

# Spatial ecology of crested porcupine in a metropolitan landscape

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**Running title:** Urban ecology of the porcupine.

## Abstract

Human settlements, including cities, may provide wildlife with new ecological niches, in terms of habitat types and food availability, thus requiring plasticity for adaptation. The crested porcupine *Hystrix cristata* is a habitat-generalist, large-sized rodent, also recorded in some suburban areas, but no information is available on its habitat use in metropolitan landscapes.

26 Here, we assessed the land-use factors influencing the presence of crested porcupines in a  
27 metropolitan area of Central Italy. We collected data on the occurrence of crested porcupines  
28 from the metropolitan area of Rome following an observer-oriented approach to record  
29 occurrences and retrieve pseudo-absences. We then related the presence/absence of *H. cristata*  
30 to the landscape composition. Occupancy models showed that cultivations and scrubland were  
31 positively related to porcupine presence, most likely as they provide food resources and shelter  
32 sites, respectively. Although the crested porcupine has been confirmed as a “generalist” species  
33 in terms of habitat selection, a strong preference for areas limiting the risk of being killed and  
34 providing enough food and shelter was observed. We therefore suggest that the crested  
35 porcupine may adapt to deeply modified landscapes such as large cities by selecting specific  
36 favourable land-use types.

37

38 **Keywords.** Cultivations; *Hystrix cristata*; occupancy models; scrublands; urban areas.

39

## 40 **Introduction**

41

42 Urbanisation is one of the main land-use modifications occurring at large scales globally, as  
43 human settlements are encroaching into rural areas and natural habitats (Ditchkoff et al. 2006;  
44 McKinney 2006). Behavioural flexibility and generalist ecological niche has helped mammal  
45 species to thrive and form self-sustaining populations in urban areas, with a process called  
46 synurbisation (Santini et al. 2019). Besides species that only occasionally cross cities (“urban-  
47 visitors” and “urban-explorers”), several taxa, usually defined as “urban-dwellers” or “urban-  
48 adapters”, thrive and successfully exploit urban environments (Baker et al. 2003; Grimm et al.  
49 2008; Bateman and Fleming 2012; Balestrieri et al. 2016; Uchida et al. 2021). Synurbisation  
50 may pose a challenge to wildlife managers, as there is a strong need to find a trade-off between  
51 limiting human-wildlife conflicts and movements of animal-right groups (Don Carlos et al.

52 2009; La Morgia et al. 2017; Honda et al. 2018). Moreover, synurbic species may be relatively  
53 rare or legally protected taxa, i.e. representing a further management issue. Thus, analysing the  
54 spatial ecology of species of conservation concern and species generating human-wildlife  
55 conflict in urban ecosystems is crucial for their long-term management (Gehrt et al. 2009;  
56 Ancillotto et al. 2016; Cronk and Pillay 2021).

57 A pool of native and introduced species has benefited by the expansion of human  
58 settlements, which may provide increased food availability and shelter sites, as well as  
59 decreased predation risk (Sever and Mendelsohn 1989; Contesse et al. 2004; Marks and  
60 Bloomfield 2006). Wild mammals living in or around urban areas may exhibit different traits  
61 as their rural counterparts because of a different predation pressure or adaptation to human-  
62 induced stresses (Ditchkoff et al. 2006; Santini et al. 2019). As to mammals, about 3.5% known  
63 species worldwide is regularly recorded in urban areas, with a peak of species in Southern and  
64 Central Europe, i.e. areas with a long history of deep landscape modifications. Carnivores and  
65 rodents are the most represented mammalian orders in urban environments (Santini et al. 2019).  
66 The crested porcupine *Hystrix cristata* is one of the largest rodents inhabiting urban areas, and  
67 has been recorded in at least 10 cities within its range of introduction (Grano 2016; Lovari et  
68 al. 2017; Santini et al. 2019; Manenti et al. 2020). This species is generally described as a  
69 “habitat generalist” as it can exploit a wide range of habitat types from woodland to farmlands,  
70 despite being linked to covered habitats (e.g. woodland and scrubland) for denning (Mohr 1965;  
71 Sonnino 1998; Monetti et al. 2005; Mori et al. 2014a; Lovari et al. 2017). Porcupines are widely  
72 poached in Central and Southern Italy, mainly because they are considered as crop raiders, even  
73 though it has been shown that most damage only occurs in small unprotected vegetable gardens  
74 (Ghigi 1917; Laurenzi et al. 2016; Lovari et al. 2017). In suburban areas, where poaching  
75 pressure might be the highest (Lovari et al. 2017), the crested porcupine mostly select thorny  
76 thickets for denning and feed mostly on fruits (Lovari et al. 2017). In the suburbs, farmlands

77 and fallows are avoided by porcupines, whereas no data are available on the ecology of this  
78 large rodent in metropolitan areas.

79 The aim of this study is assessing the spatial ecology of the crested porcupine population in  
80 Rome (Italy), which currently is the only European metropolitan area hosting a self-sustaining  
81 population of crested porcupine (Grano 2016; Santini et al. 2019). Specifically, we ran  
82 occupancy models to evaluate how landscape composition affects the presence of the crested  
83 porcupine within the urban area, using occurrence data collected over a 16 years time window,  
84 i.e. since the first available records of this species in Rome. We predicted that porcupines, as  
85 being generalist rodents, would prefer areas providing the best trade-off between the availability  
86 of food resources and avoidance of predation risk, thus selecting urban environments with  
87 cultivated (i.e. exploited for foraging) and vegetation-covered areas (exploited for shelter). Our  
88 results also provide information on how limiting human-porcupine conflict (cf. Cerri et al.  
89 2017; Lovari et al. 2017), by showing the spatial behaviour of this urban-dwelling generalist  
90 species in a metropolitan area, where contacts between this species and humans are the highest.

91

## 92 **Materials and methods**

93

### 94 *Study area*

95

96 We focused on the area included in the Rome beltway (“Grande Raccordo Anulare” ring  
97 highway, hereafter GRA), i.e. within the closed ring highway that embraces the metropolitan  
98 area of Rome without discontinuity, separating the city from the countryside (average diameter:  
99 21 km; total length: 68 km). The GRA entails an area of 46,000 ha within the municipal territory  
100 of Rome. Rome represents the Italian metropolis with the highest density of green public areas  
101 (urban parks and cemeteries), i.e. the 5.1% of the study area. Rome is also the third Italian

102 municipality for the surface of agricultural land (after Florence and Bari), with cultivations  
103 (orchards, vineyards, olive groves, arable lands, and horticultural crops) covering the 29.9% of  
104 our study area (www.istat.it, accessed on 01.02.2021). Woodlands and scrublands cover  
105 respectively 3.8% and 2.5% of the study area. The remaining part of the study area is covered  
106 with human settlements (58.4%) and archaeological areas (0.3%) (Figure 1).

107 Rome is a rich city in animal biodiversity (e.g. Zapparoli 1997; Capotorti et al. 2019), hosting  
108 at least 39 mammal species, including medium to large-sized ones such as the wild boar *Sus*  
109 *scrofa*, the red fox *Vulpes vulpes*, the stone marten *Martes foina* and the crested porcupine  
110 (Amori et al. 2009; Todini and Crosti 2020). The latter is known to occur in the study area at  
111 least since the early XX century (Lepri 1911; Miller 1912), and it was confirmed continuously  
112 since the early 2000s (Gippoliti and Amori 2006; Grano 2016), thus suggesting that the  
113 population within the study area is relatively stable.

114

#### 115 *Data collection and validation*

116

117 Occurrence data of the crested porcupine used in this study were collected between April 2005  
118 and December 2020, and uploaded on Ornitho and iNaturalist citizen science platforms by one  
119 of the authors (LA). We used this time span, as the stable presence of the crested porcupine  
120 within the Rome metropolitan area was only confirmed in the early 2000s, despite occasional  
121 records since the early XX Century (Gippoliti and Amori 2006; Amori et al. 2009). All data  
122 were collected and/or verified year by year by LA during the 16 year period during extensive  
123 field-work throughout the metropolitan area to describe and monitor the local mammal  
124 diversity. Occurrences were then uploaded by the same author after 2017 for the Italian  
125 Mammal Atlas project ([https://www.inaturalist.org/observations?project\\_id=mammiferi-d-](https://www.inaturalist.org/observations?project_id=mammiferi-d-italia)  
126 [italia](https://www.inaturalist.org/observations?project_id=mammiferi-d-italia)). Data were validated through an expert-based process, as described in the regulation of

127 this platform. Most observations were represented by quills, dead animals, or footprints. Also,  
128 faecal pellets of the crested porcupine are easily identifiable, showing an unmistakable oblong  
129 and curved-olive shape (Mori et al. 2021). All data were georeferenced and entered into a  
130 database.

131

### 132 *Occupancy models*

133

134 The study area was divided into 460 cells of 1 km<sup>2</sup> each using QGIS (ver. 3.16.1: QGIS  
135 Development Team 2019). The average home range size of the crested porcupine in  
136 Mediterranean environments is ~0.5 km<sup>2</sup> (Lovari et al. 2013; Mori et al. 2014a); thus the cell  
137 size we adopted limits the risk of pseudoreplication (i.e. the same individual detected in multiple  
138 cells).

139 We used a static (single-season) occupancy model as most of the sites were monitored in one  
140 single sampling year. Following Milanesi et al. (2021), pseudo-absences were assigned to  
141 records of all the species detected by the same observer, excluding porcupine records. For cells  
142 monitored during more than one year, the year with the largest number of records of any species  
143 was selected for analyses. We considered the percentage of cover of seven habitat typologies  
144 describing land-use cover as covariates of occupancy: human settlements, scrubland,  
145 archaeological areas, woodland, urban green areas, cultivations and fallows. These habitat  
146 typologies were obtained by reclassifying the land-use map of the Latium Region of the year  
147 2016 (original land-use map available at <https://dati.lazio.it/>). For each study site (1 km cell),  
148 we extracted the percentage cover of each habitat typology.

149 Statistical analyses were performed in the software R 3.5.1 (R Core Team 2013). We used the  
150 unmarked and MuMIN packages respectively to conduct occupancy models and to select the  
151 best models (Fiske and Chandler 2011; Bartòn 2018). Animal species are rarely observed with

152 perfect accuracy, particularly when nocturnal and elusive as the crested porcupine (Corsini et  
153 al. 1995; Lovari et al. 2017). Occupancy models allow to estimate species distribution, and to  
154 evaluate relationships between occupancy and environmental features, taking into account  
155 possibility that the target species remained undetected during sampling (MacKenzie et al.  
156 2003), and are thus particularly important for the analysis of data collected through citizen  
157 science campaigns (Altwegg and Nichols 2019; Marta et al. 2019). Occupancy models allow  
158 estimating the detection probability of species based on a series of detection / non-detection  
159 data at fixed sites (Kéry et al. 2013). This approach thus requires information on non-detections,  
160 i.e. on surveys during which the target species was not detected. These data are not easy to  
161 obtain from citizen science datasets (MacKenzie et al. 2003; Altwegg and Nichols 2019). In  
162 our study pseudo-absences were estimated through an “observer-oriented” approach (Milanesi  
163 et al. 2020), i.e. by considering records of species other than the target one. Specifically, we  
164 assumed that a cell was surveyed in a specific date if the database included at least one record  
165 of a species, recorded by an observer that has detected target species (Milanesi et al. 2020) as a  
166 valuable method to inform species distribution models (Milanesi et al. 2020). Multiple records  
167 collected having the same date and the same cell were considered to be one single observation.  
168 We related detection probability to the date of the survey (day of the year), also considering a  
169 quadratic term. Pearson's correlation coefficient was used to test for independence between  
170 pairs of covariates: pairs of covariates with  $r > |0.70|$  were considered as strongly correlated;  
171 thus, only one covariate (i.e. the most important one for the porcupine: Mori et al. 2014a) of the  
172 pair was included in the model. The cover of human settlements was excluded from the models  
173 as being significantly and negatively correlated with cultivations ( $r = -0.80$ ), which is an  
174 important habitat type for the crested porcupine (Mori et al. 2014a). We ran a total of 256  
175 competing models, considering each possible combination of independent variables on  
176 detection and occupancy. Models were ranked through the Akaike's Information Criterion

177 corrected for small samples (AICc): the best model was the one with the lowest AICc (Burnham  
178 and Anderson 2004). Models with an AICc difference  $< 2$  were considered equally supported.  
179 We estimated the significance of the variables included in the best model through a likelihood  
180 ratio test, considering as significant variables when  $p < 0.05$ .

181

## 182 **Results**

183

184 Between April 2005 and December 2020, our survey provided records from 129 cells. The  
185 presence of the crested porcupine was recorded in 65 out of 129 sampled cells, for a total of  
186 100 detections of crested porcupine (Figure 1). The best-occupancy model suggested that the  
187 occupancy of the crested porcupine was positively and significantly related to the cover of  
188 scrubland and cultivations (Tables 1 and 2). The second best model included only the cover of  
189 cultivations and had a difference of AICc of 2.04 (Table 1), hence it was not considered. None  
190 of the other covariates was included in a model with high support, on the basis of AICc values.  
191 The detection probability of the porcupine was unrelated to the date of survey. The average  
192 detection probability per survey was 0.89 (95% confidence interval: 0.74 – 0.96).

193

## 194 **Discussion**

195

196 In our work, we showed that the probability of occurrence of the crested porcupine in our urban  
197 ecosystem was positively correlated to increasing coverage of cultivations and scrublands. The  
198 crested porcupine is a monogamous species who pair for life and show a sedentary behaviour  
199 after dispersal and settlement in a territory (Mori et al. 2016); therefore, the movements of  
200 adults are mostly determined by food search and not by mate search (Lovari et al. 2013;  
201 Mazzamuto et al. 2019). This may provide support to the importance of cultivations within

202 urban environments, which provide porcupines with clumped and abundant food resources  
203 (Lovari et al. 2017), even within human settlements. Scrublands are mostly selected as den  
204 sites, particularly where human pressure (i.e. poaching risk) is highest, which may support the  
205 use of this habitat types in dense human settlements (Tinelli and Tinelli 1980; Monetti et al.  
206 2005; Lovari et al. 2017). Accordingly, within the Rome urban area, the few dens of crested  
207 porcupines whose location is known, occur in one archaeological area (“Catacombe di  
208 Priscilla”, n = 1; Grano 2016), as well as in a semi-natural scrubland area within a protected  
209 natural reserve (n = 2), and in a densely vegetated area of a large recreational park (n = 1;  
210 Ancillotto L. pers. obs.). Therefore, results support the prediction that the crested porcupine in  
211 a metropolitan area would select habitats providing it with the best trade-off between food  
212 abundance and shelter site.

213 In natural habitats, the crested porcupine mainly feeds on underground storage organs of plants  
214 (e.g. bulbs, tubers and rhizomes), but can also eat fruits and vegetables (Bruno and Riccardi  
215 1995; Mori et al. 2020). Crested porcupines may exploit nearby cultivated areas which provide  
216 easy access to food resources (e.g. figs and pumpkins) and do not require time-consuming active  
217 excavation which may limit vigilance (Lovari et al. 2017). Most likely, the positive correlation  
218 between cultivations and occupancy in the urban environment could also be explained by  
219 limited food resources in some areas of the city (e.g. recreational parks characterised by deeply  
220 modified floras), thus leading porcupine individuals to expose themselves to open and,  
221 therefore, risky habitats. Accordingly, few data occurred in recreational areas, possibly  
222 underused to limit encounters with humans and potential natural predators, e.g. red foxes and  
223 domestic dogs, which are often abundant in urban parks in Rome (Amori et al. 2009). Local  
224 high densities of wild boar (Todini and Crosti 2020) may also limit the occupancy by the crested  
225 porcupines in some areas (Mazzamuto et al. 2019). Furthermore, artificial lights at night may  
226 limit the use of these areas by crested porcupines, which are known to avoid bright areas and

227 bright moonlight nights (Mori et al. 2014b). In fact, it is much more likely that these areas, as  
228 well as archaeological sites, wetlands, and human settlements, are avoided as not providing  
229 sufficient food resources. Therefore, all these habitats are avoided by porcupines also in natural  
230 contexts, yet some individuals, especially sub-adults, may visit them occasionally and create  
231 temporary or seasonal burrows (Pigozzi and Patterson 1990; Börger 2002; Mori and Assandri  
232 2019).

233 Noise pollution and vehicular traffic have also been reported to alter the spatial behaviour of  
234 the porcupine (Mori et al. 2013; Mori 2017), and long-distance roads are known to hinder  
235 wildlife movements (Forman and Alexander 1998; Seidler et al. 2015). Accordingly, records  
236 of crested porcupines in Italian urban areas increase when vehicular traffic (and related human  
237 pressure) is the lowest (e.g. during the lockdown following the SARS-CoV 2 pandemic  
238 outbreak: Manenti et al. 2020). In this context, the ring highway in Rome may represent a  
239 barrier to the transit of porcupines, as green corridors between green areas inside and outside  
240 the city centre are few.

241 Crop damages by crested porcupines may occur in areas covered by cultivations, including  
242 vegetable gardens, potentially triggering conflict with humans (Sforzi et al. 1999; Laurenzi et  
243 al., 2016). No conflict between humans and porcupines has been reported in Rome to date  
244 though; strictly nocturnal habits and local protection of cultivations through fences may have  
245 in fact promoted coexistence between porcupines and humans in urban and suburban areas  
246 (Lovari et al. 2017), as evidenced in the closely related Indian crested porcupine *Hystrix indica*  
247 in Israel (Sever and Mendelsohn 1989). However, the intense illumination of the highway  
248 between Haifa and Tel-Aviv (National Road 2, Israel) did not prevent Indian porcupines from  
249 foraging in the nearby of the roadside, contrary to what expected from a nocturnal species that  
250 avoids brightest nights (Sever and Mendelsohn 1989).

251 Our results highlight that a large generalist rodent such as *H. cristata* may become an actual  
252 urban-dwelling species (cf. Santini et al. 2019), by occupying spots of suitable habitats, namely  
253 represented by patches of natural or agricultural areas, eventually persisting in one of the largest  
254 metropolitan areas in southern Europe. The behavioural and physiological mechanisms that  
255 allow such persistence without eliciting conflicts, as well as whether urban populations exhibit  
256 gene flow with nearby non-urban ones, is still to be cleared. Thus, the urban population of *H.*  
257 *cristata* in Rome provides a suitable study system to furtherly shed light on mechanisms and  
258 consequences of synurbization in mammals.

259

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263

264 **Author's contributions** EM and LA conceived the research, LA collected data on the field,  
265 MF, RM and GFF ran the analyses; EM wrote the first draft of the manuscript. All authors  
266 contributed to and approved the final draft.

267

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269

270 **Data availability** All data are available on iNaturalist platform ([www.inaturalist.org](http://www.inaturalist.org)).

271

272 **Declaration**

273

274 **Ethics approval and consent to participate** This study did not involve human subjects or  
275 animal manipulation or maintenance in captivity or laboratory.

276

277 **Consent for publication** All authors agree and consent with the publication of the study.

278

279 **Competing interests** Authors declare that they have no competing interest.

280

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423

424 **Table 1.** Occupancy models of the crested porcupine in Rome ranked according to the AICc

425 value; df = degrees of freedom; AICc = Akaike Information Criterion corrected; “-“ indicates

426 that the variable was not included in the model.

427

Detection covariates			Occupancy covariates							df	AICc	Weight
Inercept	Day	Day <sup>2</sup>	Intercept	Scrub lands	Archaeological areas	Woodlands	Urban green areas	Cultivations	Fallows			
2.05	-	-	-0.68	8.23	-	-	-	3.94	-	4	187.02	0.73
2.10	-	-	-0.56	-	-	-	-	4.24	-	3	189.06	0.26
1.95	-	-	0.27	11.23	-	-	-3.32	-	-	4	199.04	0.002
1.91	-	-	-0.22	12.78	-	2.93	-	-	-	4	201.08	<0.001
2.06	-	-	0.56	-	-17.44	-	-3.99	-	-	4	201.35	<0.001
2.07	-	-	0.51	-	-	-	-4.16	-	-	3	201.69	<0.001
1.91	-	-	0.01	13.94	-13.67	-	-	-	-	4	201.82	<0.001
1.91	-	-	-0.06	14.67	-	-	-	-	-	3	202.03	<0.001
2.04	-	-	0.03	-	-13.97	2.98	-	-	-	4	205.48	<0.001
2.05	-	-	-0.04	-	-	3.22	-	-	-	3	205.82	<0.001
2.06	-	-	0.23	-	-16.43	-	-	-	-	3	206.94	<0.001
2.07	-	-	0.17	-	-	-	-	-	-	2	207.91	<0.001

428

429

430 **Table 2.** Estimates of the coefficient of variables included in the best occupancy model for the  
431 crested porcupine.

432

	Estimate	Standard Error	z	P
<b>Scrublands</b>	8.23	5.60	1.47	0.0411
<b>Cultivations</b>	3.94	1.17	3.38	0.0003

433

434

435 Figure legends

436

437 Figure 1. Study area, land-cover typologies, and occurrence records used for analyses. Outside  
438 the frame we report the UTM 32 coordinates of the study area; the grid used for analyses (1  
439 km) is also shown.