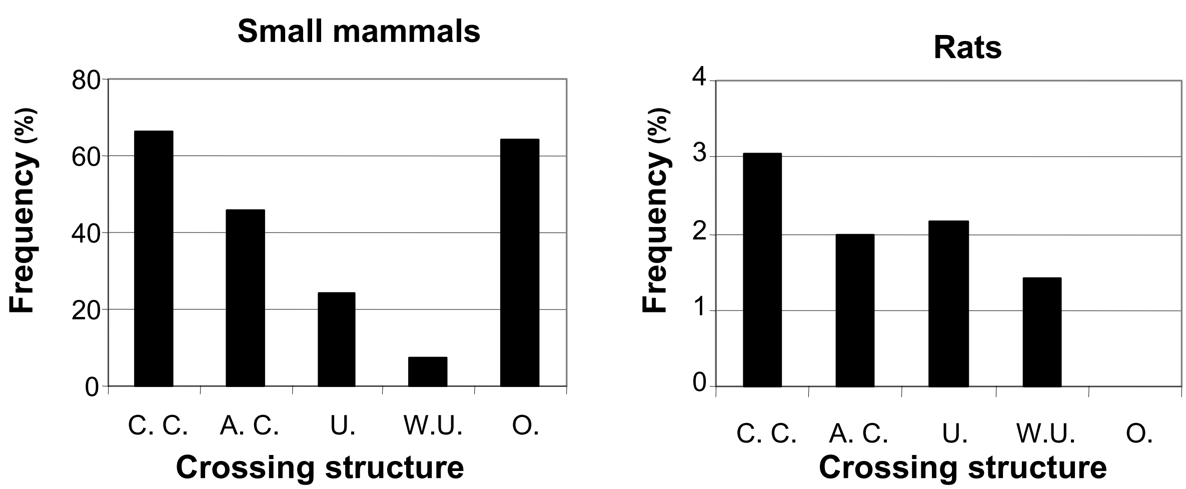

Fig. 6. Use frequency of different structure types by small mammals and rats. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Rats showed a preferential use of circular culverts (UI=1.55) and narrow passageways, but differences among all types were not significant (Chi=4.25; 4 d.f.; P=0.373). They were never detected in overpasses nor in ecoducts.

Western Hedgehog *(Erinaceus europaeus)* and Eurasian Badger *(Meles meles)*

All hedgehog records were found in structures under the motorway, mainly in wildlife-engineered underpasses (UI= 5.86, fig. 7.). The use differed significantly among structure types (Chi=9.74; 4 d.f.; P=0.045) with a tendency to select wide passes (UI= 1.75), though circular culverts were also used (UI= 0.41).

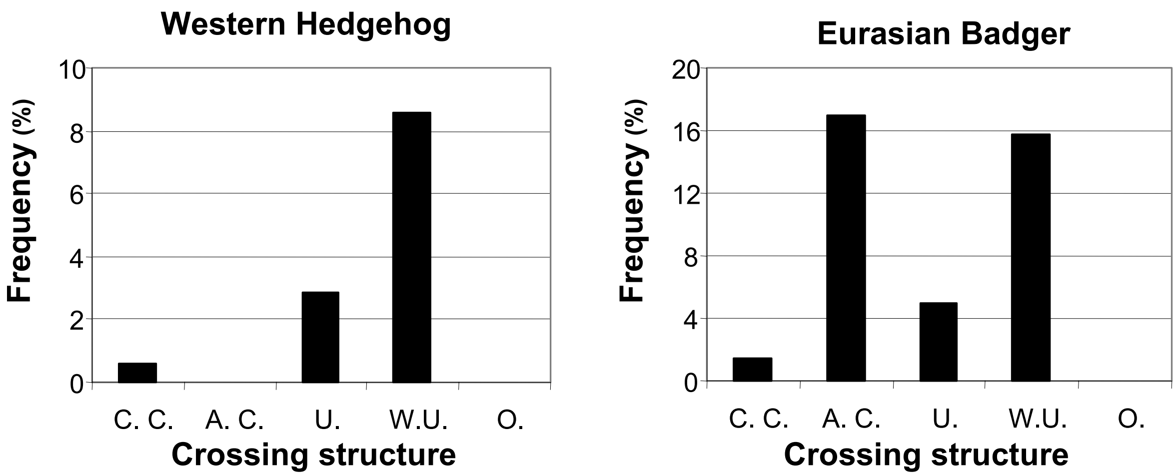

Fig. 7. Use frequency of different structure types by Western hedgehog and Eurasian badger. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Eurasian badger used exclusively passageways under the motorway, thus showing a significant selection (Chi=12.79; 4 d.f.; P=0.012). Adapted culverts ranked highest in selection (UI=3.49) followed by wildlife-engineered underpasses (UI=3.22). Circular culverts were occasionally used (UI= 0.31).

Small Mustelids and Cats

Small mustelids show clear preferences among structure types (fig. 8.; Chi=11.23; 4 df; P=0.024) selecting in all cases culverts, both circular (UI= 2.19) and adapted (UI=0.98). All pictures from small mustelids (N=12) corresponded to weasel (*Mustela nivalis*).

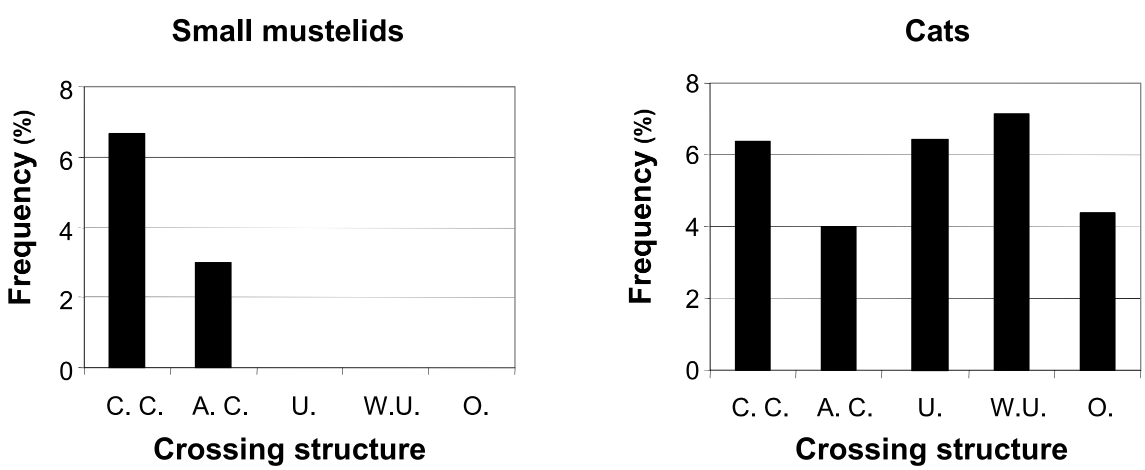

Fig. 8. Use frequency of different structure types by small mustelids and cats. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Cats used all structure types but wildlife engineered overpasses (fig. 8.), and did not show preferences among them (Chi=2.57; 4 d.f.; P=0.632). Both types of underpasses and circular culverts ranked over the average (UI in the 1.13-1.27 range) and the rest wwas less used than expected. Twenty-six out of 27 photographic contacts corresponded to feral cats, and only one showed a wildcat using a wildlife-engineered underpass.

Red Fox (*Vulpes vulpes*) and Canids
Foxes used all types of crossing structures except wildlife-engineered overpasses, and they showed a significant selection among types (fig. 9.; Chi=18.58; 4 d.f.; P=0.001). Non-wildlife-engineered underpasses ranked the highest in preference (UI=2.05) followed by wildlife-engineered passageways (UI=1.88). Thus, foxes preferred wide passes (UI= 1.43), and used more frequently underpasses (UI=1.40) than structures over the motorway (UI= 0.54).

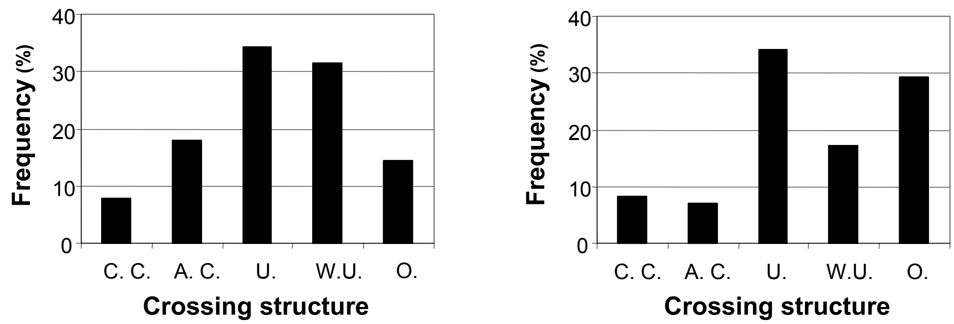

Fig. 9. Use frequency of different structure types by foxes and canids. CC: circular culverts, AC: adapted culverts, U: wide underpasses, WU: wildlife underpasses, O: overpasses.

Canid crossing was detected in all structure types, but a significant selection among them is found (fig. 9.; Chi=18.55; 4 d.f.; P=0.001). The highest use indexes were found for non-wildlife-engineered structures, both underpasses (UI=1.70) and overpasses (UI = 1.98). Wide passes are most frequently selected, but culverts are sometimes used by canids to cross the motorway (UI=0.47 and 0.40 for circular and adapted culverts respectively). Most records correspond to dogs as shown by the photographic system: only one in 33 snaps from canids was from a wolf. This picture was taken in a non-wildlife-engineered overpass.

Other Species
Finally, other species were detected on only a few occasions. Thus, a picture showed a garden dormouse (*Elyomis quercinus*) crossing through a circular culvert, and the only record of Red squirrel (*Sciurus vulgaris*) was taken in an adapted culvert. All records of water vole (*Arvicola* sp.) coincided in culverts, mainly in adapted ones (UI=4.92) and secondarily in circular (UI = 0.99). Photographic records (N=9) also point to a more intense use of adapted culverts (6 pictures) than circular ones (3), but species identification was not possible. Small-spotted genet (*Genetta genetta*) was found to use circular culverts (1 occasion) and wildlife-engineered underpasses (2 cases).

Red deer (*Cervus elaphus*) were detected in seven instances: four records were taken in wildlife-engineered overpasses and the rest in non-wildlife-engineered underpasses. On the contrary, roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) were never detected in crossing structures, even though both species are rather abundant in the area.

Discussion
Our results show two interesting points: (1) all structure types, be they specifically designed for wildlife or not, are used by vertebrates, and (2) most species show some selectivity among passageway types, thus opening the possibility for various structures to play complementary roles in the connectivity of vertebrate communities.

The passageway width seems to be the structural characteristic that most determines the species that use it. This fact had been detected before for some taxa, as shown by the positive relation between ungulate and other mammal use of crossing structures and their width (Reed *et al*. 1975, Reed 1981, Veenbass and Brandjes 1999).

This relationship seems to be linked to animal size, as the narrowest structures were mainly selected by small vertebrates. Thus, circular culverts were selected by lacertids, small mammals, rats and small mustelids, though they were more or less frequently used by most other species except ungulates. Due to the frequency of culverts, it is noteworthy the role they may play in the restoration of connectivity for small- and mid-sized mammal populations dissected by roads (Huijser *et al.* 1999, Clevenger 2001). With respect to this, it is worth nothing the high number of records produced by small mammals and the number of tracks that can be found in any structure in just one day (even more than 10). Such an intense use of crossing structures may probably be more related to their inclusion as part of the daily home range of small mammals than to their use as specific crossing points for long-distance movements (Clark *et al.* 2001). Moreover, the high number of records within passageways may be associated with an increase in small-mammal populations in the surrounding roads (Adams and Geis 1983).

Adapted culverts have been extensively used by anurans, water voles and ophidians, probably as a result of their affinity for wet habitats, a typical location for most passage structures under roads. Apart from a tendency of the most frequent snakes in the area (*Natrix* spp.) to live close to water, this finding for ophidians may be also linked to poiquilothermy, as the same trend is common to lacertids. Thus, it is possible that the role of culverts for reptiles is not only to offer them an opportunity to safely cross the road, but to provide them with a microhabitat with more constant temperature (Rodríguez *et a*l. 1996). It is also worth noting the use of adapted culverts by badgers, a result coherent with the findings by Broekhuizen *et al.* (1986) of a preferential use of underpasses.

The four types of wide passageways, over and under the road, specific and non-wildlife-engineered ones, are selected by lagomorphs, canids and red fox. Among them, fox also showed a tendency to use underpasses, as stated before by several authors (Trewhella and Harris 1990, Rodríguez *et al.* 1997). Such a tendency is shared by hedgehogs and small-spotted genets, though the low number of records precludes generalizations to be made for these species.

Canids also used wide passes, and the fact that most of them were feral and semi-domestic dogs wandering near villages probably led to their preference for the non-wildlife-engineered ones. In the case of cat records, most of them being from the domestic species, there raises more doubts for the implementation of conservation measures. Cats did not show preferences among passage types, but the extrapolation of the results to wildcats is especially risky as the wildcat is classified as a vulnerable species under IUNC criteria in the Spanish Red Data Book (Palomo and Gisbert 2002). The fact that only one picture is of a wildcat in a specific underpass reinforces this claim to caution.

Unexpectedly, small mammals were frequently detected crossing over bare-ground, non-wildlife-engineered overpasses. This observation contradicts the results of previous studies pointing to very infrequent road crossing by small mammals due to their avoidance of low-cover habitats where they can be easily predated (Oxeley *et al.* 1974, Mader 1984, Swihart and Slade 1984). Thus, differences arising from landscape structure or differential behaviour among populations cannot be disregarded.

Wildlife engineering of structures is also relevant for connectivity at the vertebrate community level, though our results could look somewhat disappointing at first sight. On the one hand, our green bridges (wildlife-engineered overpasses) had low use indexes and were among the least selected structures for many species, though the fact that we could only work with two cases may underlie this result. However, red deer used them almost exclusively, a very noteworthy point, taking into account that it is one of the species most reluctant to cross through any passageway. Specific underpasses, on the other hand, were selected by lagomorphs, hedgehogs, badgers and probably small-spotted genets.

With these results in mind, what can we say about the permeability of the motorway? Along the study section (71.5km) there is one crossing structure every 0.47km, an average distance that should be enough to allow a good permeability of the road (Keller and Pfister 1997). However, this theoretical permeability would only be valid for species like small mammals, lacertids, cats, red fox and canids that use most structures indifferently. Considering only wide passes, a structure used by most species, the average distance rises to 0.85km, and for the case of specific designs distance goes up to 4.76km. Such distance is out of daily ranging areas for most species, thus stressing the relevance of non-wildlife-engineered structures to avoid the barrier effect (Camby & Maizeret 1987, Singleton and Lehmkuhl 1999). In our case, non-wildlife-engineered structures were used by most species.

Special attention should be given to ungulates, as this group was rather under-represented in our records. Our results point to a low effectivity of crossing structures for ungulates, a finding common in literature (Thirion and Mallet 1984, Vassant *et al*. 1993a,b). Roe deer and wild boar were not detected in any structure, a result that points to serious fragmentation effects to both species (Virgós 2002). The infrequent use of crossing structures by roe deer had been reported previously (Jacques and Garnier 1982), but other studies suggest that wild boar acclimate quickly to motorway passageways (Vassant *et al.* 1993a).

Back to questions introduced at the beginning of the paper, several applied recommendations arise from this study. Firstly, the all-large versus all-small trade-off for crossing structures appears senseless, as using several kinds of passageways seems to be the best option due to their complementarity. The fact that some animals like ungulates will only cross through very wide passes suggests the need for investment in such structures, but the preference of other species points to the need of smaller structures aa well. The extensive use of non-wildlife-engineered structures by many species suggests in many instances the best solution may be to adapt the functional structures of the motorway for wildlife, thus reducing the costs of implementing mainly wildlife-specific passes.

Second, as most wild species show some preferences among crossing structure types, it would be theoretically feasible to design permeable systems in linear infrastructures based on the knowledge about vertebrate communities. The relative size of vertebrate species and passes, and their location with respect to road lanes, are the best predictors of fauna crossings at present, but we are still far from having the whole picture of animals' reaction to the establishment of passageways. This is especially noteworthy for the case of endangered or special interest species that may show unpredictable behaviour.

Moreover, some species may be especially reluctant to use even the widest crossing structures (in our case at least roe deer and wild boar), and special attention should be given to the design of crossing areas for them. In our study, pass size seems to underlie the lack of use by roe deer and wild boar, as populations of both species are dense in the area, and deep tree cover is present even up to both ends of many over- and underpasses. Therefore, the disturbing effect of the motorway may be enough to impede the crossing of these animals even through 20-meter-wide passes, and the only solution for such shy species may be the presence of larger stretches of road running above or below the ground (in viaducts and/or tunnels).

Finally, it should be stressed that there is a strong need to carry out extensive studies such as the present one and to improve the systems used for passageway monitoring. Relevant data on fauna use of crossing structures are still scarce, and results are conditioned by the fact that present-day methods do not allow the precise identification of many species. Thus, some species included within track species-groups could be threatened by the barrier effect of roads, but this problem may remain undetected due to poor monitoring devices.

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