RESEARCH ARTICLE

Stay home, stay safe? High habitat suitability and environmental connectivity increases road mortality in a colonizing mesocarnivore

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Abstract

Context Anthropogenic structures have considerable effects on ecosystems, disrupting natural population processes and representing a serious risk in terms of vehicle collisions. The golden jackal (*Canis aureus*) is a mesocarnivore species whose range is expanding in Europe. Roadkills are one of the main human-induced mortalities in Italy to the species.
Objectives Identify road-related characteristics and ecological factors related to golden jackal roadkill risk in Italy.
Methods We used habitat suitability (Maxent) and connectivity (Circuit theory) models to derive 15 metrics potentially affecting roadkill risk. We tested their influence using Bayesian generalized linear models and generalized linear models comparing golden jackal roadkill locations to random locations. Furthermore, we tested if there were significant sex, age-related and seasonal differences among road-killed individuals.
Results We found that roadkill risk was higher in areas characterized by higher values of habitat suitability and connectivity, habitat fragmentation and along highways. It was lower with increasing distance to the source population and in the presence of guardrails. No significant differences were detected in terms of roadkill risk between sexes, age classes and season
Conclusions The identified factors affecting road mortality of golden jackals in Italy provide insights on how to mitigate wildlife-vehicle collisions. Crossing areas, and visual and acoustic warnings for wildlife, as well as the importance of managing fences along high traffic volume roads could help mitigate further damage. Finally, there is a need to further investigate the effectiveness of mitigation measures in the light of the golden jackal's ongoing expansion in a human-modified landscape.

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Introduction

The destruction of natural ecosystems is one of the primary causes leading to biodiversity decline at a global level (Pereira et al. 2010); (Rands et al. 2010).

Indeed, habitat degradation leads to fragmentation of more extensive areas into smaller and more isolated patches intermixed within human-modified landscapes. This leads to unpredicted, deleterious and long-lasting effects, seriously undermining both ecosystem stability and health (Haddad et al. 2015). Anthropogenic structures may even disrupt population processes of wildlife species affecting both activity pattern (Watabe and Saito 2021) and dispersal capacity (Poessel et al. 2014), as well as representing a serious risk in terms of vehicle collisions (Poessel et al. 2014; Schmidt et al. 2020). Roadkill is the most visible effect of linear infrastructures and, globally, it is affecting the long-term survival of some vertebrate species (González-Gallina et al. 2013;(D'Amico et al. 2015), possibly damaging population size and affecting dynamics (Fahrig and Rytwinski 2009) as well as genetic diversity (Jackson and Fahrig 2011; Litvaitis et al. 2015). Furthermore, wildlife-vehicle collisions represent a serious risk to human safety and already cause substantial economic damage (Conover et al. 1995; Seiler 2005). Colonizing species may be particularly affected by the detrimental effects derived by vehicle collisions, especially within a rising metapopulation. Indeed, the persistence of a metapopulation is strictly linked with dispersal (Clobert et al. 2004), whose costs typically depend not only on energy and time spent during the relocation of individuals, but also on the probability of suffering harm or death during the movement (Bonte et al. 2012). The negative impact of roadkill on dispersal (and metapopulation) has been highlighted through simulation studies: roads lead to a significant population decline through direct mortality (Cullen et al. 2016) or habitat fragmentation and consequent isolation (Barbosa et al. 2020). In summary, addressing the impact of vehicle collisions on wildlife communities provides crucial information for conservation purposes.

Predictive modelling approaches provide strong support in the investigation of the environmental factors affecting roadkill risk, thus enabling researchers to relate roadkill events to road-related characteristics (e.g., Malo et al. 2004; Green-Barber and Old 2019; Collinson et al. 2019), as well as to predict areas where roadkill risk is higher, integrating data on habitat suitability and connectivity (Girardet et al. 2015; Fabrizio et al. 2019a, b; Russo et al. 2020). Such studies provide important information that can be used by road managers to develop adequate road designs

through the implementation of mitigation measures (Malo et al. 2004; Plante et al. 2019).

Carnivores are especially vulnerable to vehicle collisions due to their large home ranges, low population densities and their often low reproductive rates (Ginsberg 2001; Grilo et al. 2009; Litvaitis et al. 2015; Ceia-Hasse et al. 2017; Fabrizio et al. 2019a, b; Russo et al. 2020). In addition, they show a seasonal pattern of road casualties, probably related to biological features such as breeding and dispersal. The latter, along with daily movements, seems to be influenced by human disturbance with consequent negative effects on wildlife abundance (Grilo et al. 2009).

The golden jackal (*Canis aureus*) is a medium-sized mesocarnivore that has been showing a notable expansion in Europe over the last five decades (Spassov and Acosta-Pankov 2019). In Europe, one of the four golden jackal subpopulations extends along the eastern coast of the Adriatic Region along the border of Italy (Ranc et al. 2018a). In 2020, the Italian population was estimated to be composed of about 150 individuals (Franchini et al. 2020), showing an increasing trend. The highest density of golden jackals is reported in the Friuli Venezia Giulia (FVG) Region, mainly within the Karst (south-eastern part of the Region) and pre-Alpine areas (Franchini et al. 2020). Reproductive nuclei located in FVG therefore exert an important ecological role as a source area for the colonization of northern Italy. The species has been classified as being of 'Least Concern' by the International Union for the Conservation of Nature (IUCN) in Europe (Ranc et al. 2018a) and in Italy, due to its spatial connectivity with the Adriatic subpopulation (Lapini and Rondinini 2013). In FVG the golden jackal population is connected with the Slovenian one, which is mainly located in the southwest of the country (Krofel, 2008, 2009; Mihelič and Krofel 2012). Despite the golden jackal being a very adaptable species, it still faces human-related threats such as road mortality (Lapini and Rondinini 2013; Ranc et al. 2018a). Although there are several papers concerning road-related accidents of golden jackals in Asia (e.g., Mohammadi et al. 2018; Akrim et al. 2019; Rezaei et al. 2021), to the best of our knowledge, no previous research has focused on the impact of roadkill on the golden jackal population in Europe. Because of their opportunistic dietary habits (Lanszki et al. 2015; Ćirović et al. 2016), golden jackals may be subject to a high mortality risk as a consequence

of their scavenging behaviour (e.g., individuals feeding on carcasses close to roads) (Mohammadi et al. 2018). Furthermore, in India, dogs and golden jackals are among the most common mammalian victims on rural roads, with an increasing incidence during the breeding season (Sillero-Zubiri et al. 2004), likely due to their significant dispersal capabilities toward new breeding areas (Lanszki et al. 2018). In conclusion, when put together, this evidence (i.e., the current golden jackal range expansion, its feeding behaviour and dispersal capabilities) draw attention to the exposure of the species to roadkill mortality.

The purpose of this study is to assess the factors affecting the road mortality risk for golden jackal, both through the analysis of habitat suitability and connectivity and by exploring the landscape metrics at sites of roadkill incidents. We predicted to observe that golden jackal roadkill risk may increase in response to (*i*) habitat suitability and connectivity, with higher mortality risk near less favourable areas and higher landscape connectivity, (*ii*) human-modified landscapes (i.e., higher risk closer to human infrastructures and in highly fragmented habitats), and (*iii*) intrinsic biological and seasonal factors (i.e., higher risk biased toward males and subadults and during breeding season).

Materials and methods

Study area and road network

Friuli Venezia Giulia (FVG) is the most north-easterly administrative Region of Italy, covering 7,921 km^2 with 1.2 million inhabitants. Human population density decreases from the lowlands toward the mountainous areas in the North. Its location and geographical conformation support a great range of biodiversity (Regione Autonoma Friuli Venezia Giulia, 2021) with more than 90 native mammal species (Loy et al. 2019). Most of the Region is dominated by the Alps, followed by plains, which is crossed by near-pristine rivers with the remaining land surface represented by hilly landscapes (the Karst and the Alpine foothills). FVG encompasses a wide range of habitats, varying from natural mountainous areas with few urban settlements and roads to intensively human-modified landscapes with highways and high volumes of road traffic. The road network includes

13,392 km of roads, mainly represented by local roads (86.01%), followed by regional roads (5.27%), highways (4.72%) and state roads (4%) (Fig. 1).

Data collection

We detected golden jackal presence through acoustic stimulations (i.e., jackal-howling), from 2010 to 2020 following the protocol suggested by Comazzi et al. (2016). Jackal-howling is the emission of a pre-recorded howl from a specific position (calling station) to induce a response. If a response is obtained, the operators estimate the distance, azimuth and number of individuals (Giannatos et al. 2005). The distance is the most difficult parameter to estimate. Therefore, operators were trained to estimate this figure via empirical trials using a 100 m-step approach (e.g., 100 m, 200 m, etc.) before field surveys. We investigated 1,423 calling stations which were located in Karst areas, rivers, pre-Alpine and Alpine valleys, and pre-Alpine areas (Fig. S1). The locations of the calling stations were chosen to minimize potential background noise produced by anthropogenic factors (e.g., main roads, towns and airports). The calling stations were located at least two kilometres from each other. During each emission, we broadcasted a group howl with increasing volume, from 88 to 98 dB, with each emission lasting for 30 s, alternating with three minutes of listening. The procedure was repeated five times at each calling station and golden jackal locations were georeferenced using QGIS (QGIS Development Team 2021). We excluded positions recorded within towns from the analysis. This was done to avoid false positives due to domestic dog responses.

Locations of 41 road-killed golden jackals were collected between February 2009 and January 2021. Both the age and sex of the individuals were determined by experts (researchers and veterinarians), taking into account either body and/or teeth eruption, when available.

Environmental variables

We selected five meaningful environmental variables (Fourcade et al. 2017), according to golden jackal habitat requirements (Šálek et al. 2013; Spassov and Acosta-Pankov 2019; Wennink et al. 2019): land use/land cover (LULC), tree cover density, imperviousness, elevation and slope (Table 1). Golden jackals
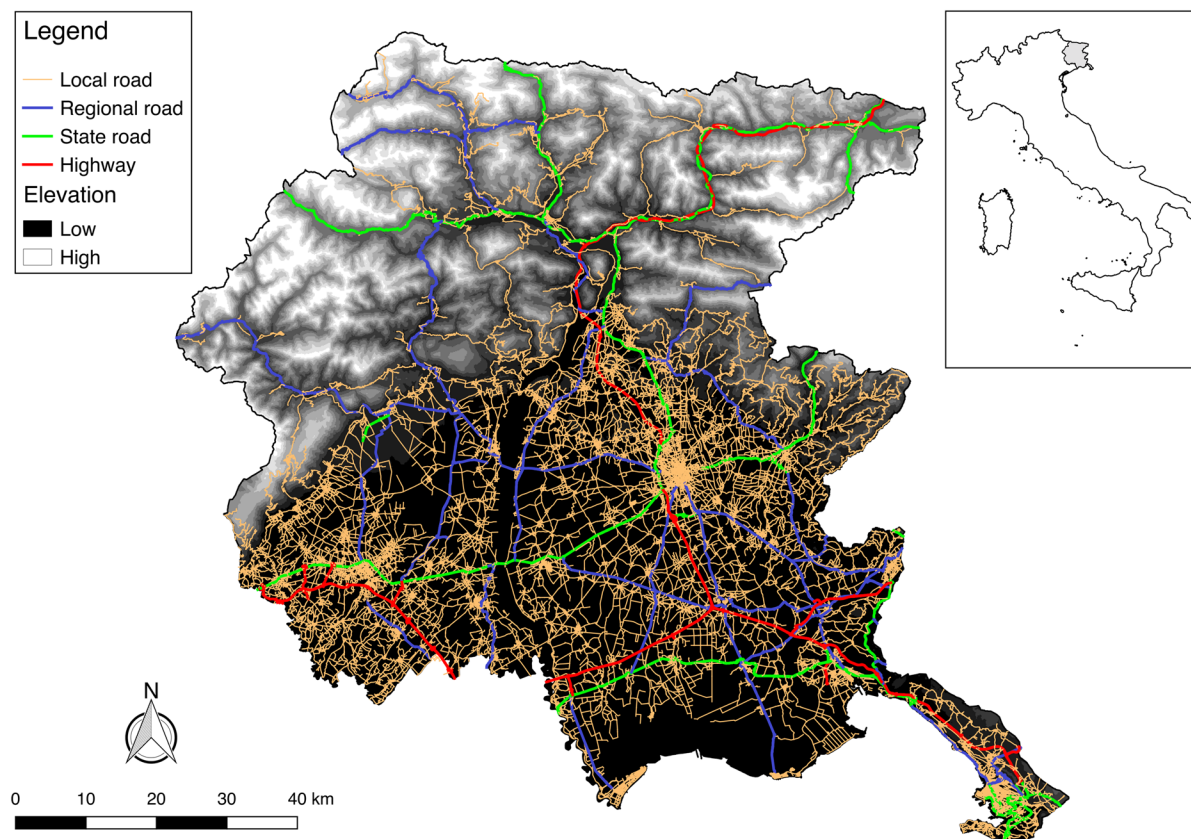
Fig. 1 Road network of Friuli Venezia Giulia Region. Background colours represent elevation: lighter colours correspond to higher elevations. The road network lies mainly within the lowlands.

Table 1 Predictors used to calibrate the habitat suitability model (HSM)

Predictor	Category	Description
Land cover	Categorical	11 land cover categories derived from Corine Land Cover 2018
Tree cover density	Continuous	Percentage of tree cover in each cell
Elevation	Categorical	14 altitudinal categories (e.g. 0-200 m asl, 200-400 m asl, 400-600 m asl, etc.) derived from DEM
Slope	Continuous	Slope derived from DEM
Imperviousness	Continuous	Percentage of the soil sealing in each cell

can colonize a wide range of natural and/or semi-natural habitats, including human-dominated agricultural landscapes (Šálek et al. 2013). In accordance with the species' distribution in Europe, it is mainly associated with shrub vegetation and a mosaic of agricultural landscapes and lowland wetlands (Giannatos 2004; Sillero-Zubiri et al. 2004). Furthermore, dense shrub vegetation is considered as an important habitat for golden jackals, because of the resource availability it represents, including both prey availability and denning sites, as well as refuge shelters (Giannatos 2004). LULC was derived from the Corine Land Cover (CLC) 2018, which we reclassified in 11 categories following Torretta et al. (2020) (Table 1 and S1). The tree cover density layer (TCD) represents the percentage tree cover in each cell. Furthermore, we investigated the degree of human-modified landscapes through the imperviousness (IMP)

layer, which represents the percentage of sealed soil. Two topographic variables were chosen, since stable golden jackals do not occur at high elevations due to harsh winters characterized by extended periods of deep snow cover (Giannatos 2004). Specifically, a digital elevation model (DEM) and slope, which was derived from the DEM, were used. The DEM was reclassified into 200 m step categories to avoid potential errors during model calibration due to removal of low altitude presence locations after spatial filtering (see below). All environmental variables were obtained from the Copernicus service (© European Union, Copernicus Land Monitoring Service 2020, European Environment Agency) and represented as raster layers of 100 m cells. Multicollinearity was tested using the variance inflation factor (VIF) which measures to what extent the variance of a regression coefficient is inflated due to multicollinearity in the model (Zuur et al. 2010). Because the VIF was < 5 (Akinwande et al. 2015), all variables were included in the analysis.

Habitat suitability

We used golden jackal presence data obtained from jackal-howling to calibrate a habitat suitability model (HSM) through the implementation of the maximum entropy algorithm in MAXENT Software (v. 3.4.1; Phillips et al. 2006). MAXENT is a popular machine learning method for predictions of species distributions using presence-only data (Elith et al. 2006; Phillips et al. 2006) and it is little sensitive to small sample sizes (Wisz et al. 2008). Predictor values are compared at species locations with a sample of random background points and a map of occurrence probability is created (Phillips et al. 2006). Our data were treated as presence-only data because calling stations without any response may not reflect a real absence (Filacorda *unpublished data*). Moreover, the golden jackal is still in expansion and may not have reached all potentially suitable areas (Bassi et al . 2015). However, HSMs may be affected by sampling bias (i.e., unequal survey effort; Leitão et al. 2011 (Bystriakova et al. 2012), which may artificially increase spatial auto-correlation of locations, potentially leading to model overfitting (Boria et al. 2014). Among the various ways to account for sampling bias, Fourcade et al. (2014) found that spatial filtering (i.e., subsampling regularly in the geographical space

of the species' locations) performed well among different types of sample bias. Therefore, we used the 'spThin' R package (Aiello-Lammens et al. 2015) to spatially thin our initial dataset while retaining the maximum number of locations that were at least 500 m apart. Such a cut-off was chosen after filtering experiments, as recommended by Boria et al. (2014), as well as because of FVG's high habitat diversity in a relatively small area. Furthermore, we tested different MAXENT implementations using the 'ENMeval' R package (Muscarella et al. 2014) because MAXENT outputs are sensitive to initial modelling settings (Merow et al. 2013). 'ENMeval' helps to find the best settings configuration which optimizes the trade-off between the goodness-of-fit and overfitting (Muscarella et al. 2014). We tested for different regularization values and feature classes using default settings, resulting in 48 combinations of the latter. The model which showed the lowest Akaike information criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2004) was considered the best model. To further reduce the degree of overfitting we used the *checkerboard2* partitioning method (Muscarella et al. 2014) which represents a variation of the 'masked geographically structured' data partitioning proposed by Radosavljevic and Anderson (2014). We randomly sampled 10,000 locations across our study area as background points. The predictive performance of the model was assessed by measuring the area under the receiver operating characteristic curve (AUC) (Hanley and McNeil 1982) and the difference between calibration and evaluation AUCs (AUCdiff) (Warren and Seifert 2011). Furthermore, we evaluated the predictive performance of the model with the Boyce index (Hirzel et al. 2006) using an independent dataset of golden jackal presence locations (n = 69) derived from opportunistic camera-trapping.

Habitat connectivity

To understand the influence of landscape connectivity on roadkill locations, we developed a connectivity model using the circuit theory, implemented in the Circuitscape Software (v. 4.0.5; McRae and Shah 2009). The choice of circuit theory relies on the assumption that, like other wild canids (Gutman et al. 2002; Cohen et al. 2013), the golden jackal may be particularly vulnerable to roadkill during the dispersal period and daily displacements. Indeed,

circuit theory is based on a Markovian random walk, i.e., random walkers do not have knowledge regarding landscape (McRae et al. 2008) and it is a more realistic approximation of dispersal movements than other analyses (McClure et al. 2016). Furthermore, it incorporates multiple pathways (McRae et al. 2008). Circuitscape runs current across raster resistance surfaces, which can typically be defined as the inverse of habitat suitability maps (Zeller et al. 2012). Higher densities of current among habitat patches indicate areas through which successful dispersers are more likely to move. Moreover, pinch points can be identified, i.e., features through which dispersers have high probabilities of crossing due to the bottleneck effect of high resistance values of the landscape (McRae et al. 2008). The current is conducted between source and sink locations (hereafter focal nodes) (McRae et al. 2008). However, our focus was to evaluate the connectivity across the entire study area, without any *a-priori* reason to place focal nodes. Therefore, we predicted the HSM to a 40 km buffer area along our study area (approx. 30% of the greatest length in our study area) and we used the inverse of the HSM as a resistance surface. We rescaled values in five discrete resistance categories (i.e., 1, 25, 50, 75, 100) (Boyle et al. 2017) based on the percentile values distribution of the HSM map, where higher values corresponded to higher resistance. The buffer area was used in order

to remove the effects of high current densities in the proximity of the node placement (Koen et al. 2014). Afterwards, we randomly placed 100 focal nodes on the edge of the buffer (Koen et al. 2014). We ran the algorithm in a pairwise mode, and after the analysis, the buffer was removed.

Roadkill site characteristics

To assess the influence of landscape features on golden jackal roadkill sites, we investigated a set of 15 landscape metrics comparing the 41 roadkill locations to 80 randomly generated points along the road network (Table 2). Specifically, we derived eight microscale metrics (i.e., at the roadkill sites), and seven macroscale metrics calculated within a 1400 m radius buffer, which represents the minimum home-range size for a golden jackal pack in Europe (Ćirović et al. 2018; Lanszki et al. 2018). Microscale metrics were represented by four presence/absence variables (i.e., topographic elements along road borders, vegetation, guardrail and/or fences, and culverts) derived from Google Maps Street View, three distance variables (i.e., from road intersections, human infrastructures and from Slovenian source population located in the Karst following the species distribution provided by Ranc et al. 2018a) and road type (highway, state roads,

Table 2 Predictors tested in the Bayesian generalized linear model (BGLM) and generalized linear model (GLM)

Variable	Description	Scale
Topography	Presence of road embankments and/or steep slopes along road edge	Microscale
Vegetation	Presence of vegetation on the road verge	Microscale
Guardrail	Presence of guardrails and/or lateral fences	Microscale
Culvert	Presence of culverts within the proximity of the roadkill site	Microscale
Dist_slo	Euclidean distance from the nearest Slovenian source population	Microscale
Dist_cross	Euclidean distance from road intersections	Microscale
Dist_settl	Euclidean distance from human settlements	Microscale
Road_type	Road category (highway, state road, regional road, local road)	Microscale
HS3_perc	Percentage of the most suitable habitat category within the buffer	Macroscale
Road_dens	Road density (km/km^2) within the buffer	Macroscale
Cur_mean	Mean current value within the buffer	Macroscale
Number of patches	Number of patches of the most suitable habitat category	Macroscale
Mean patch area	Mean value of the area (km^2) of the most suitable habitat category	Macroscale
Euclidean Nearest-Neighbour Distance	Euclidean distance (km) among the most suitable habitat patches	Macroscale
Landscape division index	1—(the sum of the most suitable habitat area/buffer area)	Macroscale

Table 3 Bayesian generalized linear models (BGLMs) with the best model marked in *italics*

Model ID	Predictors	K	2logLik	BIC	ΔBIC	ωi
1	*guardrail + dist_slo + road_type*	*4*	*114.86*	*123.19*	*0.00*	*0.67*
2	guardrail + culvert + dist_slo + road_type	5	114.71	125.13	1.94	0.25
3	vegetation + guardrail + culvert + dist_slo + road_type	6	115.39	127.88	4.69	0.06
4	vegetation + guardrail + culvert + dist_cross + dist_slo + road_type	7	116.24	130.82	7.63	0.01
5	topography + vegetation + guardrail + culvert + dist_cross + dist_slo + road_type	8	118.81	135.48	12.28	0.00
6	topography + vegetation + guardrail + culvert + dist_cross + dist_settl + dist_slo + road_type	9	121.53	140.27	17.08	0.00

D*ist_cross* distance from the nearest crossroad (m)

Dist_settl distance from the nearest urban settlements (m)

Dist_slo distance from the nearest Slovenian source population (m)

K number of parameters

logLik logarithmic likelihood

BIC Bayesian information criterion

Wi Schwarz's weight

regional roads and local roads), where each road category incorporates information about speed limits and traffic volumes (Jaeger and Fahrig, 2004; D'Amico et al. 2015). To derive macroscale metrics, we first rescaled the habitat suitability values in three equal categories representing three levels of suitability (low, medium and high). Thus, macroscale variables were represented by road density, percentage of the highest suitability category, mean connectivity value and four habitat fragmentation indices for the most suitable level from the rescaled map (number of patches, mean patch area, Euclidean nearest-neighbour distance and landscape division index) (Turner et al. 2001).

Statistical analyses

Statistical analysis was carried out using the Software R (v 4.0) and the level of significance (i.e., alpha) was set at 0.05. Following Zuur et al. (2009), in order to test the effect of different environmental and ecological predictors without resulting in model overfitting, data were analysed using both Bayesian generalized linear models (BGLMs) (Table 3) and generalized linear models (GLMs) (Table 4) through the R packages 'glm2' (Marschner 2011) and 'arm' (Gelman and Hill 2006), respectively. The roadkill risk was considered as the binomial dependent variable in which road-killed individuals were considered as observed values while random points as expected values. Overdispersion was checked through dividing the residual deviance of the maximal model (i.e., the one with more predictors) with the respective degrees of freedom. The choice to use Bayesian models was taken to best cope with binomial probabilities of presence/absence predictors, i.e., topography, vegetation, guardrail, culverts (Table 3) which may have affected the computation of p-values as a consequence of the prediction of absolute probabilities of 0 and 1 (Gelman and Hill 2006). For a given predictor, multicollinearity was tested through the VIF. Variables which showed the highest VIF values (> 5) were considered as highly correlated (Akinwande et al. 2015) and then dropped from the model. Model simplification was done based on the *principle of parsimony* (Occam's razor), fitting a maximal model and then simplifying it by removing non-significant explanatory variables. At last, model ranking was performed based on both the Bayesian information criterion (BIC) (Burnham and Anderson 2004) and Schwarz's weight (ωi) (Schwarz 1978) for BGLMs, and Akaike's information criterion (AIC) and Akaike's weight (ωi) (Burnham and Anderson 2004) for GLMs. Models with ΔBIC or ΔAIC < 2 were considered as competitors of the best model (Burnham and Anderson 2004). Furthermore, to compare the difference in terms of number of road-killed individuals between sexes, age classes and seasonal periods (autumn–winter vs. spring–summer) the

Table 4 Generalized linear models (GLMs) with the best model marked in *italics*

Model ID	Predictors	K	2logLik	AIC	ΔAIC	ωi
1	*habitat + connectivity + npatch + landscape*	*5*	*112.48*	*122.48*	*0.00*	*0.46*
2	habitat + connectivity + npatch + mean_patch + landscape	6	112.33	124.33	1.85	0.18
3	habitat + connectivity + landscape	4	116.38	124.38	1.90	0.18
4	connectivity + landscape	3	119.58	125.58	3.10	0.10
5	habitat + road_dens + connectivity + npatch + mean_patch + landscape	7	112.33	126.33	3.85	0.07
6	habitat + road_dens + connectivity + npatch + mean_patch + euclidean + landscape	8	112.33	128.33	5.85	0.02

habitat Percentage of the most suitable habitat around each buffer; *road_dens* road density (km of road/km^2 of the buffer surface); *connectivity* landscape connectivity; *npatch* number of patches of suitable habitats; *mean_patch* mean patch area of suitable habitats (km^2); *euclidean* Euclidean distance among patches of suitable habitats (km); *landscape* landscape division index (0 = poorly fragmented habitat, 1 highly fragmented habitat); *K* number of parameters; *logLik* logarithmic likelihood; *AIC* Akaike's information criterion; *ωi* = Akaike's weight

Two-Tailed One-Proportion Z-Test was applied using the *prop.test()* as sample size was > 30.

Results

Overall, we obtained 479 golden jackal responses and after applying spatial filtering, we kept a final dataset of 159 golden jackal locations. Of the 41 road-killed golden jackals collected in the study area, most of them (n = 34, 83%) have been found in the last four years (2018–2021) (Fig. S2). Sex was documented for 32 individuals and age class was able to be estimated for 33 individuals.

Among the 48 combinations of model settings, the one with the lowest ΔAICc had a regularization multiplier set to 0.5 and included linear + quadratic feature classes (Fig. 2). The model showed very good predictive performance based on the AUC (0.872, var = 0.0002) and the difference between calibration and evaluation AUCs was very low (0.024, var = 0.0002). The Boyce index showed high predictive abilities of the HSM because it assumed a value of 0.952.

LULC, elevation and slope were the environmental variables mostly affecting the HSM (Fig. S3 and Table. S2). The most suitable LULC types were broad-leaved woodlands and shrublands, coniferous and mixed forests, as well as areas without vegetation. Pastures and grasslands and cultivations with natural elements played a secondary role. Furthermore, suitability decreased with increasing elevation and slope. Even though the effect of tree cover density was not as pronounced as for other previously described

variables, its response curve exhibited a bell shape, reaching highest suitability at 50–60% of coverage. Finally, the IMP affected the HSM only marginally and it assumed high constant values with a slightly decreasing trend (Fig. S3 and Table S2).

Highly suitable areas covered 6% of the surface of FVG and were mostly represented by the Karst (Fig. 2), the hilly areas bordering the lowlands, the main rivers and the natural areas in the southern part of the lowlands. Conversely, upper elevations and most of the lowlands occupied by intensive agriculture exhibited the lowest suitability levels (Fig. 2).

The connectivity map showed high current values mainly in the Karst and along rivers, and secondly within the hilly areas. Pinch points of current were highlighted in the lowlands representing pathways most likely to be used by jackals (Fig. 3).

From the best model resulted from the BGLMs analysis (Table 3) we obtained that the distance from the nearest Slovenian source population (BGLM, *ResD* = 104.01, *p* = 0.04), the presence of guardrails and/or fences (BGLM, *ResD* = 104.01, *p* = 0.01), and the type of road (BGLM, *ResD* = 104.01, *p* < 0.001) represent those predictors significantly affecting the risk for golden jackals of being road-killed. However, because the difference in terms of ΔBIC with the second model was < 2 (Table 3), also the latter model could be considered as adequate as the first in describing the relationship between response variable and covariates. Moreover, the second model confirms that the distance from the nearest Slovenian source population (BGLM, *ResD* = 101.15, *p* = 0.03), the presence of guardrails and/or fences (BGLM, *ResD* = 101.15, *p* = 0.01), and the type of road
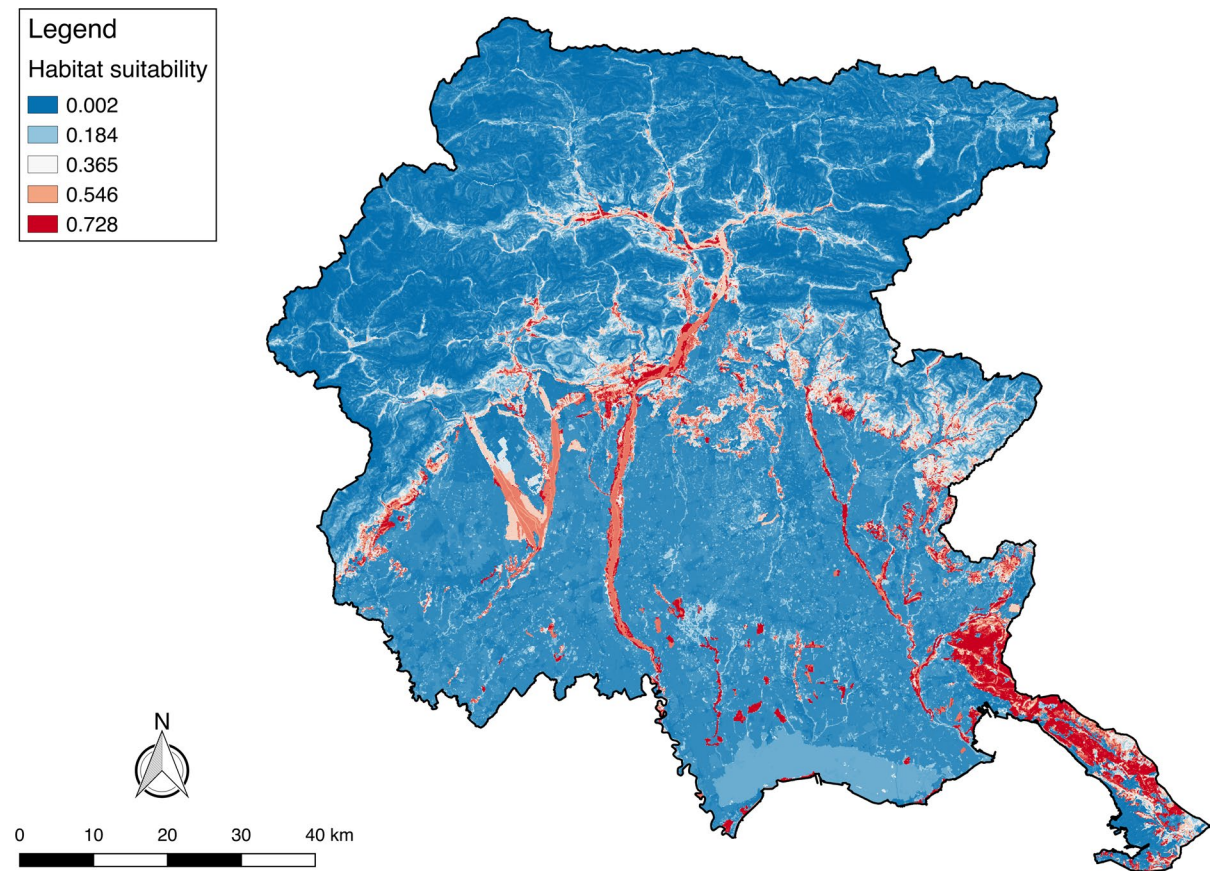
Fig. 2 Habitat suitability map for golden jackal. Highly suitable areas are shown in red and are represented mainly by the Karst (south-eastern FVG), river valleys, hilly areas bordering the lowlands and the natural areas within the lowlands (the southern part of FVG). Lowlands and uplands, as well as steep areas are depicted as poor habitats for golden jackals.

(BGLM, $ResD = 101.15$, $p < 0.001$) are predictors significantly affecting the risk for golden jackals of being road-killed. From the best model, it turned out that the risk for golden jackals of being road-killed decreases in response to increasing distance from the nearest Slovenian source population, presence of guardrails and/or fences and type of road (Fig. 4).

From the best model of the GLMs analysis (Table 4) we obtained that the percentage of suitable habitat calculated within each buffer (GLM, $ResD = 122.48$, $p = 0.02$) and habitat fragmentation expressed through the landscape division index (GLM, $ResD = 122.48$, $p = 0.006$) were those predictors significantly affecting the risk for golden jackals of being road-killed. However, because the difference in terms of ΔAIC with the second and third model was <2 (Table 4), they were adequate as well

in describing the effect of the different environmental covariates. The second model revealed that the landscape division index (GLM, $ResD = 112.33$, $p = 0.007$) was the only predictor significantly affecting the risk for golden jackals of being road-killed; while the third model showed that the landscape division index (GLM, $ResD = 116.38$, $p = 0.03$) and the landscape connectivity (GLM, $ResD = 116.38$, $p = 0.03$) were those predictors significantly affecting the risk for golden jackals of being road-killed. Specifically, it turned out that the risk for golden jackals of being road-killed increases in response to increasing percentage of suitable habitat and both higher habitat fragmentation and connectivity (Fig. 5).

No significant difference was obtained comparing the number of road-killed males (n = 18, 56.25%) and females (n = 14, 43.75%) ($\chi^2 = 0.28$, CI
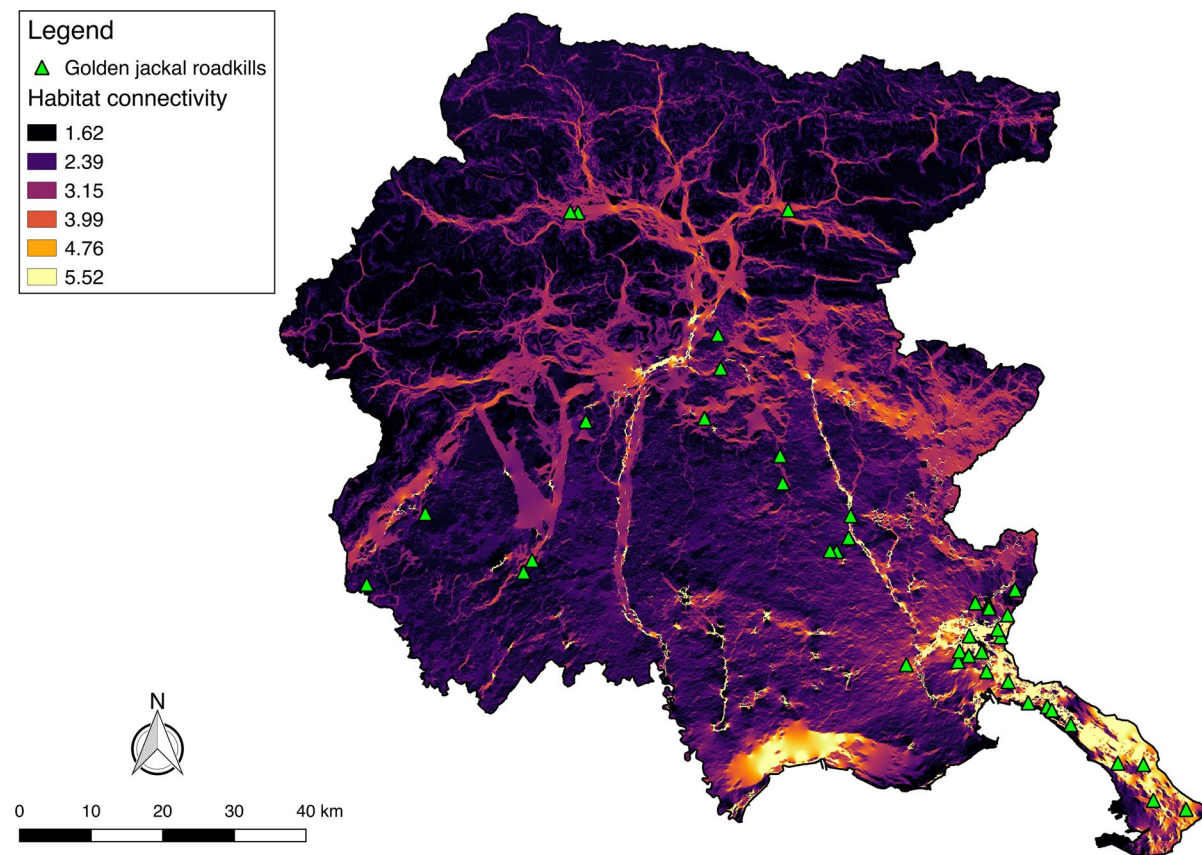
Fig. 3 Habitat connectivity map for golden jackal. Areas with high connectivity values are represented mostly by the Karst, river valleys and hilly areas. Most of the road-killed golden jackals were found within the Karst, since it is a permeable area, as depicted by its high connectivity values

95% = 0.38 – 0.73, PoS = 0.56, p = 0.59) and between periods, i.e., autumn–winter (n = 25, 64.10%) and spring–summer (n = 14, 35.90%) (χ^2 = 2.56, CI 95% = 0.47 – 0.78, PoS = 0.64, p = 0.10). Moreover, no significant difference (χ^2 = 1.09, CI 95% = 0.42 – 0.76, PoS = 0.61, p = 0.30) was registered in terms of roadkill risk between sub-adults (n = 20, 60.6%) and adult individuals (n = 13, 39.4%).

Discussion

The increase on the recovery of road-killed golden jackals within FVG in the last years, most likely as a consequence of population growth and prior range expansion, highlights how roadkill represents a rising threat to the species' colonization and human safety. We built habitat suitability and connectivity models which enabled us to assess how (*i*) such factors influenced the roadkill risk for golden jackal, along with (*ii*) the influence of microscale elements. However, we did not find any significant difference in roadkill mortality when inspecting (*iii*) biological and seasonal factors.

Habitat suitability and connectivity for the golden jackal in FVG

Due to its high degree of adaptability and ecological plasticity the golden jackal has recently expanded its range in many areas of south-eastern and central Europe (Šálek et al. 2013; Trouwborst et al. 2015), meaning habitat suitability assessments represent an important conservation tool (Ranc et al. 2018b; Wennink et al. 2019; Torretta et al. 2020). Although our HSM was calibrated using locations obtained from
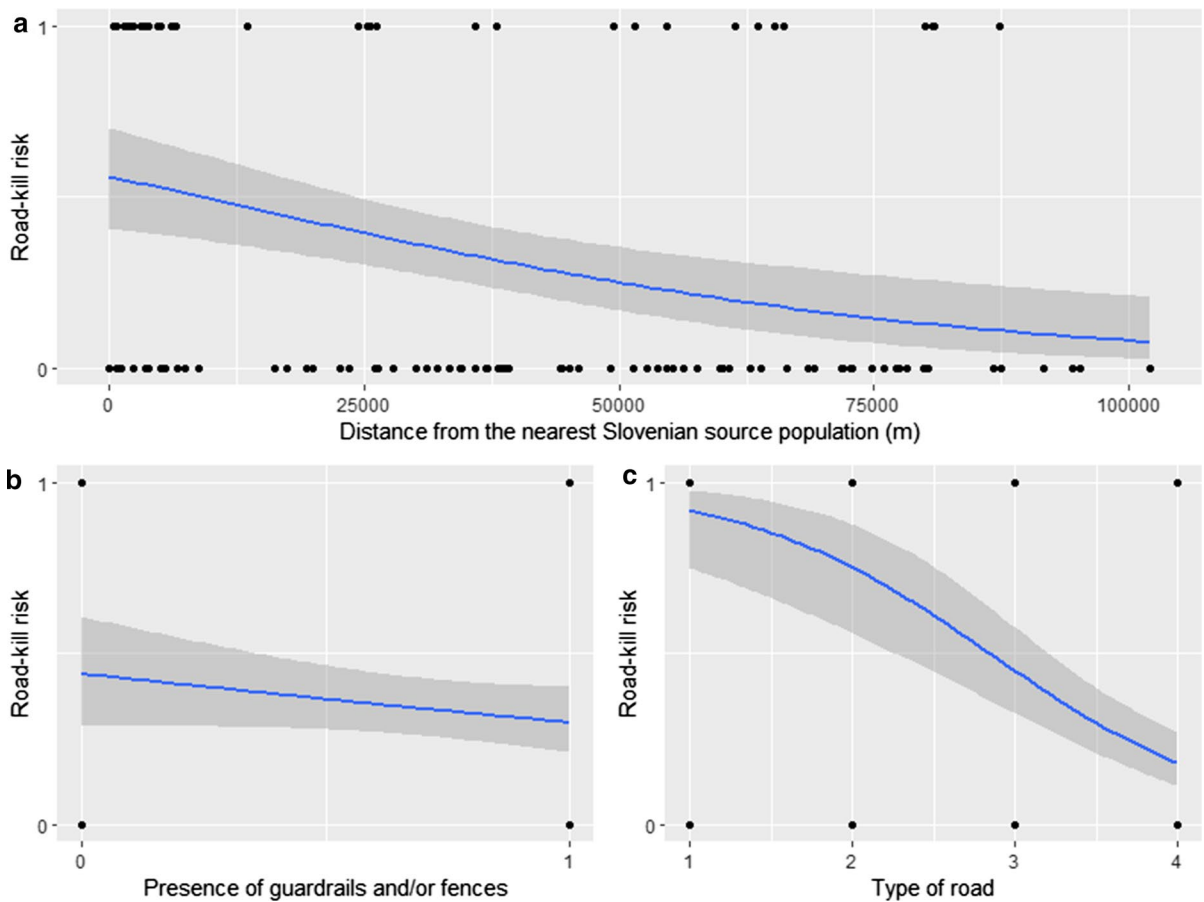
Fig. 4 Effect of **a** distance from the nearest Slovenian source population (m), **b** presence of guardrails and fences (0 = no, 1 = yes), and **c** type of road (1 = highway, 2 = state roads, 3 = regional roads, 4 = local road) in terms of roadkill risk for jackals

jackal-howling monitoring sessions, which are potentially affected by bias produced by different operator skills in terms of the perceived distance of the response, its predictions best reflect the ecological needs of the species (Giannatos 2004; Giannatos et al. 2005; Šálek et al. 2013; Spassov and Acosta-Pankov 2019).

The HSM highlighted the main role of natural habitats for golden jackal persistence, as well as a non-negligible influence of grasslands and cultivations intermixed with natural patches. These findings are in accordance with other habitat requirement studies carried out on golden jackals. Natural areas have been described as key factors affecting the species' presence (Torretta et al. 2020), especially dense broad-leaved vegetation, both because it offers sheltered areas and a high abundance of prey

(Giannatos 2004). Furthermore, it was not surprising to discover that golden jackal presence was linked to heterogeneous human cultivations (i.e., intermixed with natural elements), as it can take advantage of anthropogenic resources because of its opportunistic dietary habits (Lanszki et al. 2015) and can find protection against human pressure (Giannatos 2004; Šálek et al. 2013). Furthermore, our results match those obtained from previous research in which a negative correlation of both elevation (Giannatos 2004; Ranc et al. 2018b; Spassov and Acosta-Pankov 2019) and slope (Spassov and Acosta-Pankov 2019; Rather et al. 2020) with habitat suitability was shown. Indeed, higher values of these covariates were associated with lower habitat suitability values and vice versa. Finally, tree cover density and imperviousness showed negligible influence on the HSM. However,
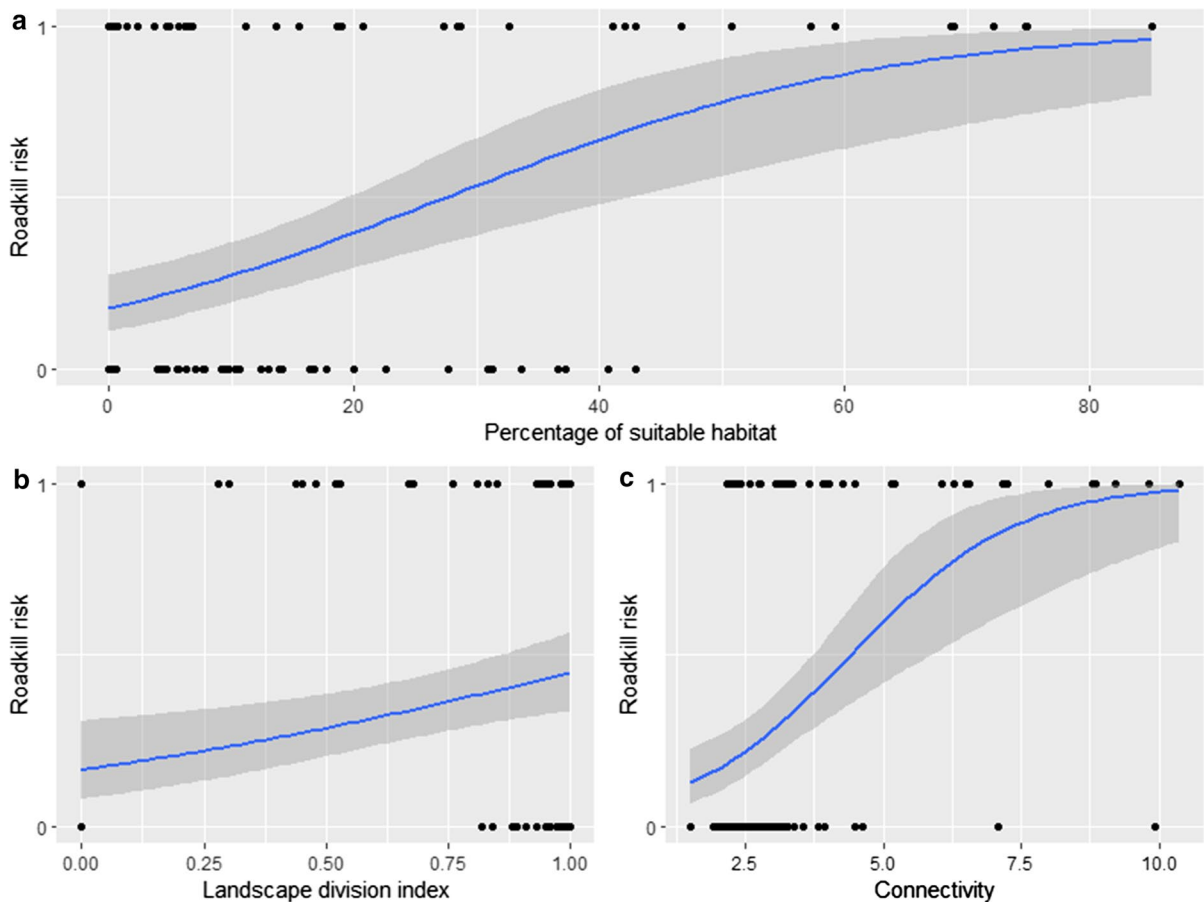
Fig. 5 Effect of **a** percentage of suitable habitats calculated within each buffer, **b** habitat fragmentation, expressed through the landscape division index (0=poorly fragmented habitat, 1=highly fragmented habitat), and **c** habitat connectivity in terms of roadkill risk for golden jackals

tree cover density exhibited a bell-shaped response curve (Fig. S3) and it may be related to the preference of the species for small woods with open canopies (Giannatos 2004; Spassov and Acosta-Pankov 2019). The response to the degree of anthropization slightly decreased when imperviousness increased, assuming high constant values of probability of occurrence. However, even though it is widely recognized that the golden jackal may use forest patches near human settlements (Giannatos et al. 2005; Markov 2012), we caution when considering this result as a decisive predictor, due to its very low variable importance on the HSM (Fig. S3 and Table. S2).

A visual inspection of our connectivity map enabled us to investigate the dispersion pattern that golden jackal individuals may use, without any *a-priori* assumption on source populations. Most of the

roadkill sites (n=33, 80.5%) were located near areas with high connectivity values, especially in the Karst where the highest species densities were recorded. Indeed, the connectivity map suggests that dispersion may occur through several pathways (Fig. 3) with the river network and the Karst representing the most likely dispersion routes. Rivers exert a key role especially in lowlands due to low levels of human disturbance and the presence of patches of vegetation along their courses, which provide shelter and food resources. Furthermore, in the mountainous area, rivers may offer a flat, natural and safe network corridor that can be used to colonize new areas. On the other hand, the Karst is the main area of golden jackal presence as it holds suitable environmental conditions which facilitate the movements of individuals. Finally, another important natural corridor is

represented by the hilly area bordering the lowlands. Apart from the rivers, current values in the lowlands are very low, suggesting that it is unlikely that golden jackals are able to cross heavily anthropized environments. However, during dispersal movements canids are even known to cross unsuitable areas (Ciucci et al. 2009; Lanski et al. 2018). Therefore, the presence of pinch points in these areas leads us to assume that dispersal routes may also include less favorable areas.

Golden jackal roadkill risk: a matter of source population

Through the multiscale approach we were able to assess patterns comparing roadkill sites with random locations, partially verifying predictions (*i*) and (*ii*). Indeed, in FVG the roadkill sites of golden jackals were influenced by ecological macroscale metrics, i.e., (*i*) habitat suitability, connectivity and habitat fragmentation, as well as by microscale elements (metrics), such as (*ii*) the distance from the Slovenian source population, the presence of guardrails and/or fences and the road type. We believe that the statistical significances found in our study are strongly connected with the spatial distribution of the species, as highlighted by the roadkill locations. However, we are aware that some potentially explanatory variables may be overlooked, thus representing one of the main limits of our study.

Our model highlighted the role of habitat suitability and connectivity on roadkill risk. As stated above, ecological modelling has been increasingly used on roadkill studies, as it provides crucial ecological information on the studied species (Santos et al. 2013; Girardet et al. 2015; Fabrizio et al. 2019a). In our analysis, higher roadkill risk was related to higher values of suitability and connectivity, i.e., within or nearby highly permeable areas. This might be explained mainly by the clustered roadkill sites, as most of them were located within the Karst area and/ or not far from rivers (Fig. 3). Therefore, golden jackals may be subject to road mortality during daily displacements, as well as when they use roads as feeding sites, scavenging on road-killed carcasses (Prosser et al. 2008; Akrim et al. 2019). This is particularly true in areas where the overall habitat connectivity is very low (i.e., in lowlands or mountainous areas) and only few dispersal routes are present (e.g., rivers). Moreover, the Karst represents a risky area as a result

of several factors, with higher densities of the species compared to FVG overall, suitable areas facilitating the movements of individuals and the presence of high speed limits and high traffic volume roads may enhance roadkill within this area.

With their great capacity for dispersal and large home-ranges some carnivore species are either behaviourally or spatially affected by habitat fragmentation, especially in relation to road density. Watabe and Saito (2021) showed that the night-time activity of the red fox (*Vulpes vulpes*), the racoon dog (*Nyctereutes procyonoides*) and the Asiatic black bear (*Ursus thibetanus*) was significantly higher on forestry roads with high vehicle-passing frequency compared to those with lower frequency, highlighting the potential trade-off effects produced by roads and vehicular transit on carnivore behaviour. Other studies revealed that despite felids being well adapted to life in urban areas, bobcats (*Lynx rufus*) and ocelots (*Leopardus pardalis*) are particularly sensitive to habitat fragmentation, as roadkill risk increased markedly as a consequence of increased road-crossing events (Poessel et al. 2014; Schmidt et al. 2020). In the case of the golden jackal, we calculated that higher mortality risk was associated with higher habitat fragmentation values (expressed through the landscape division index) which in turn was linked to a higher proportion of roads and human settlements, as well as higher habitat connectivity values. This may be linked to the evidence that the golden jackal may use forest patches near human settlements (Giannatos et al. 2005; Markov 2012), i.e., highly fragmented areas.

Contrary to our expectations, the roadkill risk was lower when the distance to the Slovenian source population increased. Indeed, within a colonization scenario one may expect that the greater the distance from the natal home range, the roadkill risk would increase as well, since dispersal represents a sensitive phase for individuals (Bonte et al. 2012). However, our results should be interpreted taking into account the spatial distribution of the species (this paper and Ranc et al. 2018a). As stated above, most of the roadkill events occurred within the Karst, which represents the area showing the highest density of the species (Franchini et al. 2020) also thanks to the presence of ecological corridors with the Slovenian source population. Moreover, as displayed in the Fig. 3, rivers represent safe routes which may be used by the species for dispersal. Therefore, combining

these two factors (i.e., high density of the species and dispersal routes), the influence of the proximity to the source population can be explained.

With the presence of guardrails and/or fences, the roadkill risk was lower. Although our results may suggest that these elements may effectively prevent the risk of fatal collisions, they should be interpreted cautiously. Indeed, most of the golden jackal carcasses (n=26, 63%) were found in close proximity to roads along which guardrails and/or fences were present. Many studies investigated the effect of roadside fences with different and, likely, context-dependent results. Malo et al. (2004) found that guardrails prevented wildlife-vehicle collisions for large and medium-sized mammals. Furthermore, Plante et al. (2019) highlighted how fence length represents a critical feature to discourage small and medium-sized mammals from crossing a road. Kreling et al. (2019) on the other hand were not able to detect such a prevention effect for coyotes (*Canis latrans*), which are ecologically similar to the golden jackal. Therefore, the reason behind these contrasting results may be linked to different study areas and designs, as well as different target species. Furthermore, in our study we did not investigate the influence of different types of guardrails or fences (Green-Barber and Old 2019) and, in addition, a considerable number of the road-killed golden jackals (n=12, 29%) were found along highways, where both guardrails and wire mesh fences were present. Such observations might confuse the interpretation of our model results. However, since golden jackals are scavengers (Lanszki et al. 2015), they may be attracted by carcasses distributed along the highway, as highlighted by GPS collared specimen (Frangini et al. 2022), and they may pass through gaps in fences (Filacorda *pers. comm.*). Furthermore, a possible explanation for the great number of golden jackals road-killed within the highway where fences are present is a *cage effect*, as they make it difficult to escape. Lateral fences and 2-lane guardrails might represent an optimal solution to prevent golden jackals reaching the road verge, thus lowering the risk for the animals of being killed. However, to ensure the effectiveness of such barriers, attention should be given to their maintenance. On the other hand, to counteract the fragmentation effect of fences, we stress the importance of implementing further mitigation measures such as animal crossings (e.g., underpasses and green bridges).

The highest roadkill risk was associated with highways (motorways), while the risk decreased in the association with local roads, suggesting that high traffic volume and speed limit may represent risk factors in terms of vehicle collisions. In Italy, recent research on other carnivores has yielded varying results. For the Eurasian otter (*Lutra lutra*) (Fabrizio et al. 2019b) and the polecat (*Mustela putorius*) (Russo et al. 2020) the density of state roads was shown as being most influential, whereas for the European badger (*Meles meles*) the density of regional roads mostly affected the roadkill risk (Fabrizio et al. 2019a). However, these differences are most probably linked to the varying ecological requirements of the target species, population dynamics (e.g., stable or expanding populations) and different study designs. Even though the greatest proportion of golden jackal carcasses were found on local roads (n=14, 34%) our model placed this road category as the least important in determining roadkill risk. Although such a result is quite intuitive due to the low traffic volume and speed limit of local roads, several factors may be involved in the explanation of this result. The main one, the road type represented most frequently in FVG are local roads, thus the random locations were more likely to be sampled from this road category (Fig. S4). Another factor is represented by the speed limit. State and regional roads have higher speed limits than local roads, and this may hamper drivers in recognizing road-killed animals. Motorists are the most important source of data when recollecting golden jackal carcasses. Furthermore, on highways the higher speed limit reduces the response time of drivers (Van Langevelde and Jaarsma 2004) and the animal frequently dies immediately after collision, lying on the road verge or in close proximity. On the contrary, on state and regional roads, because of the lower speed limits the animal may not die instantly following collision and thus carcasses identification may be more difficult if individuals cover some distances before collapsing (Meza-Joya et al. 2019).

Biological and seasonal factors vs. roadkill risk

Our results showed no statistical significance when analysed for differences in sex, age and seasonal factors. Some studies on mammals found a significant bias toward males, likely due to their larger home ranges, greater dispersal capabilities and less

cautious behaviour compared to females (Coulson 1997; Philcox et al. 2001). However, Admasu et al. (2004) did not find differences when comparing male and female home ranges on seven radio-collared golden jackals. Similar results were observed by Fenton et al. (2021), even though the only golden jackal male showed greater movement patterns compared to females. Moreover, carnivores show seasonal patterns in road mortality likely due to dispersal and breeding (Grilo et al. 2009). Indeed, evidence from GPS telemetry showed that a yearling female settled in a different area from the natal home range and successfully reproduced, after crossing several roads during dispersal (Lanszki et al. 2018). The reason why we were unable to detect a significant trend towards an age- or sex-class in our data may be found in the localization of the majority of roadkill sites. Most of them are located within the Karst (Fig. 3), which is the core area of the species distribution (Franchini et al. 2020) in FVG. Therefore, the individuals are more likely to be killed during daily displacements rather than dispersal events, the former involving all sex and age-classes. However, we should point out that a quasi-significant finding referred to the analysis of seasonal differences, suggesting that with a greater sample size we might have obtained different results. In conclusion, we suggest further investigations to overcome such spatial and sample biases.

Conclusion

Ongoing monitoring of the golden jackal population in FVG has allowed us to predict both habitat suitability and connectivity models for the species. We found that a key factor which increased the risk for jackals of being roadkill was the proximity to the source population located in the Italian and Slovenian Karst, an area characterized by highly suitable habitats and high densities of the species. Furthermore, golden jackals suffered high mortality rates within more fragmented areas. Finally, we have pointed out the great impact of high traffic volume roads and the need for proper management of fences and guardrails, in order to ensure their preventative function. To sum up, this study pointed out some of the factors impacting the safety of golden jackals and humans and paves the way for management suggestions. We believe that the creation of crossing areas (i.e., wildlife underpasses or overpasses) along with the maintenance of the existing fences to prevent animals crossing them represent a feasible solution to reduce wildlife-vehicle collisions. Introducing proper fences and guardrails along road verges may represent a rapid solution in areas of high risk, with the potential to reduce the numbers of animals road-killed. Furthermore, because crossing areas or newly-fenced road segments may not be economically feasible right across FVG, acoustic warnings and light reflectors could be implemented along sections of road more exposed to roadkill risk. We suggest that future research should focus on testing the effectiveness of these mitigation measures in order to identify which are best at preventing vehicle collisions for golden jackals, especially within a metapopulation context, considering its ongoing colonization in highly anthropized environments, such as the Italian lowlands.

Data availability The exact location data cannot be shared due to the sensitivity of golden jackal packs locations.

Code availability Codes are available on request.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication   Not applicable.

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