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The permeability of highway in Gorski kotar (Croatia) for large mammals

Josip Kusak · Djuro Huber · Tomislav Gomerčić · Gabriel Schwaderer · Goran Gužvica

Abstract The highway from Zagreb to Rijeka stretches 68.5 km through a wildlife core area in Gorski kotar (Croatia). It has 43 viaducts and tunnels, and one specifically constructed (100 m wide) green bridge (Dedin). One quarter of the total highway length consists of possible crossing structures. At Dedin green bridge, a total of 12,519 crossings have been recorded during 793 different days of active infrared monitors being in operation, or 15.8 crossings per day. Two monitored tunnel overpasses had 11.2 and 37.0 crossings per day, respectively, whilst 4.3 crossings occurred per day under one monitored viaduct. Of those crossings, 83.2% were by ungulates and 14.6% by large carnivores. Radio-tracked large carnivores, brown bear (*Ursus arctos*), grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*), expressed strong positive selection for tunnels and viaducts, whilst avoiding small underpasses or bridges. Selection for the use of Dedin green bridge was equal to its availability. We conclude that this green bridge, constructed as a measure to mitigate the negative effects of the studied highway, served its purpose acceptably. Territorial and dispersing radio-tracked large carnivores crossed the highway 41 times, using both sides of the highway as parts of their home ranges. Overall, the highway in Gorski kotar does not seem to be a barrier. This demonstrates that it is possible to maintain habitat connectivity during the process of planning the highway route.

Keywords Brown bear · Grey wolf · Eurasian lynx · Green bridge · Habitat continuity

Introduction

The pressure of modern life demands various new constructions in previously undisturbed natural areas. Legal provisions nowadays require environmental impact assessment studies prior to such interventions in nature, as well as the monitoring of the effect of the intervention. The construction of the new highway from Karlovac to Rijeka, in Croatia, did meet most of the mitigation measures required for wildlife. We studied the effect of the critical section of the highway once it was being used.

Modifications of animals' behaviour (home range shift, changed home range sizes, changed movement patterns and altered gene flow) is one of the ways in which roads affect terrestrial and aquatic ecosystems (Trombulak and Frissel 2000; Coulon et al. 2004). Habitat fragmentation has been recognised as one of the most significant factors contributing to the decline of biodiversity in Europe (Damarad and Bekker 2003). Large mammals and especially large carnivores are sensitive to habitat fragmentation and destruction because of their low numbers, large ranges and direct persecution by humans (Linnell et al. 1996; Noss et al. 1996). Due to their high conflict rate with humans and

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their broad habitat quality tolerance, large carnivores cannot always be used as flagship animals for preserving biodiversity (Linnell et al. 2000), but, as the most space-demanding terrestrial animals, they are ideal as indicators for continuity of large areas (Crooks 2002). Preserving or restoring habitat continuity is recognised as one of main tasks when the conservation of large mammals is the goal (Clevenger and Waltho 2000; Chruszcz et al. 2003; Kaczensky et al. 2003). Unfenced roads and highways are not usually a barrier for most large mammals, but they can have a significant share in human-caused mortality due to collisions with vehicles (Huber et al. 1998; Kusak et al. 2000; Huber et al. 2002; Seiler 2005), whilst fenced highways are almost impermeable barrier for most large mammals (Kaczensky et al. 2003; Epps et al. 2005). Construction of appropriate crossing structures on suitable and ecologically important places and other mitigation measures are necessary if we want to minimise the negative effects of roads and highways (Clevenger and Waltho 2000; Kaczensky et al. 2003). Activities have to start from the very beginning of planning the new development, where a target-oriented approach that integrates natural and socio-cultural assets in road management allows consideration of non-monetary landscape values that have been largely ignored due to lack of assessment tools and insufficient knowledge (Seiler and Sjölund 2005).

Brown bears (*Ursus arctos*), grey wolves (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) inhabiting the Dinara Mountains of Croatia belong to the large and stable population of these large carnivores nearest to the Alps. Together with the neighbouring Slovenian population segment, they comprise the source for recolonisation of the Alps and much of Western Europe either through natural migrations or transplanting of captured animals. The new highway has been constructed through the main portion of the large carnivore's core area in Gorski kotar during the period from 1996 to 2004. When the last three concatenating sections were finished (1997, 2003 and 2004), the remaining large carnivores range in Croatia was intersected with a fenced highway, possibly splitting the Dinaric mountain range into a northern (half of Gorski kotar and adjacent Slovenian part) and a larger southern part. The highway has a number of viaducts, tunnels and one specifically constructed (100-m wide) green bridge, named Dedin, for bears and other wild animals. We studied the impact of the highway on large- and medium-sized mammal movements, and estimated the highway permeability for those animals.

The importance of such data may be crucial for future management of the population integrity and gene flow in the east–west direction. The data were very useful when designing other new roads and highways in the large

carnivore habitat in Croatia, like the newly constructed highway from Bosiljevo to Split. Additional importance is the potential of avoiding collision accidents. With this work, we tried to document the performance of Dedin green bridge, two tunnels and one viaduct as highway crossing structures for large mammals. By radio tracking [very high frequency (VHF) and global positioning system (GPS)] of bears, wolves and lynx, we related their movements to the newly constructed highway and to all highway objects that could be used as places where animals could cross the highway (highway crossing structures).

Study area

Gorski kotar (1,800 km²) is situated in Croatia in the narrowest part of the Dinarids (Fig. 1) from 14°22′30″ to 15°15′00″ east and from 45°07′30″ to 45°37′30″ north. It comprises the northwest end of the Dinara mountain range, which divides Mediterranean from the continental part of Croatia and the Adriatic Sea from the Black Sea drainage. The climate of Gorski kotar is diverse as a result of Mediterranean, continental, Alpine, and Dinaric influences. In general, Gorski kotar has a moderately cold climate (yearly average about 8°C) with relatively large amount of precipitation (up to 3,770 mm/year) and high snow cover, which lasts on average 139 days (Penzar 1959). Three large carnivore species inhabit the area: brown bear (*Ursus arctos*), with a density of 20/100 km² (Huber et al. 2008); grey wolf (*Canis lupus*), with a density of 1.5/100 km² (Štrbenac et al. 2005); and Eurasian lynx (*Lynx lynx*), with a density of about 0.5/100 km² (Firšt et al. 2005). The later has been reintroduced to Slovenia from Carpathian Mountains in 1973, as the native Balkan lynx has been extinct since 1903 (Koritnik 1974; Frković 2001). Other large mammal species present in the study area are wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Their combined density is 169/100 km² (Firšt et al. 2005). The calculated ratio of the number of large carnivores to ungulates would then be 11.5% to 88.5%, respectively. The group of medium-sized mammals is represented by badger (*Meles meles*), fox (*Canis vulpes*), hare (*Lepus europaeus*) and occasional golden jackal (*Canis aureus*). The area is inhabited by 236,000 people living in 308 settlements, but the majority (74%) of them live in three towns on the Adriatic coast (i.e., in the 10% of marginal habitat). The rest (90%) is mountainous area inhabited by 24 humans per square kilometer (Anonymous 1993).

The new highway was constructed through the large carnivore area in Gorski kotar in several phases (sections) during the period from 1998 to 2004. The highway

Fig. 1 Part of Gorski kotar area with new highway and railroad at the end of 2004. On the highway, *highlighted* are tunnels, viaducts and green bridge as possible crossing structures
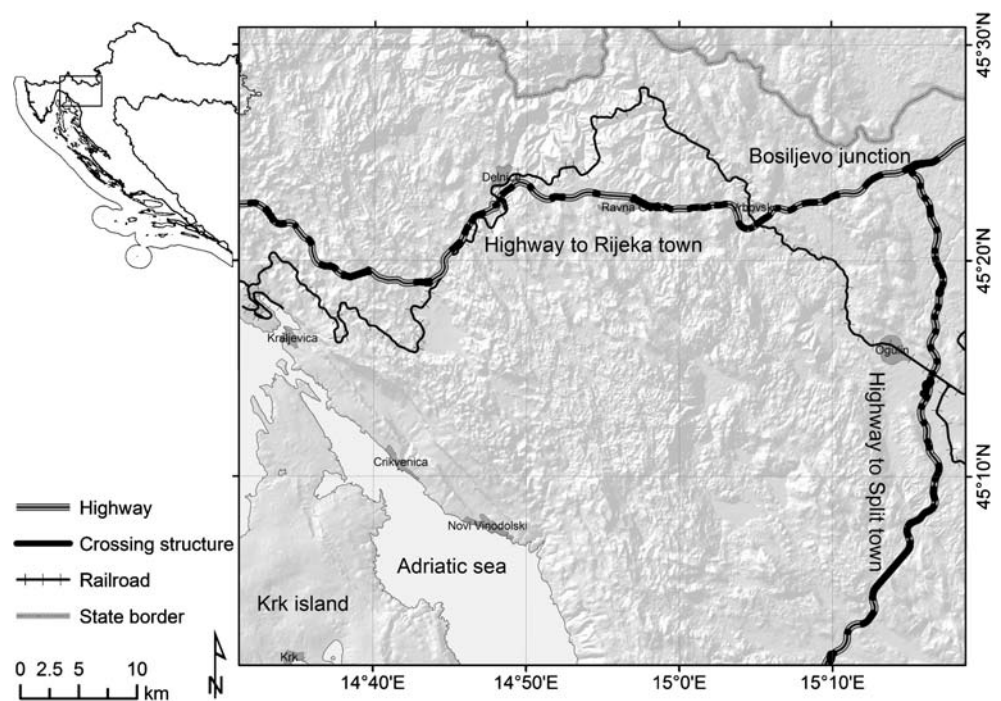
connects inland Croatia (Zagreb) with the northern Adriatic coast (Rijeka). The total length of highway through the large carnivore range is 68.53 km (Fig. 1). The inland end is at a highway junction Bosiljevo, where the southern section splits to the town of Split, whilst the western part connects to the town of Rijeka. The highway is fenced with a 210-cm-high wire mesh along its entire length. The 100-m-wide green bridge, named Dedin, was the first such object ever constructed in Croatia. The need for such an object was recognised in part due to previous studies of bear movements (Huber and Roth 1993) and bear mortality caused by traffic (Huber et al. 1998).

Materials and methods

We measured the length of the monitored highway, and all potential crossing structures were listed by type and width (Table 1). Four potential crossing structures were monitored by track searches; one of them was monitored by infrared (IR) sensor counters and another one also by automatic camera (photo trap). Clevenger and Waltho (2000) have found that the most limiting factors for the use of highway underpasses by large mammals are structural openness, followed by the distance to a town site. The first factor (structural openness) does not apply for crossing structures monitored by us (tunnels, green bridge and a high viaduct), as they were not like underpasses studied in Banff (Canada), so the second variable

(distance to town) moves to first place. The distance to the nearest town was measured for four monitored objects and used in evaluation of possible differences in crossing structure use.

Monitoring by tracks and automatic photo camera

We counted animal tracks under one viaduct, over two tunnels and one green bridge on the highway through the large carnivore core area in Gorski kotar. Tracks were searched as footprints in snow, mud or sand, or as scats, digging sites and specific marks on trees or ground. We were aware that, during dry seasons, passage of animals could produce no visible footprints. Therefore, the count of tracks was used in the first place to make the list of species passing through and to reveal the share of each species in the total. Additionally, we used one automatic photo camera (IR sensor activated) to document the use of one well-defined animal trail crossing above the Sopač tunnel. Photo monitoring also gave us the ratio of different animals crossing the highway via that trail. We calculated and tested (x^2 test) the ratio of species found by track searches against species ratio determined by photo trap. The purpose was to determine whether the frequencies of some of monitored species (e.g. lighter digitigrades like wolves and lynx) could be underestimated by track searches.

All four monitored objects were on a 9-km highway stretch, surrounded by the same habitat type (mixed beech and fir forest; Corine classification), and without any other

Table 1 List and widths (m) of all potential crossing structures on the Zagreb–Rijeka highway (68,534 m long) in Gorski kotar

Number	Object name	Object type	Width (m)
1	Severinske Drage	Viaduct	724
2	Osojnik	Viaduct	435
3	Veliki Gložac	Tunnel	1,130
4	Zečeve Drage	Viaduct	942
5	Underpass	Underpass	10
6	Underpass	Underpass	10
7	Hambarište	Viaduct	107
8	Rožman Brdo	Tunnel	508
9	Overpass	Overpass	10
10	Dobra	Bridge	173
11	Overpass	Overpass	10
12	Kamačnik	Bridge	240
13	Overpass	Overpass	10
14	Lazi	Viaduct	74
15	Jablan II	Viaduct	206
16	Overpass	Overpass	10
17	Jablan I	Viaduct	105
18	Čardak	Tunnel	601
19	Stara Sušica	Viaduct	430
20	Pod Vugleš	Tunnel	640
21	Javorova Kosa	Tunnel	1,460
22	Zalesina	Viaduct	200
23	Vršek	Tunnel	868
24	Dedin	Green bridge	100
25	Delnice	Viaduct	105
26	Underpass	Underpass	20
27	Lučice	Tunnel	576
28	Underpass	Underpass	20
29	Sopač	Tunnel	752
30	Golubinjak	Viaduct	569
31	Sleme	Tunnel	835
32	Vrata	Tunnel	257
33	Bajer	Bridge	485
34	Tuhobić	Tunnel	2,140
35	Hreljin	Viaduct	537
36	Hrasten	Tunnel	278
37	Bukovo	Viaduct	395
38	Kamenjak	Underpass	15
39	Melnik	Viaduct	140
40	Mali Svib	Viaduct	215
41	Veliki Svib	Viaduct	385
42	Čičave	Viaduct	300
43	Kikovica	Underpass	50
44	Konj	Underpass	50
	Total		17,127

We monitored Dedin green bridge by IR sensors and tracks, Golubinjak viaduct by tracks, Sopač tunnel by tracks and photo trap, and Sleme tunnel by tracks. All objects were potential crossing structures for radio-tracked animals, i.e. were monitored by VHF radio or GPS telemetry.

major habitat-dividing feature. Because of this, we assumed that the density of monitored species was the same around all four objects. The differences in use of monitored objects would then be the result of differences in structural and

spatial attributes of each crossing structure. We considered possible site-specific differences (Clevenger and Waltho 2000) and, for each object tested (χ^2 test), the observed ratio of large carnivore and ungulate crossings against general densities of those animal groups in the area around the highway.

Monitoring by IR counters

Three sets of IR emitters and sensors (Trailmaster, USA) were placed in concrete tubes set along the Dedin green bridge width: Three sections of the bridge surface useable for wildlife crossing were monitored separately. We named the sections A, B and C, counting from east to west. The distances between the sets of IR devices, i.e. the lengths of sections A, B and C were 24.4, 23.1 and 24.8 m, respectively. The remaining 3.1 and 2.8 m of bridge width between the edge fences were blocked for larger animals by branches. The height of IR beams was set at 40 cm above the ground to permit the smaller animals (up to the size of fox, hare and badger) to cross the bridge unrecorded. The IR recorder holds in memory up to 1,000 beam inter-ruptions whilst noting the date and time of each record.

We noticed certain malfunctions of IR recorders due to weather and other external conditions. Strong snowfall and rain could have interrupted the IR beams, as well as occasional tall grass and other weeds growing along the IR beams line, thus producing false records. There is also reasonable evidence that a herd of roe deer used to graze or rest on the bridge, causing multiple records. We adapted the method of IR sensor use to mitigate these problems. We calculated the mean values (M) and standard deviations (SD) of the number of records per hour per section of the bridge before evaluating the strings of records. Hence, we accepted up to six records per hour, but each hour that had seven or more records (more than one SD above the mean) was cancelled; i.e. we calculated that hour as zero records. It is possible that, on rare occasions, seven or more animals crossed the same section of bridge in the same hour, but we wanted to make sure not to overestimate the use of the bridge, and we presented the collected data as the minimum use of this green bridge.

To calculate the frequencies of Dedin green bridge crossings for each species monitored, we used a combina-tion of IR record counts and counting of tracks on a sand track placed across the width of the bridge (Fig. 2b): The IR sensors only count but do not distinguish the species that crossed. Therefore, we periodically examined animal tracks on the green bridge where a sand track 1.5 m wide was placed across the entire width of the bridge. The count of tracks per species was used to determine the share of each species in the total crossings of bridge. Hence, it was possible to estimate the use of bridge for each

Fig. 2 Green bridge Dedin (**a**) is at the level of the surrounding terrain, so the approaching animal has a clear overview from the forest edge to the 100-m wide passage over the highway and to the forest edge on the other side. Stand poles (**b**) for infrared sensors and the sand bed for animal tracks on the Dedin green bridge
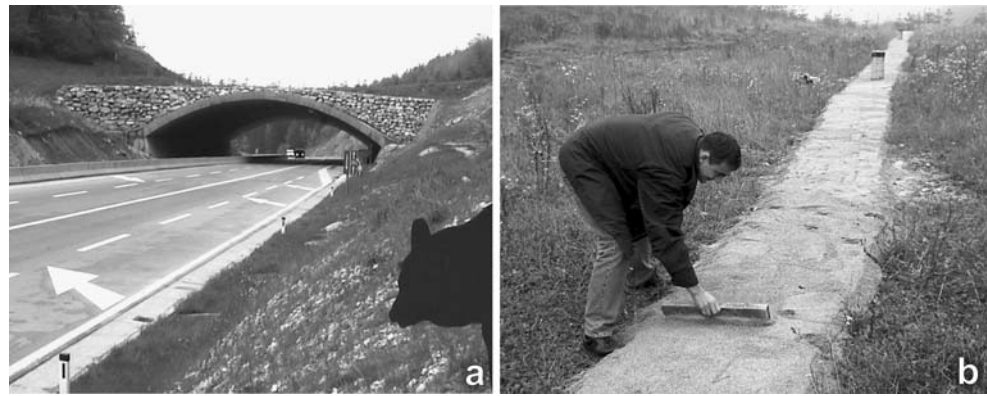
species that was taller than 40 cm and therefore counted by IR sensors.

After calculating the number of crossings for Dedin green bridge, we calculated the ratio (index) for the numbers of crossings per day and the number of tracks found per check. Applying this index to other objects where we did not have IR sensors but only numbers of tracks found per each check, we calculated possible number of crosses per day for those objects as well. With this extrapolation, each crossing structure retained the species ratio and possible differences of tracks found (site-specific difference), whilst only the possible total number of crosses for each species was calculated.

Monitoring by VHF radio and GPS telemetry

To evaluate animal movements in relation to the highway and the use of available crossing structures, we radio-tracked two bears, three wolves and two lynx by the use of VHF or GPS radio collars. Animals were captured in relative proximity (5 to 15 km) to the highway: wolves from the northern side; bears and lynx from the southern side of the highway. Bears were captured by the use of modified Aldrich snares manufactured by us, whilst wolves and lynx were captured by the use of Belisle snares (Entreprises Belisle, Canada). Wolves and lynx were immobilised with the use of Zoletil 100 (100 mg/ml of tiletamine and 100 mg/ml of zolazepam, Vibrac Laboratories, 06516 Carros, France), whilst bears were immobilised with ketamine hydrochloride (11 mg/kg, Ketalar, Parke-Davis, Berlin, Germany) and xylazine hydrochloride (6 mg/kg, Rompun, Bayer, Leverkusen, Germany). Drugs for bears were administered by a CO_2-powered immobilising gun from an approximate distance of 10 m, whilst for wolves and lynx, we used a blowpipe or pole stick. All doses were according to literature (Ballard et al. 1991; Kreeger et al. 2002). Sex and reproductive status were determined, whilst age was estimated on the basis of body size, tooth wear (Nowak et al. 2000) and the date of capture. Two wolves and

one lynx were marked with VHF radio-collars (MOD-500 and MOD-400; Telonics, Messa, AZ, USA), whilst one wolf, one lynx and two bears were marked with GPS collars (GPS-Plus and GPS-Pro; Vectronic Aerospace GmbH, Berlin, Germany). Due to the high density of local roads, almost all VHF radio tracking was done by the use of a field vehicle. For VHF collars, the routine protocol included a 3-day-long telemetry sessions at 10-day intervals throughout the year. We used a DOS-based palmtop PC and Locate II program (Nams 1993) set to maximum likelihood estimator method (Lenth 1981) to calculate locations and the size of 95% confidence areas. Locations were calculated immediately in the field from at least three bearings. The time interval between the first and last successful bearing was between 20 and 40 min. Bearings were measured until the desired accuracy (95% confidence area of size ≤0.3 km²) of calculated location was achieved. Wolf and lynx GPS collars were set to get a GPS fix every 6 h, whilst bear GPS collars were set to attempt a GPS fix every 2 h. Animal locations and their movement were analysed in relation to the highway and possible highway crossing structures. We used the minimum-convex polygon (MCP; White and Garrot 1990) and kernel methods (Worton 1989) to calculate the size of home ranges. For calculating kernel home ranges, we used the fixed kernel method with the smoothing factor (band-width) calculated by least-square cross-validation of animal locations (Seaman et al. 1999). Animal home ranges were overlaid with highway lane to determine the ratio of overlapping. The distance between every location, the closest highway edge and the closest crossing structure was measured and tested for normality (Shapiro–Wilk's W test). A number of random locations were generated within each animal's corresponding 100% MCP home range. The shortest distances from those random locations to the closest highway edge and to the closest highway crossing structure were measured and compared (Mann–Whitney U test) with distances of animal locations to determine if animals preferred or avoided the highway and possible highway crossing structure. Successive locations were connected with

lines into movement path to count the number of highway crossings and to identify where they crossed the highway. The frequency of GPS fixes on bear collars was set to 2 h, and considering that daily movements of bears in Croatia are 1,500 m (Huber and Roth 1993), this data resolution was sufficient for distinguishing where bears were crossing the highway. The determination of crossing sites for GPS-tracked wolves and lynxes were not attempted because of their faster movements and GPS set to 6-h intervals. The exceptions to this were locations and movements tracking done by triangulations, when the tracker was in real time documenting animal crossings over the crossing structure. Animal locations, movements and home ranges were calculated and analysed with the use of ArcView 3.1 GIS software (Anonymous 1996), Animal Movement extension ver. 2 (Hooge et al. 1999). All distances were measured with Nearest Features 3.8a (Jenness 2005a), whilst random points were generated with the use of Random Points Generator 1.3 (Jenness 2005b). Statistical tests were done with Statistica 7 (Anonymous 2004).

Results

The total length of the Zagreb–Rijeka highway through the large carnivore range in Gorski kotar was 68,534 m. The highway had 44 potential crossing structures whose total width was 17,127 m or 25.0% of the highway length (Table 1). The distances from the four monitored crossing structures to the nearest town were Dedin, 1,050 m; Sopač, 900 m; Golubinjak, 550 m; and Sleme, 970 m.

Monitoring by tracks and automatic photo camera

We checked the four monitored crossing structures for tracks 118 times in the period from January 1999 to January 2001. The average interval between two checks was 37 days.

The Dedin green bridge was 100 m wide, but the useable surface for animal crossings, between the highway fences on both sides, was 77.4 m. A total of ten different mammal species (including man and excluding rodents and other

Table 2 Number of tracks of large mammals found on ground above two tunnels, one green bridge and under one viaduct, with the number of photos taken by automatic camera on the animal trail over the Sopač tunnel. The ratio of species found by tracks on Sopač tunnel was compared (χ^2 test), with the ratio determined by the photo trap on one trail on the same hill. The tracks ratio of large carnivores and ungulates was compared (χ^2 test) with corresponding densities (11.5% of LC and 88.5% of LU) of those animal groups in the study area around the highway. The monitoring was done in the period from January 1998 to January 2001.

Species	Dedin green bridge 64 checks for tracks			Viaduct Golubinjak 23 checks for tracks			Tunnel Sopač 23 checks for tracks			Tunnel Sopač photo trap		Tunnel Sopač N tracks vs N photos (χ^2 test, 1 df)		Tunnel Sleme 8 checks for tracks		
	N	Percent	N/check	N	Percent	N/check	N	Percent	N/check	N	Percent	χ^2	P	N	Percent	N/check
Roe deer	166	42.0	2.59	20	51.3	0.87	40	39.6	1.74	3	20.0	1.1100	0.2926	37	31.9	4.63
Red deer	103	26.1	1.61	12	30.8	0.52	22	21.8	0.96	0	0.0	3.1900	0.0740	52	44.8	6.50
Wild boar	66	16.7	1.03	1	2.6	0.04	6	5.9	0.26	1	6.7	0.0100	0.9176	15	12.9	1.88
Bear	39	9.9	0.61	4	10.3	0.17	29	28.7	1.26	3	20.0	0.3000	0.5858	10	8.6	1.25
Wolf	4	1.0	0.06	1	2.6	0.04	2	2.0	0.09	2	13.3	4.3700	0.0366	1	0.9	0.13
Lynx	1	0.3	0.02	1	2.6	0.04	2	2.0	0.09	0	0	0.3000	0.5862	1	0.9	0.13
Badger	–	–	–	–	–	–	0	0	0	4	26.7	22.0000	0.0000	–	–	–
Red fox	–	–	–	–	–	–	0	0	0	2	13.3	12.0900	0.0005	–	–	–
Man	16	4.1	0.25	0	0.0	0.00	0	0	0.00	–	–	–	–	0	0	14.50
Total UN[a]	335	88.4	5.23	33	84.6	1.43	68	67.3	2.96	4	44.4	–	–	104	89.7	13.00
Total LC[a]	44	11.6	0.69	6	15.4	0.26	33	32.7	1.43	5	55.6	–	–	12	10.3	1.50
Total LM	379	100	5.92	39	100	1.70	101	100	4.39	9	100	–	–	116	100	14.50
Grand total	395	100	6.17	39	100	1.70	101	100	4.39	15	100			116	100	5.52
	Observed vs expected ratio (χ^2 test, 1 df)			Observed vs expected ratio (χ^2 test, 1 df)			Observed vs expected ratio (χ^2 test, 1 df)			Observed vs expected ratio (χ^2 test, 1 df)		Not applicable		Observed vs expected ratio (χ^2 test, 1 df)		
Ungulates and large carnivores	$\chi^2=0.004$ $0.975>p>0.95$			$\chi^2=0.578$ $0.90>p>0.10$			$\chi^2=44.489$ $p<0.01$			$\chi^2=17.163$ $p<0.01$				$\chi^2=0.152$ $0.90>p>0.10$		

UN ungulates, *LC* large carnivores, *LM* large mammals (UN+LC)
[a] Percentage totals of large carnivores and ungulates are expressed as percent of all large mammals, not including medium-sized mammals and man.

Fig. 3 Animals photographed by trap camera at the hillside above tunnel Sopač: **a** brown bear, **b** wolf with roe deer prey in mouth, **c** red deer doe and **d** fox

small mammals) were determined by 529 animal tracks found in 64 checks on the sand track across the bridge. Out of this total, 134 (25%) tracks belonged to animals lower than 40 cm (fox, $N=83$; hare, $N=49$; and badger, $N=2$) and thus were not counted by the IR sensors. The remaining 395 tracks belonged to animals taller than 40 cm (Table 2).

Golubinjak is a 569-m-wide underpass where the highway is on a 25-m-high viaduct. It was checked 23 times for signs of animal crossings. On the ground under this viaduct, we determined tracks of a minimum of ten medium- and large-size wild mammal species, and of man, dog and cat. It is important to note that all three species of large carnivores have been observed to pass under this viaduct. The count, share (percent of the wild large mammals' tracks) and number of tracks per single check are shown in Table 2.

On the forested ridge above the Sopač tunnel (742 m width), we determined the tracks of a minimum of ten wild mammal species (of medium and large size), and of dogs and humans, whose count, share (percent of the wild large mammals' tracks) and number of tracks per single check is shown in Table 2. A total of 24 successful photographs of animals were made on one well-defined animal trail on Sopač hill during 339 days of active use of the IR-activated photo camera. After exclusion of squirrels ($N=7$; 29.2%) and birds ($N=2$; 8.3%), the remaining 15 photographs were

shared among bear ($N=3$; 20.0%), roe deer ($N=3$; 20.0%), badger ($N=4$; 26.7%), fox ($N=2$; 13.3%), wolf ($N=2$; 13.3%) and wild boar ($N=1$; 6.7%). A significantly larger (χ^2 test; Table 2; Fig. 3) proportion of lighter digitigrades (fox, badger and wolf) was recorded by the automatic photo camera than was found by tracks searches on the same crossing structure.

On the forested ridge above the Sleme tunnel (835 m width), we determined the tracks of a minimum of nine wild mammal species of medium and large size. All data on distribution of a total of 116 tracks are shown in Table 2. It is important to note that all three species of large carnivores have been determined to walk over both surveyed tunnels.

We compared (χ^2 test) the ratio of tracks found for two animal groups (large carnivores, LC; ungulates, UN) for each object, with the density ratio of those groups present in the study area. For three crossing structures (Dedin, Golubinjak and Sleme), there was no significant difference. On the contrary, the ratio of large carnivores that crossed the Sopač tunnel was significantly higher than expected [$\chi^2(1\ df)=44.489$, $p<0.01$], whilst ungulates used this crossing structure less than expected (Table 2).

Monitoring by IR counters

IR sensors were installed on the Dedin green bridge from 25 May 1999 to 13 January 2003 (1,329 days). A total of

Table 3 Number of accepted IR records (N of crossings) of Dedin green bridge per sections (A, B and C) from 25 May 1999 to 13 January 2003 and the number or crossings per day

Section of bridge	Year 1999	Year 2000	Year 2001	Year 2002	Year 2003	Total crosses	N days	N crosses/day	Percent crosses
A	112	1,346	978	2,308	0	4,744	877.5	5.4	34.1
B	99	1,070	1,230	1,737	6	4,142	707.5	5.9	37.0
C	221	1,260	633	1,465	54	3,633	794.2	4.6	28.9
Total	432	3,676	2,841	5,510	60	12,519	793.1	15.8	100.0

72,510 beam interruptions were recorded in a total of 109 accepted sessions. A total of 12,519 (17.3%) records were used for further elaboration when only up to six records in the same hour were accepted. IR sensors were active in total for 877.5, 707.5 and 794.2 days for the A, B and C bridge sections, respectively. The whole bridge was under IR crossing control during 793.1 different days on average, when the total accepted number of crossings (N=12,519) occurred. Both lateral portions of the bridge (A and C) were used slightly less than the central part (B; Table 3): Those differences were not statistically significant (χ^2=0.1598; 2 df, p<0.9231), and for further analyses, the three sections' data were pooled together. Recalculated to the yearly level (365 days), IR count gave an estimate of a total of 5,761 bridge crossings per year or 15.8 per day (Table 3). Tracks percentage ratio of animals taller than 40 cm (N=395) allowed the quantitative analyses of IR records, i.e. by species of animals. Using the 12,519 accepted IR records, we calculated that a minimum of 5,258 roe deer, 3,267 red deer, 2,091 wild boar, 1,239 bear, 513 human, 125 wolf and 25 lynx crossings of the bridge occurred in 793.1 days. Recalculated daily crossings of the Dedin green bridge are given in Table 4.

Relating the average number of tracks found during each check to the estimated number of crosses per day on the Dedin green bridge, we got the ratio of 2.56 (range, 1.5 to 2.67). The number of tracks found during checks represented a fraction and an index of the total number of crosses of that object. We applied this new index to the number of tracks found in each check for the other objects that did not have IR sensors and approximately calculated the total number of crosses for those objects (Table 4). This calculation was possible because all four monitored objects were within the core area, where the surrounding habitat was uniform and the densities of monitored mammal populations were not expected to differ significantly. Overpasses (two tunnels and green bridge) had five times more crosses per day, compared to one wide underpass (viaduct Golubinjak). Even a relatively narrow overpass like Dedin green bridge (100 m) was used 3.7 times more than the surface under 569 m long and 25 m high viaduct Golubinjak. Daily distribution of animal use of Dedin green bridge indicated a certain activity level during all hours of the day. The times of low use were during late afternoon hours. In general, the night activity level was higher than that for the daytime (Fig. 4).

Table 4 Estimation of total numbers of large mammal crossings for studied objects

Species	Dedin				Golubinjak		Sopač		Sleme		Total	
	Total N from IR count	N/day est.	N tracks/ check	Ratio per day IR count to tracks per check	N tracks/ check	N/day est.	N tracks/ check	N/day est.	N tracks/ check	N/day est.	N tracks/ check	N/day est.
Roe deer	5,258	6.63	2.59	2.56	0.87	2.23	1.74	4.45	4.63	11.85	2.23	25.16
Red deer	3,267	4.12	1.61	2.56	0.52	1.33	0.96	2.46	6.50	16.63	1.60	24.54
Wild boar	2,091	2.64	1.03	2.56	0.04	0.10	0.26	0.67	1.88	4.82	0.75	8.23
Bear	1,239	1.56	0.61	2.56	0.17	0.43	1.26	3.22	1.25	3.20	0.69	8.41
Wolf	125	0.16	0.06	2.67	0.04	0.11	0.09	0.24	0.13	0.35	0.07	0.85
Lynx	25	0.03	0.02	1.50	0.04	0.06	0.09	0.14	0.13	0.20	0.04	0.42
Man	513	0.65	0.25	2.60	0	0.00	0.00	0.00	0.00	0.00	0.14	0.65
Total	12,519	15.78	6.17	2.56	1.7	4.26	4.39	11.17	14.50	37.04	5.52	68.27

For the Dedin green bridge, the total number of crossings was calculated based on the percent of the share of tracks of each species in the total number of IR records (N=12,519 in 793 days). For three other objects, the estimated number of crossings was calculated from number of tracks found per check multiplied by the ratio between the number of crosses determined by IR sensors and number of tracks found during checks of Dedin green bridge. The obtained numbers are of orientation value only.
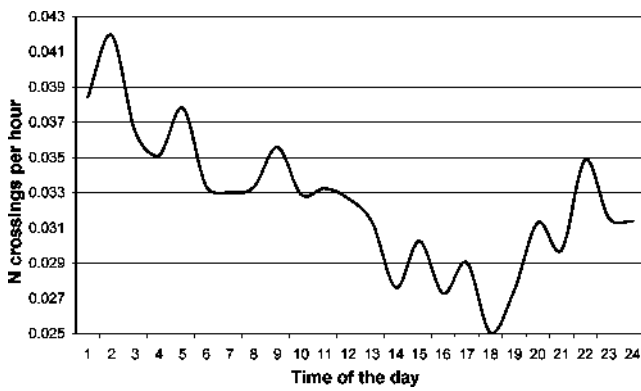
Fig. 4 Distribution of animal crossings over Dedin green bridge by hours of day

Monitoring by VHF radio and GPS telemetry

We radio-tracked two bears, three wolves and two lynx around the highway area in the period from 2 July 2002 to 18 March 2007 (1,720 days). We collected altogether 4,087 locations, of which 3,641 (89.1%) were for two bears, 383 (9.4%) for three wolves and only 63 (1.5%) locations were for two lynx (Table 5). Most of the highway crossings were made by a bear B30, which alone made 32 (78.1%) of the crossings (Fig. 5), whilst wolves W09 and W10 made four (9.8%) crossings each and lynx L02 crossed the highway once (Table 6). Thirteen crossings of all animals (31.7%) were over the tunnel Sleme, 16 (39.0%) over the tunnel Sopač, two (4.9%) over the Dedin green bridge and 11 (26.8%) over other, undetermined, places. It was not possible to tell where the wolves and lynx crossed the highway because their GPS were taking fixes every 6 h and that seemed to be too long a period for the movements of those carnivores.

There was no significant difference (Mann–Whitney U test) between the distances of animal locations from the highway route and from animal locations to crossing structures, and in further analyses, we used only distances to the nearest crossing structure. The average straight line distance of animal locations to the nearest highway crossing structure was 7,409.0 m (range, 746.8 to 16,408.7 m). Shortest recorded distance from the highway crossing structure (19.2 m) was documented for a bear B30, whilst bear B29 had, of all tracked animals, the farthest minimal distance to the crossing structure (2,153.2 m, Table 6).

Various numbers of random points were generated within corresponding 100% MCP home ranges of each tracked animal. We have found significant differences for six out of seven tracked animals after comparing (Mann–Whitney U test) distances of animal locations to the nearest crossing structure with random points distance (Table 6). Bear B29 preferred to stay away from highway and crossing structures, and has never crossed the highway during the tracking time. Bear B30 chose to stay closer to the highway and crossing structures, and it crossed the highway 32 times. Both of these tracked bears were young males at ages 2.5 and 3.5 years, predisposed for long range movements. Lynx L02 strongly avoided the highway and crossing structures but, in spite of that, managed to cross to the other side in one occasion and stayed there. Lynx L03 showed a slight avoidance of possible crossing structures, and it did not cross the highway during the tracking time. Wolf W05, a young non-reproducing female, preferred to stay close to crossing structures but was not documented crossing to the other side of the highway. Wolf W10, a reproducing female, stayed significantly farther from crossing structures, but it also crossed the highway on four occasions, probably to hunt roe deer, as documented with the automatic camera on a Sopač hill (Fig. 3). Wolf W09, a young dispersing female, crossed the highway four times (sites not determined), but distances of her locations to the highway objects were not significantly different from random (Table 6).

We found tunnels to be most often ($N=3,040$, 74.8%) the closest crossing structure. Testing (χ^2 test) the availability (count) of all crossing structures and the animal selection (proximity to structure), we have found that animals had strong positive selection for tunnels and viaducts but were using small underpasses or bridges over

Table 5 Basic data of animals radio-tracked around the highway area in Gorski kotar in the period from 2 July 2002 to 18 March 2007 (1,720 days)

Animal	Species	Gender	Age at capture (years)	Start tracking	N days	N locations	MCP100 (km^2)	50% kernel (km^2)
B29	Bear	M	2.5	25.09.2003	224	881	79.0	2.2
B30	Bear	M	3.5	10.09.2004	409	2,760	653.5	42.0
L02	Lynx	M	0.5	25.10.2005	425	12	92.3	39.2
L03	Lynx	M	2	01.12.2006	118	51	174.6	33.4
W05	Wolf	F	2.5	02.07.2002	267	84	140.5	9.1
W09	Wolf	F	2.5	11.09.2004	91	202	939.1	76.5
W10	Wolf	F	6	17.09.2004	637	97	160.4	10.6
						4,087		

Fig. 5 Locations and lines connecting consecutive locations of two radio-tracked bears in relation to highway and crossing structures in Gorski kotar during the tracking period from 25 September 2003 to 24 October 2005. A total of 32 crossings of bear B30 have been recorded
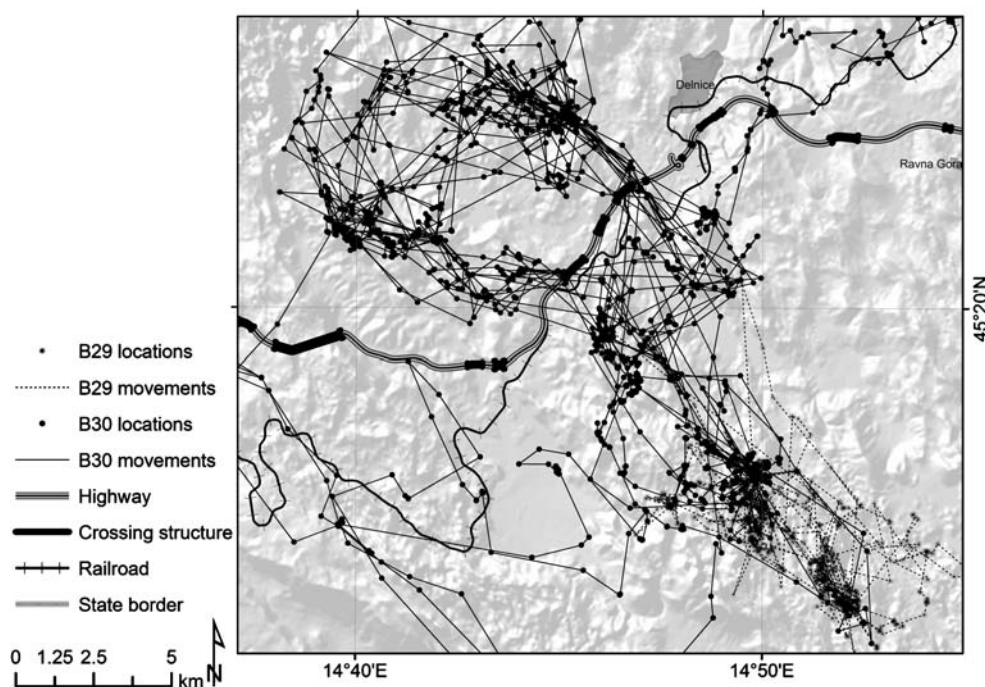

Table 6 Individual number of crossings of the highway and distances of locations of radio-tracked animals to the nearest highway crossing structure in Gorski kotar in the period from 2 July 2002 to 18 March 2007 (1,720 days), compared (Mann–Whitney U test) with random points distances generated within each animal corresponding 100% MCP home range

Animals		Animal location distances (m) to the nearest crossing structure					Random points distances (m) to the nearest crossing structure					Mann–Whitney U test
Code	N highway crosses	N	Mean	SE	Min	Max	N	Mean	SE	Min	Max	Statistical significance (p)
B29	0	881	10,365.1	222.1	2,153.2	15,384.5	279	8,823.5	194.3	2,637.5	14,946.0	0.000999
B30	32	2,760	4,897.2	139.6	19.2	14,751.6	2,238	5,680.0	77.4	4.2	14,403.6	0.003023
L02	1	12	5,039.6	937.1	1,832.7	9,398.2	296	2,270.5	95.1	18.3	8,234.0	0.000772
L03	0	51	6,819.0	785.1	148.1	14,753.3	564	7,490.9	150.9	355.1	14,431.4	0.048533
W05	0	84	6,010.2	458.5	205.0	15,000.3	460	7,894.1	153.6	391.9	15,020.0	0.000007
W09	4	202	11,495.9	850.9	396.7	31,067.6	3,143	12,078.9	149.6	4.2	31,608.9	0.907637
W10	4	97	7,236.2	345.0	472.7	14,505.4	530	6,158.5	150.0	4.3	13,922.8	0.003199
All	41	4,087	7,409.0	534.04	746.8	16,408.7	7,510	7,199.49	138.7	487.93	16,080.96	

Table 7 Distances of all radio-tracked animals to the nearest highway crossing structure in Gorski kotar in the period from 2 July 2002 to 18 March 2007 (1,720 days)

Crossing structure	N distances to nearest locations	Percent count locations	N objects	Percent objects count	χ^2 test (1 df)	P	Mean distance (m)	Min distance (m)	Max distance (m)	SD
Bridge	76	1.86	3	6.8	6.39	0.016	4,097.1	87.6	14,254.1	2,582.3
Underpass	81	1.98	5	11.4	9.48	0.002	12,712.1	332.9	30,588.5	8,570.4
Tunnel	3,157	77.24	12	27.3	10.37	0.001	6,256.4	74.4	15,829.0	3,659.4
Viaduct	718	17.57	17	38.6	9.26	0.020	6,773.3	542.9	30,965.5	3,791.1
Green bridge	55	1.35	1	2.3	0.26	0.607	2,122.9	43.3	7,609.1	1,768.6
Sum/Average	4,087	100	38	100.0			6,392.4	216.2	19,849.2	4,074.3

Fig. 6 Home ranges (100% MCP and 50% kernel) of two bears (B29 and B30), three wolves (W05, W09 and W10) and two lynx (L02 and L03) radio-tracked in Gorski kotar in the period from 2 July 2002 to 18 March 2007
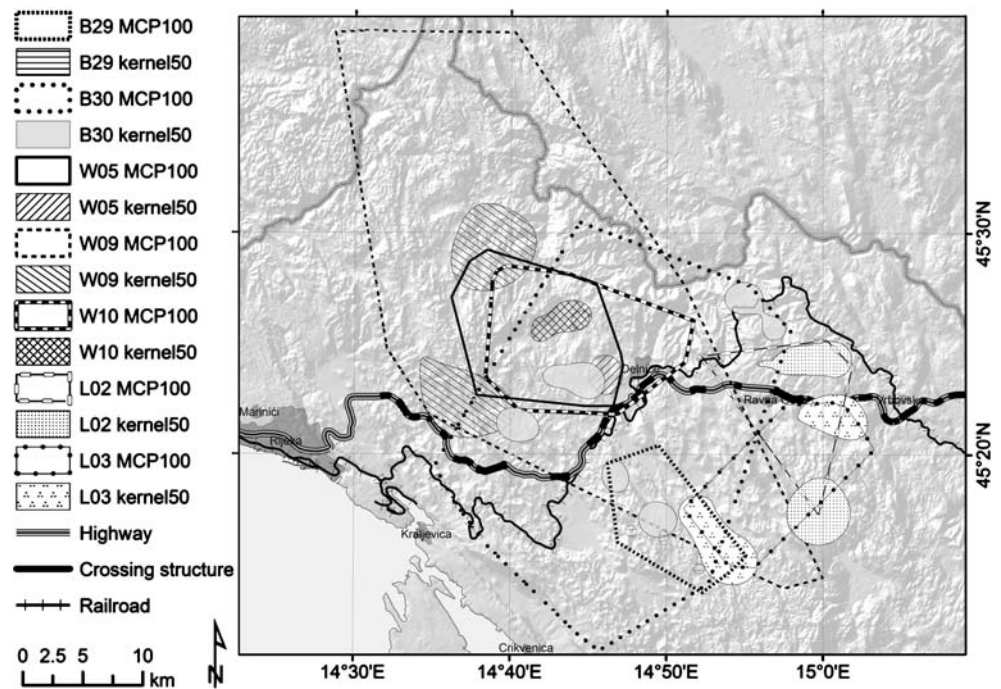
rivers and lakes less frequently than expected. Selection for Dedin green bridge was equal to its availability (Table 7).

Home ranges of two male bears were 8.3 times different in size (Table 5) and different in relation to the highway (Fig. 6). Bear B30 used areas on both sides of the highway, with 336 km^2 north and 317 km^2 south of it. Core areas (50% kernel) of B30 were on both sides of the highway; three patches on the north and two on the south side (Fig. 6). Wolves W05 and W10 (offspring and a reproducing female) were using the same area north of the highway and adjacent to it, with a core area north of the highway (Fig. 6). Contrary to this, wolf W09, a young female that was dispersing during all 3 months of tracking, used both highway sides, with MCP100 of 740.4 km^2 on the north and 198.6 km^2 on the south side, but patches of core areas were on the northern side only. Both lynx had core areas divided in two parts: L02 was using one area south of the highway and another north of it, whilst both parts of L03 core area were south of the highway (Fig. 6).

Discussion

The fact that as much as 25% of the analysed 68.5 km of the highway were potential crossing structures is a fortunate consequence of perpendicularity between mountains and the highway route, resulting in numerous long tunnels and viaducts. During highway planning, a need for only one additional crossing structure was recognised at the place where bear movements and collision with cars and trains on

a parallel old road and railroad had been documented earlier (Huber et al. 1998). The first "green bridge" in Croatia, a highway overpass 100 m wide was constructed on that site in 1999. Well-studied highway (Clevenger and Waltho 2000, 2005) of comparable length (76 km of highway sections named phases 1, 2 and 3A) in Bow Valley of Banff National Park; stretches along the bottom of the valley where 22 relatively narrow (average=7.5 m wide; range, 2.0–14.9 m) underpasses and two green bridges (overpasses, each 50 m wide) were constructed to re-establish habitat continuity: The total width of all 24 crossing structures in Banff NP is 237.6 m, giving a total highway permeability of 0.31% or 80.6 times less than on the highway in Gorski kotar. Apart from this highway, there were no other significant habitat dividing features in our study area. We could assume that all highway crossing structures were equally available to the large mammal populations.

Monitoring by tracks and automatic photo camera

The ratio of animal tracks documented by our searches on two monitored overpasses and one underpass, with 83.2% of all signs left by ungulates and 14.6% by large carnivores, was not significantly different to the density ratio of their populations in the area. The ratio of underpasses use by large carnivores in Banff NP was 5% only, and the most limiting factors for use of highway underpasses by large mammals were structural openness and then distances to the town site (Clevenger and Waltho 2000). Large

ungulates in Banff NP are sensitive to structural attributes of the underpasses, whilst large carnivores are sensitive to distance to town and human activity level. The first factor (structural openness) does not apply for crossing structures monitored by us (tunnels, green bridge and high viaduct) because they were very open and submerged in the surrounding habitat, so the second variable (distance to town) moved to first place. If the crossing structure, overpass or large viaduct is good enough for large carnivores, which were found to be sensitive to the level of human presence and activity, it is likely that it will also be used by ungulates. However, as an exception, one of our monitored overpasses (tunnel Sopač) had significantly higher proportion of use by large carnivores, followed by consequent lover use by ungulates. This was presumably due to a site-specific difference influenced by factors that we did not evaluate.

The large carnivore's ratio for Sopač tunnel was probably even higher because the use of crossing structures by large- and medium-sized carnivores (wolf, lynx, fox and badger) can be easily underestimated, as shown by the tracks-to-photo ratio for the same place. Clevenger and Waltho (2000, 2005) used a track pad to count the absolute number of animal crossings. In our approach, track pad counting was used only to determine the relative ratio of crossings by different species. For that reason, it was not necessary to check for tracks every 3 to 5 days. We do agree that the observed ratio of animals that are lighter or rarer can be underestimated. Underestimating the carnivores crossing ratio and consequently higher ratio of other large mammals (bears and ungulates) would not change the total crossing ratio of all large mammals, i.e. would not change their crossing frequency, which we determined by IR counter. Thus, by the use of IR counter, we avoided possible pitfalls of track pad use (erasure of tracks by rain or wind; missing tracks of species with low densities or relatively low weight).

Large carnivores can cross the highway even if only relatively narrow underpasses, such as those in Banff NP (Clevenger and Waltho 2000, 2005) or Florida (Foster and Humphrey 1995), are available to them: Our study showed that their ratio of crossing can be three to six times higher if they have the opportunity to use wide (100 m and more) overpasses.

Monitoring by IR counters

The use of IR trail monitors requires a certain degree of caution, as we had to reject 82.7% of records, as explained in "Materials and methods". However, we believe that the remaining numbers of records were true crossings of the Dedin green bridge, with 15.8 passes per day. This is comparable to the daily use (12.2 to 16.3 passes) by

ungulates of one overpass (50 by 95 m) in The Netherlands (van Wieren and Worm 1997) and by sum of 13.7 passed per day under all monitored (N=11) underpasses in Banff NP (Clevenger and Waltho 2000). The total number of crosses per day over/under four monitored crossing structures in Gorski kotar was five times higher than under all underpasses on phases 1 and 2 of the highway in Banff NP. The length of our monitored crossing structures represents only 16% of all crossing structures on the length of the highway through Gorski kotar, so the total highway permeability, with included unmonitored structures, could be three to four times higher.

Observed use of the Dedin green bridge by all large mammal species in the area supported the assumption stating that, if the object was appropriate for the most demanding species (large carnivores), it will also be suitable for other, less disturbance-sensitive species. Of course, site-specific differences can change the ratio of carnivores to ungulates use of the structure but will not entirely stop ungulates crossing the site if it is highly used by carnivores. Lower use of the Golubinjak viaduct could not only be attributed to its structural difference from monitored overpasses: Whilst all three overpasses were surrounded by forest on both sides, Golubinjak underpass had a local picnic resort on the eastern side, and from the western side, had a relatively narrow forest belt (250 m wide) that opened into a village with 650 inhabitants, only 550 m away. Low use of the Golubinjak underpass can also be attributed to the proximity (650 m away) of Sopač overpass that took 72.4% share of the total number (15.4) of crossings/day. Predominant night use of Dedin green bridge indicates the general nocturnal preference of the species in concern, as well as presence of human disturbance of the object during the day, similar to findings on a Florida highway (Foster and Humphrey 1995), where carnivores used four underpasses at night, whilst deer were crossing during the day, probably to avoid these carnivores.

It was speculated earlier (Gloyne and Clevenger 2001) that two overpasses (50 m wide) in Banff NP were unsuitable for cougars because of obstructed cross-highway view due to overpass arches above the ground. The green bridge Dedin was the only purposely constructed animal crossing structure on the monitored highway in Gorski kotar. High frequency of both large carnivores and ungulates crossing Dedin overpass could be attributed to its optimal spatial location, at a place known for animal activity and crossing (Huber et al. 1998), away from settlements (1,050 m) and surrounded by forest, in addition to its dimensions and shape. An approaching animal has a clear overview from the forest edge to the 100-m-wide green bridge over the highway, which is buried into the terrain, and of views to the forest edge on the other side (Fig. 2a).

Monitoring by VHF radio and GPS telemetry

Our tracked animals clearly preferred wide overpasses, compared to narrow underpasses that were also used by humans. This preference could be partly because of human disturbance but also because of structural differences between overpasses and underpasses: We believe that any large mammal, especially a large carnivore, would rather walk on a wide, possibly forested bridge, than go into narrow, long and dark corridors.

Contrary to Clevenger and Waltho (2005), who did not find that large carnivores preferred two open overpasses in Banff NP, we have found a clear preference to overpasses by telemetry tracked bears, wolves and lynxes. The explanation of this difference could be in the great difference of structural attributes between Banff NP overpasses and overpasses monitored in this study: Two of the Banff overpasses are only 50 m wide and prominent from the surrounding terrain; the narrowest overpass monitored by us was twice as wide (Dedin green bridge, 100 m wide), whilst the other two monitored tunnels were more than 700 m wide. The average width of all 12 tunnels and potential crossing structures for radio-tracked large carnivores was 837 m, whilst the average width of seven underpasses on the same highway in our study area was 25 m. Our telemetry tracking has found strong positive selection to those very wide overpasses and negative selection to relatively narrow underpasses. The selection of Dedin green bridge (100 m) was equal to its availability. This leads to the conclusion that 50 m wide and prominent overpasses, such as in Banff NP, are not any better than 2–14.9 m wide underpasses (same highway in Bannf NP), as found by Clevenger and Waltho (2005), and that the intensity of use of 100-m-wide overpasses (Dedin green bridge, this study) could be equal to their availability, whilst more than 100 m wide overpasses will be selected more than expected (as found in this study), i.e. will function as funnels, attracting animals from farther distances.

Several studies have shown that four lane-fenced highways can be a barrier to large carnivores (Gibeau et al. 2002; Kaczensky et al. 2003). All three species of radio GPS tracked large carnivores in Croatia crossed the highway at least once and up to 32 times. One bear was using both sides of the highway as if there was no highway at all, whilst the other tracked bear never approached it during the time of the survey, probably because of territoriality. Lynx L02 crossed the lane once and established itself on the other side of the highway. Lynx L03, an adult male, had part of its core area (Fig. 6) very close to the highway fence but had never crossed it. It could be that this animal had found a good hunting area there, consisting of interspersed meadows and forest, with highway fence blocking the escape of roe deer from one side: Such hunting

pattern may be adopted by some predators (Waters 1988). A wolf pack (tracked by radio-collared wolves W05 and W09) living next to the north edge of the highway and was crossing it sometimes (four telemetry records) over Sopač hill to hunt for roe deer on the meadows south of the highway (Fig. 3b), but their core area, dens and rendezvous sites, were north of it (Fig. 6). Wolf W09 was a dispersing female, which wandered in large areas on both sides of the highway, crossing it four times in 3 months of tracking before it was illegally shot.

Satellite collars set to take GPS fixes at 6-h intervals may have too wide a time window for fast-moving animals like the wolf and may miss some crossings of the highway. GPS collars on two tracked bears were set to 2-h intervals of GPS fixes, and it was possible to track their movements with more accuracy. It was clearly visible (Fig. 5) where bear B30 was crossing the highway 32 times (including Dedin green bridge). Our tracked animals were crossing the highway to find denning sites, to find or to hunt for food on the other side of the highway, or maybe even used the highway fence for cornering their prey. Bears in Slovenia (Kaczensky et al. 2003) did not avoid the highway, but because the monitored section of the highway did not have tunnels or viaducts, the highway was a barrier for home ranges of resident bears: This was not the case for either resident or dispersing large carnivores in Gorski kotar.

Conclusions

The absolute counting by IR sensors of crossings of the highway, combined with track readings and a photo trap for the determination of species ratio, provide cost-effective and reliable data of the crossing structure use by large mammals.

The share of lighter digitigrades (wolf, fox and badger) could be underestimated by track searches but may be corrected by the use of photo trap.

Large mammals of Gorski kotar (Croatia) preferred to use wide overpasses (100 m and wider) instead of narrow (10 to 50 m) underpasses.

The Dedin green bridge (100 m wide overpass) in our study showed comparable effectiveness (13.3% more crossing per day) to the total effectiveness of all 11 underpasses (10 to 15 m wide, each) of phases 1 and 2 of the highway in Banff NP (Clevenger and Waltho 2000).

The ratio of large carnivores crossing the highway via wide overpasses can be three to six times higher compared to crossings through 10- to 15-m wide underpasses.

The highway in Gorski kotar, with 25% of the highway length in the crossing structures themselves, seemed not to be a barrier either for large carnivores (resident or dispersing) or for large ungulates.

Based on experience gained with the Dedin green bridge, a new highway to the south of Croatia (to Split and Dubrovnik towns), including 200 planned objects (potential crossing structures), included eight dedicated overpasses (green bridges in widths of 120, 150 and 200 m), one additional tunnel and five additional viaducts. The permeability of that highway is about 12%, i.e. 50% less than the highway through Gorski kotar. With this study, we have found that the 25% of highway permeability ensures habitat connectivity: What level of connectivity is provided by this 12.5% of highway permeability remains to be discovered.

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