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Research Article

Brown bear occurrence along a proposed highway route in Romania's Carpathian Mountains

Csaba Domokos[1], Sebastian Collet[2], Carsten Nowak[2], Ferenc Jánoska[3], Bogdan Cristescu[4]

1 Milvus Group Bird and Nature Protection Association, str. Crinului 22, 540343 Tîrgu Mureş, Romania
2 Senckenberg Research Institute and Natural History Museum Frankfurt, Centre for Wildlife Genetics, Clamecystraße 12, 63571 Gelnhausen, Germany
3 Institute of Game Biology and Management, University of Sopron, Bajcsy-Zsilinszky u. 4, 9400 Sopron, Hungary
4 Institute for Communities and Wildlife in Africa (iCWild), Department of Biological Sciences, University of Cape Town, 7701 Cape Town, Western Cape, South Africa
Corresponding author: Csaba Domokos (csaba.domokos@milvus.ro)

Abstract

Linear transportation infrastructure threatens terrestrial mammals by altering their habitats, creating barriers to movement and increasing mortality risk. Large carnivores are especially susceptible to the negative effects of roads due to their wide-ranging movements. Major road developments are planned or ongoing throughout the range of the Romanian brown bear (*Ursus arctos*) population, which is numerically the largest in the European Union. The planned A8 (Tîrgu Mureș–Iași–Ungheni) highway crosses the Romanian Eastern Carpathians on their entire width, posing a risk to the Romanian and broader Carpathian transboundary bear population. In the summers of 2014, 2017 and 2020, we surveyed an 80 km-long section of the planned highway using 68 hair traps with lure mounted in pairs along the route. We aimed to assess bear occurrence, genetic connectivity across the proposed highway and to estimate the minimum number and sex ratio of bears present in the area. With an effort of 3,519 hair trapping days (17 days / trap / session), we identified 24 individuals from the 45 collected hair samples, with a higher prevalence of female bears (male:female sex ratio of 1:1.3). We documented functional connectivity across the planned highway through parent-offspring (4 cases), full-sib (2 cases) and half-sib (24 cases) genetic relationships amongst sampled individuals. Terrain ruggedness and longitude were the most important predictors of bear occurrence from our analysis of detections at hair trap locations. Bears consistently occurred in the vicinity of the planned highway when in rugged terrain of the western section of the study area and were often detected close to human settlements (< 1 km). Even at this stage, without the A8 highway constructed, connectivity is likely already limited by the existing extensive network of settlements and restricted to a few important linkage areas still free of developments. Additional threats to bears and other wildlife in the area include poaching and large numbers of free-ranging dogs. We provide recommendations to mitigate these threats.

Key words: Carpații Orientali, detection survey, habitat fragmentation, hair trapping, non-invasive survey, road ecology, *Ursus arctos*

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Introduction

The loss, degradation and fragmentation of habitats represent major threats to terrestrial mammal diversity around the globe (Rands et al. 2010; Crooks et al. 2017; Kuipers et al. 2021). In recent decades, the impacts of roads on ecosystems have received concerted attention (Coffin 2007) and roads have been recognised as a main driving force behind the global alteration of natural habitats (Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000; Rhodes et al. 2014). Roads can affect many components of ecosystems and their associated edge effects can manifest at local and landscape levels (Coffin 2007). Animal species with wide ranging movements, large home ranges and long dispersal distances are especially vulnerable to roads (Rytwinski and Fahrig 2012). In particular, possible adverse effects of roads have been documented for large carnivores, including canids (Jędrzejewski et al. 2004; Riley et al. 2006), felids (Palma et al. 1999; Kerley et al. 2002; Niedziałkowska et al. 2006; Colchero et al. 2011; Litvaitis et al. 2015) and ursids (Proctor et al. 2018; Morales-González et al. 2020).

The relationship between roads and brown bears (*Ursus arctos*) is complex, because road effects can be area- and/or sex-specific, may vary by time of day and season and can be influenced by traffic volume (Penteriani et al. 2018). Roads facilitate access of people to bear habitats, increasing the chances of human-bear encounters and bear mortality risk (Benn and Herrero 2002; Ciarniello et al. 2009; McLellan 2015). In some areas, collisions with vehicles represent a major cause of documented bear mortalities (Huber et al. 1998; Kaczensky et al. 2003; Gunther et al. 2004). Certain components of roadside vegetation, especially during spring and early summer (Nielsen et al. 2004a; Roever et al. 2008a), as well as other food sources associated with human presence on roads, such as waste (Huber et al. 1998), can lure bears close or onto roads. While seasonally attractive roadside vegetation can potentially improve female body condition and reproductive success, the benefits of roadsides are countered by high mortality (Boulanger et al. 2013). Road placement, for example, in areas of low ruggedness, can combine with previously enumerated factors to further increase the attraction of roads (Roever et al. 2008a).

Some bears decrease their use of areas near roads or avoid these altogether, suggesting that roads can cause effective habitat loss at varying scales (McLellan and Shackleton 1988; Kasworm and Manley 1990; Mace et al. 1996; Waller and Servheen 2005). Displacement from habitats near roads reduces habitat extent and might affect body condition, reproductive rates and, ultimately, population density of bears (McLellan and Shackleton 1988; Mace et al. 1996). Adult males generally avoid roadsides (McLellan and Shackleton 1988; Boulanger and Stenhouse 2014). Females with cubs (McLellan and Shackleton 1988; Graham et al. 2010) and subadults (Mueller et al. 2004; Graham et al. 2010) tend to exploit the vicinity of roads more often, due to preferred forage availability (e.g. herbaceous vegetation layer for grazing) and/or as an avoidance mechanism against potentially aggressive/infanticidal adult males.

Traffic volumes are negatively correlated with road permeability for bears (Gibeau 2000; Waller and Servheen 2005; Northrup et al. 2012). High traffic levels (e.g. along highways) can create home range boundaries for resident animals (Kaczensky et al. 2003; Find'o et al. 2019). Once traffic volumes exceed a threshold of 5,000 vehicles/24 hrs, roads may become absolute barriers to bear movements (Skuban et al. 2017). Roads can also offset the social structure of bear populations, because females are less likely to cross busy roads than males (Gibeau and Heuer 1996; Waller and Servheen 2005) and stop crossing roads altogether at a lower traffic threshold than males (4,000 vs. 5,000 vehicles/24 hrs; Skuban et al. 2017).

North American studies advocate for limiting road access (Mace et al. 1996; Wielgus et al. 2002; Graves et al. 2006; Roever et al. 2008a, 2008b) and reduction of road density in bear habitat by targeted road closure and removal (Nielsen et al. 2006; Ciarniello et al. 2007; Nielsen et al. 2008; Switalski and Nelson 2011). In Europe, on the other hand, bears mostly have to contend with crowded, highly fragmented, multi-use landscapes, with little wilderness areas left (Swenson et al. 2000; van Maanen et al. 2006; Linnell et al. 2008), where they are frequently exposed to roads (Torres et al. 2016; Psaralexi et al. 2017).

Romania is an important stronghold for brown bears in Europe, hosting approximately 6,000 individuals (Swenson et al. 2000; van Maanen et al. 2006; Linnell et al. 2008; Kaczensky et al. 2013), although this number might be overestimated (Salvatori et al. 2002; Popescu et al. 2016). As a European Union (EU) Member State since 2007, Romania has plans to extend and modernise its transport infrastructure to meet EU standards, with the aid of both national and dedicated EU funding (Romanian Ministry of Transport 2008). The goal is to cope with steadily increasing traffic levels: in the period 2007–2019, the number of vehicles has almost doubled, reaching more than 8 million in 2019 (Eurostat 2021). In 2020, the total length of Romanian highways was 904 km, with a highway density of 3.8 km/1,000 km^2. Major transport infrastructure developments are envisioned to enlarge this network to a total of 2,416 km of highways and 1,784 km of express roads (Papp et al. 2022). The country's best bear habitats are in the Carpathian Mountains and their foothills (Swenson et al. 2000; van Maanen et al. 2006; Cristescu et al. 2019), with many of the planned highways intersecting bear habitat. As a result, there is a potential risk that, without proper road mitigation measures in place, the Romanian bear population and its habitats will become severely fragmented.

The planned A8 (Tîrgu Mureș–Iași–Ungheni) highway, linking the city of Tîrgu Mureș in the west to the national border between Romania and the Republic of Moldova in the east, has been identified as a major threat to brown bear habitat connectivity (Fedorca et al. 2019). In particular, its westernmost section will intersect both important bear denning habitats (Faure et al. 2020) and critical movement corridors linking denning habitats to seasonal feeding grounds, as indicated by telemetry data from bears fitted with GPS collars (Domokos, unpublished data). The goals of this study were to evaluate brown bear occurrence, habitat use and genetic connectivity along a central section of the planned A8 highway. We aimed to identify locations on the landscape that are conducive to 1) bear occurrence, 2) bear movement and 3) to estimate the minimum number and sex ratio of bears using the planned highway route prior to the highway's construction. Our overarching hypothesis was that the distribution of the brown bear population would be ubiquitous and relatively homogeneous within a landscape that maintains some permeability despite human settlements, given that highway construction had not started at the time of the study. We anticipated that specific landscape characteristics might influence local patterns of bear occurrence.

Materials and methods

Study area

The planned A8 highway is designed to traverse the Romanian Eastern Carpathians and their foothills on a west–east axis. This study covers an 80 km-long segment of the central section (Section 2) of the highway, between the villages of Ditrău in the west and Leghin in the east, representing 37.4% of the total length (Fig. 1A). Here, the planned highway will follow and upgrade an existing network of county and national roads (DJ127, DN15, DN15B). Most (approximately 55 km) of the planned highway section considered in the study also parallels human settlements, which, in Romania, are often linear when following valleys. The primary land cover in the area is forest, dominated by coniferous or mixed coniferous-broadleaf tree species, including Norway spruce (*Picea abies*), silver fir (*Abies alba*), European larch (*Larix decidua*) and European beech (*Fagus sylvatica*). Deciduous forests composed of European beech, European hornbeam (*Carpinus betulus*) and sometimes oak (*Quercus* sp.) occur infrequently mainly in some regenerating, previously logged parcels. Agriculture is mostly limited to animal husbandry and agricultural lands comprise pastures grazed from late spring to early autumn, as well as hayfields.

Even without the planned A8 highway, the study area is partially fragmented by human settlements which are contiguous in some areas. Unlike for the western section of this highway, no purpose-built wildlife crossing structures have been planned for this 80 km-long section by the Environmental Permit (Neamț County Environmental Protection Agency 2023). Instead, a series of tunnels (23), viaducts (63) and bridges (60) that were planned due to the rugged topography, were considered adequate to also function as large mammal over- or underpasses, with a cumulative length of 26.5 km (33.1% of the section of interest).

Study design

We designed a sampling scheme to quantify the occurrence, functional connectivity across the planned highway, minimum population size and sex ratio of brown bears in the vicinity of the proposed highway. Using a Geographic Information System (GIS), we divided a shapefile of the highway route into 1 km-long segments. We generated points in pairs at the end of each 1-km highway segment, with one point on either side of the highway and all points at a set 500 m from the route. Pairs of points of which at least one fell inside a GIS layer of settlements were discarded, resulting in a total of 74 points arranged in 37 pairs (Fig. 1B).

Hair trapping

We entered the coordinates of each of the 74 points described above in a handheld GPS unit and accessed the points by driving and hiking to the sites. We deployed a hair trap station at each point during three survey sessions (2014, 2017, 2020). Surveys occurred in summer (June–July in 2014, July–August in 2017 and 2020). Hair traps were active for 17 days during each survey, after which the stations were retrieved from the field. Hair-trap stations were deployed within a 50 m buffer of each predetermined point, selecting areas with trees whenever

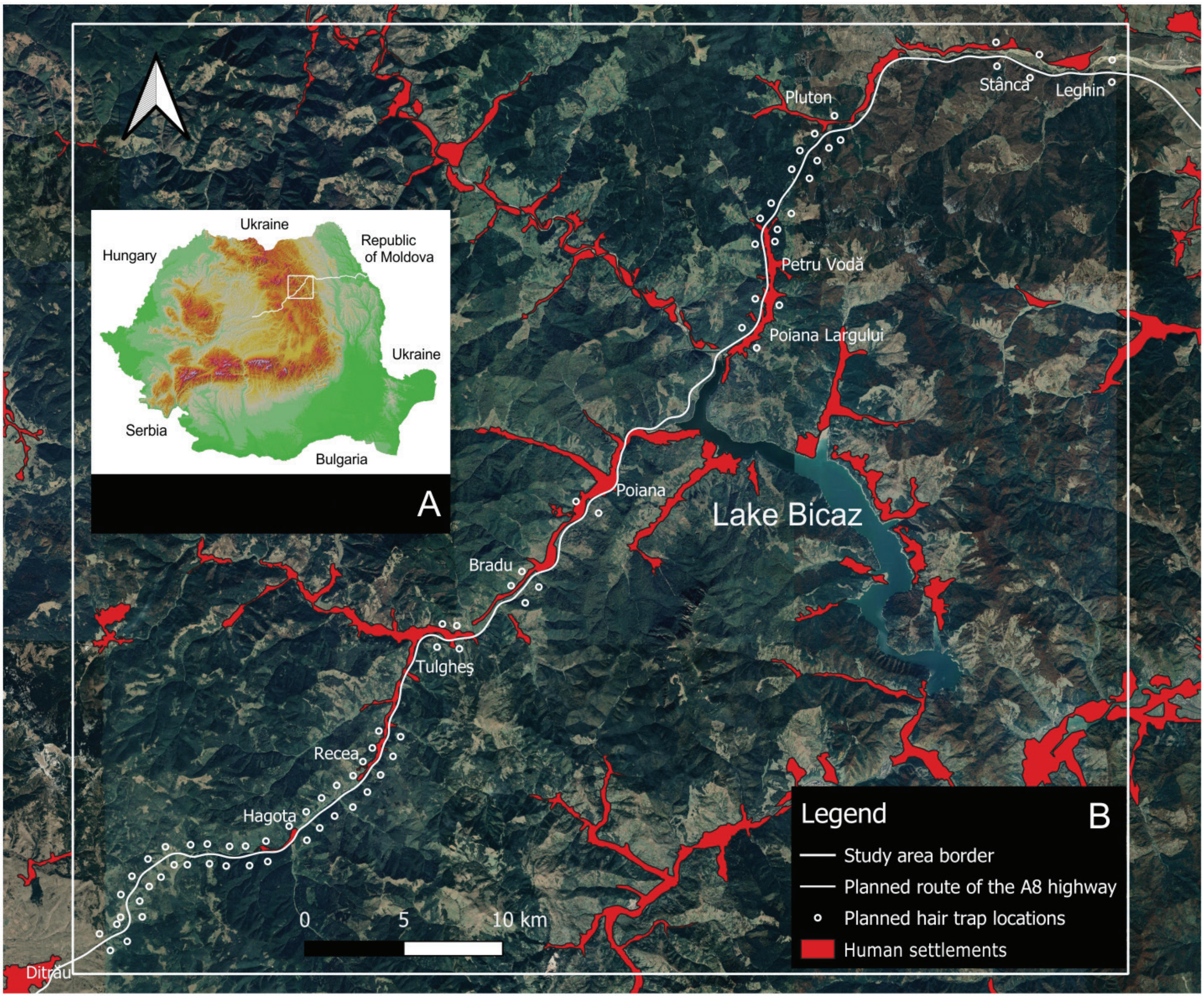

Figure 1. Route of the planned A8 highway and location of the study area in Romania's Eastern Carpathians (**A**) and detailed map of the study area, with planned brown bear hair trap locations (n = 74) situated in pairs along an 80 km-long section of the planned A8 highway (**B**).

possible. Stations consisted of a single strand of 4-prong barbed wire, mounted at a height of 50 cm that delimited a small area (6–16 m^2). The barbed wire was secured with U nails to at least three trees, if present or to 1.5 m-long, sharpened poles that we carried to the site and hammered into the ground.

At the centre of the area enclosed by the barbed wire, we constructed a small mound from locally available woody debris and rocks, onto which we poured 0.5 l of scent lure. The scented mound was unreachable for bears unless they crossed the barbed wire. We prepared the lure prior to each survey session, using 40 kg of Atlantic mackerel (*Scomber scombrus*) that we left rotting for 12 months in sealed plastic barrels. We then added 30 l of fresh, salted cattle blood and left the mixture to rot for an additional 3 months, before bottling it.

We checked the barbed wire at each station after 17 days for hair samples. Obtained hairs were visually examined to classify them as brown bear vs. other species. Examiners were experienced wildlife biologists accompanied by gamekeepers who had handled hairs of bears and other mammals, as well as physically handled bears for > 10 years. Hairs from other, clearly identifiable species were discarded after recording the non-target species. Hair samples from bears or of unclear origin were collected and labelled. Hairs located on the same group of four barbs were always collected as a single sample. Hairs located on neighbouring or almost neighbouring groups of barbs (i.e. 10–20 cm apart) were also collected as part of the same sample, unless they were obviously different in colour, length or texture. Hairs located further than 20 cm apart were always collected as separate samples, even if they seemed similar. We used medical tweezers to transfer samples from the barbed wire to envelopes, cleansing them after each use through burning with a lighter to avoid cross-sample contamination. Samples were stored individually in filter paper envelopes placed inside individual ziplock plastic bags that contained a bag of silica gel.

Genetic analysis

All pre-PCR molecular steps were conducted in a laboratory dedicated to the processing of environmental samples following standard routines for avoidance of contamination (Taberlet et al. 1999). DNA from collected hairs was extracted using the QIAamp DNA Investigator Kit (Qiagen, Hilden, Germany) with two final elution steps of 40 µl each. A part of the hypervariable domain of the mitochondrial control region (D-loop) was sequenced for general species identification (Pun et al. 2009) and haplotype assignment using the primers L15995 (Taberlet and Bouvet 1994) and H16498 (Fumagalli et al. 1996). For samples collected in the last sampling season (2020), the reverse primer was replaced through WdloopH (Caniglia et al. 2013). Obtained sequences were compared to the NCBI GenBank via BLAST search and bear haplotypes were assigned according to Frosch et al. (2014) (BG1, KJ638591.1; Ro2, X75873.1) and Matosiuk et al. (2019) (H7, MG254055.1).

For confirmed bear samples we amplified 13 unlinked autosomal microsatellite markers: Msut2 (Kitahara et al. 2000); G1A, G10C, G10P, G10D, G10L (Paetkau et al. 1995); G10H, G10J, G10U (Paetkau and Strobeck 1994); UarMU26 (Taberlet et al. 1997); Mu10, Mu23, Mu51 (Bellemain and Taberlet 2004). Reactions were performed in three multiplexes and four PCR replicates to account for genotyping errors (Navidi et al. 1992; Taberlet et al. 1999). PCR reactions were as described in Frosch et al. (2011) and microsatellite fragment analysis (including sex identification) was conducted as in Frosch et al. (2014).

The software ML-relate (Kalinowski et al. 2006) was used to infer genealogical relationships amongst individuals, based on the microsatellite data. ML-relate uses a Maximum Likelihood approach to estimate the likely relationship between pairs of individuals for four relationship categories: PO (parent-offspring), FS (full-sib), HS (half-sib) and U (unrelated). Related genotypes were manually compared to check for potential 1st grade relatives in the dataset.

Error rates for microsatellite genotyping were assessed via three basic statistics: Allelic dropout (AD) was calculated for heterozygote consensus genotypes as the proportion of one of the two consensus alleles missing across replicates (including wrong alleles); false allele rate (FA) was calculated for homozygote consensus genotypes as the proportion of additional alleles present across replicates; amplification success was calculated as the proportion of failed loci across all replicates. Error rates were calculated within samples across replicates and summarised over all samples.

Environmental covariates

We considered a suite of covariates that could *a priori* be hypothesised to influence bear occurrence (Table 1). We categorised land cover ("Habitat") in four classes which we assigned in the field when deploying hair-trap stations. We derived a terrain ruggedness index ("TRI") from a 30-m Digital Elevation Model (DEM) from the GMES RDA project (EU-DEM, https://www.eea.europa.eu/) using the GDAL Terrain Ruggedness Index algorithm in Q-GIS (v.3.18, QGIS Development Team 2013). From the resulting raster, we extracted TRI values for hair trap locations with the SAGA Add Grid/Raster Values to Points algorithm. The TRI provides a quantitative measure of topographic heterogeneity, calculating the sum change in elevation between a grid cell and its neighbouring cells (Riley et al. 1999). We calculated the distance of each hair-trap location to the nearest human settlement ("DistSett") using the GRASS v.distance algorithm. Human settlements were available as a polygon shapefile from CORINE Land Cover 2012 ("discontinuous urban fabric"; CORINE Land Cover database 2012). As human influence in the form of poaching was suspected to occur on a west to east gradient (with easternmost areas having higher poaching pressure, based on local information and our experiences in the field), we also considered a "Longitude" covariate.

Statistical analyses

We used ordinal logistic regression to investigate brown bear occurrence as a function of covariates hypothesised to influence bear habitat use. In ordinal logistic regression, the dependent variable is structured to have multiple discrete values in an assigned order. Although our data involved repeated surveys at the same set of stations, an occupancy modelling approach was not appropriate because the assumption of population closure for the survey duration was not fulfilled. Occurrence in our analytical framework took three values corresponding to

Table 1. Covariates for modelling brown bear occurrence along a planned highway in Romania's Eastern Carpathians.

Covariate	Code	Units	Data range	Linearity	Covariate justification (*potential influence to be tested in the models*)	References
Habitat						
Abiotic						
Terrain Ruggedness Index	TRI	Unitless (index)	0.43–13.86	Non-linear	Rugged terrain offers habitat security by limiting human access and providing better cover	Nielsen et al. (2004b); Martin et al. (2010); Sahlén et al. (2011)
Biotic						
Habitat	Habitat	Categorical	Pasture, mixed forest, conifer forest, deciduous forest	Non-linear	Pastures, deciduous and mixed forests provide feeding opportunities for bears. All three forest types provide cover for the species.	Dorresteijn et al. (2014); Pop et al. (2018)
Human Influence						
Longitude	Longitude	Degree	25.55–26.22	Linear	Poaching was suspected to occur on a west to east gradient, with easternmost areas having higher poaching pressure	none (area specific)
Distance to nearest settlement	DistSett	Metre	0–4,484.54	Non-linear	The proximity of settlements can filter the bear population for individuals more tolerant towards people and/or actively avoiding larger/more aggressive conspecifics	Kaczensky et al. (2006); Nellemann et al. (2007); Elfström et al. (2014)

situations where a bear was detected: no detection in the three survey sessions (1), detection in one of the three sessions (2) and detection in two or three of the three sessions (3). This method follows the approach of Chapron et al. (2014) and aims to identify areas with greatest probability of bear occurrence. Detection was defined as confirmed brown bear presence irrespective of the number of samples collected at a hair trapping station in a specific survey year and regardless of how many bear individuals were confirmed present at the site through genetic analysis.

We generated a set of 15 candidate models that were either univariate or included combinations of covariates. A correlation matrix including all covariates showed that the variables were not highly correlated (r <|0.6|) and could, therefore, be included in the same model structure. The models were included in three categories corresponding to three hypotheses: Habitat (n = 1), Human (n = 7) and combined Habitat and Human influences (n = 7). We ranked models using delta AICc and calculated evidence ratios for supported models (delta AICc < 2 and delta AICc < delta AICc of the null model).

We report the results as odds ratios, which we obtained through using the exponential of the parameter estimate(s) of the predictor(s) in the top model(s). For a one-unit increase in each predictor, odds ratios > 1 indicate an increase and odds ratios < 1 a decrease in the odds of bear occurrence.

We used QGIS v.3.16.15 for GIS procedures and R Studio v.2021.09.0 Build 351 for all statistical analyses.

Results

Overall, 68 hair-trap stations were active for 17 consecutive days across all sessions. Sampling effort was 1,156 trapping days in 2014 and 2017, respectively 1,207 trapping days in 2020. Three additional hair-trap stations active only in 2020 were excluded from modelling bear occurrence, but included in all other analyses. Three other locations that had been planned for sampling were excluded due to the presence of shepherd camps or livestock water troughs in all survey years.

Brown bear detection

During the three survey sessions, we collected a total of 89 hair samples. Mitochondrial control region sequencing was successful for 86 of the 89 analysed samples (96.6%). Half of the samples (n = 45, 50.6%) could be assigned to brown bears: 12 in 2014, 27 in 2017 and six in 2020. The samples originated from 12 hair traps in 2014 (17.7% of all mounted traps), 11 in 2017 (16.2% of all mounted traps) and five in 2020 (7% of all mounted traps). Bear hair was almost exclusively collected from hair trap locations west of Lake Bicaz (43 of the 45 samples). The two exceptions were samples collected in 2017 from the same hair trap that was the westernmost location sampled east of Lake Bicaz. During fieldwork east of the Lake, we only observed bear sign (tracks of a single animal) once in 2017. In contrast, we often encountered bear sign (tracks, scats, excavated anthills, peeled tree bark) west of Lake Bicaz.

Twenty of the 68 traps active across all three sessions registered bear hair (29.4%). Additionally, one trap active only in 2020 also captured bear hair. Fourteen traps were successful during a single session (including one active only in 2020), whereas seven traps yielded bear hair samples in two sessions each (Fig. 2A–C). Ten traps on each side of the planned highway route detected bears, whereas an additional trap only active in 2020 on the north side of the route also registered bear detection. Successful hair traps were distributed across all habitat classes surveyed: pasture (8), mixed forest (5), conifer forest (4) and deciduous forest (4).

We identified a total of three haplotypes, namely BG1 and Ro2 (Frosch et al. 2014; NCBI accession numbers KJ638591.1, X75873.1) and a third one matching to H7 (Matosiuk et al. 2019; MG254055.1, although the H7 sequence is slightly longer compared to our fragment).

Non-target species detection

We documented other wildlife and domestic species depositing hair at the hair trapping stations. Domestic dogs as the most frequently detected species overall (more than bears) were detected in all three survey years (2014, 2017, 2020: 15, 28, 22 locations, respectively) and so were wild boar (*Sus scrofa*; 2, 1, 4 locations) and red deer (*Cervus elaphus*; 1, 1, 3 locations). Roe deer (*Capreolus capreolus*) were detected in two survey years (2014, 2017: 1, 2 locations), just as cattle (2014, 2017: 2, 8 locations) and horses (2014, 2020: 1, 1 locations). Red fox (*Vulpes vulpes*; 2020: 2 locations) and sheep (2014: 1 location) were each detected in one survey year. Additionally, unidentified *Canis* sp. (either dogs or wolves [*Canis lupus*], as mitochondrial haplotypes w4, w11 and w19 following Pilot et al. (2010) have been identified in both European wolves and in dogs; data not shown) were detected in two survey years (2017, 2020: 13, 3 locations). We confirmed the presence of dogs at 10 out of the 13 locations in 2017 and all three locations in 2020 where we detected unidentified *Canis* sp. genetically.

Modelled bear occurrence

Only one model that had an intermediate number of parameters received support (model 7 with two parameters; Table 2). The model had good fit compared to the null model (Likelihood Ratio Test LR = 14.25, df = 2, P = 0.0008). Bears occurred consistently in areas of high terrain ruggedness. For 1-unit increase in ruggedness, the odds of bear occurrence increased by 32% (95% CI 8–63%). Longitude also influenced bear occurrence, with hair traps in the west having higher probability of occurrence than those in the east. As longitude of the trap location increased by 1-unit, the odds of bear presence decreased by 99%, with the decrease up to 98-fold as illustrated by the confidence interval (95% CI 45–9800%). Although distance to human settlement was not included in the supported model, it is noteworthy to mention that 15 of the 20 (75%) hair traps where bears were detected were located < 1 km from the edge of the nearest human settlement.

Minimum number of identified bears

Genotyping of brown bear hair samples was successful for 34 (75.6%) samples. Calculation of error rates showed a mean allelic dropout rate of 0.17 (SD = 0.28), a mean false allele rate of 0.03 (SD = 0.14) and a mean amplification

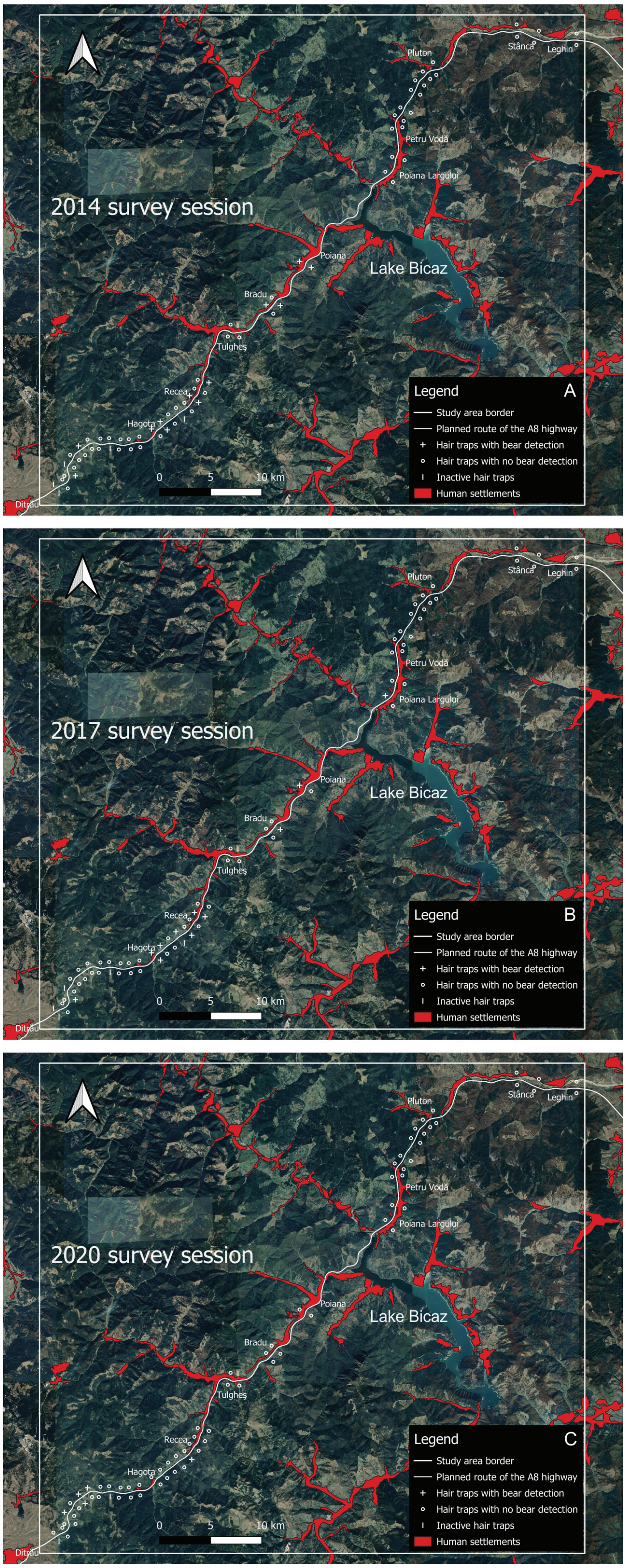

Figure 2. Brown bear hair trapping success along an 80 km-long section of the planned A8 highway during three survey sessions in the summers of 2014, 2017 and 2020 (**A–C**).

success of 0.78 (SD = 0.27). Out of the 34 samples, nine were excluded from further analysis, as they originated from four individuals that had already been identified on the same hair traps, during the same survey year (2017). We identified a total of 24 individual bears across the three survey sessions. Sex was successfully determined for 21 (87.5%) of the 24 individuals: nine were males and 12 females, resulting in a sex ratio (male:female) of 1:1.3. The largest number of individuals was identified in the year 2017 (n_{female} = 7, n_{male} = 3, $n_{unknown}$ = 2), followed by year 2014 (n_{female} = 4, n_{male} = 5) and 2020 (n_{female} = 2, n_{male} = 1, $n_{unknown}$ = 1).

Table 2. Ranking of brown bear occurrence models across a planned highway route in Romania's Eastern Carpathians. The supported model is illustrated in bold font.

Model_code	Model_set	Model_structure	K	ResDev	AIC	AICc	dAICc	ER
7	**Human Influence**	***TRI + Longitude***	**4**	**94.0**	**102.0**	**102.7**	**0.0**	**1.0**
8	Human Influence	DistSett + TRI + Longitude	5	93.9	103.9	104.8	2.2	2.9
3	Human Influence	TRI	3	100.4	106.4	106.8	4.1	8.0
6	Human Influence	DistSett + Longitude	4	98.8	106.8	107.4	4.7	10.6
5	Human Influence	DistSett + TRI	4	99.3	107.3	108.0	5.3	14.1
14	Human Influence & Habitat	Habitat + TRI + Longitude	7	92.5	106.5	108.4	5.7	17.3
4	Human Influence	Longitude	3	102.0	108.0	108.4	5.7	17.4
15	Human Influence & Habitat	Habitat + DistSett + TRI + Longitude	8	92.2	108.2	110.6	8.0	54.0
10	Human Influence & Habitat	Habitat + TRI	6	98.4	110.4	111.7	9.1	92.9
0	Null	Null	2	108.3	112.3	112.5	9.8	134.2
13	Human Influence & Habitat	Habitat + DistSett + Longitude	7	97.2	111.2	113.0	10.4	178.3
12	Human Influence & Habitat	Habitat + DistSett + TRI	7	97.6	111.6	113.5	10.8	219.1
11	Human Influence & Habitat	Habitat + Longitude	6	100.5	112.5	113.9	11.2	274.2
2	Human Influence	DistSett	3	108.3	114.3	114.7	12.0	401.0
1	Habitat	Habitat	5	107.1	117.1	118.1	15.4	2198.3
9	Human Influence & Habitat	Habitat + DistSett	6	107.1	119.1	120.4	17.8	7194.3

Bear recapture, relatedness and connectivity

Only one female bear was recaptured in our study, both within and across survey years, amongst different hair trap locations. The animal was detected in 2014 and 2017 on neighbouring hair traps located on the same side (south) of the planned highway route.

We found four cases of parent-offspring (PO) relationships and two full-sibs (FS) in the dataset (Table 3). Some potential degree of more distant relatedness (half-sibs [HS]) was identified for a total of 24 additional pairs. Eleven (9 × HS; 2 × FS) of the 30 related pairs of animals were found on opposite sides of the planned highway, which suggests gene flow across the envisioned highway route. The remaining 19 related pairs of animals (4 × PO; 15 × HS) were detected on the same sides of the planned highway (either north or south). Two of these pairs were detected on the same two hair traps. The remaining 17 pairs, however, detected on different hair traps indicate that movement is not impeded along a given side.

Table 3. Successfully genotyped bears (n = 24), relatedness and movements in relation to the planned highway route implied by detected relatedness. Hair traps A were located to the north, hair traps B to the south of the planned highway route, with numbers increasing from west to east.

Individual	Sex	Detected on hair trap (survey year)	Haplotype	Clade/ lineage	Related with (relatedness)	Movement implied by relatedness in relation to highway route
RO_UA001	♂	A06 (2014)	BG1	west	RO_UA004 (HS); RO_UA011 (HS); RO_UA022 (HS)	along; across; along
RO_UA002	♀	A13 (2014)	Ro2	east	RO_UA014 (PO); RO_UA015 (PO); RO_UA018 (HS); RO_UA021 (HS)	along; along; along; across
RO_UA003	♂	A18 (2014)	Ro2	east	RO_UA007 (FS); RO_UA009 (HS); RO_UA022 (HS)	across; across; along
RO_UA004	♀	A25 (2014)	BG1	west	RO_UA001 (HS); RO_UA011 (HS)	along; across
RO_UA005	♀	B03 (2014)	BG1	west	RO_UA006 (HS); RO_UA013 (HS); RO_UA025 (HS)	along; across; along
RO_UA006	♀	B14 (2014); B13 (2017)	BG1	west	RO_UA005 (HS); RO_UA019 (HS)	along; along
RO_UA007	♂	B18 (2014)	Ro2	east	RO_UA003 (FS); RO_UA020 (FS)	across; across
RO_UA008	♂	B20 (2014)	BG1	west	RO_UA016 (HS); RO_UA019 (HS)	across; along
RO_UA009	♂	B24 (2014)	BG1	west	RO_UA003 (HS); RO_UA019 (HS)	across; along
RO_UA011	♂	B03 (2017)	Ro2	east	RO_UA001 (HS); RO_UA004 (HS);	across; across
RO_UA012	♀	A13 (2017)	Ro2	east	RO_UA013 (PO); RO_UA022 (HS)	none (same hair trap); along
RO_UA013	?	A13 (2017)	Ro2	east	RO_UA005 (HS); RO_UA012 (PO); RO_UA015 (HS)	across; none (same hair trap); along
RO_UA014	♀	A14 (2017)	Ro2	east	RO_UA002 (PO); RO_UA016 (HS); RO_UA018 (HS)	along; along; along
RO_UA015	♀	A14 (2017)	Ro2	east	RO_UA002 (PO); RO_UA013 (HS); RO_UA018 (HS)	along; along; along
RO_UA016	♀	A25 (2017)	H7	west	RO_UA008 (HS); RO_UA014 (HS); RO_UA017 (PO)	across; along; none (same hair trap)
RO_UA017	♀	A25 (2017)	H7	west	RO_UA016 (PO); RO_UA018 (HS); RO_UA019 (HS)	none (same hair trap); along; across
RO_UA018	♂	A16 (2017)	Ro2	east	RO_UA002 (HS); RO_UA014 (HS); RO_UA015 (HS); RO_UA017 (HS)	along; along; along; along
RO_UA019	♂	B17 (2017)	BG1	west	RO_UA006 (HS); RO_UA008 (HS); RO_UA009 (HS); RO_UA017 (HS)	along; along; along; across
RO_UA020	♀	A19 (2017)	Ro2	east	RO_UA007 (FS); RO_UA021 (HS); RO_UA024 (HS)	across; across; across

Individual	Sex	Detected on hair trap (survey year)	Haplotype	Clade/ lineage	Related with (relatedness)	Movement implied by relatedness in relation to highway route
RO_UA021	?	B19 (2017)	Ro2	east	RO_UA002 (HS); RO_UA020 (HS)	across; across
RO_UA022	♀	A04 (2020)	Ro2	east	RO_UA001 (HS); RO_UA003 (HS); RO_UA012 (HS)	along; along; along
RO_UA023	?	A06 (2020)	BG1	west	–	–
RO_UA024	♂	B06 (2020)	BG1	west	RO_UA020 (HS)	across
RO_UA025	♀	B17 (2020)	Ro2	east	RO_UA005 (HS)	along

Discussion

Using non-invasive repeat survey methodology, we assessed the distribution and documented the minimum local population size of brown bears along a planned highway route in Romania, as part of an effort to collect information before highway construction. We detected bears at 21 sampling stations along the planned highway route, but with a more restricted distribution than expected and a concentration of presence in the western part of the study area. Our study did not succeed in producing direct evidence of bears crossing the planned highway route (e.g. same individual detected by hair traps on both sides of the future highway). Nevertheless, we provide genetic evidence that the population uses both sides of the planned development, including the detection of related animals on both sides of the highway route.

We found a positive association between bear occurrence and terrain ruggedness. When confronted with human disturbance, such as in human-dominated landscapes of Europe, bears may select rugged terrain (Martin et al. 2010; Dorresteijn et al. 2014; Roellig et al. 2014). Rugged terrain limits human access and provides secure habitat, minimising the risk of human-bear encounters and of human-induced bear mortalities (Nielsen et al. 2004b). With decreasing distance to human settlements, the use of increasingly rugged terrain has also been documented in the case of denning bears (Sahlén et al. 2011).

Most hair traps that detected bears were close (< 1 km) to human settlements (mean ± SD distance of all hair traps to human settlements was 1.35 ± 1.33 km). Mountainous villages in Romania commonly comprise solitary houses or small groups of homesteads, which are often not recorded as part of settlements in Corine Land Cover (i.e. discontinuous urban fabric). Thus, some hair traps that registered bears were even closer to buildings than revealed by the land-cover layer. Our results are in accordance with previous studies reporting that in Romania bears regularly use human-dominated landscapes and in general habitats in the proximity of human settlements (Dorresteijn et al. 2014; Roellig et al. 2014; Borka-Vitális et al. 2017), without necessarily coming into conflict with humans. After investigating the mechanisms underlying the occurrence of bears near settlements, Elfström et al. (2014) concluded that bears approaching settlements display a natural behaviour, best explained through avoidance of intraspecific aggression and/or interference competition. This adaptive behaviour is shaped by the despotic distribution of conspecifics more than by naivety, food conditioning or human habituation. In despotic distribution, dominant individuals exploit high quality habitats more often than subordinate conspecifics, whereas subordinate bears seem to fear dominant conspecifics more than they fear people. We can confirm that during the extended periods of fieldwork in the area, despite frequent interactions with locals, we have never heard complaints about habituated/nuisance bears, although this can be an issue elsewhere (Cristescu et al. 2016). When close to human settlements or human activity, bears may adjust their behaviour to avoid encounters with people (Ordiz et al. 2011), being most active at crepuscular or nocturnal hours to avoid overlap with human diel activity patterns (Kaczensky et al. 2006; Martin et al. 2010; Schwartz et al. 2010; Ordiz et al. 2014; Oberosler et al. 2017). Habitat selection may also vary with time of day and season according to risks associated with people, with bears near settlements selecting steep slopes and highly concealed resting sites during daylight hours (Martin et al. 2010; Ordiz et al. 2011; Cristescu et al. 2013; Skuban et al. 2018).

Longitude of the hair trap location was a good predictor of bear presence, with westernmost hair traps more successful. One possible explanation for this pattern is habitat fragmentation of the region in the west–east direction by Lake Bicaz due to its large size, as well as numerous contiguous settlements around it. However, poaching with firearms is also an issue of concern around the Lake and in the region east of it (Anonymous, Harghita County Police Inspectorate, Miercurea Ciuc, Romania, personal communication 2015, 2016). As these are some of the best bear habitats in Romania (Pop et al. 2018; Cristescu et al. 2019), widespread poaching can transform them into ecological traps for bears (e.g. attractive habitats with high mortality risk; Schlaepfer et al. 2002), also affecting bears originating from other source areas (Robertson and Hutto 2006; Lamb et al. 2017). While it is possible that some bear individuals may avoid areas with high poaching risk as an evolutionarily adaptive response to fear of humans (Ordiz et al. 2013), in general, poaching is an activity that may be difficult to predict and adapt to and could impact bear populations substantially (Kaczensky et al. 2011).

The habitat types in which the hair traps were mounted did not influence the success rate of collecting bear hair samples. In Romania, during summer when our surveys were conducted, female bears typically select mixed forests, whereas males select all three forest types: deciduous, mixed and conifer (Pop et al. 2018). Pastures are important feeding grounds for brown bears during the same period mainly because of the availability of ants (Dorresteijn et al. 2014), an important food source for the species (Swenson et al. 1999; Große et al. 2003; Roellig et al. 2014).

Although we identified 24 distinct bear individuals in the three surveys, we expected to detect a larger number of individuals. A possible reason is the close proximity of sampling stations to human settlements, which can act as a filter for the bear population, selecting for subordinate individuals or demographics of age or reproductive classes that are more tolerant towards human presence and/or actively avoid larger/more aggressive conspecifics. Nellemann et al. (2007) found that 52% of bears in the wider surroundings of settlements in Sweden were subadults of both sexes, with only 8% of adult males present in the < 10 km radius of larger settlements and resorts. While the techniques used in this study did not allow us to differentiate between age classes of bears that we sampled, we know that at least some of the detected bears were adults, as confirmed by four documented PO relationships.

Proctor et al. (2012) demonstrated that mortality associated with settlements has been a major force impacting bear populations and connectivity in western Canada, the northern United States and southeast Alaska. In our study system, we documented gene flow through PO, FS and HS relationships, both on the north–south and west–east axis and across the existing network of settlements. On the west–east axis (e.g. along the planned highway route), with the exception of some human settlement barriers near Lake Bicaz, bear movements are mostly unobstructed by human habitation, at least parallel with the planned highway route. However, because of often contiguous settlements spread along valleys stretching from west to east, bear movements on the north–south axis (e.g. across the planned highway route) are likely already limited and possibly restricted to the remaining undeveloped areas. Tunnels, viaducts and bridges that are planned for highway development could help maintain some of the remaining functional connectivity for bears and other wildlife, especially because these structures will be relatively close to each other (mean distance between structures 326.2 m (range 20–2,072 m); Silvia Borlea, EPC Environmental Consulting, Bucharest, Romania, personal communication 2023). The mean length of the planned tunnels is 188 m (range 16–940 m), while the mean Openness Index (width × height / length of the structure) of the selected viaducts and bridges is 120.6 (range 4.4–853.9). The most significant linkage areas on the north–south axis are situated between villages, such as Ditrău and Hagota (12 km), Hagota and Recea (4 km) and Petru Vodă and Pluton (4.8 km). The latter area, however, is situated east of Lake Bicaz and our study did not document bear presence in its surroundings.

Widespread, cryptic poaching could have contributed to relatively low bear detection rates in our study. Due to low densities and slow reproductive rates, large carnivores are especially vulnerable to poaching and previous studies have documented substantial effects of illegal killings on large carnivore demography (Kruckenhauser et al. 2009; Liberg et al. 2012; Persson et al. 2015; Červený et al. 2019; Benson et al. 2023). Additionally, the timing of our surveys might have also influenced bear detection rates, with part of the bear population moving during the summer to richer feeding grounds situated at lower altitudes, either to the west or to the east from the surveyed area. This pattern of significant seasonal movements of at least part of the population has been observed in another area of the Romanian Eastern Carpathians (Domokos, unpublished data) and other regions (Cozzi et al. 2016; De Angelis et al. 2021). The timing of our surveys might have influenced bear detection rates in other ways too. While our surveys took place during summer, bears are more likely to respond to scent lures in spring (Gervasi et al. 2008). Lamb et al. (2016) found that starting hair trapping at lure-scented sites towards the end of the mating season (which corresponds to early June in Romania) maximises female detections, while starting early in the mating season (late April - early May in Romania) maximises male detections. Another potential limitation of our survey design could have been the fact that scent lures do not offer a reward to the visiting bear, which might thus become trap-wise and lose interest in revisiting the site or visiting other hair-trap locations.

Even if we were unable to determine the sex of three of the 24 individual bears we identified, the data are indicative of a large population segment of females (1:1.3 [male:female]). This is comparable to the 1:1.6 sex ratio estimated for the Romanian Southern Carpathians (Skrbinšek et al. 2019) or to the 1:1.5 documented in Slovenia and 1:1.4 in Croatia (Skrbinšek et al. 2017). Prior to a ban introduced in October 2016, bear trophy hunting was a common, decades-old practice in Romania (Salvatori et al. 2002; Popescu et al. 2019). With male-biased hunting, a sex ratio skewed in favour of females is to be expected.

We showed that domestic dogs are present throughout the region, at least during the summer. The frequent detection of dogs at the hair traps is likely due to the presence of large numbers of guardian dogs accompanying livestock, stray dogs or dogs associated with human settlements. A similar finding was recorded in a study of wolf diet which revealed the importance of dogs in the diet of wolves in the south-eastern Carpathian Mountains (Sin et al. 2019). Although their benefits for protecting livestock from carnivore attacks have been demonstrated (Smith et al. 2000; van Eeden et al. 2018), domestic dogs can have negative impacts on wildlife when not under human supervision (Potgieter et al. 2016; Wierzbowska et al. 2016; Drouilly et al. 2020). If dogs as a depredation mitigation strategy are adequately applied, they can be an effective strategy for livestock protection (van Eeden et al. 2018), but may enable disease transmission at the wildlife-domestic animal interface (Borka-Vitális et al. 2017). Bears are susceptible to a number of pathogens of domestic dogs, such as canine distemper virus (CDV, the etiological agent of distemper; Di Francesco et al. 2015; Vitásková et al. 2019; Balseiro et al. 2024), canine parvovirus type 2 (CPV-2; Di Francesco et al. 2015; Vitásková et al. 2019) and canine adenovirus type-1 (CAdV-1, the etiological agent of infectious canine hepatitis; García Marín et al. 2018; Balseiro et al. 2024). Measures to decrease the risk of disease transmission between domestic dogs and bears and between livestock and wildlife in general should be incorporated into decision-making programmes for livestock husbandry under free-ranging conditions.

We also genetically confirmed the presence of unidentified *Canis* sp. (either dogs or wolves) in several locations. There is a possibility that at least some of these samples originated from wolves, in particular, the ones identified as haplotype w4, which occasionally occurs in dogs, but is commonly found in Romanian wolves (Jarausch et al. 2023). We did document wolf scats and a partially consumed livestock guardian dog in the area in spring 2015. However, our evidence indicate that most unidentified *Canis* sp. samples originated from dogs. Firstly, we confirmed the presence of dogs (either through visual inspection or genetic analysis of hair samples) at the majority of locations where unidentified *Canis* sp. samples were collected. Secondly, we collected samples later confirmed as originating from unidentified *Canis* sp. due to their resemblance to bear hair. These samples consisted of long, dark-coloured, undulating, soft guard hairs, which are also characteristic of dark-coloured, large bodied, mixed breed livestock guardian dogs. Dark-coloured dogs are traditionally used in the area, although less commonly than light-coloured animals, as shepherds appear to gradually replace mixed breed dogs with purpose-bred shepherd breeds such as Caucasian, Central Asian or Anatolian.

Conclusions

Connectivity on the north-south axis is relatively limited in the study area due to existing human settlements. Completion of the A8 highway could potentially further impede bear movements in important bear habitats centrally located in the Romanian Eastern Carpathians and their foothills. This area provides a vital link to other national-level populations located further North, including Ukraine, Slovakia and Poland (Straka et al. 2012). Together, these national populations form the vast majority of the transboundary Carpathian bear population, completed by a small population in eastern Serbia (Kaczensky et al. 2013; Chapron et al. 2014). Preserving and enhancing functional connectivity within the Carpathian bear population (Matosiuk et al. 2019; Papp et al. 2022), including maintaining permeability of Romania's Eastern Carpathians is of crucial importance (Fedorca et al. 2019). In this respect, dedicated wildlife crossing structures could have been planned by the responsible authorities during the pre-construction phase of the highway, based on the best available information concerning bear presence and movement in the area. Given the decisions already made through the environmental permit, we recommend permeability studies post-completion of the A8 highway section, with a particular focus in the area of the potential crossing structures associated with highway development as imposed by topography; and after bears have had the time to explore and start using them. If the structural features of the highway meant to bypass topographical challenges prove insufficient for wildlife connectivity, dedicated wildlife crossing structures (e.g. wide overpasses, Ford et al. 2017) might be required, even though their construction costs would be much higher at that stage. To maximise their effectiveness, these should be located in the vicinity of the still undeveloped areas identified in this study. Permanent development should be limited as movement is somewhat constricted already by the high density of human settlements, although for the time being i.e. before highway construction bear population connectivity is not yet fully curtailed. In parallel with maintaining habitat connectivity, the issues of poaching and dogs in the wild should be addressed by wildlife managers and law enforcement authorities.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

B. Cristescu and C. Domokos conceived and designed the study. C. Domokos collected the data. S. Collet and C. Nowak analyzed the genetic data. B. Cristescu and C. Domokos analyzed the occurrence data. C. Domokos led the writing of the manuscript. All authors contributed critically to drafts and approved the final draft.

Author ORCIDs

Csaba Domokos https://orcid.org/0000-0002-9973-7779
Sebastian Collet https://orcid.org/0000-0002-7309-5448
Carsten Nowak https://orcid.org/0000-0002-3139-1951
Ferenc Jánoska https://orcid.org/0000-0002-6200-0829
Bogdan Cristescu https://orcid.org/0000-0003-2964-5040

Data availability

All of the data that support the findings of this study are available in the main text.

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