1 **Title:** Spatial bias in dietary studies can limit our understanding of the feeding ecology of large

2 carnivores

3

4 **Authors**: Cerri, J.[1], Brogi, R.[1], Musto, C.[2], Bassi, E.[1], Ventura, G.[3], Bianchi, A.[3], Delogu, M.[2],

5 Scandura, M.[1], Apollonio, M.[1]

6

7 **Affiliations**:

8   1. Department of Veterinary Medicine, University of Sassari, 07100, Sassari, Italy. email

9   2. Department of Veterinary Medical Sciences, University of Bologna, 40064, Bologna, Italy

10   3. Istituto Zooprofilattico della Lombardia e dell'Emilia-Romagna "B. Ubertini", 25124,

11   Brescia, Italy

12

13 **Corresponding author**:

14 ● Jacopo Cerri, Department of Veterinary Medicine, University of Sassari, 07100, Sassari,

15   Italy. email: jcerri@uniss.it

16

17 **Abstract**

18 Many large carnivores have broad geographical ranges, encompassing ecosystems with a different

19 prey base. Our understanding of their diet could therefore be biased by the spatial concentration of

20 dietary studies into few areas. We propose a protocol to divide the geographical range of large

21 carnivores, into areas that are homogeneous with respect to available food sources, by using the

22 grey wolf (*Canis lupus*) in Italy, as a case study.

23 We mapped the potential maximum distribution of wolves, on a 10 km grid (n = 2,497), and then

24 performed cluster analysis to classify cells according to their: *i*) abundance of domestic and wild

25 ungulates, *ii*) suitability for the coypu (*Myocastor coypus*) and *iii*) landscape anthropization.

26 Finally, we checked the percentage of cells in each cluster that were covered by dietary studies in

27 2007-2013, 2014-2018 and 2019-2023.

28 The distribution range of wolves in Italy can be divided into 5 areas, characterized by different

29 food sources but also by a different spatial coverage from dietary studies. The Alps and some

30 sectors of the Apennines, with low anthropization and abundant wild ungulates, were oversampled.

31 More anthropized areas in Central and Southern Italy, rich in sheep and wild ungulates, as well as

32 anthropized lowlands, with abundant food waste and coypu, were undersampled. Finally, no study

33 was carried out in intensive farming districts of Northern Italy.

34 Our protocol indicates that future studies about the diet of wolves in Italy should focus on

35 anthropized landscapes. There, the consumption of pets could trigger wolf persecution and pathogen

36 transmission, and predation on coypu and the consumption of food waste could increase the

37 exposure to toxic compounds.

38 More broadly, our protocol can improve our understanding about the feeding ecology of large

39 carnivores, as it can be used to: *i*) assess and put into perspective meta-analytic findings, *ii*) identify

40 knowledge gaps arising from spatial bias and prioritize new studies in undersampled areas and *iii*)

41 design sampling schemes for large-scale research.

42

44

Introduction

Meta-analyses summarize and advance existing knowledge about the biology, ecology, evolution, and conservation of animals and plants (Gurevitch et al., 2018), and reveal the occurrence, magnitude, and spatiotemporal variation of ecological dynamics (Peters, 2010).

However, the increase in meta-analyses in ecology and evolution, since the early 2000s (Cadotte et al., 2012; Vetter et al., 2013), came hand-in-hand with the growing awareness that aggregating different studies is challenging, particularly in fast-evolving fields like ecology, ethology or evolutionary biology. On the one hand, the reliability of a meta-analysis depends upon the transparency and standardization of data collection protocols across studies, with differences in measurements and/or analytical methods resulting into spurious findings (Gurevitch et al., 2018; Nakagawa et al., 2017; Whittaker, 2010). On the other hand, the generalizability of its conclusions depends upon the quality of the sampling strategy and, for ecological dynamics that vary in space, the geographical balance of the various studies that are summarized. A well-known example is spatial-bias, with most peer-reviewed studies being conducted in the Global North, in more accessible areas, or in parks and natural reserves (Christie et al., 2020; Di Marco et al., 2017; Hughes et al., 2021).

Large carnivores have been the focus of many reviews and meta-analyses that covered, among the others, their long-term population dynamics and range shifts (Ingeman et al., 2022; Jacobson et al., 2016; Murphy et al., 2022; Strampelli et al., 2022; Wolf and Ripple, 2017), movement ecology (Gonzalez-Borrajo et al., 2016; Morales-González et al., 2022), genetic diversity (Hindrikson et al., 2017; O'Brien et al., 2017), and interspecific relationships (Franchini and de las Mercedes Guerisoli, 2023; Périquet et al., 2014). Perhaps, one of the most covered topics is carnivores diet (Table 1), due to its major implications for ecosystem dynamics. Many large carnivores rely on wild ungulates as a prey base: once these are depleted, they can either perish (Carbone et al., 2011; Wolf and Ripple, 2017) or shift to alternative food sources (Creel et al., 2017), including livestock or human food waste, two food sources that may create conflicts with humans (van Eeden et al., 2017;

71 Newsome et al., 2014). Reviews about the diet of large carnivores are therefore fundamental to

72 understand how they can respond to human impacts on wildlife and ecosystem, and therefore result

73 crucial to plan their management. It may be the case of top predators with a wide dietary breadth,

74 which, differently from strictly specialist carnivores, can shift to livestock or other anthropogenic

75 resources according to the local availability of the different items (Ferretti et al., 2020), which in

76 turn depends on human impacts and landscape transformations (Kuijper et al., 2024; Newsome et

77 al., 2014).

78 Understanding dietary breadth was the scope of many reviews about large carnivores, particularly

79 for adaptable species with a large geographical range and living alongside humans. Nevertheless,

80 spatial bias is likely to limit the generalizability of their findings. As resource selection is an

81 adaptive process (Manly et al., 2007), with predators adapting to available prey in a certain area, a

82 review based on studies covering only part of the geographical range and only specific

83 environmental types among those inhabited by a large carnivore is unlikely to capture its whole

84 dietary breadth. This problem is exacerbated for those species whose geographical distribution

85 expands or shifts through time, often to environmental types which were not included in their

86 former range. Some large carnivores in Europe and North America are in facts recovering part of

87 their historical range (Chapron et al., 2014; Miller et al., 2013), with human-dominated landscapes

88 being increasingly represented within their distribution ranges (Kuijper et al., 2024, Zanni et al.,

89 2023). As dietary studies require time for data collection and processing, the rhythm to which they

90 are published might not match these fast spatiotemporal dynamics, resulting in increased spatial

91 bias through time.

92 While spatial-bias has already been mentioned as a potential limitation for research about large

93 carnivore diet (Newsome et al. 2016), to the best of our knowledge no study quantified it, nor

94 proposed a workflow to detect it. Evaluating if published literature is biased, with respect to the

95 ecological conditions characterizing the whole range of a certain species, can be used both

96 beforehand and retrospectively. By checking for spatial bias in advance, researchers can decide

97 whether existing literature is suitable to carry out a meta-analysis or even to study the diet of a

98 certain species in a geographical region where no study has been conducted before. Conversely, the

99 post-hoc exploration of spatial-bias could be used to put existing scientific evidence into

100 perspective.

101 In this study we aim to show how spatial and ecological bias in dietary studies involving large

102 carnivores could be assessed and evaluated, by using the expansion of the gray wolf (*Canis lupus*)

103 in Italy as a case study. Gray wolf can indeed be considered the most successful large carnivore at

104 recolonizing the human-dominated portion of its former range in Europe (Kuijper et al. 2024) and

105 Italy is among the European countries that, since the 1970s, had the most marked increase in wolves

106 (Boitani et al., 2022, Zanni et al. 2023). Starting from a small population of a few hundred

107 individuals in remote areas of Central Italy (Zimen and Boitani, 1975; Cagnolaro et al., 1974), at

108 least 2,945 – 3,608 individuals are nowadays thought to be present (La Morgia et al., 2022),

109 upsetting the scenarios for wolf conservation and coexistence in the country.

110 Even though wolves are known to have a wide trophic niche, and can include in their diet also

111 unexpected resources (Adams et al., 2010; Barocas et al., 2018; Mohammadi et al., 2019; Roffler et

112 al., 2022) most reviews regard wild ungulates, or alternatively livestock, as the cornerstone of their

113 diet, with other food sources playing a minor role (Capitani et al. 2004; Janeiro-Otero et al., 2020;

114 Meriggi et al., 2011; Mattioli et al. 2011, Meriggi and Lovari, 1996; Mori et al., 2017; Newsome et

115 al., 2016; Zlatanova et al., 2014). However, if wolves had truly relied on wild ungulates, it is

116 unclear how they could be colonizing peri-urban areas and croplands (Torretta et al., 2022; Zanni et

117 al., 2023), where ungulates are less abundant and where recent evidence suggests they rely on

118 alternative food sources (Ciucci et al., 2020; Ferretti et al., 2019; Musto et al., 2024).

119 The surprising speed of wolf expansion in Italy, leading to the recovery of most of its historical

120 range (differently from other European countries, e.g., Spain, Clavero et al., 2023), made Italy a

121 perfect workbench to highlight potential spatial biases in wolf diet literature. We did so by

122 considering three temporal windows for which wolf occupancy data are available (2007-2012,

123 2013-2018 and 2019-2023) and then by comparing the ecological conditions characterizing *i*) the

124 spatial distribution of wolves in Italy and *ii*) that of study areas of wolf diet research.

125

126 **Methods**

127 **Collection of studies and inclusion criteria**

128 Data collection adopted a threefold approach. First, we extracted all those studies that were

129 mentioned in reviews about wolf diet (Janeiro-Otero et al., 2020; Meriggi et al., 2011; Mori et al.,

130 2017; Newsome et al., 2016; Zlatanova et al., 2014), and that were conducted in Italy between 2007

131 and 2023.

132 Moreover, we also searched for the keywords "*Canis lupus*", "*wolf*" and "*diet*" (similarly to

133 Newsome et al., 2016) on three large datasets of scientific publications: Scopus, Web of Science,

134 and Google Scholar. Then, from this second pool of studies, we selected those which had been

135 carried out in Italy, and were published between 2007 and 2023. As the period when data had been

136 collected was not always reported, and results were often not splitted between different years, we

137 used the year of publication to assign each study to one of our three periods. By doing so we

138 obtained insights about studies that were carried out after the most recent review about wolf diet

139 (Janeiro-Otero et al., 2020), or that had been discarded by previous reviews, but whose spatial

140 location was informative about potential spatial biases.

141 Finally, we also collected available gray literature about wolf diet in Italy. This included non-peer

142 reviewed documents, such as dissertations of MSc and PhD students that had not been subsequently

143 published in a peer-reviewed journal, or reports published by local authorities and protected areas.

144 As dissertations are not always adequately indexed on the archives of Italian universities, we used

145 snowballing. First, we queried "*Dieta lupo*", the Italian translation of "*Wolf diet*" on university

146 archives and Google. Then, starting from an initial sample of Msc thesis that we previously knew

147 about, we asked mentors if they had supervised other students on the same topic, between 2007 and

148 2023. Finally, we also asked colleagues from other research groups if they could indicate some gray

149   literature on the topic, until no new studies were detected. From the pool of studies that we had

150   obtained, we retained those for which it was possible to understand where data had been collected,

151   with respect to the grid used by the Ministry for the Environment to quantify wolf occupancy in

152   2019-2021 (La Morgia et al., 2022).

153   Although different methods for investigating wolf diet may provide different results (Klare et al.,

154   2011), we did not discard studies according to the method they used as our meta-analysis focused

155   on assessing spatial bias. So, we pooled together studies relying on scat analysis, barcoding,

156   stomach contents and isotopes.

157

158   **Quantification of spatial location, measurements and statistical analysis**

159   We used a 10-km resolution grid produced by the Ministry of the Environment (La Morgia et al.

160   2022), to identify: *i*) the distribution of wolves, *ii*) environmental conditions and *iii*) the spatial

161   coverage of studies about wolf diet in peninsular Italy.

162   For the 2019 – 2023 period, for peninsular Italy we used the whole grid produced by La Morgia et

163   al. (2022), whose cells had an occupancy probability different from zero. Moreover, we also added

164   those cells in the Alps, where the presence of wolves was confirmed (La Morgia et al., 2022). For

165   the 2007-2013 and 2014-2018 periods, we used official distribution maps from official reports of

166   the Habitat directive (http://reportingdirettivahabitat.isprambiente.it/). To ensure consistency

167   between the three different periods these maps were aligned to the grid developed by La Morgia et

168   al. (2022). A complete overview of wolf distribution in these three periods is available in Fig. 1.

169   Then, for each cell of the grid we extracted variables related to the main food sources available to

170   wolves. These included: anthropization and the presence of domestic livestock, wild ungulates, and

171   the coypu (*Myocastor coypus*).

172   Anthropization is an important factor affecting wolf diet, mostly through food waste, which is a

173   nearly unlimited food source. Although wolves do not fully exploit carbohydrates (Axelsson et al.,

174   2013), evidence from non-European countries indicate that they exploit food waste whenever

175 available (Barocas et al., 2018; Mohammadi et al., 2019), probably by selecting for meat scraps and

176 bones. Moreover, wolves living around human settlements could also prey on pets (Bassi et al.,

177 2017; Kojola et al., 2022; Nowak et al., 2011). We quantified anthropization by calculating

178 evenness of human density, quantified at a 1km resolution through the Global Human Settlement

179 Layer (https://human-settlement.emergency.copernicus.eu/index.php), for each cell of our grid.

180 Evenness was quantified through the Gini index, which varies from 0, when all the units of a

181 sample have the same value of a certain measure, to 1 when one unit has the entire amount of that

182 value. Therefore, the Gini index in our case was negatively associated with human presence, with

183 cells having the lowest values being characterized by widespread human settlements and having a

184 higher amount of food waste.

185 We also considered the abundance of domestic livestock, particularly sheep, cattle, and domestic

186 pigs, that can be regularly preyed on by wolves (Gervasi et al., 2021). Moreover, the abundance of

187 livestock could also account for the availability of carrion and slaughterhouses in the environment,

188 important supplementary food sources for wolves (Ciucci et al., 2020; Ćirović and Penezić, 2019).

189 For domestic livestock, we used 10km abundance projections generated by the Food and

190 Agriculture Organization and structured in the Gridded Livestock of the World database (GLW4,

191 https://data.apps.fao.org/catalog/dataset/15f8c56c-5499-45d5-bd89-59ef6c026704), related to the

192 abundance of sheep, cattle, and domestic pigs.

193 For wild ungulates, we considered the five most preyed on by wolves in Italy: roe deer (*Capreolus*

194 *capreolus*), deer (*Cervus elaphus*), wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and Northern

195 chamois (*Rupicapra rupicapra*) (Gazzola et al. 2007, Mattioli et al. 2011). We did not consider the

196 mouflon (*Ovis gmelini musimon*), which is distributed with scattered populations in the Italian

197 peninsula, although occasionally it could represent an important prey (Capitani et al. 2004).

198 Moreover, we did not consider the Sika deer (*Cervus nippon*), because its distribution in Central

199 and Northern Italy is still uncertain (Mori et al., 2024). Neither we considered the Alpine ibex

200 (*Capra ibex*), as it seems to play a minor role in the diet of alpine wolves (Palmegiani et al. 2013).

201 For wild ungulates, we relied on 10-km hunting yield density maps elaborated within the

202 ENETWILD project (ENETWILD consortium, 2022), using them as relative indexes for the local

203 abundance of each wild ungulate species. Although the ENETWILD maps predict low values for

204 the abundance of a certain species, even in areas lying outside of its actual distribution range, we

205 used them as they were the only available information about the occurrence and abundance of

206 multiple ungulate species at the national scale, in Italy. Moreover, in cluster analysis (see the

207 following lines), areas with a different prey base were identified mostly by high densities of the

208 various species, and therefore this bias was not deemed to affect our results.

209 Finally, we also included the potential environmental suitability of the Italian peninsula for the

210 coypu. Recent studies found out that the coypu can be an important prey, in some agricultural

211 ecosystems of Central and Northern Italy (Musto et al., 2024; Ferretti et al., 2019), probably

212 because it is easy to prey and can attain very high densities, providing wolves with a relevant

213 biomass (Balestrieri et al., 2016). As no abundance map was available for this species, we rather use

214 the potential suitability of the Italian landscape, at a 1 km resolution, obtained from Schertler et al.

215 (2020). For each cell of our grid, we calculated the median for the abundance of wild ungulates and

216 livestock and the geometric mean for the suitability for the coypus. Although wolves in many areas

217 of Central and Northern Europe regularly prey on other aquatic rodents, such as the Eurasian beaver

218 (*Castor fiber*, Gable et al., 2018), we did not include this species, because its population in Central

219 and Northern Italy is still extremely small and confined to few areas (Bertolino et al., 2024).

220 Finally, we assigned our studies to the various cells of the grid. As each study provided us with

221 different information about its study area, and the location where data had been collected, we

222 identified the location of each study area as the geographical center of the area where biological

223 samples had been collected. Then, we assumed that wolves for which biological samples had been

224 collected on the centroid, could have moved in a home range of approximately 113 km^2 (Mancinelli

225 et al., 2018; Mattioli et al., 2018) and so we generated a buffer with a radius of 6 km around each

226 point and classified all those cells of the grid that overlapped with it. As our scope was to assess the

227 spatial coverage of existing studies about wolf diet, and because many studies refer to the same

228 research project, we only classified the cells of our grid as being covered by studies or not, with a

229 dichotomous variable.

230 Finally, we identified environmentally homogeneous areas within the entire Italian peninsula, based

231 on: *i*) the Gini index of human density, *ii*) the median abundance of roe deer, red deer, wild boar,

232 fallow deer and Northern chamois, *iii*) the median abundance of domestic pigs, sheep and cattle, i*v*)

233 the geometric mean of the potential suitability for the coypu. To this end, we used the CLARA

234 algorithm, an extension of Partitioning Around Medoids cluster analysis (Kaufman and Rousseeuw,

235 2009). We chose the CLARA algorithm due to the high number of cells (n = 2,497) and its

236 robustness against non-normal data and outliers. The number of clusters was chosen by graphically

237 exploring the silhouette width method, the elbow method, and the gap statistics method

238 (Kassambara, 2017). Before clustering our cells, we standardized and centered our variables.

239 Once we identified environmental clusters, we graphically inspected how studies about wolf diet

240 were distributed between different clusters, across the three different periods. Although we

241 clusterized environmental variables in the entire Italian peninsula, we then only explored coverage

242 in those cells that corresponded to the maximum distribution range of the wolf. This range (n. cells

243 = 1,974) was obtained by considering all cells where the species was reported at least in one of the

244 three time periods. We calculated both *i*) the portion of dietary studies being conducted in each

245 different cluster and *ii*) the portion of cells of each cluster being involved in at least a dietary study,

246 both overall and across the three different time periods.

247 Statistical analyses were carried out in R (R Core Team 2023). A completely reproducible dataset

248 and software code are available at https://osf.io/76cx4/

249

250 **Results**

251 Our final dataset included 36 studies: 27 of them were published in peer-reviewed journals, 8 of

252 them were MSc dissertations and 1 was a study published in the proceedings of a scientific

conference (see the file "StudiesDiet_20240624.xlsx" in the "Data" folder of Supplementary Information). Most studies were published during the 2019-2023 (n = 15) and the 2014-2018 periods (n = 13). As for MSc dissertations, 6 studies out of 8 were from the 2019-2023 period, probably because older dissertations had not been archived in a digital format.

Cluster analysis identified 5 groups of areas that were homogeneous in terms of food resources (Fig. 2-4). The first group (Cluster 1) coincided with the Alps and with high-elevation areas of Central Apennines. Cells in this cluster had a high abundance of wild ungulates, particularly of Northern chamois and red deer, extremely low anthropization and little animal husbandry. These areas were unsuitable for the coypu.

The second group (Cluster 2) included areas with sheep herding, medium-low values of anthropization, high abundance of roe deer, wild boar, and fallow deer, and that were moderately suitable for the coypu. These areas have low abundance of the red deer. The third group (Cluster 3) included cells with high abundance of wild ungulates, including the red deer, but characterized by lower values of anthropization, sheep herding and suitability for the coypu than cells from Cluster 2. Overall, Cluster 2 and Cluster 3 were common in Central and Southern Italy, where they account for most Apennines areas, and in the Prealps in Northern Italy.

The fourth (Cluster 4) and the fifth group (Cluster 5) included anthropized areas. Namely, Cluster 4 included cells with high urban sprawl and the highest suitability for the coypu, characterized by little animal husbandry and intermediate abundances of the roe deer and the wild boar. Cluster 5 instead corresponded to areas of intensive animal husbandry, with high densities of sheep, cattle and domestic pigs. Cluster 5 was also suitable for the coypu and had intermediate values of anthropization. Overall, all cells from Cluster 5 and most cells from Cluster 4 occurred in the Po Plain in Northern Italy, but some cells from Cluster 4 also occurred in lowlands of Central and Southern Italy.

When considering the entire 2007-2023 period, most cells covered by studies about wolf diet were in Cluster 3 (43%). The proportion was lower in Cluster 1 (28%), Cluster 2 (22%) and Cluster 4

279   (8%). Conversely, when checking the percentage of cells that covered by studies in each cluster,

280   both Cluster 1 and Cluster 3 attained the highest coverage, with 19% and 18% of cells. Coverage

281   was much lower for Cluster 4 and Cluster 2 (5%). Moreover, although Cluster 5 accounted only for

282   an area of 400km2 in the distribution range of wolves, its cells were never interested by dietary

283   studies.

284   When considering the spatial distribution of dietary studies through time, we noticed that the

285   distribution of cells interested by studies has become more even between 2007-2013 and 2019-

286   2023, with the progressive inclusion of Cluster 4 (Table 2).

287

288   **Discussion**

289   Systematic reviews are crucial to summarize existing knowledge about the feeding ecology of

290   species of conservation concern, and prone to conflict with humans, such as large carnivores.

291   However, spatial bias can limit the generalizability of their findings. In this study we showed how

292   researchers can quantify the magnitude of spatial bias, by identifying areas that result homogeneous

293   in terms of prey they can offer to a large carnivore and then checking the allocation of existing

294   studies between them. Namely, we used data about the distribution of important food sources for

295   the gray wolf in Italy, to identify 5 ecologically homogeneous areas at the national level, and then

296   understand the extent to which these were interested by dietary studies that had been carried out

297   since 2007.

298   From a research viewpoint, our protocol can be used either before conducting a systematic review

299   or after having produced one. In the first case, whenever existing literature is limited to specific

300   environments, researchers might decide not to synthesize knowledge at all, as knowledge gaps

301   could interest a significant portion of a species range. Alternatively, and perhaps more

302   pragmatically, researchers could review existing literature, and then put their findings into

303   perspective, by specifying that areas with certain types of prey species or other source of food were

304   not covered. Identifying spatial bias in existing dietary studies could also be useful to plan future

305 research, by assisting the design of large-scale surveys for scat collection. To ensure unbiased

306 findings, or at least minimize bias associated with scat collection, Steenweg et al., (2015) suggested

307 the adoption of spatially balanced random sampling, like generalized random tessellation

308 stratification. Although spatially balanced sampling is robust against unobserved bias (Kermorvant

309 et al., 2019), we believe that our approach, by identifying strata that are homogeneous in terms of

310 environmental resources, could be useful to develop advanced sampling designs with a higher

311 accuracy (Robertson and Price, 2024).

312 There is much to be gained from a similar process both in terms of ecological research and

313 management, and we will make a few examples from our case study about wolves.

314 Concerning the 5 homogeneous areas we identified by clustering food sources; our findings clearly

315 highlight that existing literature about the diet of wolves is severely unbalanced. Most research

316 referred to Cluster 3 and Cluster 1, areas with little landscape anthropization and abundant wild

317 ungulates. In these areas wolves have been found to rely mostly on deer and wild boar, which are

318 nevertheless much less abundant in Cluster 4 and 5. However, with the progressive recolonization

319 of the Italian peninsula by wolf packs (Bassi et al., 2015), wolves indeed expanded in human-

320 modified areas as those included in Clusters 4 and 5 (Torretta et al., 2022; Zanni et al., 2023). Since

321 these areas are also those more likely to host conflicts with humans, due to their high human

322 presence and activities, the knowledge gaps concerning wolf ecology in these areas may prevent the

323 application of evidence-based conservation and conflict management policies (Kuijper et al., 2024).

324 It indeed remains unclear the extent to which wolves in these human-dominated areas could shift to

325 coypus, food waste, livestock, pets and animal byproducts, with major possible alterations of their

326 fitness and behavior. Indeed, beside the direct effects on behavior, diet shifts towards anthropogenic

327 items may also induce modifications of wolf's genetics through an increased proximity with

328 commensal domestic or feral dogs, likely more abundant in human-dominated areas, ultimately

329 leading to an enhanced likelihood of hybridization (Hughes & Macdonald, 2013). Moreover, the

330 analysis of scats collected in these environments, coupled with a genetic assessment of the

331 hybridization level, can also be useful to see if wolves and wolf-dog hybrids segregate their trophic

332 niche, something that does not seem to happen in less anthropized environments (Bassi et al., 2017).

333 In the case of peri-urban wolves, the presence of remains attributable to pets was observed in the

334 stomach contents (see Appendix 1). The consumption of domestic cats can also be inferred from the

335 detection in the intestinal matrix of wolves of viruses typical of felines (e.g., Feline Panleukopenia

336 Virus, Balboni et al., 2021). Beside directly threatening wolves through an increased share of

337 parasites and other pathogens, and being their loss both an emotional and economic harm for

338 owners, the predation of pets may drive negative attitudes towards wolf conservation (Lescureux &

339 Linnell, 2014). Fulfilling our knowledge gaps on the wolf dietary patterns in anthropized

340 environments, hosting more domestic dogs and cats, may thus enhance our understanding of wolf

341 predation on pets and its possible implications for wolf conservation.

342 Also, researchers frequently attempt to monitor temporal changes in the diet of large carnivores. In

343 our case study, if we want to monitor changes in the diet of wolves through time, apart from being

344 sure about potential issues of sampling bias (Gable et al., 2015), it is important that comparisons are

345 based on areas with similar prey composition. For example, our findings indicate that dietary

346 studies in livestock districts (Cluster 5, currently not sampled) are urgently needed to quantify

347 dietary habits of wolves inhabiting these environments. Moreover, assessing dietary shifts between

348 2007-2013 and 2019-2023 by pooling together multiple studies with a cross-sectional approach is

349 questionable, as studies were initially concentrated in less anthropized environments. Combining

350 longitudinal studies carried out on single wolf packs (Bassi et al. 2020) or at least populations (e.g.

351 Mattioli et al., 1995; 2011), seems certainly more appropriate for this purpose.

352 Our protocol could also be used to study the role played by underrated prey in the diet of a large

353 carnivore. For example, areas from Cluster 4 and Cluster 5 are also rich in coypu. So far, few

354 studies explored the extent to which wolves could rely on this species (Ferretti et al., 2019) and

355 none was carried out in areas, like Cluster 4 and 5, where domestic or wild ungulates are scarce. As

356 coypu are easy to catch in agricultural channels and could attain significant densities (Balestrieri et

357 al., 2016), it is plausible that they are indeed a major prey for wolves. Empirical evidence seems to

358 confirm this point: by analyzing the stomach content of 64 wolves that were found dead in the Po

359 Plain (Cremona, Mantua, and Bologna provinces), we found remains of coypu in 10 individuals

360 (15.6%) (see Appendix 2). Beyond the necropsy findings, we believe that rodents (rats and coypus)

361 are increasingly contributing to the diet of peri-urban wolves in Italy, as 61.8% of the wolf

362 carcasses analyzed by Musto et al. (2024) were positive to the presence of Second-Generation

363 Anticoagulant Rodenticides (SGARs), particularly in highly anthropized areas, due to probable

364 ingestion of poisoned rodents. Therefore, it is plausible that rodents, particularly coypu (similarly to

365 beavers, Gable et al., 2018), might be an important species which is fueling the expansion of wolves

366 in lowlands, particularly that of dispersing individuals or couples. This could explain the significant

367 expansion of wolves along the Po Plain, where two packs are nowadays present in the Po delta.

368 In conclusion we provided a rigorous and standardized approach to assess spatial and ecological

369 bias in dietary studies, which may be profitably replicated with other large carnivores and even

370 other animal group such as scavengers, herbivores, marine predators and mesocarnivores to identify

371 and address gaps in our knowledge of their feeding ecology, with the ultimate goals to increase our

372 understanding of the context-dependent variations of their ecological impacts and to improve their

373 conservation.

374

375

376 **References**

377 Adams, L. G., Farley, S. D., Stricker, C. A., Demma, D. J., Roffler, G. H., Miller, D. C., & Rye, R.

378 O. (2010). Are inland wolf–ungulate systems influenced by marine subsidies of Pacific salmon?.

379 *Ecological Applications*, *20*(1), 251-262. https://doi.org/10.1890/08-1437.1

380 Apollonio M, Bassi E, Berzi D, Bongi P, Caniglia R, Canu A, Fabbri E, Galaverni M, Luccarini S,

381 Mattioli L, Merli E, Morimando F, Passilongo D, Scandura M, Viviani V. Esperienze di

382 monitoraggio e conservazione del lupo in Toscana (2013-2016). 2016. Available from:

383 https://www.isprambiente.gov.it/files2018/eventi/verso-piano-monitoraggio-lupo/

384 APOLLONIOROMADICEMBRE2018DEFINITIVA.pdf

385 Axelsson, E., Ratnakumar, A., Arendt, M. L., Maqbool, K., Webster, M. T., Perloski, M., ... &

386 Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a

387 starch-rich diet. *Nature*, *495*(7441), 360-364. https://doi.org/10.1038/nature11837

388 Balboni, A., Urbani, L., Delogu, M., Musto, C., Fontana, M.C., Merialdi, G., Lucifora, G., Terrusi,

389 A., Dondi, F., Battilani, M. (2021). Integrated Use of Molecular Techniques to Detect and

390 Genetically Characterise DNA Viruses in Italian Wolves (*Canis lupus italicus*). *Animals*, 11, 2198.

391 https://doi.org/10.3390/ani11082198

392 Balestrieri, A., Zenato, M., Fontana, E., Vezza, P., Remonti, L., Caronni, F. E., ... & Prigioni, C.

393 (2016). An indirect method for assessing the abundance of introduced pest *Myocastor coypus*

394 (Rodentia) in agricultural landscapes. *Journal of Zoology*, 298(1), 37-45.

395 https://doi.org/10.1111/jzo.12284

396 Barocas, A., Hefner, R., Ucko, M., Merkle, J. A., & Geffen, E. (2018). Behavioral adaptations of a

397 large carnivore to human activity in an extremely arid landscape. *Animal Conservation*, *21*(5), 433-

398 443. https://doi.org/10.1111/acv.12414

399 Bassi, E., Canu, A., Firmo, I., Mattioli, L., Scandura, M., & Apollonio, M. (2017). Trophic overlap

400 between wolves and free-ranging wolf× dog hybrids in the Apennine Mountains, Italy. *Global*

401 *Ecology and Conservation*, 9, 39-49. https://doi.org/10.1016/j.gecco.2016.11.002

402 Bassi, E., Pervan, I., Ugarković, D., Kavčić, K., Maksan, M. T., Krofel, M., & Šprem, N. (2021).

403 Attacks on hunting dogs: the case of wolf–dog interactions in Croatia. *European Journal of Wildlife*

404 *Research*, *67*, 1-9. https://doi.org/10.1007/s10344-020-01451-5

405 Bassi, E., Gazzola, A., Bongi, P., Scandura, M., Apollonio, M. (2020). Relative

406 impact of human harvest and wolf predation on two ungulate species in Central Italy. *Ecological*

407 *Research, 35,* 662–674. https://doi.org/10.1111/1440-1703.12130

408 Bassi, E., Willis, S. G., Passilongo, D., Mattioli, L., & Apollonio, M. (2015). Predicting the spatial

409 distribution of wolf (*Canis lupus*) breeding areas in a mountainous region of Central Italy. *PloS one,*

410 *10*(6), e0124698. https://doi.org/10.1371/journal.pone.0124698

411 Bertolino, S., Bartolommei, P., Ferri, M., Gasperini, S., Grignolio, S., Lapini, L., ... & Cerri, J.

412 (2023). The strange case of beaver return in Italy: origins and management. *Hystrix, the Italian*

413 *Journal of Mammalogy.* https://doi.org/10.4404/hystrix-00654-2023

414 Blanco, G., Cortés-Avizanda, A., Frías, Ó., Arrondo, E., & Donázar, J. A. (2019). Livestock

415 farming practices modulate vulture diet-disease interactions. *Global Ecology and Conservation*, 17,

416 e00518. https://doi.org/10.1016/j.gecco.2018.e00518

417 Boitani, L. (1992). Wolf research and conservation in Italy. *Biological conservation, 61*(2), 125-

418 132. https://doi.org/10.1016/0006-3207(92)91102-X

419 Boitani L., Kaczensky, P., Alvares, F., Andrén, H., Balys, V., Blanco, J.C., Chapron, G., Chiriac,

420 S., Cirovic, D., Drouet-Houguet, N., Groff, C., Huber, D., Iliopoulos, Y., Ionescu, O., Kojola, I.,

421 Krofel, M., Kutal, M., Linnell, J., Majic, A., Mannil, P., Marucco, F., Melovski, D., Mengüllüoğlu,

422 D., Mergeay, J., Nowak, S., Ozolins, J., Perovic, A., Rauer, G., Reinhardt, I., Rigg, R., Salvatori,

423 V., Sanaja, B., Schley, L., Shkvyria, M., Sunde, P., Tirronen, K., Trajce, A., Trbojevic, I.,

424 Trouwborst, A., von Arx, M., Wolfl, M., Zlatanova, D., Patkó, L. (2022). Assessment of the

425 conservation status of the wolf (*Canis lupus*) in Europe. Convention on the conservation of

426 European wildlife and natural habitats. Standing Committee, 42nd meeting, 28 November – 2

427 December   2022.

428 https://purews.inbo.be/ws/files/87214845/638036032684557257_LCIE_CoE_Wolf_status_report_2

429 022.pdf

430 Bojarska, K., & Selva, N. (2012). Spatial patterns in brown bear *Ursus arctos* diet: the role of

431 geographical and environmental factors. *Mammal Review, 42*(2), 120-143.

432 https://doi.org/10.1111/j.1365-2907.2011.00192.x

433 Cadotte, M. W., Mehrkens, L. R., & Menge, D. N. (2012). Gauging the impact of meta-analysis on

434 ecology. *Evolutionary Ecology*, 26, 1153-1167. https://doi.org/10.1007/s10682-012-9585-z

435 Cagnolaro, L., Rosso D., Spagnesi M., & Venturi B. (1974). *Inchiesta sulla distribuzione del lupo*

436 *(Canis lupus L.) in Italia e nei cantoni Ticino e Grigioni (Svizzera)*. Ricerche di Biologia della

437 Selvaggina, 59, 1-91.

438 Caniglia, R., Fabbri, E., Galaverni, M., Milanesi, P., & Randi, E. (2014). Noninvasive sampling and

439 genetic variability, pack structure, and dynamics in an expanding wolf population. *Journal of*

440 *Mammalogy*, *95*(1), 41-59. https://doi.org/10.1644/13-MAMM-A-039

441 Capitani, C., Bertelli, I., Varuzza, P., Scandura, M., & Apollonio, M. (2004). A comparative

442 analysis of wolf (*Canis lupus*) diet in three different Italian ecosystems. *Mammalian biology*, 69(1),

443 1-10. https://doi.org/10.1078/1616-5047-112

444 Carbone, C., Pettorelli, N., & Stephens, P. A. (2011). The bigger they come, the harder they fall:

445 body size and prey abundance influence predator–prey ratios. *Biology letters*, *7*(2), 312-315.

446 https://doi.org/10.1098/rsbl.2010.0996

447 Cerri, J., Musto, C., Stefanini, F. M., di Nicola, U., Riganelli, N., Fontana, M. C., Rossi, A.,

448 Garbarino, C., Merialdi, G., Ciuti, F., & Apollonio, M. (2023). A human-neutral large carnivore?

449 No patterns in the body mass of gray wolves across a gradient of anthropization. *PloS One*.

450 https://doi.org/10.1371/journal.pone/0282232

451 Chapron, G., Kaczensky, P., Linnell, J. D., Von Arx, M., Huber, D., Andrén, H., ... & Boitani, L.

452 (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*,

453 *346*(6216), 1517-1519. https://doi.org/10.1126/science.1257553

454 Chiang, P. J., & Allen, M. L. (2017). A review of our current knowledge of clouded leopards

455 (Neofelis nebulosa). *arXiv preprint arXiv:1712.04377*. https://doi.org/10.48550/arXiv.1712.04377

456 Christie, A. P., Amano, T., Martin, P. A., Petrovan, S. O., Shackelford, G. E., Simmons, B. I., ... &

457 Sutherland, W. J. (2021). The challenge of biased evidence in conservation. *Conservation Biology*,

458 *35*(1), 249-262. https://doi.org/10.1111/cobi.13577

459 Cimatti, M., Ranc, N., Benítez-López, A., Maiorano, L., Boitani, L., Cagnacci, F., ... & Santini, L.

460 (2021). Large carnivore expansion in Europe is associated with human population density and land

461 cover changes. *Diversity and Distributions*, *27*(4), 602-617. https://doi.org/10.1111/ddi.13219

462 Ćirović, D., & Penezić, A. (2019). Importance of slaughter waste in winter diet of wolves (*Canis*

463 *lupus*)   in   Serbia.   *North-Western   Journal   of   Zoology*,   *15*(2).

464 https://www.researchgate.net/profile/Aleksandra-Penezic/publication/

465 339141349_Importance_of_slaughter_waste_in_winter_diet_of_wolves_Canis_lupus_in_Serbia/

466 links/5e4136c4458515072d8e2be7/Importance-of-slaughter-waste-in-winter-diet-of-wolves-Canis-

467 lupus-in-Serbia.pdf

468 Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O., & Grottoli, L. (2020). Anthropogenic food

469 subsidies hinder the ecological role of wolves: Insights for conservation of apex predators in

470 human-modified   landscapes.   *Global   Ecology   and   Conservation*,   *21*,   e00841.

471 https://doi.org/10.1016/j.gecco.2019.e00841

472 Clavero, M., García-Reyes, A., Fernández-Gil, A., Revilla, E., & Fernández, N. (2023). Where

473 wolves were: setting historical baselines for wolf recovery in Spain. *Animal Conservation*, 26(2),

474 239-249. https://doi.org/10.1111/acv.12814

475 Creel, S., Matandiko, W., Schuette, P., Rosenblatt, E., Sanguinetti, C., Banda, K., ... & Becker, M.

476 (2018). Changes in African large carnivore diets over the past half-century reveal the loss of large

477 prey. *Journal of Applied Ecology*, *55*(6), 2908-2916. https://doi.org/10.1111/1365-2664.13227

478 Cruz, L. R., Muylaert, R. L., Galetti, M., & Pires, M. M. (2022). The geography of diet variation in

479 Neotropical Carnivora. *Mammal Review*, *52*(1), 112-128. https://doi.org/10.1111/mam.12266

480 Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., ... & Watson, J. E.

481 (2017). Changing trends and persisting biases in three decades of conservation science. *Global*

482 *Ecology and Conservation*, *10*, 32-42. https://doi.org/10.1016/j.gecco.2017.01.008

483 Ditmer, M. A., Stoner, D. C., Francis, C. D., Barber, J. R., Forester, J. D., Choate, D. M., ... &

484 Carter, N. H. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore.

485 *Ecography*, *44*(2), 149-161. https://doi.org/10.1111/ecog.05251

486 ENETWILD-consortium, Illanas, S., Croft, S., Smith, G. C., López-Padilla, S., Vicente, J., ... &

487 Acevedo, P. (2022). New models for wild ungulates occurrence and hunting yield abundance at

488 European   scale.   *EFSA   Supporting   Publications*,   *19*(10),   7631E.

489 https://doi.org/10.2903/sp.efsa.2022.EN-7631

490 Esattore, B., Rossi, A. C., Bazzoni, F., Riggio, C., Oliveira, R., Leggiero, I., & Ferretti, F. (2022).

491 Same place, different time, head up: multiple antipredator responses to a recolonizing apex

492 predator. *Current Zoology*. https://doi.org/10.1093/cz/zoac083

493 Falconi, N., Carlo, T. A., Fuller, T. K., Destefano, S., & Organ, J. F. (2022). Bear diets and human–

494 bear   conflicts: insights   from   isotopic   ecology.   *Mammal   Review*,   *52*(3),   322-327.

495 https://doi.org/10.1111/mam.12285

496 Farrington, J. D., & Li, J. (2024). Climate change impacts on snow leopard range. In *Snow leopards*

497 (pp. 81-93). Academic Press. https://doi.org/10.1016/B978-0-323-85775-8.00037-6

498 Fauvel, M., Lopes, M., Dubo, T., Rivers-Moore, J., Frison, P. L., Gross, N., & Ouin, A. (2020).

499 Prediction of plant diversity in grasslands using Sentinel-1 and -2 satellite image time series. *Remote*

500 *Sensing of Environment*, 237, 111536. https://doi.org/10.1016/j.rse.2019.111536

501 Ferretti, F., Lovari, S., Lucherini, M., Hayward, M., & Stephens, P. A. (2020). Only the largest

502 terrestrial carnivores increase their dietary breadth with increasing prey richness. *Mammal Review*,

503 *50*(3), 291-303. https://doi.org/10.1111/mam.12197

504 Ferretti, F., Lovari, S., Mancino, V., Burrini, L., & Rossa, M. (2019). Food habits of wolves and

505 selection of wild ungulates in a prey-rich Mediterranean coastal area. *Mammalian Biology*, *99*, 119-

506 127. https://doi.org/10.1016/j.mambio.2019.10.008

507   Fleming, P. A., Stobo-Wilson, A. M., Crawford, H. M., Dawson, S. J., Dickman, C. R., Doherty, T.

508   S., ... & Woinarski, J. C. (2022). Distinctive diets of eutherian predators in Australia. *Royal Society*

509   *Open Science*, *9*(10), 220792. https://doi.org/10.1098/rsos.220792

510   Franchini, M., & Guerisoli, M. D. L. M. (2023). Interference competition driven by co-occurrence

511   with tigers Panthera tigris may increase livestock predation by leopards *Panthera pardus*: a first

512   step meta-analysis. *Mammal Review*, *53*(4), 271-286. https://doi.org/10.1111/mam.12323

513   Gable, T. D., Windels, S. K., & Bruggink, J. G. (2017). The problems with pooling poop:

514   confronting sampling method biases in wolf (*Canis lupus*) diet studies. *Canadian Journal of*

515   *Zoology*, 95(11), 843-851. https://doi.org/10.1139/cjz-2016-0308

516   Gable, T. D., Windels, S. K., Romanski, M. C., & Rosell, F. (2018). The forgotten prey of an iconic

517   predator: a review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp.

518   *Mammal review*, 48(2), 123-138. https://doi.org/10.1111/mam.12118

519   Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R., & Apollonio, M.

520   (2007). The role of the wolf in shaping a multi-species ungulate community in the Italian western

521   Alps. *Italian Journal of Zoology*, 74(3), 297-307. https://doi.org/10.1080/11250000701447074

522   Gervasi, V., Linnell, J. D., Berce, T., Boitani, L., Ciucci, P., Cretois, B., ... & Gimenez, O. (2021).

523   Ecological correlates of large carnivore depredation on sheep in Europe. *Global Ecology and*

524   *Conservation*, 30, e01798. https://doi.org/10.1016/j.gecco.2021.e01798

525   González, C. A. L., & Miller, B. J. (2002). Do jaguars (Panthera onca) depend on large prey?.

526   *Western North American Naturalist*, 218-222. https://www.jstor.org/stable/41717194

527   Gonzalez-Borrajo, N., López-Bao, J. V., & Palomares, F. (2017). Spatial ecology of jaguars, pumas,

528   and ocelots: a review of the state of knowledge. *Mammal review*, *47*(1), 62-75.

529   https://doi.org/10.1111/mam.12081

530   Groff C., Angeli F., Baggia M., Bragalanti N., Pedrotti L., Zanghellini P., Zeni M. (2022). Rapporto

531   Grandi carnivori 2021 del Servizio Faunistico della Provincia Autonoma di Trento"

532 https://grandicarnivori.provincia.tn.it/content/download/14995/257640/file/Rapporto%20Grandi

533 %20Carnivori%202021.pdf

534 Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of

535 research synthesis. *Nature*, *555*(7695), 175-182. https://doi.org/10.1038/nature25753

536 Gurevitch, J., & Nakagawa, S. (2015). Research synthesis methods in ecology. *Ecological*

537 *statistics: Contemporary theory and application*, 200-227.

538 https://doi.org/10.1093/acprof:oso/9780199672547.001.0001

539 Hankin, D., Mohr, M. S., & Newman, K. B. (2019). *Sampling theory: For the ecological and*

540 *natural resource sciences*. Oxford University Press, USA.

541 Hayward, M. W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of

542 dietary overlap with the lion (*Panthera leo*). *Journal of Zoology*, 270(4), 606-614.

543 https://doi.org/10.1111/j.1469-7998.2006.00183.x

544 Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. (2006). Prey

545 preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, *270*(2), 298-313.

546 https://doi.org/10.1111/j.1469-7998.2006.00139.x

547 Hayward, M. W., Hofmeyr, M., O'brien, J., & Kerley, G. I. (2006). Prey preferences of the cheetah

548 (*Acinonyx jubatus*)(Felidae: Carnivora): morphological limitations or the need to capture rapidly

549 consumable prey before kleptoparasites arrive?. *Journal of Zoology*, *270*(4), 615-627.

550 https://doi.org/10.1111/j.1469-7998.2006.00184.x

551 Hayward, M. W., Jędrzejewski, W., & Jedrzejewska, B. (2012). Prey preferences of the tiger

552 *Panthera tigris*. *Journal of Zoology*, *286*(3), 221-231. https://doi.org/10.1111/j.1469-

553 7998.2011.00871.x

554 Hayward, M. W., Kamler, J. F., Montgomery, R. A., Newlove, A., Rostro-García, S., Sales, L. P.,

555 & Van Valkenburgh, B. (2016). Prey preferences of the jaguar *Panthera onca* reflect the post-

556 Pleistocene demise of large prey. *Frontiers in Ecology and Evolution*, *3*, 148.

557 https://doi.org/10.3389/fevo.2015.00148

Hayward, M. W., & Kerley, G. I. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of zoology*, *267*(3), 309-322. https://doi.org/10.1017/S0952836905007508

Hayward, M. W., O'Brien, J., Hofmeyr, M., & Kerley, G. I. (2006). Prey preferences of the African wild dog *Lycaon pictus* (Canidae: Carnivora): ecological requirements for conservation. *Journal of Mammalogy*, 87(6), 1122-1131. https://doi.org/10.1644/05-MAMM-A-304R2.1

Hindrikson, M., Remm, J., Pilot, M., Godinho, R., Stronen, A. V., Baltrūnaité, L., ... & Saarma, U. (2017). Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. *Biological Reviews*, *92*(3), 1601-1629. https://doi.org/10.1111/brv.12298

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological conservation*, 157, 341-351. https://doi.org/10.1016/j.biocon.2012.07.005

Hughes, A. C., Orr, M. C., Ma, K., Costello, M. J., Waller, J., Provoost, P., ... & Qiao, H. (2021). Sampling biases shape our view of the natural world. *Ecography*, *44*(9), 1259-1269. https://doi.org/10.1111/ecog.05926

Ingeman, K. E., Zhao, L. Z., Wolf, C., Williams, D. R., Ritger, A. L., Ripple, W. J., ... & Stier, A. C. (2022). Glimmers of hope in large carnivore recoveries. *Scientific Reports*, *12*(1), 10005. https://doi.org/10.1038/s41598-022-13671-7

Jacobson, A. P., Gerngross, P., Lemeris Jr, J. R., Schoonover, R. F., Anco, C., Breitenmoser-Würsten, C., ... & Dollar, L. (2016). Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ*, *4*, e1974. https://doi.org/10.7717/peerj.1974

Janeiro-Otero, A., Newsome, T. M., Van Eeden, L. M., Ripple, W. J., & Dormann, C. F. (2020). Grey wolf (*Canis lupus*) predation on livestock in relation to prey availability. *Biological conservation*, *243*, 108433. https://doi.org/10.1016/j.biocon.2020.108433

Karandikar, H., Serota, M. W., Sherman, W. C., Green, J. R., Verta, G., Kremen, C., & Middleton, A. D. (2022). Dietary patterns of a versatile large carnivore, the puma (*Puma concolor*). *Ecology and Evolution*, *12*(6), e9002. https://doi.org/10.1002/ece3.9002

Kassambara, A. (2017). *Practical guide to cluster analysis in R: Unsupervised machine learning* (Vol. 1). Sthda.

Kaufman, L., & Rousseeuw, P. J. (2009). Finding groups in data: an introduction to cluster analysis. John Wiley & Sons.

Kermorvant, C., D'amico, F., Bru, N., Caill-Milly, N., & Robertson, B. (2019). Spatially balanced sampling designs for environmental surveys. *Environmental monitoring and assessment*, 191(8), 524. https://doi.org/10.1007/s10661-019-7666-y

Khorozyan, I., & Heurich, M. (2023). Patterns of predation by the Eurasian lynx Lynx lynx throughout its range: ecological and conservation implications. Mammal Review. https://doi.org/10.1111/mam.12317

Khorozyan, I., & Heurich, M. (2023). Where, why and how carnivores kill domestic animals in different parts of their ranges: An example of the Eurasian lynx. *Global Ecology and Conservation*, e02585. https://doi.org/10.1016/j.gecco.2023.e02585

Klare, U., Kamler, J. F., & Macdonald, D. W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, *41*(4), 294-312. https://doi.org/10.1111/j.1365-2907.2011.00183.x

Kojola, I., Hallikainen, V., Kübarsepp, M., Männil, P., Tikkunen, M., & Heikkinen, S. (2022). Does prey scarcity increase the risk of wolf attacks on domestic dogs?. *Wildlife Biology*, *2022*(5), e01038. https://doi.org/10.1002/wlb3.01038

Kuijper, D. P. J., Diserens, T. A., Say-Sallaz, E., Kasper, K., Szafrańska, P. A., Szewczyk, M., ... & Churski, M. (2024). Wolves recolonize novel ecosystems leading to novel interactions. *Journal of Applied Ecology*. https://doi.org/10.1111/1365-2664.14602

607   LaBarge, L. R., Evans, M. J., Miller, J. R., Cannataro, G., Hunt, C., & Elbroch, L. M. (2022).

608   Pumas *Puma concolor* as ecological brokers: a review of their biotic relationships. *Mammal*

609   *Review*, *52*(3), 360-376. https://doi.org/10.1111/mam.12281

610   La Morgia, V., Marucco, F., Aragno, P., Salvatori V., Gervasi V., De Angelis D., Fabbri E.,

611   Caniglia R., Velli E., Avanzinelli E., Boiani M.V., & Genovesi P. (2022). Stima della distribuzione

612   e consistenza del lupo a scala nazionale 2020/2021. Relazione tecnica realizzata nell'ambito della

613   convenzione ISPRA-Ministero della Transizione Ecologica "Attività di monitoraggio nazionale

614   nell'ambito del Piano di Azione del lupo".

615   Lambertucci, S. A., Navarro, J., Sanchez Zapata, J. A., Hobson, K. A., Alarcón, P. A., Wiemeyer,

616   G., ... & Donázar, J. A. (2018). Tracking data and retrospective analyses of diet reveal the

617   consequences of loss of marine subsidies for an obligate scavenger, the Andean condor.

618   *Proceedings of the Royal Society B: Biological Sciences*, 285(1879), 20180550.

619   https://doi.org/10.1098/rspb.2018.0550

620   Lescureux, N., & Linnell, J. D. (2014). Warring brothers: The complex interactions between wolves

621   (*Canis lupus*) and dogs (*Canis familiaris*) in a conservation context. Biological conservation, 171,

622   232-245. https://doi.org/10.1016/j.biocon.2014.01.032

623   Li, Z., & Wang, T. (2022). Competition and coexistence between tigers and leopards in Asia.

624   *Biodiversity Science*, *30*(9), 22271. https://doi.org/10.17520/biods.2022271

625   Lyngdoh, S., Shrotriya, S., Goyal, S. P., Clements, H., Hayward, M. W., & Habib, B. (2014). Prey

626   preferences of the snow leopard (*Panthera uncia*): regional diet specificity holds global significance

627   for conservation. *PloS one*, *9*(2), e88349. https://doi.org/10.1371/journal.pone.0088349

628   Mallon, D., Harris, R. B., & Wegge, P. (2016). Snow leopard prey and diet. In *Snow leopards* (pp.

629   43-55). Academic Press.

630   Mancinelli, S., Boitani, L., & Ciucci, P. (2018). Determinants of home range size and space use

631   patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. *Canadian*

632   *Journal of Zoology*, 96(8), 828-838. https://doi.org/10.1139/cjz-2017-0210

633   Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007).

634   *Resource selection by animals: statistical design and analysis for field studies*. Springer Science &

635   Business Media.

636   Marucco, F., Pilgrim, K. L., Avanzinelli, E., Schwartz, M. K., & Rossi, L. (2022). Wolf dispersal

637   patterns in the Italian Alps and implications for wildlife diseases spreading. *Animals*, 12(10), 1260.

638   https://doi.org/10.3390/ani12101260

639   Mattioli, L., Apollonio, M., Mazzarone, V., & Centofanti, E. (1995). Wolf food habits and wild

640   ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta theriologica*, 40(4), 387-

641   402. https://rcin.org.pl/Content/12376/PDF/BI002_2613_Cz-40-2_Acta-T40-nr31-387-402_o.pdf

642   Mattioli, L., Canu, A., Passilongo, D., Scandura, M., & Apollonio, M. (2018). Estimation of pack

643   density in grey wolf (*Canis lupus*) by applying spatially explicit capture-recapture models to camera

644   trap data supported by genetic monitoring. *Frontiers in zoology*, 15, 1-15.

645   https://doi.org/10.1186/s12983-018-0281-x

646   Mattioli, L., Capitani, C., Gazzola, A., Scandura, M., & Apollonio, M. (2011). Prey selection and

647   dietary response by wolves in a high-density multi-species ungulate community. *European Journal*

648   *of Wildlife Research*, 57, 909-922. https://doi.org/10.1007/s10344-011-0503-4

649   Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., & Milanesi, P. (2011). Changes of wolf

650   (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology*

651   *& Evolution*, 23(3), 195-210. https://doi.org/10.1080/03949370.2011.577814

652   Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: does the wolf

653   prefer wild prey to livestock?. *Journal of applied ecology*, 1561-1571.

654   https://doi.org/10.2307/2404794

655   Miller, S. D., McLellan, B. N., & Derocher, A. E. (2013). Conservation and management of large

656   carnivores in North America. *International journal of environmental studies*, *70*(3), 383-398.

657   https://doi.org/10.1080/00207233.2013.801628

658   Mohammadi, A., Kaboli, M., Sazatornil, V., & López-Bao, J. V. (2019). Anthropogenic food

659   resources sustain wolves in conflict scenarios of Western Iran. *PloS one, 14*(6), e0218345.

660   https://doi.org/10.1371/journal.pone.0218345

661   Morales-González, A., Fernández-Gil, A., Quevedo, M., & Revilla, E. (2022). Patterns and

662   determinants of dispersal in grey wolves (*Canis lupus*). *Biological Reviews, 97*(2), 466-480.

663   https://doi.org/10.1111/brv.12807

664   Mori, E., Benatti, L., Lovari, S., & Ferretti, F. (2017). What does the wild boar mean to the wolf?.

665   *European journal of wildlife research, 63*, 1-5. https://doi.org/10.1007/s10344-016-1060-7

666   Mori, E., Viviano, A., Ferri, M., Ancillotto, L., Grignolio, S., Merli, E., ... & Baratti, M. (2024).

667   Sika deer *Cervus nippon* out of the blue: a cryptic invasion in Italy. Mammalian Biology, 1-6.

668   https://doi.org/10.1007/s42991-023-00395-y

669   Murphy, S. M., Beausoleil, R. A., Stewart, H., & Cox, J. J. (2022). Review of puma density

670   estimates reveals sources of bias and variation, and the need for standardization. *Global Ecology*

671   *and Conservation, 35,* e02109. https://doi.org/10.1016/j.gecco.2022.e02109

672   Musto, C., Cerri, J., Capizzi, D., Fontana, M. C., Rubini, S., Merialdi, G., ... & Garbarino, C.

673   (2024). First evidence of widespread positivity to anticoagulant rodenticides in grey wolves (*Canis*

674   *lupus*). *Science of the Total Environment*, 915, 169990.

675   https://doi.org/10.1016/j.scitotenv.2024.169990

676   Nakagawa, S., Noble, D. W., Senior, A. M., & Lagisz, M. (2017). Meta-evaluation of meta-

677   analysis: ten appraisal questions for biologists. *BMC biology, 15*(1), 1-14.

678   https://doi.org/10.1186/s12915-017-0357-7

679   Newsome, T. M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C. R., Dellinger, J. A., ... &

680   Ripple, W. J. (2016). Food habits of the world's grey wolves. *Mammal Review, 46*(4), 255-269.

681   https://doi.org/10.1111/mam.12067

682 Newsome, T. M., Dellinger, J. A., Pavey, C. R., Ripple, W. J., Shores, C. R., Wirsing, A. J., &

683 Dickman, C. R. (2015). The ecological effects of providing resource subsidies to predators. *Global*

684 *Ecology and Biogeography*, *24*(1), 1-11. https://doi.org/10.1111/geb.12236

685 Nickel, B. A., Suraci, J. P., Nisi, A. C., & Wilmers, C. C. (2021). Energetics and fear of humans

686 constrain the spatial ecology of pumas. *Proceedings of the National Academy of Sciences*, *118*(5),

687 e2004592118. https://doi.org/10.1073/pnas.2004592118

688 Niedziałkowska, M., Hayward, M. W., Borowik, T., Jędrzejewski, W., & Jędrzejewska, B. (2019).

689 A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus arctos* in

690 Eurasia. *Mammal Research*, *64*, 1-9. https://doi.org/10.1007/s13364-018-0396-7

691 Nowak, S., Mysłajek, R. W., Kłosińska, A., & Gabryś, G. (2011). Diet and prey selection of wolves

692 (*Canis lupus*) recolonising Western and Central Poland. *Mammalian Biology*, 76(6), 709-715.

693 https://doi.org/10.1016/j.mambio.2011.06.007

694 O'Brien, S. J., Johnson, W. E., Driscoll, C. A., Dobrynin, P., & Marker, L. (2017). Conservation

695 genetics of the cheetah: lessons learned and new opportunities. *Journal of Heredity*, *108*(6), 671-

696 677. https://doi.org/10.1093/jhered/esx047

697 Palmegiani, I., Gazzola, A., Apollonio, M. (2013). Wolf diet and its impact on the ungulates

698 community in a new recolonized area of Western Alps: Gran Paradiso National Park. *Folia*

699 *Zoologica, 62(1)*, 59-66. https://doi.org/10.25225/fozo.v62.i1.a9.2013

700 Périquet, S., Fritz, H., & Revilla, E. (2015). The Lion King and the Hyaena Queen: large carnivore

701 interactions and coexistence. *Biological reviews*, *90*(4), 1197-1214.

702 https://doi.org/10.1111/brv.12152

703 Peters, D. P. (2010). Accessible ecology: synthesis of the long, deep, and broad. *Trends in ecology*

704 *& evolution*, *25*(10), 592-601. https://doi.org/10.1016/j.tree.2010.07.005

705 Prugh, L. R., & Sivy, K. J. (2020). Enemies with benefits: integrating positive and negative

706 interactions among terrestrial carnivores. *Ecology Letters*, 23(5), 902-918.

707 https://doi.org/10.1111/ele.13489

708   R Core Team (2023). R: A language and environment for statistical computing. R Foundation for

709   Statistical Computing, Vienna, Austria. https://www.R-project.org/

710   Robertson, B., & Price, C. (2024). One point per cluster spatially balanced sampling.

711   *Computational Statistics & Data Analysis*, 191, 107888. https://doi.org/10.1016/j.csda.2023.107888

712   Roffler, G. H., Eriksson, C. E., Allen, J. M., & Levi, T. (2023). Recovery of a marine keystone

713   predator transforms terrestrial predator–prey dynamics. *Proceedings of the National Academy of*

714   *Sciences, 120*(5), e2209037120. https://doi.org/10.1073/pnas.2209037120

715   Rubio-Rocha, Y. G., Gaxiola, S. M., Chávez, C., Ceballos, G., Bojorquez, C., & Diaz, D. (2023).

716   Jaguar (*Panthera onca*) food resource use and its interaction with humans: scoping review.

717   *Veterinaria México OA, 10*. https://doi.org/10.22201/fmvz.24486760e.2023.1107

718   Schepens, G., Pigeon, K., Loosen, A., Forshner, A., & Jacob, A. L. (2023). Synthesis of habitat

719   models for management of wolverine (*Gulo gulo*): Identifying key habitat and snow refugia in the

720   Columbia and Rocky Mountains, Canada. *Global Ecology and Conservation*, e02540.

721   https://doi.org/10.1016/j.gecco.2023.e02540

722   Schertler, A., Rabitsch, W., Moser, D., Wessely, J., & Essl, F. (2020). The potential current

723   distribution of the coypu (*Myocastor coypus*) in Europe and climate change induced shifts in the

724   near future. *NeoBiota*, 58, 129-160. https://doi.org/10.3897/neobiota.58.33118

725   Schmidt, P. A., & Mech, L. D. (1997). Wolf pack size and food acquisition. *The American*

726   *Naturalist, 150*(4), 513-517. https://doi.org/10.1086/286079

727   Shultz, S., Baral, H. S., Charman, S., Cunningham, A. A., Das, D., Ghalsasi, G. R., ... & Prakash,

728   V. (2004). Diclofenac poisoning is widespread in declining vulture populations across the Indian

729   subcontinent. *Proceedings of the Royal Society of London. Series B: Biological Sciences*,

730   271(suppl_6), S458-S460. https://doi.org/10.1098/rsbl.2004.0223

731   Srivathsa, A., Ramachandran, V., Saravanan, P., Sureshbabu, A., Ganguly, D., & Ramakrishnan, U.

732   (2023). Topcats and underdogs: intraguild interactions among three apex carnivores across Asia's

733   forestscapes. *Biological Reviews*. https://doi.org/10.1111/brv.12998

734 Srivathsa, A., Sharma, S., & Oli, M. K. (2020). Every dog has its prey: Range-wide assessment of

735 links between diet patterns, livestock depredation and human interactions for an endangered

736 carnivore. *Science of the Total Environment*, *714*, 136798.

737 https://doi.org/10.1016/j.scitotenv.2020.136798

738 Steenweg, R., Gillingham, M. P., Parker, K. L., & Heard, D. C. (2015). Considering sampling

739 approaches when determining carnivore diets: the importance of where, how, and when scats are

740 collected. *Mammal Research*, 60, 207-216. https://doi.org/10.1007/s13364-015-0222-4

741 Stein, A. B., & Hayssen, V. (2013). *Panthera pardus* (Carnivora: Felidae). *Mammalian Species*,

742 *45*(900), 30-48. https://doi.org/10.1644/900.1

743 Strampelli, P., Campbell, L. A., Henschel, P., Nicholson, S. K., Macdonald, D. W., & Dickman, A.

744 J. (2022). Trends and biases in African large carnivore population assessments: identifying

745 priorities and opportunities from a systematic review of two decades of research. *PeerJ*, *10*, e14354.

746 https://doi.org/10.7717/peerj.14354

747 Stumpf, F., Schneider, M. K., Keller, A., Mayr, A., Rentschler, T., Meuli, R. G., ... & Liebisch, F.

748 (2020). Spatial monitoring of grassland management using multi-temporal satellite imagery.

749 *Ecological Indicators*, 113, 106201. https://doi.org/10.1016/j.ecolind.2020.106201

750 Tatler, J., Prowse, T. A., Roshier, D. A., Allen, B. L., & Cassey, P. (2019). Resource pulses affect

751 prey selection and reduce dietary diversity of dingoes in arid Australia. *Mammal Review*, *49*(3),

752 263-275. https://doi.org/10.1111/mam.12157

753 Torretta, E., Corradini, A., Pedrotti, L., Bani, L., Bisi, F., & Dondina, O. (2022). Hide-and-Seek in

754 a Highly Human-Dominated Landscape: Insights into Movement Patterns and Selection of Resting

755 Sites of Rehabilitated Wolves (*Canis lupus*) in Northern Italy. *Animals*, *13*(1), 46.

756 https://doi.org/10.3390/ani13010046

757 Van Eeden, L. M., Crowther, M. S., Dickman, C. R., Macdonald, D. W., Ripple, W. J., Ritchie, E.

758 G., & Newsome, T. M. (2018). Managing conflict between large carnivores and livestock.

759 *Conservation Biology*, *32*(1), 26-34. https://doi.org/10.1111/cobi.12959

760 Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., ... & Watson, J. E.

761 (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific data*, *3*(1), 1-10.

762 https://doi.org/10.1038/sdata.2016.67

763 Vetter, D., Ruecker, G., & Storch, I. (2013). Meta-analysis: A need for well-defined usage in

764 ecology and conservation biology. *Ecosphere*, *4*(6), 1-24. https://doi.org/10.1890/ES13-00062.1

765 Whittaker, R. J. (2010). Meta-analyses and mega-mistakes: calling time on meta-analysis of the

766 species richness–productivity relationship. *Ecology*, *91*(9), 2522-2533. https://doi.org/10.1890/08-

767 0968.1

768 Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal*

769 *Society open science*, *3*(8), 160252 https://doi.org/10.1098/rsos.160252

770 Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society*

771 *open science*, *4*(7), 170052. https://doi.org/10.1098/rsos.170052

772 Wilson, M. F., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain

773 analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine*

774 *Geodesy*, *30*(1-2), 3-35. https://doi.org/10.1080/01490410701295962

775 Zanni, M., Brogi, R., Merli, E., & Apollonio, M. (2023). The wolf and the city: insights on wolves

776 conservation in the anthropocene. *Animal Conservation*. https://doi.org/10.1111/acv.12858

777 Zimen, E. & Boitani, L. (1975). Number and distribution of wolves in Italy. Z. Säugetierkunde 40:

778 102-112.   https://pascal-francis.inist.fr/vibad/index.php?

779 action=getRecordDetail&idt=PASCAL7536013162

780 Zlatanova, D., Ahmed, A., Valasseva, A., & Genov, P. (2014). Adaptive diet strategy of the wolf

781 (*Canis lupus*) in Europe: a review. *Acta zoologica bulgarica*, *66*(4), 439-452.

782

783

Supplementary material

The supplementary information, as well as the reproducible data and software code, are available at:

https://osf.io/76cx4/

Ethical approval

Not applicable

CRediT authorship contribution statement

Conceptualization: JC, RB, CM, EB **Methodology:** JC, RB, CM, EB **Software:** JC **Validation:** JC, RB, CM, EB, GV, AB, MD, MS, MA **Formal analysis:** JC **Investigation:** JC, RB, CM, EB,

810   GV, AB **Resources:** GV, AB, MD, MS, MA **Data curation:** CM, EB, GV, AB **Writing - original**

811   **draft:** JC, RB, CM, EB **Writing- review and editing:** JC, RB, CM, EB, GV, AB, MD, MS, MA

812   **Visualization:** JC, RB, CM, EB **Supervision:** MD, MS, MA **Project administration:** MD, MA

813   **Funding Acquisition:** GV, AB, MD, MS, MA
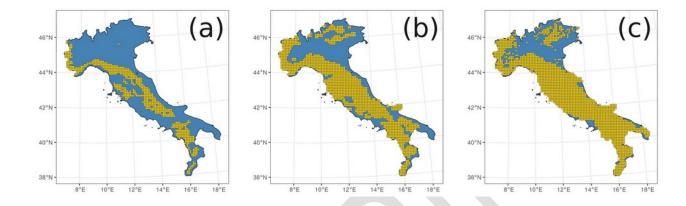
814

815

Figures

822 Fig. 1. Areas of the Italian peninsula where wolves were present in 2007-2013 (a), 2014-2019 (b)

823 and 2019-2023 (c). For data sources please see the Methods section.

824

825

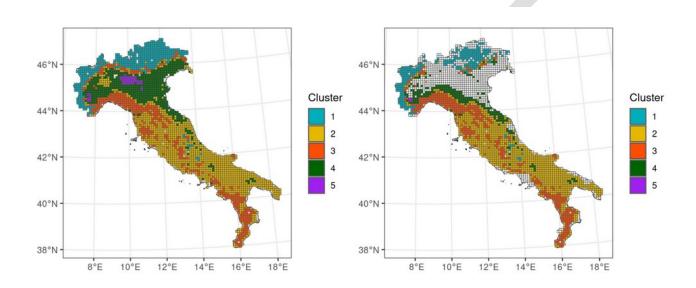826

827

828

829

830

831

Fig. 2. Spatial distribution of the five clusters obtained through CLARA. Left: distribution of clusters in the Italian peninsula. Right: distribution of clusters in the maximum distribution range of wolves in the Italian peninsula. White cells represent areas outside of the range or with missing data, for which cluster analysis was not possible.
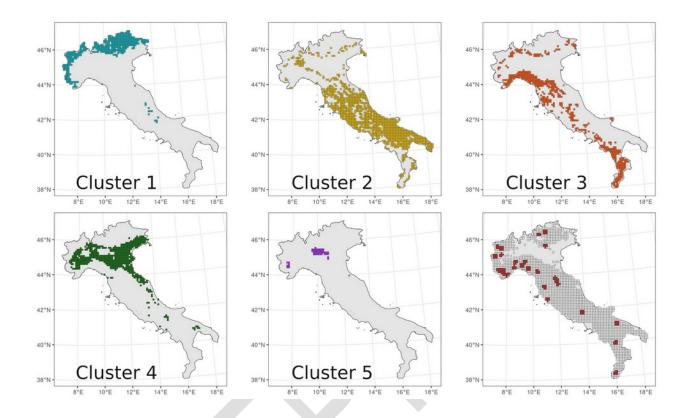
837

838

839

840

841

Fig. 3. Spatial distribution in Italy of the five clusters. In the lower-right corner of the figure we also represented the spatial distribution of cells interested by dietary studies (in dark) overlayed on the maximum distribution range of the wolf.
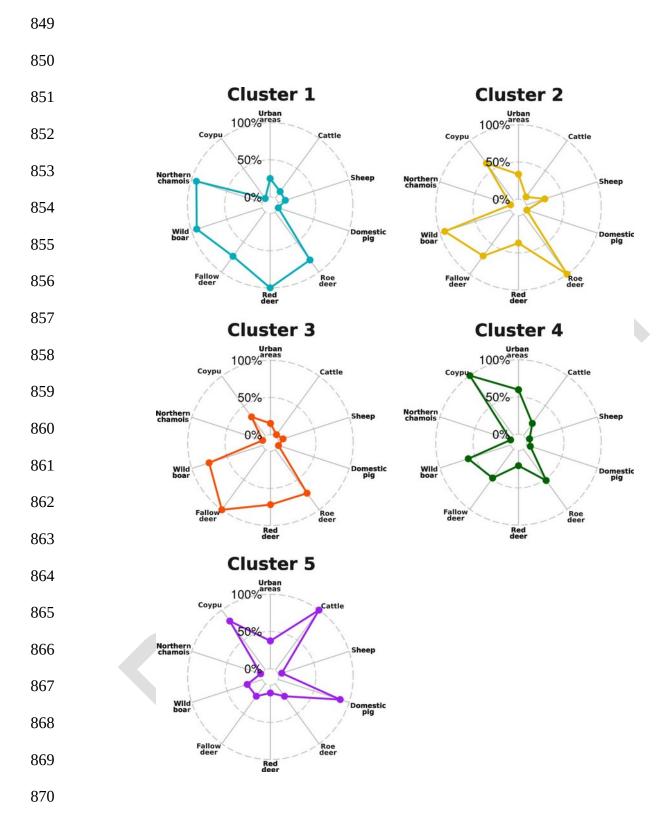
846

847

848

Fig. 4. Median values of environmental covariates in each cluster. Values have been rescaled from 0 to 100, to better interpret them.

874 **Tables**

875

876 Table 1. Overview of main systematic reviews and meta-analyses about the diet of large carnivores.

Species	Systematic reviews and meta-analyses about its diet
African wild dog (*Lycaon pictus*)	Hayward et al., (2006)
American black bear (*Ursus americanus*)	Falconi et al. (2022)
Andean black bear (*Tremarctos ornatus*)	Falconi et al. (2022)
Asiatic black bear (*Ursus thibetanus*)	Falconi et al. (2022)
Brown bear (*Ursus arctos*)	Bojarska and Selva (2012); Falconi et al. (2022); Niedziałkowska et al. (2018)
Polar bear (*Ursus maritimus*)	Falconi et al. (2022)
Brown hyaena (*Parahyaena brunnea*)	-
Cheetah (*Acinonyx jubatus*)	Hayward et al. (2006)
Clouded leopard (*Neofelis nebulosa*)	Chiang and Allen (2017)
Dhole (*Cuon alpinus*)	Srivathsa et al. (2020); Srivathsa et al., (2023)
Dingo (*Canis lupus dingo*)	Fleming et al., (2022); Tatler et al., (2019)
Ethiopian wolf (*Canis simensis*)	-
Eurasian lynx (*Lynx lynx*)	Khorozyan and Heurich (2023a,b)
Gray wolf (*Canis lupus*)	Janeiro-Otero et al., 2020; Meriggi et al., 2011; Meriggi and Lovari, 1996; Mori et al., 2017; Newsome et al., 2016; Zlatanova et al., 2014
Jaguar (*Panthera onca*)	Cruz et al. (2022); Hayward et al. (2016); López-González and Miller (2002); Rubio-Rocha et al. (2023)
Leopard (*Panthera pardus*);	Hayward et al. (2006); Franchini and Guerisoli (2023); Srivathsa et al., (2023); Stein and Hayssen (2013)
Lion (*Panthera leo*)	Hayward and Kerley (2006); Périquet et al. (2014)
Puma (*Puma concolor*)	Cruz et al. (2022); Karandikar et al. (2022); La Barge et al. (2022)
Red wolf (*Canis rufus*)	-
Sloth bear (*Melursus ursinus*)	Falconi et al. (2022)
Snow leopard (*Panthera uncia*)	Lyngdoh et al. (2014); Mallon et al. (2016)
Spotted hyena (*Crocuta crocuta*)	Hayward (2006); Périquet et al. (2014)
Striped hyena (*Hyaena hyaena*)	-
Sun bear (*Helarctos malayanus*)	Falconi et al. (2022)
Sunda clouded leopard (*Neofelis diardi*)	-

| Tiger (*Panthera tigris*) | Hayward et al. (2012); Li and Wang (2022); Srivathsa et al., (2023) |
| Wolverine (*Gulo gulo*) | Fisher et al. (2022) |

877   Table 2. Percentage of cells that were interested by dietary studies, in each one of the three periods

878   (2007-2013, 2014-2018 and 2019-2023), between the five different clusters.

879

Cluster	Extent, compared to the maximum potential range of the species	Cells covered by studies (overall period)	Cells covered by studies (2007-2013)	Cells covered by studies (2014-2018)	Cells covered by studies (2019-2023)
1	16.1%	28%	34%	21%	32%
2	40.5%	22%	16%	20%	32%
3	20.0%	43%	50%	58%	15%
4	21.6%	8%	0%	2%	22%
5	1.8%	0%	0%	0%	0%

880

881

–