

Can bear corridors support mammalian biodiversity? A case study on the Central Italian Apennines

Chiara Dragonetti¹, Niccolò Ceci¹, Stefan Rodrigo Von Kempis¹, Jan-Niklas Trei², Mario Cipollone², Piero Visconti³, Moreno Di Marco¹

¹La Sapienza University of Rome

²Rewilding Apennines ETS

³International Institute for Applied Systems Analysis (IIASA)

A - Research concept and design, B - Collection and/or assembly of data, C - Data analysis and interpretation, D - Writing the article, E - Critical revision of the article, F - Final approval of the article

Abstract:

Ecological corridors are essential for maintaining ecosystem functionality, as they facilitate the movement of species between protected areas. In the Central Italian Apennines, five corridors have been identified to enhance habitat connectivity for the critically endangered Marsican brown bear (*Ursus arctos marsicanus*). This study focuses on two of these corridors to investigate their support of other mammal species populations. We collected data from camera traps over four months, and applied a Random Encounter Model to estimate the population densities of eight meso- and macro-mammal species. We compared the densities we estimated with those reported in the literature for different locations across Europe. The results indicated higher-than-average densities for several species compared to published data, especially for ungulates. These findings underscore the broader importance of Marsican bear corridors, providing important habitats for several mammal species. This type of analysis can be replicated in the same area at different times, or in other coexistence corridors for large carnivores, to support management strategies. Effective management of these corridors, with a focus on reducing human disturbance and improving habitat connectivity, will be critical for the long-term survival of both the Marsican bear and its coexisting species.

Keywords: wildlife management, ecological corridors, camera-traps, REM, density estimation.

Received: 2025-05-19

Revised: 2025-07-23

Accepted: 2025-08-03

Final review: 2025-06-25

Short title

The density of mammals in a study area of Central Apennines

Corresponding author

Chiara Dragonetti

La Sapienza University of Rome; email: chiara.dragonetti@uniroma1.it

Introduction

Protected areas (PAs) are the cornerstone of biodiversity conservation (Watson et al. 2014), and have increased rapidly in their global extent, now covering around 16% of the Earth's land surface (UNEP-WCMC & IUCN, 2024). PAs have been effective at preventing the extinction of several species, and nowadays the populations of many threatened mammal species rely almost entirely on these sites, while threats such as habitat loss, degradation and fragmentation affect unprotected parts of their distribution ranges (Pacifici et al. 2020). Yet, even effectively managed PAs might not be sufficient to preserve species with high spatial requirements, thus maintaining ecological connectivity between PAs is essential (Hilty et al. 2020). This is the rationale behind the inclusion of ecological corridors within the 2030 EU Biodiversity Strategy “*Legally protect a minimum of 30% of the EU's land areas and 30% of the EU sea area and integrate ecological corridors*” (EC 2024). This strategy requires extending conservation intervention beyond PAs, also focussing on the restoration and maintenance of habitat corridors between isolated reserves (Fahrig 2003, Pacifici et al. 2020, EC 2022).

Ecological corridors can increase the persistence of species with large spatial requirements, by allowing migration and dispersal, and they can also help to reduce species' mortality by facilitating the avoidance of predation and human disturbance (Curcic and Djurdjic 2013). They became a key element of conservation and management strategies for endangered mammal species, as they can mitigate the impact of habitat loss and fragmentation and they can increase the resilience of PAs networks (Mateo-Sánchez et al. 2014, McGuire et al. 2016). However, the ecological value of a corridor is species-specific, as corridors intended for one species may not work for other species with different habitat preferences and movement patterns (Merenlender et al. 2022). The vast majority of ecological corridors are designed for charismatic and endangered species, which have high conservation support from stakeholders and citizens (Keeley et al. 2019). Yet, these areas might also provide important co-benefits for several other species co-occurring with the focal species for which

49 47 the corridor was designed, especially if the former have lower spatial requirements than the latter
50 48 (Wang et al. 2018).

51 49 The Marsican brown bear (*Ursus arctos marsicanus*) is a subspecies of the brown bear (*Ursus arctos*)
52 50 and an endemism of the Central Italian Apennines (Ciucci and Boitani 2008). This subspecies is
53 51 geographically isolated from other bear populations, and represents one of the most endangered
54 52 mammal in Europe, facing severe risk of extinction due to very small population size (Ciucci and
55 53 Boitani 2008, Ciucci et al. 2015, Gervasi and Ciucci 2018). While the population is almost entirely
56 54 confined within the Abruzzo, Lazio, and Molise National Park (ALMNP), five corridor areas of
57 55 suitable habitat have been identified by stakeholders and conservationists to enhance the connectivity
58 56 towards critical areas in between PAs (Carotenuto et al. 2014, Ciucci et al. 2016, Ciucci et al. 2017,
59 57 Maiorano et al. 2019). These corridors are now the focus of conservation, restoration and rewilding
60 58 activities from a group of local NGOs, with the main goal of facilitating bear recolonization of its
61 59 former range by reducing the mortality causes outside protected area (Cipollone et al. 2024).

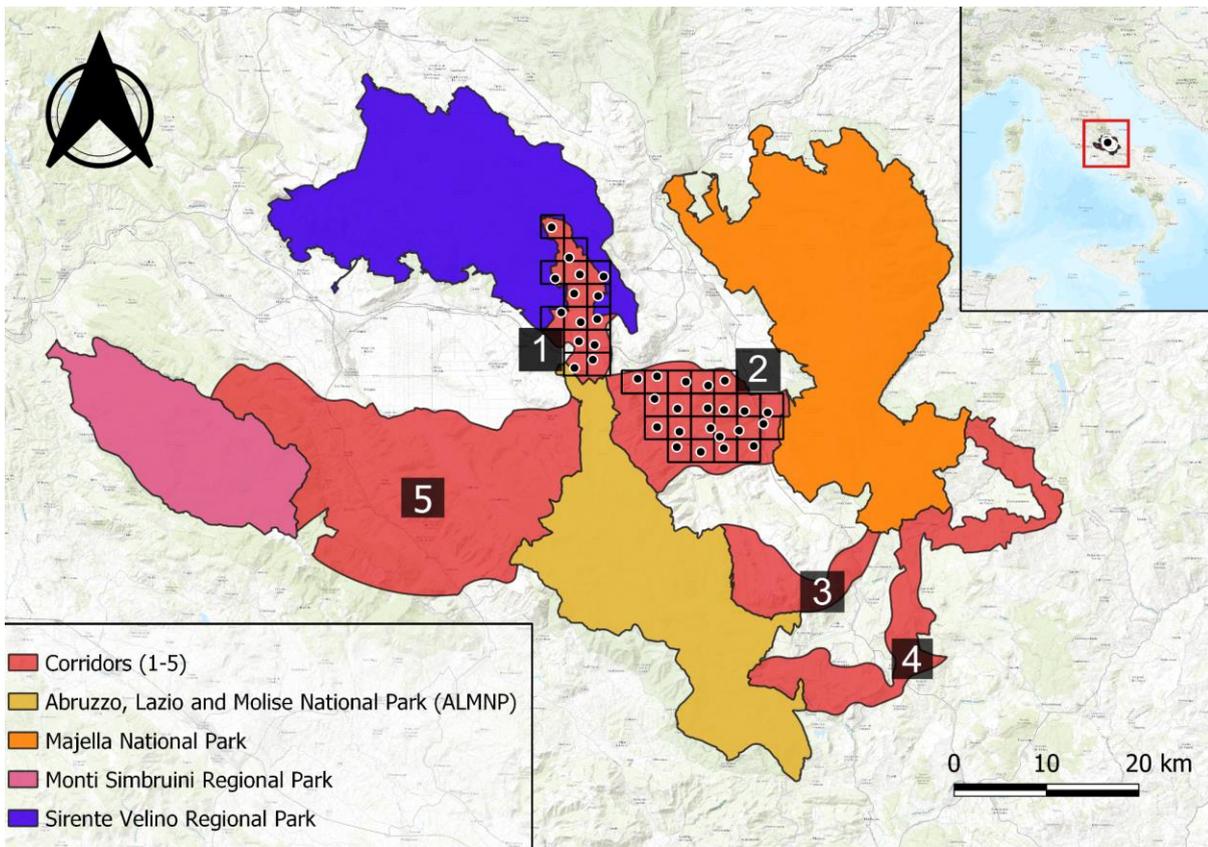
62 60 In addition to the Marsican brown bear, the Central Apennines host other charismatic mammal species
63 61 (Loy et al. 2019), including endemic subspecies such as the Apennine chamois (*Rupicapra pyrenaica*
64 62 *ornata*) and the Apennine wolf (*Canis lupus italicus*), and other species such as the red deer (*Cervus*
65 63 *elaphus*), the roe deer (*Capreolus capreolus*) and the porcupine (*Hystrix cristata*). As all these species
66 64 co-occur with the Marsican brown bear, they can in principle benefit from the management of bear
67 65 ecological corridors, because several causes of mortality and disturbance operate in a similar way
68 66 among species. Indeed, it is possible that these corridors act simultaneously as connectivity areas for
69 67 facilitating bear movement and as suitable habitats able to support meta-populations of other mammal
70 68 species with lower spatial requirements (Thornton et al. 2016). Despite the high ecological value of
71 69 these corridor areas, wildlife populations living within them are understudied. Except for the Marsican
72 70 brown bear, most wildlife monitoring is restricted to PAs, with data often unavailable or only traceable
73 71 in unpublished reports.

75 72 Here, we aim to estimate the population density of meso- and macro-mammal species within two
76 73 Marsican bear corridors in the Central Apennines, an information that is particularly underexplored in
77 74 the existing literature. In particular, we aim to provide a baseline estimate of population density
78 75 intended to be replicated over time and space, and comparable estimates of these species' densities
79 76 within these corridors. Our goal is to determine if corridors delineated and managed to enhance the
80 77 safe movements of the Marsican bear population also serve as ecologically valuable habitats for other
81 78 mammal species, thereby having a high conservation value for them. We deployed camera traps to
82 79 detect the images of meso- and macro-mammal species with smaller spatial requirements than the
83 80 brown bear. Based on data collected, we focus on eight species: European badger (*Meles meles*), hare
84 81 (*Lepus spp.*), porcupine, red deer, red fox (*Vulpes vulpes*), roe deer, wild boar (*Sus scrofa*), and wildcat
85 82 (*Felis silvestris silvestris*). To estimate population densities for each species, we used the Random
86 83 Encounter Model (REM; Rowcliffe et al. 2008), one of the most used and robust methods to estimate
87 84 population density of unmarked populations of different species (Palencia et al. 2022a).

85 Materials and Methods

86 Study area

87 Our study area is located in the Central Apennines (Italy) and includes two ecological corridors
88 designed to enhance the connectivity for the Marsican bear population (Fig. 1). The two corridors
89 connect the Abruzzo, Lazio and Molise National Park (ALMNP) with the Sirente Velino Regional
90 Park (Corridor 1) and with the Majella National Park (Corridor 2). These are part of a set of five
91 corridors identified for the National action plan for the Marsican brown bear protection (PATOM -
92 Piano d'Azione nazionale per la Tutela dell'Orso Marsicano: VV.AA, 2011 by Ciucci et al. (2016).
93 Along their extent, the corridors intersect or include additional reserves that contribute to the regional
94 ecological network, including the Monte Genzana Alto Gizio Natural Reserve (~3,160 ha), the Gole
95 del Sagittario Natural Reserve (~450 ha), and the Lago di San Domenico Natural Reserve (~60 ha).
96 The two corridors together cover an area of approximately 265 km², with Corridor 1 extending for
97 around 75 km² and Corridor 2 extending for around 190 km². Corridor 1 is dominated by grassland
98 (49%), followed by tree cover (36.5%) and a notable proportion of cropland (8.5%), while elevation
99 ranges from 472 to 1637 m asl. Instead, Corridor 2 is dominated by tree cover (68%) and grassland
100 (28.6%), with no significant cropland, and elevation ranging from 449 to 2199 m asl. The climate is
101 temperate Mediterranean continental, with frequent snowfalls, cold winters and hot summers, with a
102 temperature ranging between 24°C and 35°C during the sampling period (Fратиanni and Acquotta
103 2017).



109104

110105

111106

112107

113108

Figure 1: Map of the five corridor areas identified in the Central Apennines. The corridors (in red, marked with numbers) connect four protected areas (other coloured polygons). The study area, covering Corridor 1 and Corridor 2, is divided into 34 2.5 km grid cells, each including a camera trap (black points).

Data collection

We placed 34 camera traps from 19/04/2023 to 20/11/2023, for a total of 215 days. We selected this period to avoid winter season, when mammals are less active and snow and frost would have made access to many camera trap locations difficult or impossible. We deployed 14 camera traps in Corridor 1 and 20 in Corridor 2, using a random sampling and following a grid with cells of 2.5 km side. The camera traps were deployed as close as possible to the centroid of each cell, with a maximum distance from the centroid of 200 metres. Camera traps were placed on trees at a height ranging from 0.5 m to 1.7 m, and facing north orientation, to avoid direct exposure to the sun. We used Browning Patriot (BTC-PATRIOT-FHD) camera-traps with the following settings: trail mode (i.e., picture mode); capture delay of 1 seconds; multi shot set on 3 shots; image resolution of 3840 x 2160 (Ultra HD); night exposure on “mid-range” for confined spaces and “long-range” for open spaces. Checks were made regularly every three weeks for each camera trap, to control the status of the batteries and SD cards. During the sampling period, two camera traps were stolen, and replaced approximately 100 metres away from their original locations.

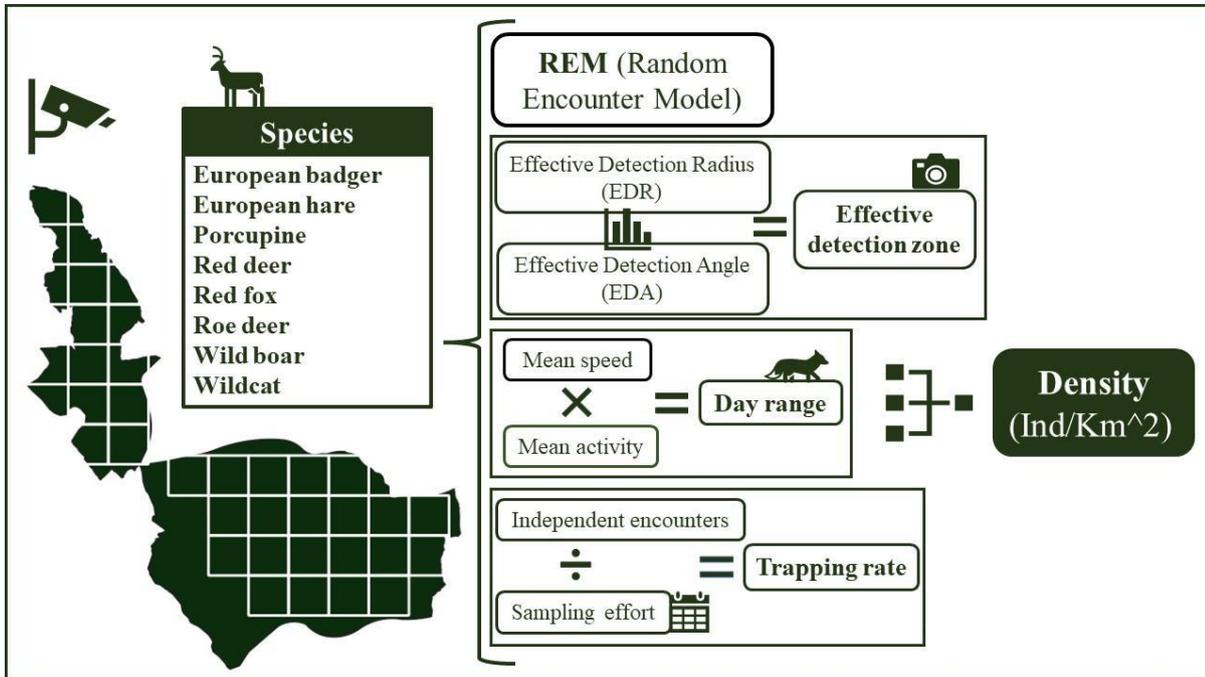
Based on a minimum number of encounters threshold >20 (Rowcliffe et al. 2008) and thus on the possibility to derive the needed parameters for the application of REM, we decided to estimate the density of 8 species of meso- and macro-mammals: European badger, hare, porcupine, red deer, red fox, roe deer, wild boar, wildcat. Since it was not possible to distinguish the European hare (*Lepus europaeus*) from the Apennine hare (*Lepus corsicanus*) in the images, we refer to the hare as *Lepus spp.* We decided to not consider the wolf in our analysis, because the home range of a wolf pack is much larger than our study area and a different sampling design would have been needed to estimate wolf density (Ciucci et al. 1997, Mancinelli et al. 2018).

Data processing

We processed camera trap data to calculate density estimates via the REM, a model that operates with unmarked animals and estimates their population density in a given area (Rowcliffe et al. 2008). The model treats animals like ideal gas particles and estimates density within the collective detection viewsheds of a camera array. REM has been proven to be a reliable method for estimating wildlife population density in a wide range of situations and scenarios, when using appropriate methods to estimate parameters and appropriate sampling designs (Palencia et al. 2022). It is also effective for monitoring more than one species using the same survey design, because for its application it is not needed for the animals to have a high detection probability (Rowcliffe et al. 2008). We estimated densities for each corridor separately, and for the entire study area (Corridor 1 + Corridor 2).

The densities are estimated based on different parameters (Fig. 2), which can be measured directly from the camera trap pictures, without the need of auxiliary data (Caravaggi et al. 2016, Hofmeester et al. 2017). Parameters estimated include: day range (i.e., the average distance travelled by an individual during the day, estimated as the product of speed –average travel speed while active– and activity rate –proportion of day that the population spent active), the camera traps' effective detection zone (EDZ; i.e., the area effectively monitored by cameras, defined by the effective detection radius –EDR– and the effective detection angle –EDA), and trapping rates (i.e., the number of independent encounters per unit time, in particular the number of encounters occurred at least 30 minutes from each other over the collective time in which the camera traps were operative) (Rowcliffe et al. 2008). To account for heterogeneity in detection distances across different camera trap models, we estimated EDR and EDA by extracting the distance and the angle from camera traps of each encounter, and then by using distance sampling models to find the threshold value at which the expected number missed within is equal to the expected number detected beyond (Rowcliffe et al. 2011; more details in Appendix SI). All the parameters were measured by using data from Corridor 1 and Corridor 2

163155 separately when estimating densities of each corridor, while we considered all the images together in
164156 calculating densities of the entire study area (Corridor 1 + Corridor 2) (Appendix SI, Table S2).
165157



166158
167159 **Figure 2:** Framework of the application of the Random Encounter Model (REM) to estimate the density of the
168160 eight mammal species analysed, in the study area.
169161

Random Encounter Model application

We applied REM following Palencia (2022b) to estimate the density of each species (D), using the formula:

$$D = \frac{y}{t} \frac{\pi}{vr(2+\alpha)} \quad [1]$$

where y is the number of independent encounters, t is total camera survey effort (in days), v is the average distance travelled by an individual during a day (i.e., day range, expressed in km/day), and r and α are the radius (metres) and angle (degrees) of the camera traps detection zone, respectively. For the wild boar, which is a highly gregarious species, most independent encounters included groups rather than solitary individuals. As a result, applying the standard REM formula directly yields an estimate of group density rather than individual density (Rowcliffe et al. 2008). To adjust this, we multiplied D by the average group size observed in our dataset ($\bar{s} = 3.31$ individuals), according to the following formula:

$$D_i = D \times \bar{s} \quad [2]$$

Where D_i is the individual density, D is the group density estimated using the REM, and \bar{s} is the average number of individuals per group.

We also represented the trapping rates estimated for each species in each grid cell.

To allow interpretation of our results, we gathered available information on species density from the literature. Previous studies have demonstrated that REM results are comparable to those obtained through other methods when all the parameters (i.e., day range, detection zone and encounter rate) are estimated accurately (e.g., Palencia et al. 2022a; Santini et al. 2018). We selected references published from the year 2000 onwards and referring to population densities estimated in Europe, giving priority

195185 to those estimated in Italy, whenever available. Since it was not possible to consider only densities
196186 estimated with the camera trap method, we took into consideration studies that used different
197187 methodologies. We collected 29 studies that reported population estimates in Europe for recent years
198188 (year 2000 and onwards). Among these, five were literature reviews that reported several density
199189 estimates (Smith et al. 2005, Melis et al. 2009, Lara-Romero et al. 2012, Mattioli et al. 2014). We
200190 found a total of 9 studies that used camera traps to estimate densities, two of which used REM. One of
201191 them is a collection of 19 works using REM to calculate the density of wild boars in different European
202192 areas (ENETWILD-consortium et al. 2022). Except for the Abruzzo Lazio and Molise National Park
203193 (ALMNP) for which we densities of red deer and roe deer were estimated using the pellet count method
204194 (Latini 2019) and the Monte Genzana reserve for which we found red deer estimates from individual
205195 recognition by camera trapping (Fabrizio et al. 2012), we have not found density data within the nearby
206196 PAs.

207197 Covariates extraction and comparison between corridors

208198 We also compared density estimated across corridors. We extracted the values (i.e., mean, median, and
209199 standard deviation) of different environmental covariates within each corridor, to highlight the main
210200 environmental differences between the two areas and therefore better explain the differences in the
211201 density results we obtained. We considered the following covariates: land-cover (i.e., tree cover,
212202 shrubland, grassland, cropland, built up) measured as the percentage values of the classes surface
213203 coverage within corridors, fractal dimension index (dimensionless), elevation (m), slope, distance from
214204 primary roads (m), distance from settlements (m), livestock density measures as livestock units per
215205 hectare (LSU/ha).

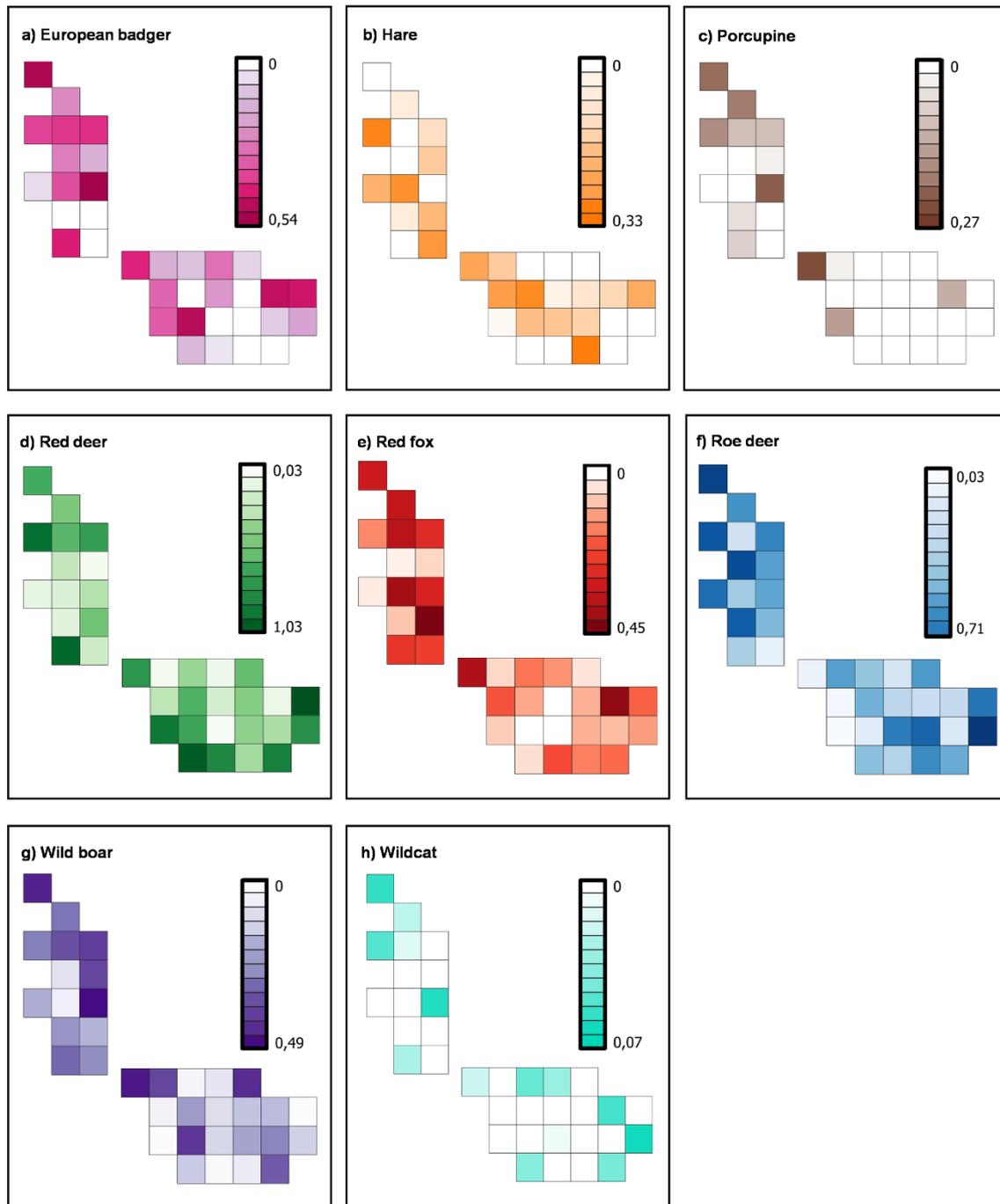
216206 We extracted land-cover variables from the European Space Agency (ESA) World Cover portal
217207 (Zanaga et al. 2022). The original raster has a resolution of 10 m, and we resampled it at a resolution
218208 of 30 m to be consistent with other covariates. Fractal dimension index is a fragmentation metric that

220209 is based on the area and perimeter of the patch and describes its complexity. It was extracted using the
221210 LecoS plugin on Qgis (3.22.12-Białowieża, 2022; Jung 2016) from the tree cover raster, thus
222211 quantifying the fragmentation of forest habitats. To calculate the statistics for the elevation and the
223212 slope, we downloaded the Digital Elevation Model DEM GLO-30 (Fahrland et al. 2022) for central
224213 Italy from the Nasa Earth Observing System Data and Information System (EOSDIS) and we then
225214 calculated the zonal statistics using Qgis Processing tools. Using Qgis, we calculated the Euclidean
226215 distance of each camera trap to the nearest village. To calculate the distances of each camera trap from
227216 the primary roads, we used the roads' shapefile downloaded from "OpenstreetMap" (Curran et al.
228217 2013). We calculated the livestock density in Corridor 1 and Corridor 2 using the dataset of Dragonetti
229218 et al. (2025).

Results

Estimating model parameters

We collected a total of 3,942 pictures of 15 species of wild mammals, including 3,379 pictures of our 8 study species (Table S1). We found high variability in the estimate of day range among species – i.e., the average distance that animals travel in a day – with values ranging from 5.91 km/day (SE = 0.89) for the European hare to 16.21 km/day (SE = 1.49) for the red fox (Table S2). The trapping rate (i.e., the number of independent encounters over time) varied widely in the study area, both among species and between the two corridors (Fig. 3, Table S3). The porcupine and the wildcat were not detected in several cells and showed the lowest trapping rates (mean = 0.02 ± 0.05 encounters per day for porcupine; mean = 0.01 ± 0.02 for wildcat). Conversely, the red deer and roe deer were detected in all cells and showed the highest trapping rates (mean = 0.21 ± 0.22 and mean = 0.21 ± 0.16 , respectively). The wild boar was also detected in the entire study area except two cells of corridor 2, with a mean trapping rate = 0.08 ± 0.12 , and showing high values in some locations (i.e., 0.50 in “Marsicana” and 0.47 in “Anversa”). The red fox showed trapping rates greater than 0 in all the cells of corridor 1 but not in all cells of corridor 2, with a mean of 0.10 ± 0.11 in the whole study area. Notably, the porcupine was only detected in three locations of Corridor 2: “Anversa” (0.27), “Lago di San Domenico” (0.05) and “Valle Santa Margherita” (0.04).



249236

250237

251238

252239

Figure 3: Trapping rates of each camera trap location of the study area, for each of the eight species of meso- and macro-mammals analysed (panels a-h). Trapping rates were obtained from the number of independent encounters divided by survey effort (i.e., the operating time of camera traps expressed in days).

254240 Species density estimates

255241 The wild boar showed the highest density in the overall study area (7.22 ± 1.75 ind./km²), followed
256242 by the roe deer (3.41 ± 0.70 ind./km²) and the hare (3.39 ± 0.86 ind./km²; Table 1). Instead, the wildcat
257243 and the red fox were the species with the lowest densities (0.43 ± 0.17 ind./km² and 1.27 ± 0.27
258244 ind./km², respectively). For the wildcat, reliable estimates could only be obtained for the entire study
259245 area, due to an insufficient number of images for each separate corridor. To aid interpretation of our
260246 results, we compared the population densities estimated in our study area with those found in the
261247 literature (Table 1, Table S4).

262248 We found that all the densities we estimated were comparable to the data collected from the literature.
263249 While important for results interpretation, it is important to clarify that this is not a formal comparison
264250 of densities inside vs outside corridors, as the study design behind different estimates was not the same
265251 (see Discussion).

266252 Comparison between the two corridors and covariates extraction

267253 The analysis of environmental covariates revealed that Corridor 1 is, on average, more cultivated, more
268254 built, more densely grazed and less forested than Corridor 2. The fractal dimension index (i.e.,
269255 fragmentation of forested habitats) was also higher in Corridor 1. Corridor 2, on average, showed a
270256 higher altitude and slope. Additionally, the camera traps in Corridor 1 were generally closer to primary
271257 roads than those in Corridor 2, but almost at the same distance from the nearest village (Fig. S2).

272258 These environmental differences between the two corridors are also reflected in different estimates of
273259 population density for several species (Table 1, Fig. S3). In Corridor 1, species with the highest density
274260 included the wild boar (14.21 ± 4.64 ind./km²), the badger (4.73 ± 2.05 ind./km²) and the roe deer
275261 (4.67 ± 1.47 ind./km²). In Corridor 2, species with the highest density included the hare (3.60 ± 2.96
276262 ind./km²), the red deer (3.36 ± 1.50 ind./km²) and the roe deer (2.94 ± 0.68 ind./km²). We found

278263 Corridor 1 showing higher densities than Corridor 2 for all species except the hare (that however
279264 showed similar estimate across corridors). Some of the most notable examples were the wild boar
280265 (14.21 ± 4.64 ind./km² in Corridor 1 vs 1.69 ± 0.71 ind./km² in Corridor 2), the badger (4.73 ± 2.05
281266 ind./km² in Corridor 1 vs 1.03 ± 0.34 ind./km² in Corridor 2) and the red fox (2.65 ± 0.63 ind./km² in
282267 Corridor 1 vs 0.49 ± 0.14 ind./km² in Corridor 2). For the wildcat, data were not sufficient to estimate
283268 the densities for the two corridors separately.

285269 **Table 1.** Density estimates and standard errors (S.E.) derived from the application of Random Encounter Model
 286270 (REM), for eight species of meso- and macro-mammals. Densities of all species are reported separately for
 287271 Corridor 1, Corridor 2, and for the whole study area, with the exception of the wildcat (*Felis silvestris silvestris*)
 288272 which could only be reported for the whole area. The last column refers to the other densities found from the
 289273 literature.

Species	Corridor 1 (ind./km ²)	Corridor 2 (ind./km ²)	Corridor 1+2 (ind./km ²)	Literature values (ind./km ²)
European badger (<i>Meles meles</i>)	4.73 ± 2.05	1.03 ± 0.34	1.83 ± 0.82	Min: 0.26 Max: 3.81 Median: 0.85
Hare (<i>Lepus spp</i>)	3.22 ± 1.58	3.60 ± 2.96	3.39 ± 0.86	Min: 0.0023 Max: 82 Median: 9.15
Porcupine (<i>Hystix cristata</i>)	1.84 ± 0.68	1.08 ± 0.67	1.40 ± 0.47	Min: 0.44 Max: 0.49 Median: 0.46
Red deer (<i>Cervus elaphus</i>)	3.36 ± 1.50	2.71 ± 0.99	3.16 ± 0.92	Min: 1.72 Max: 8.5 Median: 2.85
Red fox (<i>Vulpes vulpes</i>)	2.65 ± 0.63	0.49 ± 0.14	1.27 ± 0.27	Min: 0.21 Max: 4.4 Median: 0.66
Roe deer (<i>Capreolus capreolus</i>)	4.67 ± 1.47	2.94 ± 0.68	3.41 ± 0.70	Min: 0.11 Max: 53.8 Median: 15.45
Wild boar (<i>Sus scrofa</i>)	14.21 ± 4.64	1.69 ± 0.71	7.22 ± 1.75	Min: 0.35 Max: 47 Median: 6.54
Wildcat (<i>Felis silvestris silvestris</i>)	NA	NA	0.43 ± 0.17	Min: 0.069 Max: 1.36 Median: 0.33

301274

Discussion

We estimated the densities of eight meso- and macro-mammal species in two areas of the Central Apennines managed as connectivity corridors for the Marsican bear by local administration and NGOs (Ciucci et al. 2016, Maiorano et al. 2019, Cipollone et al. 2024). Our results on mammal density constitute important knowledge, since this information is especially scarce in our study area and, overall, in the Central Apennines. We estimated densities both at the individual corridor level and for the entire study area, and we compared these with density values from other European areas, to contextualize and validate our results, and to identify species with existing population data from nearby protected areas. We found that the densities we estimated are on average higher than those found in the literature, suggesting that these bear corridors host areas of high ecological value for several other mammal species.

The comparison between the two corridor areas allowed us to understand which environmental conditions could favour the presence of the species analysed. Corridor 1 showed higher density values than Corridor 2 for almost all species. Species that showed the greatest differences between corridors were the European badger, the red fox, the wild boar and the roe deer. The greater presence of badgers in Corridor 1 than in Corridor 2 is certainly something to further investigate, as this species is known to prefer forested environments rather than shrubland and grassland or cultivated fields, which are more present in Corridor 1 (Rosalino et al. 2008, Chiatante et al. 2017). Species such as foxes and wild boars could benefit from the more widespread (albeit not intense) anthropic presence in Corridor 1, being high generalists. Conversely, the roe deer could benefit from mosaic spaces with a high ecotone index characterised by the continuous alternation of open environments with herbaceous vegetation and broad-leaved woods, typical of Corridor 1. Corridor 1 showed a slightly higher grazing pressure than Corridor 2, placing it within the category of semi-natural habitats shaped by extensive grazing (Dragonetti et al. 2025). These habitats play a key role in maintaining open

329 300 landscapes and supporting biodiversity, particularly species that thrive in ecotonal and
330 301 transitional zones. This is consistent with the higher forest fragmentation observed in the area,
331 302 as grazing helps prevent woodland encroachment (Falcucci et al. 2007; Ponzetta et al. 2010).
332 303 In addition, the lower altitude and slope of Corridor 1 could favour most of the species
333 304 analysed, as they are not strictly mountainous or alpine species.

334 305 The three species of ungulates (i.e., roe deer, red deer, wild boar) showed the highest densities
335 306 and the highest trapping rates. This is consistent with the trend of the last few years in Italy,
336 307 which sees these species expanding their ranges and increasing their population numbers
337 308 (Rondinini et al. 2022). Italian ungulates are mostly represented by opportunistic and generalist
338 309 species. As they can adapt to several ecological conditions, they have exploited the massive
339 310 abandonment of mountains and hills by humans in the last decades in the internal areas of Italy
340 311 which facilitated the expansion of the woodlands (Acevedo et al. 2011, Falcucci et al. 2007,
341 312 Valente et al. 2020). While we could not obtain a reliable density estimate of the wildcat in
342 313 each corridor, but just for the whole area, Corridor 2 showed higher trapping rates than Corridor
343 314 1 which seem to indicate higher suitability (Fig. 3). However, a more extensive camera trapping
344 315 design would be required to validate this hypothesis.

345 316 A potential limitation of our estimates concerns the selected sampling period (19 April – 20
346 317 November), which excludes the winter season. This may have led to seasonally biased species
347 318 activity rates and detection probabilities. However, the REM framework is designed to account
348 319 for such variation: a lower trapping rate due to reduced activity should be balanced by a
349 320 correspondingly shorter day range, resulting in broadly consistent density estimates.

350 321 Density estimates for individual species

351 322 We found our estimates aligning with, or even exceeding, previously reported values in the
352 323 literature for almost all species (see Appendix SII for additional discussion). We decided to

354 324 compare our results with densities estimated with other methods when REM estimates were
355 325 not available, as unbiased densities are obtained when REM parameters are calculated
356 326 accurately (Palencia et al. 2022a; Santini et al. 2018). By comparing our values with other
357 327 estimates reported in the literature we aimed to place our findings within a broader range of
358 328 known population densities, assess their reliability, and identify which species have been
359 329 studied in nearby protected areas.

360 330 For the European badger, our estimated density (1.83 ± 0.82 ind./km²) was higher than average
361 331 but still comparable to other European studies that employed camera traps (Lara-Romero et al.
362 332 2012). Although Italy lacks comprehensive data on badger populations, one study in the river
363 333 Po plain using camera traps reported lower densities (0.93–1.4 ind./km²) in hilly regions
364 334 (Balestrieri et al. 2016).

365 335 Regarding the hare, we estimated a density of 3.39 ± 0.86 ind./km², which is on the lower end
366 336 compared to other European estimates (5.6 ind./ km² to 82 ind./ km²) (Smith et al. 2005), even
367 337 if most of these studies used old methods, such as transect counts or spotlight surveys. The
368 338 only other study conducted in Italy (Genghini and Capizzi 2005) reported much lower hare
369 339 densities (0.0027 ± 0.0007 ind./km²).

370 340 For porcupines, our density estimate (1.40 ± 0.47 ind./km²) was higher than most reported in
371 341 the literature (e.g., 0.49 ind./km² in Lombardy - Palencia et al. 2024). This difference is likely
372 342 due to our study area being located within the core range of the species, whereas Lombardy is
373 343 probably still at the periphery of the porcupine's current distribution. The species is currently
374 344 undergoing a range expansion, facilitated by habitat changes such as global warming and
375 345 agricultural abandonment (Mori et al. 2021).

376 346 Results for ungulates were mixed. Our red deer density (3.16 ± 0.92 ind./km²) closely matched
377 347 previous estimates for central Italy and aligned with estimates from the ALMNP, where a pellet
378 348 count survey recorded a density of 3.8 ind./km² (Latini 2019). We also found estimates from

380 349 the Monte Genzana Alto Gizio Reserve, where individual recognition through camera trapping
381 350 led to an estimated density of 1.3–2.5 ind./km² (Fabrizio et al. 2012). In contrast, roe deer
382 351 density in our study (3.41 ± 0.70 ind./km²) fell within the medium-to-low range of European
383 352 estimates ($0.11 - 53.80$ ind./km²) (Melis et al. 2009). Lower roe deer densities are expected in
384 353 areas such as our study site, where high predator presence tend to limit roe deer populations.
385 354 In contrast, areas with no predators, such as Ticino National Park, report much higher densities
386 355 (30.7 ind./km² - De Pasquale et al. 2019). Comparing our estimate with a regional one, we
387 356 found an average density of roe deer of 0.5 ind./km² (95% CI = 0.4-0.6) within the ALMNP
388 357 (Latini 2019), calculated with the pellet count method, with higher densities recorded in the
389 358 peripheral layers, close to our study area (0.94 ind./km², 95% CI= 0.22- 8.15).

390 359 For wild boar, our estimated density (7.34 ± 1.78 ind./km²) was consistent with other studies
391 360 that adopted REM (from 0.35 ind./km² in Croatia to 15.25 ind./km² in Italy: ENETWILD-
392 361 consortium et al. 2022). Due to their high reproductive rate, migratory behaviour, and
393 362 adaptability to various habitats, wild boar have a density that is notoriously difficult to estimate
394 363 accurately (ENETWILD-consortium et al. 2018). However, the high trapping rate of wild boars
395 364 in our study suggested a genuinely high density in the area, in line with European trends, where
396 365 wild boar numbers have steadily increased in the last decades (Massei et al. 2015). Wild boars
397 366 are highly adaptable compared to other ungulates, being omnivorous and modifying their diet
398 367 based on locally available resources, showing high reproductive rates, and the ability to adapt
399 368 in a wide range of habitats, from forests to agricultural areas (Colomer et al. 2024).

400 369 Our density estimate of the red fox (1.27 ± 0.27 ind./km²) was on the higher end compared to
401 370 other European studies (e.g., $0.23-1.62$ ind./km² in the Mediterranean area - Jimenez et al.
402 371 2019). We found Corridor 1 had more than twice the fox density of Corridor 2, likely due to
403 372 its greater degree of human presence and lower elevation. Red foxes, being highly adaptable
404 373 and able to live in human-dominated landscapes, benefit from such conditions (Alexandre et

406 374 al. 2020).

407 375 For the wildcat, we estimated a density of 0.43 ± 0.17 ind./km², consistent with previous

408 376 European studies that used camera traps. For example, Anile et al. (2014) found similar

409 377 densities (0.32–1.36 ind./km²) in Sicily using different methods, including REM. Other studies

410 378 in mountainous regions (Maronde et al. 2020, Fonda et al. 2022) reported comparable densities

411 379 (0.26 and 0.35 ind./km²) using camera traps.

412 380 Management and research implications

413 381 Our work demonstrated that ecological corridors defined for the Marsican bear host high

414 382 densities of several other mammal species, highlighting the crucial role that these areas play in

415 383 supporting mammalian biodiversity in the Central Apennines. Albeit not formally comparable

416 384 due to different analytical protocols, REM densities of the ungulates (roe deer, red deer and

417 385 wild boar) were similar to the ones found in literature. In particular, the densities of red deer

418 386 and roe deer were close to the ones in the nearby PAs, further emphasizing their conservation

419 387 value and the importance of dedicated management strategies. A focus of future studies could

420 388 be a formal comparative study in nearby PAs using the same methods we deployed in corridor

421 389 areas, that we were unable to conduct due to strict park protection policies, difficulties in

422 390 availability of data and the significantly larger sampling effort required. In this sense, our

423 391 results provide an important baseline to enable comparative studies. Similarly, the protocol

424 392 presented here should be replicated regularly in the same study area, to allow for the detection

425 393 of trends in densities and the investigation of correlations between management activities that

426 394 have recently started in the corridors to enhance bear conservation and the density of non-

427 395 target species (Cipollone et al. 2024). Analyses similar to those we presented here can support

428 396 management in other co-existence corridors and for other large carnivores. This could be the

429 397 case, for example, of the Iberian Peninsula, where two separate brown bear populations live in

431 398 the Cantabrian Mountains and the Pyrenees, coexisting with human activities (Pérez et al. 2010,
432 399 Méndez et al. 2014). Our analysis also highlighted marked differences between the two
433 400 corridors, with Corridor 1 showing higher densities for almost all species. This finding is
434 401 particularly relevant for land management, as it suggests that many species can benefit from
435 402 certain forms of human activity, such as extensive agriculture and traditional pasture, when
436 403 carried out in a non-intensive way (Halada et al. 2011; Schieltz & Rubenstein 2016).

437 404 We found that the porcupine and the ungulates are present with particularly high densities in
438 405 the bear corridors. Human-wildlife conflict, due to the frequent use by these species of
439 406 agricultural lands for foraging, increases tensions with local communities. In this sense, it is
440 407 essential to monitor the population development of those species over an extended time (White
441 408 and Ward 2010), while the installation of electric fences, already recommended for mitigating
442 409 bear-human conflicts in the LIFE project “Bear-Smart Corridors” (Cipollone et al. 2024), could
443 410 be effective in preventing also damages from porcupines. Moreover, compensation schemes
444 411 and community engagement initiatives could foster coexistence, reducing the negative impacts
445 412 of wildlife on human livelihoods while promoting the ecological benefit of maintaining healthy
446 413 mammal populations.

447 414 Since bear corridors are of great importance for the entire community of meso- and macro-
448 415 mammals, management strategies should focus on maintaining and enhancing their ecological
449 416 connectivity, facilitating species movement and dispersal beyond PAs (Fahrig 2003, Pacifici et
450 417 al. 2020). This is in line with the Kunming-Montreal Global Biodiversity Framework and the
451 418 EU Biodiversity Strategy both of which emphasize the need for ecological corridors to connect
452 419 fragmented habitats (EC 2022). Likewise, this goal is in line with the 2030 EU Biodiversity
453 420 Strategy and the Italian National Strategy for Biodiversity 2030, which stress the importance
454 421 of integrating ecological corridors to link isolated PAs (EC 2020, MASE 2023). Thus, the

456 422 management of these corridors must reduce human-induced pressures, for instance by
457 423 mitigating road impact with strict regulation of vehicular access on dirt roads and critical areas
458 424 during sensitive periods for the bears such as the mating season (Ciucci et al. 2016). Wildlife
459 425 mortality due to road accidents along main roads can be limited by measures such as road
460 426 signals and awareness campaigns implemented in projects like LIFE "Strade", which are
461 427 crucial in Central Apennine corridors (Giovacchini and Fabrizio 2022; Valfrè and Cipollone
462 428 2016).

463 429 Our findings imply that conservation actions intended for enhancing habitat connectivity for
464 430 the Marsican brown bear could also be effective for other species in the area, thereby having
465 431 an “umbrella” effect. These actions will ensure the long-term survival of the Marsican bear and
466 432 other mammal species that rely on these critical habitats (either for movement and survival).

467 433 Acknowledgments

468 434 We thank all the Rewilding Apennines team and all the volunteers of the 2023 summer season
469 435 for contributing substantially to the data collection. We thank the Genzana and Alto Gizio
470 436 reserve and in particular Antonio di Croce and Antonio Monaco for the exchange of ideas and
471 437 for intellectually supporting this research.

472 438 We acknowledge support from The European Union–NextGenerationEU as part of the
473 439 National Biodiversity Future Center, Italian National Recovery and Resilience Plan (NRRP)
474 440 Mission 4 Component 2 Investment 1.4 (CUP: B83C22002950007).

476 441 **Authors' contributions**

477 Chiara Dragonetti, Moreno Di Marco, Jan-Niklas Trej and Piero Visconti conceived the ideas
478 and designed the methodology; Chiara Dragonetti, Jan-Niklas Trej and Niccolò Ceci collected
479 the data; Niccolò Ceci, Chiara Dragonetti, Jan-Niklas Trej and Stefan Von Kempis analysed
480 the data and performed the Random Encounter Model; all authors contributed to the writing,
481 reviewing, editing and finalising of the manuscript.

482 442 **Competing interests**

483 443 The authors declare that they have no competing interests.

484 444 **Funding**

485 445 This research did not receive any specific funding from agencies in the public, commercial or
486 446 not-for-profit sectors.

487 447 **Data availability**

488 448 The datasets generated and analysed during the current study are available from the
489 449 corresponding author on reasonable request.

490 450

491 451

493 452 **Figures captions**

494 453 **Figure 1:** Map of the five corridor areas identified in the Central Apennines. The corridors (in red,
495 454 marked with numbers) connect four protected areas (other coloured polygons). The study area,
496 455 covering Corridor 1 and Corridor 2, is divided into 34 2.5 km grid cells, each including a camera trap
497 456 (black points).

498 457
499 458 **Figure 2:** Framework of the application of the Random Encounter Model (REM) to estimate the density
500 459 of the eight mammal species analysed in the study area.

501 460
502 461 **Figure 3:** Trapping rates of each camera trap location of the study area, for each of the eight species
503 462 of meso- and macro-mammals analysed (panels a-h). Trapping rates were obtained from the number
504 463 of independent encounters divided by survey effort (i.e., the operating time of camera traps expressed
505 464 in days).

506 465
507 466

508 467

509 468

511 469 References

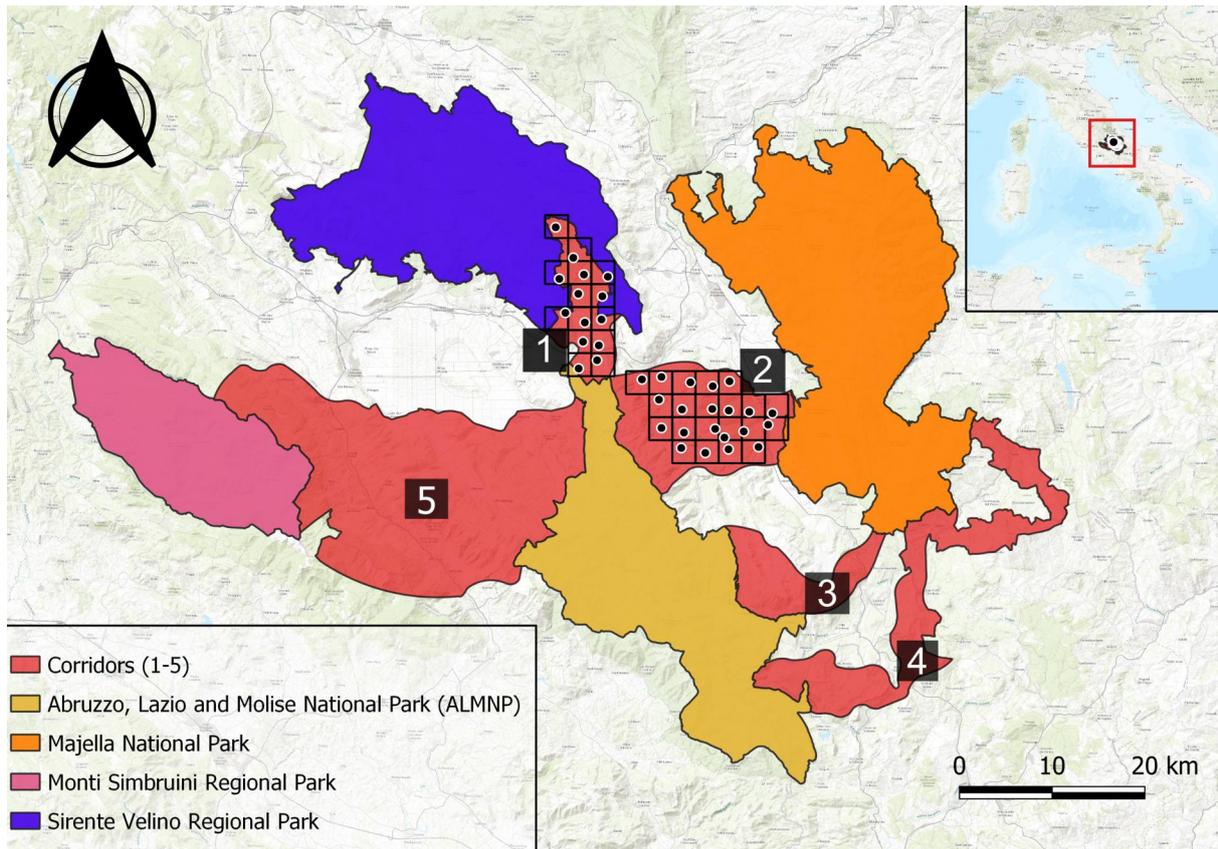
- 512 470 Acevedo, P., Farfán, M.Á., Márquez, A.L., Delibes-Mateos, M., Real, R., and J.M. Vargas.
513 471 2020. Past, present and future of wild ungulates in relation to changes in land use.
514 472 *Landscape Ecol* 26, 19–31.
- 515 473 Alexandre, M., D. Hipólito, E. Ferreira, C. Fonseca, and L. M. Rosalino. 2020. Humans do
516 474 matter: determinants of red fox (*Vulpes vulpes*) presence in a western Mediterranean
517 475 landscape. *Mammal Research* 65:203–214.
- 518 476 Anile, S., B. Ragni, E. Randi, F. Mattucci, and F. Rovero. 2014. Wildcat population density
519 477 on the Etna volcano, Italy: a comparison of density estimation methods. *Journal of*
520 478 *Zoology* 293:252–261.
- 521 479 Balestrieri, A., E. Cardarelli, M. Pandini, L. Remonti, N. Saino, and C. Prigioni. 2016. Spatial
522 480 organisation of european badger (*Meles meles*) in Northern Italy as assessed by
523 481 camera-trapping. *European Journal of Wildlife Research* 62:219–226.
- 524 482 Biodiversity strategy for 2030 - European Commission. 2024.
525 483 <https://environment.ec.europa.eu/strategy/biodiversity-strategy-2030_en>. Accessed
526 484 1 Jul 2024.
- 527 485 Caravaggi, A., M. Zaccaroni, F. Riga, S. C. Schai-Braun, J. T. A. Dick, W. I. Montgomery,
528 486 and N. Reid. 2016. An invasive-native mammalian species replacement process
529 487 captured by camera trap survey random encounter models. *Remote Sensing in*
530 488 *Ecology and Conservation* 2:45–58.
- 531 489 Carotenuto, L., Pizzol, I., Di Clemente, G., Caporioni, M., Davoli, F., Donfrancesco, S., ... &
532 490 Tarquini, L. (2014). Longdistance, long-term movements of Apennine brown bear
533 491 outside its core area. In *Proceedings of the IX Congresso Italiano di Teriologia*,
534 492 Civitella Alfedena, L'Aquila, Italy, *Hystrix* (Vol. 25, No. 6).
- 535 493 Chiatante, G., Dondina, O., Lucchelli, M., Bani, L., and A. Meriggi. 2017. Habitat selection
536 494 of European badger *Meles meles* in a highly fragmented forest landscape in northern
537 495 Italy: the importance of hedgerows and agro-forestry systems. *Hystrix, the Italian*
538 496 *Journal of Mammalogy*, 28(2), 247-252.
- 539 497 Cipollone, M., D. Bormpoudakis, A. Carrara, G. Chatzinakos, A. Chovardas, D. D'Amico,
540 498 Antonio Di Croce, Antonio Di Nunzio, S. Frau, A. Karamanlidis, V. Koutis, P. Leone,
541 499 Y. Mertzanis, E. Olivieri, S. Psaroudas, A. Tavone, and D. Vavylis. 2024.
542 500 GUIDELINES FOR A BEAR-SMART COMMUNITY. <[https://rewilding-](https://rewilding-apennines.com/wp-content/uploads/sites/9/2024/06/GUIDELINES-FOR-BSC.pdf)
543 501 [apennines.com/wp-content/uploads/sites/9/2024/06/GUIDELINES-FOR-BSC.pdf](https://rewilding-apennines.com/wp-content/uploads/sites/9/2024/06/GUIDELINES-FOR-BSC.pdf)>.
544 502 Accessed 1 Oct 2024.
- 545 503 Ciucci, P., and L. Boitani. 2008. The Apennine Brown Bear: A Critical Review of Its Status
546 504 and Conservation Problems. Volume 19.
- 547 505 Ciucci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and
548 506 movements of a wolf pack in central Italy. *Journal of Zoology* 243:803–819.
- 549 507 Ciucci, P., V. Gervasi, L. Boitani, J. Boulanger, D. Paetkau, R. Prive, and E. Tosoni. 2015.
550 508 Estimating abundance of the remnant Apennine brown bear population using multiple
551 509 noninvasive genetic data sources. *Journal of Mammalogy* 96:206–220.
- 552 510 Ciucci, P., Altea, T., Antonucci, A., Chiaverini, L., Di Croce, A., Fabrizio, M., Forconi, P.,
553 511 Latini, R., Maiorano, L., Monaco, A., Morini, P., Ricci, F., Sammarone, L., Striglioni,
554 512 F., Tosoni, E., and Regione Lazio, B. M. N. 2017. Distribution of the brown bear
555 513 (*Ursus arctos marsicanus*) in the Central Apennines, Italy, 2005-2014. *Hystrix, the*
556 514 *Italian Journal of Mammalogy*, 28(1), 86-91. Ciucci, P., L. L. Maiorano, M.
557 515 Chiaverini, and Falco. 2016. Aggiornamento della cartografia di riferimento del
558 516 PATOM su presenza e distribuzione potenziale dell'orso bruno marsicano

- 560 517 nell'Appennino centrale. Azione A2: Relazione tecnica finale. Ministero
561 518 dell'Ambiente e della Tutela del Territorio e del Mare e Unione Zoologica Italiana,
562 519 Roma. 84 pagg.
- 563 520 Colomer, J., Massei, G., Roos, D., Rosell, C., and J.D. Rodríguez-Teijeiro. 2024. What drives
564 521 wild boar density and population growth in Mediterranean environments *The Science*
565 522 of the total environment, 931, 172739. Curcic, N., and S. Djurdjic. 2013. The actual
566 523 relevance of ecological corridors in nature conservation. *Journal of the Geographical*
567 524 *Institute Jovan Cvijic, SASA* 63:21–34.
- 568 525 Curran, K., J. Crumlish, and G. Fisher. 2013. OpenStreetMap. Pages 540–549 in. *Geographic*
569 526 *Information Systems: Concepts, Methodologies, Tools, and Applications*. IGI Global.
- 570 527 De Pasquale, D. D., O. Dondina, E. Scancarello, and A. Meriggi. 2019. Long-term viability
571 528 of a reintroduced population of roe deer *Capreolus capreolus*, in a lowland area of
572 529 northern Italy. *Folia Zoologica* 68:9–20.
- 573 530 Dragonetti, C., Masiello, G., Villa, F., Von Kempis, S.R., Cipollone, M., and M. Di Marco.
574 531 2025. Map of livestock density in Central Apennines: a standardised protocol. *Nature*
575 532 *Conservation*. Accepted paper EC. 2022. Commission Staff Working Document.
576 533 Criteria and guidance for protected areas designations. SWD (2022) 23 final.
577 534 European Commission.
- 578 535 EC. 2020. Communication from the Commission to the European Parliament, the Council,
579 536 the European Economic and Social Committee and the Committee of the Regions —
580 537 EU Biodiversity Strategy for 2030 — Bringing nature back into our lives (COM
581 538 (2020) 380 final, 20.5.2020).
- 582 539 ENETWILD consortium, O. Keuling, M. Sange, P. Acevedo, T. Podgorski, G. Smith, M.
583 540 Scandura, M. Apollonio, E. Ferroglio, and J. Vicente. 2018. Guidance on estimation
584 541 of wild boar population abundance and density: methods, challenges, possibilities.
585 542 EFSA Supporting Publications 15:1449E.
- 586 543 ENETWILD-consortium, P. Acevedo, V. Aleksovski, M. Apollonio, O. Berdión, J. Blanco-
587 544 Aguiar, L. del Rio, A. Ertürk, L. Fajdiga, F. Escribano, E. Ferroglio, G. Gruychev, I.
588 545 Gutiérrez, V. Häberlein, B. Hoxha, K. Kavčić, O. Keuling, C. Martínez-Carrasco, P.
589 546 Palencia, P. Pereira, R. Plhal, K. Plis, T. Podgórski, C. Ruiz, M. Scandura, J. Santos,
590 547 J. Sereno, A. Sergejev, V. Shakun, R. Soriguer, A. Soyumert, N. Sprem, S. Stoyanov,
591 548 G. Smith, A. Trajçe, N. Urbani, S. Zanet, and J. Vicente. 2022. Wild boar density data
592 549 generated by camera trapping in nineteen European areas. EFSA Supporting
593 550 Publications 19:7214E.
- 594 551 Explore the World's Protected Areas. <<https://www.protectedplanet.net/en>>. Accessed 5 Oct
595 552 2024.
- 596 553 Fabrizio, M., Monaco, A., and F. Nonni. 2012. Stima numerica della popolazione maschile di
597 554 *Cervus elaphus* mediante identificazione individuale da fototrappolaggio. *Atti del*
598 555 *Convegno "Il foto-video trappolaggio in Italia: primi risultati di una nuova tecnica di*
599 556 *ricerca scientifica per la fauna selvatica"* 9 luglio 2011-Pettorano sul Gizio (AQ), 18
600 557 [in Italian].
- 601 558 Falcucci, A., Maiorano, L., and L. Boitani. 2007. Changes in land-use/land-cover patterns in
602 559 Italy and their implications for biodiversity conservation. *Landscape Ecol* 22, 617–
603 560 631.
- 604 561 Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. *Annual Review of*
605 562 *Ecology, Evolution, and Systematics*. Volume 34. Annual Reviews Inc.
- 606 563 Fahrland, E., H. Paschko, P. Jacob, and H. Kahabka. 2022. Copernicus DEM Delivery
607 564 Review Organisation Note (DEL-06).
- 608 565 Fonda, F., G. Bacaro, S. Battistella, G. Chiatante, S. Pecorella, and M. Pavanello. 2022.
609 566 Population density of European wildcats in a pre-alpine area (northeast Italy) and an

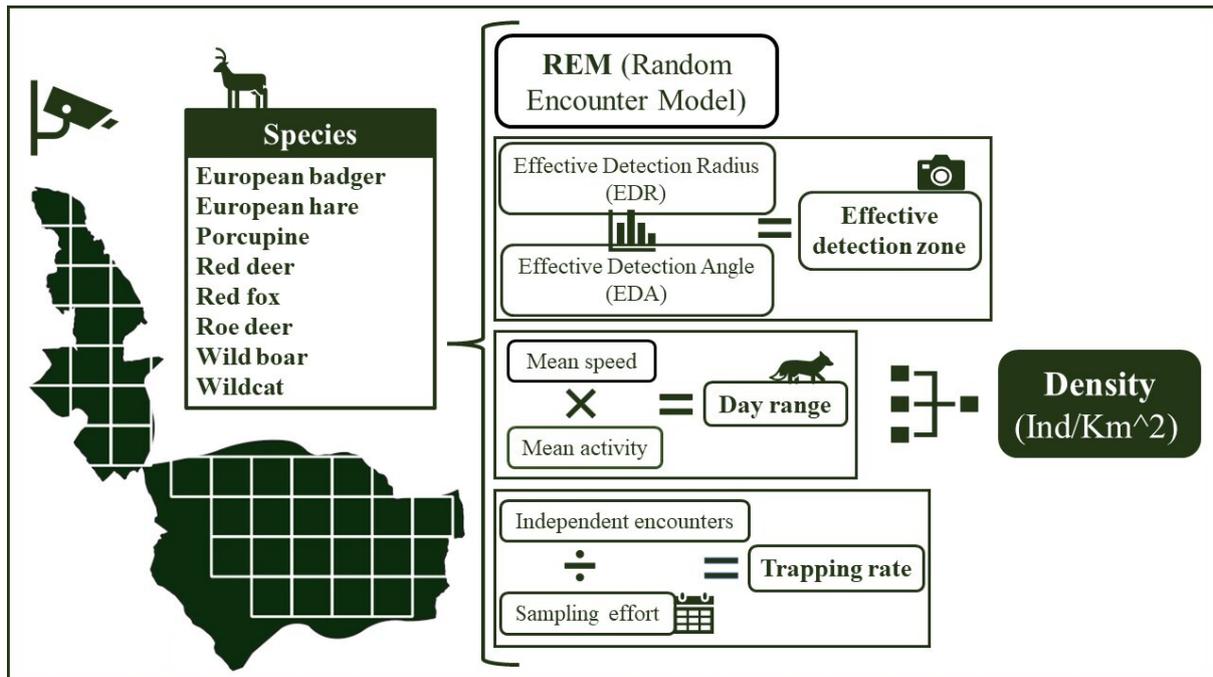
- 611 567 assessment of estimate robustness. *Mammal Research* 67:9–20.
- 612 568 Fratianni, S., and F. Acquavotta. 2017. The Climate of Italy. Pages 29–38 in M. Soldati and M.
- 613 569 Marchetti, editors. *Landscapes and Landforms of Italy*. Springer International
- 614 570 Publishing, Cham.
- 615 571 Genghini, M., and D. Capizzi. 2005. Habitat improvement and effects on brown hare *Lepus*
- 616 572 *europaeus* and roe deer *Capreolus capreolus*: a case study in northern Italy. *Wildlife*
- 617 573 *Biology* 11:319–329.
- 618 574 Gervasi, V., and P. Ciucci. 2018. Demographic projections of the Apennine brown bear
- 619 575 population *Ursus arctos marsicanus* (Mammalia: Ursidae) under alternative
- 620 576 management scenarios. *European Zoological Journal* 85:243–253.
- 621 577 Giovacchini S., and Fabrizio M. 2022. Wildlife road-kill analysis along the State Road 690
- 622 578 with specific concern on the interference for Apennine brown bear dispersal
- 623 579 movements. Technical report for International Association for Bear Research and
- 624 580 Management.
- 625 581 Halada, L., Evans, D., Romão, C., and J-E Petersen. 2011. Which habitats of European
- 626 582 importance depend on agricultural practices? *Biodiversity and Conservation* 20:
- 627 583 2365–2378. Hilty, J., G. L. Worboys, A. Keeley, S. Woodley, B. J. Lausche, H. Locke,
- 628 584 M. Carr, I. Pulsford, J. Pittock, J. W. White, D. M. Theobald, J. Levine, M. Reuling,
- 629 585 J. E. M. Watson, R. Ament, and G. M. Tabor. 2020. Guidelines for conserving
- 630 586 connectivity through ecological networks and corridors. IUCN.
- 631 587 Hofmeester, T. R., J. M. Rowcliffe, and P. A. Jansen. 2017. A simple method for estimating
- 632 588 the effective detection distance of camera traps. *Remote Sensing in Ecology and*
- 633 589 *Conservation* 3:81–89.
- 634 590 Jimenez, J., R. Chandler, J. Tobajas, E. Descalzo, R. Mateo, and P. Ferreras. 2019.
- 635 591 Generalized spatial mark–resight models with incomplete identification: An
- 636 592 application to red fox density estimates. *Ecology and Evolution* 9:4739–4748.
- 637 593 Jung, M. 2016. LecoS - A python plugin for automated landscape ecology analysis.
- 638 594 *Ecological Informatics* 31:18–21.
- 639 595 Keeley, A. T. H., P. Beier, T. Creech, K. Jones, R. H. G. Jongman, G. Stonecipher, and G. M.
- 640 596 Tabor. 2019. Thirty years of connectivity conservation planning: An assessment of
- 641 597 factors influencing plan implementation. *Environmental Research Letters* 14.
- 642 598 Lara-Romero, C., E. Virgós, and E. Revilla. 2012. Sett density as an estimator of population
- 643 599 density in the European badger *Meles meles*. *Mammal Review* 42:78–84.
- 644 600 Latini, R. 2019. Stima della densità della popolazione di cervo e di capriolo nel Parco
- 645 601 Nazionale d’Abruzzo, Lazio e Molise, Technical report.
- 646 602 Loy, A., G. Aloise, L. Ancillotto, F. M. Angelici, S. Bertolino, D. Capizzi, R. Castiglia, P.
- 647 603 Colangelo, L. Contoli, B. Cozzi, D. Fontaneto, L. Lapini, N. Maio, A. Monaco, E.
- 648 604 Mori, A. Nappi, M. Podestà, D. Russo, M. Sarà, M. Scandura, and G. Amori. 2019.
- 649 605 *Mammals of Italy: An annotated checklist*. *Hystrix* 30.
- 650 606 Maiorano, L., L. Chiaverini, M. Falco, and P. Ciucci. 2019. Combining multi-state species
- 651 607 distribution models, mortality estimates, and landscape connectivity to model
- 652 608 potential species distribution for endangered species in human dominated landscapes.
- 653 609 *Biological Conservation* 237:19–27.
- 654 610 Mancinelli, S., L. Boitani, and P. Ciucci. 2018. Determinants of home range size and space
- 655 611 use patterns in a protected wolf (*Canis lupus*) population in the central apennines,
- 656 612 Italy. *Canadian Journal of Zoology* 96:828–838.
- 657 613 Maronde, L., B. T. McClintock, U. Breitenmoser, and F. Zimmermann. 2020. Spatial
- 658 614 capture–recapture with multiple noninvasive marks: An application to camera-
- 659 615 trapping data of the European wildcat (*Felis silvestris*) using R package multimark.
- 660 616 *Ecology and Evolution* 10:13968–13979.

- 662 617 MASE. 2023. Strategia Nazionale per la Biodiversità (SNB) 2030. Ministero dell' Ambiente e
663 618 della Sicurezza Energetica Direzione Generale Patrimonio Naturalistico e Mare
664 619 Divisione III – Strategie della Biodiversità.
- 665 620 Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E.,
666 621 Hohmann, U., Monaco, A., Ozoliņš, J., Cellina, S., Podgórski, T., Fonseca, C.,
667 622 Markov, N., Pokorny, B., Rosell, C., and A. Náhlík. 2015. Wild boar populations up,
668 623 numbers of hunters down? A review of trends and implications for Europe. *Pest*
669 624 *management science*, 71(4), 492–500.
- 670 625 Mateo-Sánchez, M. C., S. A. Cushman, and S. Saura. 2014. Connecting endangered brown
671 626 bear subpopulations in the Cantabrian Range (north-western Spain). *Animal*
672 627 *Conservation* 17:430–440.
- 673 628 Mattioli, L., P. Forconi, D. Berzi, and P. Perco. 2014. WOLF POPULATION ESTIMATE IN
674 629 ITALY AND MONITORING PERSPECTIVES.
- 675 630 McGuire, J. L., J. J. Lawler, B. H. McRae, T. A. Nuñez, and D. M. Theobald. 2016.
676 631 Achieving climate connectivity in a fragmented landscape. *Proceedings of the*
677 632 *National Academy of Sciences of the United States of America* 113:7195–7200.
- 678 633 Melis, C., B. Jędrzejewska, M. Apollonio, K. A. Bartoń, W. Jędrzejewski, J. D. C. Linnell, I.
679 634 Kojola, J. Kusak, M. Adamic, S. Ciuti, I. Delehan, I. Dykyy, K. Krapinec, L. Mattioli,
680 635 A. Sagaydak, N. Samchuk, K. Schmidt, M. Shkvyrya, V. E. Sidorovich, B. Zawadzka,
681 636 and S. Zhyla. 2009. Predation has a greater impact in less productive environments:
682 637 variation in roe deer, *Capreolus capreolus*, population density across Europe. *Global*
683 638 *Ecology and Biogeography* 18:724–734.
- 684 639 Méndez, T. P., J. Naves, J. F. Vázquez, A. Fernández-Gil, J. Seijas, J. Albornoz, E. Revilla,
685 640 M. Delibes, and A. Domínguez. 2014. Estimating the population size of the
686 641 endangered Cantabrian brown bear through genetic sampling. *Wildlife Biology*
687 642 20:300–309.
- 688 643 Merenlender, A. M., A. T. H. Keeley, and J. A. Hilty. 2022. Ecological corridors for which
689 644 species? *Therya* 13:45–55.
- 690 645 Mori, E., G. F. Ficetola, R. Bartolomei, G. Capobianco, P. Varuzza, and M. Falaschi. 2021.
691 646 How the South was won: current and potential range expansion of the crested
692 647 porcupine in Southern Italy. *Mammalian Biology* 101:11–19.
- 693 648 Pacifici, M., M. D. Marco, and J. E. M. Watson. 2020. Protected areas are now the last
694 649 strongholds for many imperiled mammal species. *Conservation Letters* 13.
- 695 650 Palencia, P., P. Barroso, J. Vicente, T. R. Hofmeester, J. Ferreres, and P. Acevedo. 2022a.
696 651 Random encounter model is a reliable method for estimating population density of
697 652 multiple species using camera traps. *Remote Sensing in Ecology and Conservation*
698 653 8:670–682.
- 699 654 Palencia, P. 2022b. REM analysis vignette.
- 700 655 Palencia, P., S. Zanet, P. Barroso, R. Vada, F. Benatti, F. Occhibove, F. Meriggi, and E.
701 656 Ferroglio. 2024. How abundant is a species at the limit of its distribution range? Crested
702 657 porcupine *Hystrix cristata* and its northern population. *Ecology and Evolution*
703 658 14:e10793.
- 704 659 Pérez, T., J. Naves, J. F. Vázquez, J. Seijas, A. Corao, J. Albornoz, and A. Domínguez. 2010.
705 660 Evidence for improved connectivity between Cantabrian brown bear subpopulations.
706 661 *Ursus* 21:104–108.
- 707 662 Ponzetta, M.P., Cervasio, F., Crocetti, C., Messeri, A., and G. Argenti. 2010. Habitat
708 663 Improvements with Wildlife Purposes in a Grazed Area on the Apennine Mountains.
709 664 *Italian Journal of Agronomy* 5: 233–238.
- 710 665 Rondinini, C., A. Battistoni, V. Peronace, and C. Teofili. 2022. LISTA ROSSA DEI
711 666 VERTEBRATI ITALIANI.

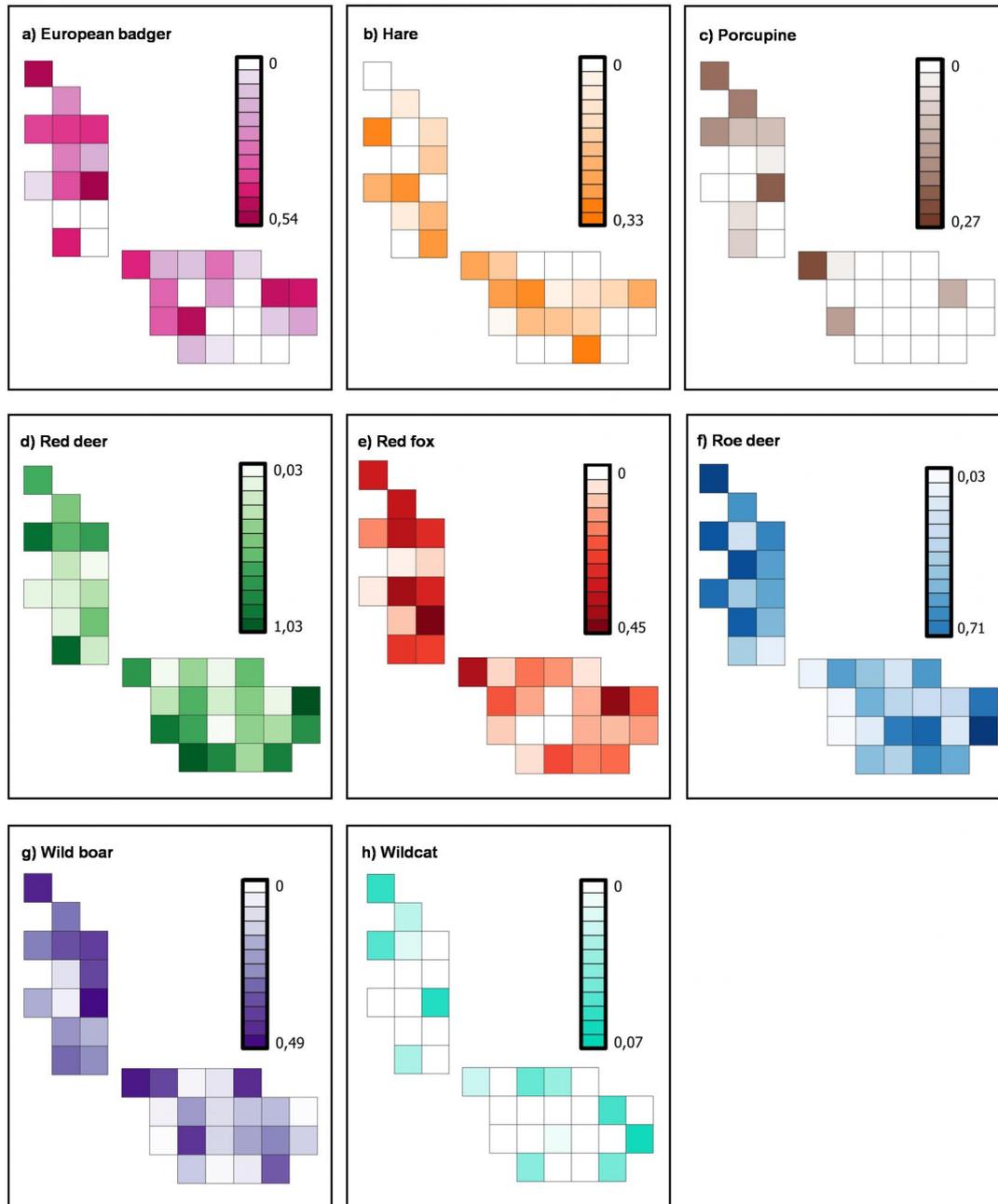
- 713 667 Rosalino, L.M., Santos, M. J., Beier, P., and M. Santos-Reis. 2008. Eurasian badger habitat
714 668 selection in Mediterranean environments: Does scale really matter?. *Mammalian*
715 669 *Biology*, 73:189-198. Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008.
716 670 Estimating animal density using camera traps without the need for individual
717 671 recognition. *Journal of Applied Ecology* 45:1228–1236.
- 718 672 Rowcliffe, J. M., Carbone, C., Jansen, P.A., Kays, R. and Kranstauber, B. 2011. Quantifying
719 673 the sensitivity of camera traps: an adapted distance sampling approach. *Methods in*
720 674 *Ecology and Evolution*, 2: 464-476.
- 721 675 Santini, L., Isaac, N.J.B., and G.F. Ficetola. 2018. TetraDENSITY: A database of population
722 676 density estimates in terrestrial vertebrates. *Global Ecol Biogeogr*; 27: 787–791.
- 723 677 Schieltz, J.M. and D.I. Rubenstein. 2016. Evidence based review: positive versus negative
724 678 effects of livestock grazing on wildlife. What do we really know? *Environmental*
725 679 *Research Letters* 11: 113003.
- 726 680 Smith, R. K., N. V. Jennings, and S. Harris. 2005. A quantitative analysis of the abundance
727 681 and demography of European hares *Lepus europaeus* in relation to habitat type,
728 682 intensity of agriculture and climate. *Mammal Review*. Volume 35. Blackwell
729 683 Publishing Ltd.
- 730 684 Thornton, D., K. Zeller, C. Rondinini, L. Boitani, K. Crooks, C. Burdett, A. Rabinowitz, and
731 685 H. Quigley. 2016. Assessing the umbrella value of a range-wide conservation network
732 686 for jaguars (*Panthera onca*). *Ecological Applications* 26:1112–1124.
- 733 687 UNEP-WCMC & IUCN. (2024) *Protected Planet: the World Database of Protected*
734 688 *Areas (WDPA)*.
- 735 689 Valente, A.M., Acevedo, P., Figueiredo, A.M., Fonseca, C. and R.T. Torres. 2020,
736 690 Overabundant wild ungulate populations in Europe: management with consideration
737 691 of socio-ecological consequences. *Mam Rev*, 50: 353-366.
- 738 692 Valfrè, D., and M. Cipollone. 2016. Realizzazione di opere di mitigazione per la messa in
739 693 sicurezza della SR 83 “Marsicana” tra gli abitati di Gioia dei Marsi e Opi a favore
740 694 dell’orso bruno marsicano (*Ursus arctos marsicanus*) nell’Appennino centrale (Italia),
741 695 International Congress “Wildlife Road Kill Prevention: Theory, Research and
742 696 Practice” October 4th-5th 2016, Perugia.
- 743 697 VV.AA., 2011 - Piano d'azione nazionale per la tutela dell'orso bruno marsicano – PATOM.
744 698 QUAD. CONS. NATURA 37. MIN AMBIENTE - ISPRA. [in Italian].
- 745 699 Wang, F., W. J. McShea, S. Li, and D. Wang. 2018. Does one size fit all? A multispecies
746 700 approach to regional landscape corridor planning. *Diversity and Distributions* 24:415–
747 701 425.
- 748 702 Watson, J. E. M., N. Dudley, D. B. Segan, and M. Hockings. 2014. The performance and
749 703 potential of protected areas. *Nature*. Volume 515. Nature Publishing Group.
- 750 704 White, P. C. L., and A. I. Ward. 2010. Interdisciplinary approaches for the management of
751 705 existing and emerging human–wildlife conflicts. *Wildlife Research* 37:623–629.
- 752 706 Zanaga, D., R. Van De Kerchove, D. Daems, W. De Keersmaecker, C. Brockmann, G.
753 707 Kirches, J. Wevers, O. Cartus, M. Santoro, S. Fritz, M. Lesiv, M. Herold, N.-E.
754 708 Tsendbazar, P. Xu, F. Ramoino, and O. Arino. 2022. *ESA WorldCover 10 m 2021*
755 709 *v200*. <<https://zenodo.org/records/7254221>>. Accessed 31 May 2024.



Map of the five corridor areas identified in the Central Apennines. The corridors (in red, marked with numbers) connect four protected areas (other coloured polygons). The study area, covering Corridor 1 and Corridor 2, is divided into 34 2.5 km grid cells, each including a camera trap (black points).



Framework of the application of the Random Encounter Model (REM) to estimate the density of the eight mammal species analysed in the study area.



Trapping rates of each camera trap location of the study area, for each of the eight species of meso- and macro-mammals analysed (panels a-h). Trapping rates were obtained from the number of independent encounters divided by survey effort (i.e., the operating time of camera traps expressed in days).

Manuscript body

[Download source file \(5.3 MB\)](#)

Figures

Figure 1 - [Download source file \(12.92 MB\)](#)

Map of the five corridor areas identified in the Central Apennines. The corridors (in red, marked with numbers) connect four protected areas (other coloured polygons). The study area, covering Corridor 1 and Corridor 2, is divided into 34 2.5 km grid cells, each including a camera trap (black points).

Figure 2 - [Download source file \(151.46 kB\)](#)

Framework of the application of the Random Encounter Model (REM) to estimate the density of the eight mammal species analysed in the study area.

Figure 3 - [Download source file \(309.9 kB\)](#)

Trapping rates of each camera trap location of the study area, for each of the eight species of meso- and macro-mammals analysed (panels a-h). Trapping rates were obtained from the number of independent encounters divided by survey effort (i.e., the operating time of camera traps expressed in days).

Supplementary Online Material

File 1 - [Download source file \(505.78 kB\)](#)

File 2 - [Download source file \(5.33 MB\)](#)

Main text track change (FOR REVIEWERS ONLY)