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1 **Feeding behaviour of red fox and domestic cat populations in suburban areas in**
2 **the south of Paris**

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18 **Abstract (150-250 words)**

19 Among medium-sized carnivores, red foxes (*Vulpes vulpes*) and domestic cats (*Felis*
20 *silvestris catus*) are the most abundant species in human-dominated landscapes
21 worldwide. Both are known to be generalist predators that exploit a wide range of
22 prey groups (e.g., mammals, birds, and invertebrates). Identifying red fox and
23 domestic cat predation pressure on shared prey could shed light on their ecological
24 role in shaping wildlife communities in human-dominated landscapes.

25 Here, we assess the seasonal diet of red foxes and domestic cats in terms of
26 composition, breadth, and overlap. Over two years, we collected their scats across
27 three human-dominated study sites: park ($n = 220$ for foxes and $n = 0$ for cats),
28 agricultural land ($n = 159$ for foxes and $n = 146$ for cats), and managed forest ($n =$
29 169 for foxes and $n = 47$ for cats). We detected similar diet breadth (B) for red foxes
30 and domestic cats (B = 0.32 and B = 0.36, respectively) as well as strong dietary
31 overlap (O = 0.83) between them. Moreover, the diet composition of both predators
32 varied according to the study sites and seasons. Our results confirm the highly
33 flexible trophic behaviour of these carnivores at the study sites, probably as a
34 consequence of prey availability, and also the simultaneity of their predation over
35 the same prey groups. Future studies should simultaneously monitor predator diet as
36 well as predator and prey abundance in human-dominated landscapes to better
37 understand the predatory impact of red foxes and domestic cats.

38 **Keywords**

39 Diet breadth; diet overlap; domestic cat; red fox; human-dominated landscapes

40 **Introduction**

41 By 2050, more than half of the world's population will live in urbanized areas (United
42 Nations 2019). Consequently, understanding the functioning of these ecosystems is
43 necessary in order to preserve both biodiversity and human life quality. Human-
44 dominated landscapes share a set of general biotic and abiotic characteristics such as the
45 alteration of species richness (McKinney 2008), the variation of microclimatic
46 conditions (Santamouris et al. 2001), the availability of new resources such as
47 anthropogenic food refuse (Fleming and Bateman 2018), and the lack or reduced
48 number of large carnivores (Crooks 2002; Iossa et al. 2010; Bateman and Fleming
49 2012). In this context, medium-sized carnivores may be “released” in the absence of
50 top-predators (Crooks and Soulé 1999), thus influencing prey populations through top-
51 down processes, as already demonstrated at continental (Ripple et al. 2013) and local
52 scales (Jiménez et al. 2019).

53 Among medium-sized carnivores, the red fox (*Vulpes vulpes*) is one of the most
54 widespread species (Schipper et al. 2008), while the domestic cat (*Felis silvestris catus*)
55 is one of the most popular pets worldwide. Out of 18.83 million pets in France, 11.4
56 million are cats. Moreover, the generalist trophic behaviour of red foxes and domestic
57 cats makes them successful species in human-dominated landscapes (Bateman and
58 Fleming 2012). Red fox diets in urban areas are mostly characterized by the presence of
59 anthropogenic food refuse (Harris 1981; Doncaster et al. 1990; Contesse et al. 2004;
60 Hegglin et al. 2007; Meckstroth et al. 2007), while in rural areas, they are more
61 diversified with mammals and birds (Goldyn et al. 2003), mammals, invertebrates, and
62 fruits (Ghoshal et al. 2016), or invertebrates and fruits (Dell'Arte et al. 2005) as the
63 principal food categories. Like red foxes, domestic cats living in urban areas consume
64 not only anthropogenic refuse (Eberhard 1954; Jackson 1951) but also mammals and

65 birds (Gordon et al. 2010; Tschanz et al. 2011; Thomas et al. 2012). In rural areas,
66 mammals and birds are among the principal prey categories in domestic cat diet (Kays
67 and Dewan 2004; Brickner-Braun et al. 2007; Flux 2007; Morgan et al. 2009; van
68 Heezik et al. 2010). Little is known, however, about how these predators interact with
69 each other or with their shared prey in human-dominated landscapes. In natural or semi-
70 natural habitats, several studies have assessed the influence of fox presence on cat
71 trophic behaviour (Molsher et al. 2017). Moreover, in other natural habitats there exist
72 some degree of trophic competition between these two predators (Catling 1988; Risbey
73 et al. 1999; Glen et al. 2011)

74 Simultaneous monitoring of red fox and domestic cat diets is needed in order to
75 determine their degree of trophic overlap, better assess their concomitant potential
76 predation pressure, and clarify their trophic role in shaping prey communities. To date,
77 however, only one study (Meckstroth et al. 2007) has carried out the simultaneous
78 monitoring of red fox and domestic cat diets in a human-dominated landscape, but none
79 has investigated their degree of diet overlap. In the present study, we firstly aimed to
80 describe red fox and domestic cat diets in three human-dominated landscapes (urban
81 park, agricultural land, and managed forest) across seasons and then estimate their diet
82 breadth and overlap. We hypothesised that both predators consumed a wide range of
83 prey (e.g., large diet breadth) and shared most of them (e.g., high degree of diet
84 overlap), will confirm their generalist trophic behaviour mainly driven by temporal and
85 local specificities.

86

87 **Materials and methods**

88 *Study sites*

89 Red fox and domestic cat populations were non-invasively monitored by collecting
90 faecal samples (hereafter, scats) at three suburban study sites (Fig. 1). Sceaux urban
91 park (hereafter, park) (48°46'03.17''N, 2°17'47.48''E), located 20 km south of Paris,
92 covers an area of 1.81 km² and comprises three main habitat types: open areas (lawns
93 and meadows), wooded areas (composed of 16% *Fraxinus* sp., 14% *Acer platanoides*,
94 12% *Acer pseudoplatanus*, and 9% *Carpinus*), and French formal gardens
95 (predominately ornamental species) (Hauts-de-Seine Conseil Général 2015). The
96 agricultural area of Saclay (hereafter, agricultural land) (48°42'32.18''N,
97 2°10'33.00''E) is located between the north of the Essonne department and the
98 southeast of the Yvelines department. This fertile agricultural land extending over 27
99 km² has a long agricultural tradition with the primary crops of colza, wheat, and barley.
100 Currently, this area is facing urbanisation pressure due to the development of a
101 university and laboratory cluster (Spaak 2013). Rambouillet forest (hereafter, forest)
102 (48°40'29.84''N, 1°48'27.17''E), located in the south of the Yvelines department, is
103 one of the largest forests in the Île-de-France region. This wooded area of 200 km²,
104 mainly composed of oaks and coniferous (68% and 25%, respectively), covers a
105 territory of 29 municipalities (Ministère de l'agriculture et de la pêche 2015).

106 *Sampling protocol*

107 One month prior to the start of predator scat sampling, all study sites were cleaned by
108 removing old scats. Scat sampling was carried out four times per year in the middle of
109 each season (October/autumn; January/winter; April/spring; July/summer) over two
110 consecutive years (2014-2016) for each of the three study sites. Carnivora scats are
111 cylindrical (i.e., sausage-shaped) with sub-division tapped at one of the extremities
112 (Chame 2003). These characteristics may therefore promote scat misidentifications
113 among mammalian carnivores of similar body size (Reid 2015; Morin et al. 2016). Red

114 fox and domestic cat scats, however, can be differentiated by their morphometry (Bang
115 and Dahlström 1975) and secondarily by their place of deposition, dietary content, and
116 odour. Red fox scats (8-10 cm length and 2 cm width) are larger than those of domestic
117 cats (6-8 cm length and 1-1.5 cm width) (Chame 2003). Moreover, red fox scats are
118 tubular, long, and twisted with pointed ends, whereas domestic cat scats are smoothed
119 and compacted with well-defined segments and only one tapered extremity (Chame
120 2003). Red foxes usually deposit scats in prominent positions along tracks to signal
121 their presence to other individuals, whereas domestic cats tend to bury theirs (Seton
122 1925, Gibbons 2008). Regarding dietary contents, domestic cat scats strictly reflect their
123 carnivorous diet with the additional presence of grass leaves ingested to aid hair
124 elimination and/or Gramineae seeds indirectly ingested with the grass leaves (Chame
125 2003). Fresh red fox scats present a strong “foxy” smell like middle skunk (Gibbons
126 2008). Scats were collected by walking along the same paths in each study site and
127 season. They were individually geolocalised, stored in separate plastic bags, and frozen
128 (- 20°C) until analysis. In this study, we aimed to detect the heterogeneity of predator
129 diet in the main suburban habitats and across seasons. Thus, though informative, within-
130 habitat site replications were not assessed; indeed, this was not possible in the park and
131 agricultural land due to their limited areas. Because of the low number of domestic cat
132 scats collected in the forest and park, we asked volunteer owners to collect the scats of
133 their own vagrant cats during each study period. Four owners from each study site
134 (forest and park) with one to three cats in their house collaborated with us.
135 Due to the small number of red fox and domestic cat scats containing prey remains in
136 some seasons and years, we decided to pool samples by season (i.e., without
137 considering the year). Only seasons with at least 10 scats with prey remains per predator
138 species were included in the following analyses (Table S1). Despite the collaboration of

139 cat owners, many of the collected scats did not contain any prey remains. As a result,
140 we did not have sufficient numbers of cat scats from the park for all seasons or from the
141 forest in spring to include them in the analyses (Table S1).

142 *Laboratory analyses*

143 Scats were analysed macroscopically and microscopically. Macroscopic analysis was
144 performed by washing the scats individually under a stream of water in a 2 µm sieve.
145 We excluded scats without prey remains (i.e., feathers, hairs, bones, seeds). Prey
146 remains were identified under a binocular to the finest taxonomic level possible using
147 the bone reference collections from the National Museum of Natural History in Paris for
148 mammals and birds, and identification keys for invertebrates and fruits before validating
149 our identifications with specialists of the targeted groups. Indigestible prey remains
150 (e.g., hair, teeth, bones, skin, scales, feathers, exoskeletons, seeds from fleshy fruits)
151 were then classified into 16 main food categories for a more accurate diet comparison:
152 Microtidae (including *Myodes glareolus*, *Microtus agrestis*, and *Microtus arvalis*),
153 Muridae (including *Apodemus sylvaticus*, *Mus musculus*, *Rattus* sp., *Rattus norvegicus*,
154 and *Rattus rattus*), Soricidae (including *Sorex coronatus*, *Crocidura leucodon*, and
155 *Crocidura russula*), Leporidae (including *Oryctolagus cuniculus* and *Lepus europaeus*),
156 small birds (~ size of Passeroidea), large-medium birds (~ size of Corvoidea),
157 Coleoptera, Hymenoptera, Dermaptera, Orthoptera, Heteroptera, Lepidoptera,
158 Arachnida, earthworms, small fruits (*Prunus cerasus*, *P. prunus*, and *Rubus ulmifolius*),
159 and large fruits (*Malus* sp. and *Pyrus* sp.). We also reported the frequency of nonorganic
160 (e.g., plastic, foil paper) anthropogenic refuse (hereafter, refuse). Coprophagous,
161 recycling, and ticks were excluded from the invertebrate prey.

162 Microscopic analysis was carried out by subsampling ~ 2.5 mg of each homogenised
163 predator scat on microscope slides to quantify earthworm consumption based on chaetae
164 counts (Reynolds and Aebischer 1991).

165 *Data analyses*

166 For each scat, we firstly determined the minimum number of consumed prey individuals
167 in each scat ($prey_{MNI}$) for the main food categories (i.e., excluding refuse). For birds,
168 mammals, and terrestrial arthropods, we counted the number of identical prey fragments
169 contained in each predator scat. For fleshy fruits, $prey_{MNI}$ per predator scat was
170 calculated based on the mean number of seeds (MNS) per fruit collected at the study
171 sites: *Rubus ulmifolius* (n=150, MNS = 52.64); *Prunus prunus* (n=39, MNS = 1); *P.*
172 *cerasus* (n=30, MNS = 1), *Malus* sp. (n=73, MNS = 4.49), and *Pyrus* sp. (n=71, MNS =
173 4.72). For earthworms, we collected the most abundant species (*Aporrectodea*
174 *caliginosa*, *A. giardi*, *Allolobophora icterica*, and *Octolasion cyaneum*) from our study
175 sites to measure and calculate their mean fresh weights (g), length (cm), number of
176 segments per individual, and number of chaetae per segment. $prey_{MNI}$ for earthworms
177 per scat was obtained as follows:

$$178 \quad (i) \text{ no. chaetae in scat} = \frac{\text{no. chaetae} \times \text{total scat weight (dry)}}{\text{weight of analysed sample (0.0025 gr)}}$$

179

$$180 \quad (ii) \text{ no. segments} = \frac{\text{no. chaetae in scat}}{\text{mean no. chaeta per segment}}$$

181

$$182 \quad (iii) \text{ prey}_{MNI} = \frac{\text{no. of segments}}{\text{no. of segments in one earthworm}}$$

183 To quantify the ingested prey biomass contained in each scat ($prey_{IBS}$), we firstly
184 calculated the total ingested biomass (TIB) by multiplying the $prey_{MNI}$ of each prey by
185 its mean mass (MM). The biomass of small mammals (MM= 57.32 g) and birds (MM=

186 302.54 g) was calculated using weight data extracted from the Amniote trait database
187 (Myhrvold et al. 2015). We estimated invertebrate MM by weighing field-collected
188 individuals from the orders most commonly consumed by the studied predators:
189 Coleoptera (n=156, MM= 0.29 g), Hymenoptera (n=26, MM= 0.01 g), Dermaptera
190 (n=20, MM= 0.03 g), Orthoptera (n=71, MM= 0.10 g), Heteroptera (n=76, MM= 0.02
191 g), and Lepidoptera (n=92, MM= 0.02 g), as well as the class Arachnida (n=87, MM=
192 0.01 g). Fruit MM was obtained by collecting and weighing the following fruits from
193 the study sites: *Rubus ulmifolius* (n=150, MM= 2.19 g), *Prunus prunus* (n=39, MM=
194 15.09 g), *P. cerasus* (n=30, MM= 3.70 g), *Malus* sp. (n=73, mean MM= 90.01 g), and
195 *Pyrus* sp. (n=71, MM= 98.55 g). Since red foxes and domestic cats are known to ingest
196 large body mass prey (e.g., Leporidae, large birds) only partially (Artois 1989; Bonnaud
197 et al. 2007), we estimated the ingested proportion of lagomorphs and large-medium
198 birds by calculating the maximum food intake per scat of each predator. To do so, we
199 selected red fox (n=75) and domestic cat (n=53) scats containing only small mammals
200 (i.e., prey entirely ingested) and multiplied their $prey_{MNI}$ by their MM to obtain a
201 maximum ingested biomass (MIB in g of fresh biomass) for each predator scat. MIB
202 was 244.09 g and 232.40 g for red fox and domestic cat, respectively. We then
203 calculated the ingested biomass of each prey category per scat ($prey_{IBS}$) by using one of
204 the two following formulas. If the TIB did not exceed the MIB, we applied the formula:

205

$$206 \quad (iv) \text{ prey}_{IBS} = \text{small prey}_i \text{ MM} \times \text{small prey}_i \text{ MNI}$$

207

208 If the TIB exceeded the MIB due to the consumption of large prey_j like lagomorph and
209 large-medium birds, for instance, we applied the following formula:

210

211
$$(v) \text{prey}_{IBS} = \frac{MIB - \sum_i^n (\text{small prey}_i \text{ MM} \times \text{small prey}_i \text{ MNI})}{RIB_j}$$

212
 213 Where RIB_j is the relative ingested biomass of each large prey calculated as follows:

214

215
$$(vi) RIB_j = \frac{(\text{large prey}_j \text{ biomass} \times \text{large prey}_j \text{ number})}{\sum_1^n (\text{large prey}_j \text{ biomass} \times \text{large prey}_j \text{ number})}$$

216

217 *Effects of study sites and seasons on predator diet*

218 We chose multivariate generalised linear models (hereafter, GLMs) to detect factors
 219 (i.e., predator, study site, and season) that could affect diet composition, because our
 220 dietary data had a strong mean-variance relationship that was taken into account in these
 221 models (Wang et al. 2016). Firstly, we fitted one global GLM using the following
 222 formula: $\text{diet} \sim \text{predator} + \text{study site} * \text{season}$. Secondly, we fitted one GLM for each
 223 predator species using the following formula: $\text{predator diet} \sim \text{study site} * \text{season}$. We
 224 then ran univariate analysis of variance for each prey category and adjusted the p-value
 225 for multiple testing with a step-down resampling procedure (Wang et al. 2016). We
 226 used 999 bootstrap iterations to sample multivariate GLM residuals. Models were fitted
 227 with the *manyglm* function from the *mvabund* package (Wang et al. 2016). Although we
 228 only discuss the results from the models with prey_{IBS} as the response variable, as it is
 229 the best approximation of the true diet of predators (Klare et al. 2011), we also included
 230 the results from the global model for each of the two diet descriptors (prey_{MNI} and
 231 prey_{MNI}) as response variables (Table S2) and from the model using prey_{MNI} as the
 232 response variable (Table S3).

233 *Predator diet breadths and overlaps*

234 We used `preyMNI` to calculate the degree of trophic specialisation for each studied
235 predator by estimating their diet breadth (B) and degree of diet overlap (O) using the
236 *nichevar* and *nicheoverlap* functions from the *indicspecies* package, respectively
237 (Caceres and Legendre 2009). Diet breadth ranges from 0 to 1, with values close to 0 for
238 specialised populations and values close to 1 for generalists. Diet overlap ranges from 0
239 to 1, with values close to 0 for low diet overlap between predator populations and
240 values close to 1 for high diet overlap.

241 We visually assessed dietary overlap between predators, study sites, and seasons using
242 nonmetric multidimensional scaling (NMDS) plots. This multivariate method is based
243 on a triangular resemblance matrix of Bray-Curtis similarities among all pairs of
244 samples. We used the *metaMDS* function from the *vegan* package (Oksanen et al. 2018)
245 to produce NMDS plots. All statistical analyses were carried out using R Studio version
246 1.1.463. (R Core Team 2019).

247

248 **Results**

249 In total, we collected 1,073 scats, but 332 did not contain any wild prey remains (i.e.,
250 only highly digestible organic matter like industrial food and/or refuse), with 55% of
251 them belonging to red foxes (park: $n = 94$, agricultural land: $n = 24$, managed forest: $n =$
252 65) and 45% to domestic cats (park: $n = 85$, agricultural land: $n = 21$, managed forest: $n =$
253 43) (Table S1). From the remaining 741 scats containing prey remains, 74% belonged
254 to red foxes (park: $n = 220$, agricultural land: $n = 159$, managed forest: $n = 169$) and
255 26% to domestic cats (park: $n = 0$, agricultural land: $n = 146$, managed forest: $n = 47$)
256 (Table S1). Out of these 741 scats, 41 scats contained prey remains that were not
257 attributable to the 16 main prey groups defined above (e.g., scats containing
258 unidentifiable parts of invertebrates, seeds, feathers, or hairs). This resulted in the

259 inclusion of 700 scats in prey_{IBS} and prey_{MNI} models, corresponding to 699 degrees of
260 freedom in general models and 521 and 177 degrees of freedom in red fox ($n = 522$) and
261 domestic cat ($n = 178$) models, respectively.

262 We identified a total of 6,742 prey items. Based on prey_{IBS}, red fox diet was mainly
263 composed of Rodentia (37%) and large-medium birds (28%), and domestic cat diet of
264 Leporidae (41%) and large-medium birds (27%) (Table 1). Based on the prey_{MNI}, red
265 fox diet was mainly composed of earthworms (53%), and domestic cat diet of
266 earthworms (40%) and Microtidae (21%) (Table 1).

267 The composition of both predators' diets (prey_{IBS}) was influenced by predator species,
268 study sites, seasons, and the interaction between study sites and seasons (Table S2a).

269 Predator species affected diet prey_{IBS} in terms of Leporidae, Microtidae, Coleoptera,
270 earthworms, and small fruits. Study site affected both predators' consumption of
271 Leporidae, Microtidae, Muridae, Soricidae, large-medium birds, Coleoptera, and
272 earthworms. Seasons influenced both predators' diets in terms of Coleoptera,
273 earthworms, and small fruits. The interaction between study site and season also
274 affected both predators' diets in terms of Leporidae, large-medium birds, Coleoptera,
275 and small fruits (Table S2a).

276 *Red fox diet*

277 The composition of red fox diet (prey_{IBS}) was influenced by study sites, seasons, and the
278 interaction between study sites and seasons (Table 2a). Study site affected red fox
279 prey_{IBS} in terms of Microtidae, Muridae, large-medium birds, Coleoptera, earthworms,
280 and small fruits. Seasons influenced red fox consumption of Coleoptera, earthworms,
281 and small fruits. The interaction between study site and season also affected red fox
282 prey_{IBS} in terms of large-medium birds, Coleoptera, and small fruits (Table 2a).

283 Based on the ingested prey biomass ($prey_{IBS}$), in the park, red fox diet was mainly
284 composed of large-medium birds (66%), especially in autumn (73%), spring, (99%),
285 and summer (60%) (Table 1). In agricultural land, red fox diet principally comprised
286 large-medium birds (35%), especially in autumn (50%) and summer (37%), followed by
287 Leporidae (28%), mainly in autumn (37%), winter (20%), and summer (30%) (Table 1).
288 In the forest, red fox diet was mainly composed of Leporidae (36%), especially in
289 autumn (98%) and spring (98%), followed by Muridae (29%), principally in winter
290 (53%) (Table 1).

291 Based on the minimum number of ingested individuals ($prey_{MNI}$), in the park, red fox
292 diet was mainly composed of earthworms (61%), particularly in autumn (90%), winter
293 (77%), and spring (87%). In agricultural land, red fox diet principally comprised small
294 fruits (38%), especially in summer (55%), followed by earthworms (33%), mostly in
295 autumn (61%), winter (36%), and spring (64%). In the forest, earthworms were the
296 principal food category in red fox diets (56%), especially in winter (79%) and spring
297 (64%) (Table 1).

298 *Domestic cat diet*

299 Domestic cat diet composition was influenced by the seasons as well as the interaction
300 between study site and season. In particular, seasons had an influence on domestic cat
301 $prey_{IBS}$ in terms of earthworm biomass (Table 2b).

302 Based on the ingested prey biomass ($prey_{IBS}$), in agricultural land, domestic cat diet was
303 mainly composed of Leporidae (57%), especially in autumn (67%), winter (52%), and
304 spring (77%) (Table 1). In the forest, domestic cat diet principally comprised Muridae
305 (43%), particularly in summer (70%), followed by large-medium birds (18%),
306 especially in summer (64%) (Table 1).

307 Based on the minimum number of ingested individuals ($prey_{MNI}$), in agricultural land,
308 domestic cat diet was mainly composed of earthworms (48%), particularly in autumn
309 (60%), winter (64%), and spring (34%), followed by Microtidae (20%), especially in
310 summer (34%) (Table 1). In the forest, domestic cat diet mainly comprised earthworms
311 (22%), particularly in autumn (65%) and winter (47%), followed by Microtidae (22%),
312 especially in summer (52%) (Table 1).

313 *Diet breadth and overlap*

314 According to the results of the diet breadth index, both predators exhibited a narrow diet
315 breadth at all study sites and across seasons ($B < 0.40$), with the diet breadth of each
316 predator being similar (red fox: $B = 0.32$, 95% CI [0.29, 0.34]; domestic cat: $B = 0.36$,
317 95% CI [0.31, 0.39]) across study sites and seasons (Fig. 2).

318 Interestingly, in agricultural land, we found a high degree of diet overlap between red
319 fox and domestic cat populations across all seasons ($O > 0.75$) except summer ($O =$
320 0.33 , 95% CI [0.20, 0.56]) (Table S4). During this season, dissimilarity between red fox
321 and domestic cat diet (i.e., points located far from each other with little or no overlap)
322 was higher compared to the other seasons (Fig. 3a). By contrast, we detected higher
323 variations in the diet overlap between red fox and domestic cat populations in the forest
324 compared to agricultural land, with the highest value found in winter ($O = 0.92$ 95% CI
325 [0.05, 0.99]) and the lowest in summer ($O = 0.25$ 95% CI [0.04, 0.60]) (Table S4). In
326 winter, red fox and domestic cat diet showed the highest similarity (i.e., most points are
327 spatially close to each other or overlapping), while the lowest diet similarity was
328 observed in summer (Fig. 3b). Due to the limited number of collected cat scats in some
329 habitats and seasons, we did not calculate the diet overlap between red fox and domestic
330 cat populations in the forest in spring or in the park for all seasons.

331

332 **Discussion**

333 Results obtained in this study were only based on the analysis of scats containing wild
334 prey remains (i.e., 75% and 56% of red fox and domestic cat scats, respectively). The
335 high proportion of domestic cat scats without any wild prey remains (i.e., containing
336 only highly digestible organic matter like industrial food and/or refuse) is partly due to
337 the high percentage (70%) of scats that were provided by cat owners, meaning that
338 domestic cats were primarily sustained by human-mediated food while having the
339 opportunity to wander and feed on wild prey. Even if the percentage of red fox scats
340 containing only refuse and/or industrial food is lower than that of domestic cat scats,
341 this indicates that red foxes, particularly in suburban areas, are able to feed on human-
342 mediated food. This feeding habit may provide them with some adaptive and/or survival
343 advantages.

344 *Red fox and domestic cat diets*

345 The trophic index based on ingested prey biomass (prey_{IBS}) revealed that large-medium
346 birds and mammals were the prey categories most contributing to red fox and domestic
347 cat food bolus. Invariably, red fox and domestic cat diets were dominated by large prey
348 (i.e., large-medium birds and Leporidae) and/or medium-sized prey (Muridae) across all
349 study sites and seasons. This result suggests that the survival of both predators mainly
350 depends on prey with a large biomass (e.g., medium-large birds, Leporidae), probably
351 because one killed individual represents a large source of metabolizable energy.

352 The trophic index based on the minimum number of ingested individuals (prey_{MNI})
353 revealed that earthworms were the most abundantly consumed prey in red fox diet. This
354 result is in good agreement with other studies once refuse is removed from red fox diet
355 (MacDonald 1980; Harris 1981; Doncaster et al. 1990; Reynolds and Aebischer 1991;
356 Saunders et al. 1993; Soulsbury et al. 2008). In domestic cat diet, earthworms along

357 with Microtidae were the most abundantly consumed prey. While the presence of
358 chaetae in predator scats may be increased by phenomena such as soil contamination
359 and secondary predation (i.e., chaetae would have persisted after two digestions),
360 potentially leading to a slight overestimation of earthworm consumption, the high
361 number of consumed earthworms stresses the importance of this prey type for both red
362 foxes and domestic cats, as it may supply these predators with their protein
363 requirements within human-dominated landscapes. Even if striking, the consumption of
364 earthworms (protein-rich prey) by domestic cats is probably opportunistic and focussed
365 on anecic and/or epigeic earthworms (Lee 1985), which are readily available and easy to
366 catch in agricultural and forest soils. This interesting result should be confirmed (i.e.,
367 earthworm species identification) in future studies using metabarcoding approaches, for
368 example (Bienert et al. 2012; Boyer et al. 2013; Pansu et al. 2015). In general, the
369 macro- and microscopic diet analyses of predator diets would benefit from
370 metabarcoding approaches to verify prey identification, detect and identify digested
371 soft-bodied prey (e.g., insect larvae, egg content), and confirm predator scat
372 identification (Pompanon et al. 2012; Galan et al. 2018).

373 *Specific spatiotemporal diet patterns for red foxes and domestic cats*

374 Red fox populations showed study site specificities in terms of the proportion of
375 ingested biomass for certain prey categories (Microtidae, Muridae, large-medium birds,
376 Coleoptera, earthworms, and small fruits) as well as seasonal dietary shifts for some of
377 these resources (Coleoptera, earthworms, and small fruits) (Tables 1 and 2a).
378 These results are in good agreement with and support the generalist and opportunistic
379 trophic behaviour of red foxes (Sillero et al. 2004). Thanks to this trophic behaviour, red
380 foxes could adapt their diet in contrasting human-dominated landscapes according to the

381 abundance and availability of associated prey communities and fruit resources (e.g.,
382 emergence of Coleoptera, fructification of fleshy fruits) (Díaz-Ruiz et al. 2013).

383 In contrast to red fox diet, domestic cat diet (in terms of ingested prey biomass) was
384 relatively homogeneous across study sites and mainly focussed on mammals (Leporidae
385 and Muridae; Gillies and Fitzgerald 2005 (New Zealand); Kays and Dewan 2004 (US);
386 Krauze-Gryz et al. 2012 (Europe)) and secondarily on large-medium birds, with only
387 the proportion of ingested earthworm biomass changing seasonally (Tables 1 and 2b).

388 This suggests that cats are highly adaptable and efficient hunters, which allows them to
389 survive and reproduce without regard to the type of habitat, thus confirming the
390 opportunistic but strictly carnivore trophic behaviour of domestic cats (Bradshaw et al.
391 1996; Medina et al. 2011). By consequence, the increased number of vagrant domestic
392 cats due to the higher human population density can lead to negative effects on bird,
393 mammal, and reptile population dynamics in many different types of habitats (Woods et
394 al. 2003; Dauphiné and Cooper 2009; Blancher 2013; Loss et al. 2013; Doherty et al.
395 2015). As the opportunistic behaviour of these predators likely depends on resource
396 abundance and availability, which are rarely monitored and quantified, this should be
397 investigated in future studies to detect potential patterns of prey preferences.

398 At all the study sites, both red foxes and domestic cats abundantly consumed
399 earthworms (in prey_{MNI}) in autumn, winter, and spring, probably due to the scarcity of
400 other prey categories during these seasons of relatively low productivity. The use of this
401 alternative high-protein prey may allow red foxes and domestic cats to maintain stable
402 populations all year round within degraded human-dominated landscapes. Interestingly,
403 in agricultural land, domestic cats turned to the consumption of *Microtus agrestis*
404 individuals as observed in other rural areas in Europe (Krauze-Gryz et al. 2012), while
405 red foxes shifted their diet to temporarily abundant small fruits that are rich in

406 carbohydrates, minerals, and vitamins (e.g., *Prunus cerasus*, *P. prunus*, *Rubus*
407 *ulmifolius*) (Table 1). Red fox consumption of fruits has already been described in other
408 studies in Europe (Contesse et al. 2004) and Asia (Dell'Arte et al. 2005; Ghoshal et al.
409 2016). In addition to being an alternative source of nutrient for foxes, these fruits
410 contained seeds that can be efficiently dispersed (Herrera 1989; Matías et al. 2010),
411 leading to the conservation of the vegetation structure of these habitats. Last but not
412 least, the consumption of voles by domestic cats in summer likely corresponds to a peak
413 abundance of this prey, which supports the opportunistic trophic behaviour of cats. As
414 domestic cats are one of the major predators of voles (Lin and Batzli 1995), they could
415 modify the cyclicity of the prey population dynamics (Hansson 1988) and indirectly
416 affect the trophic behaviour of other predators sharing this prey such as red foxes.

417 *Diet breadth and overlap*

418 Although we showed that red foxes and domestic cats are able to exploit a wide
419 spectrum of trophic resources (i.e., mammals, birds, invertebrates, and fruits) within
420 human-dominated landscapes, these predators exhibit quite a narrow diet breadth
421 similarly to those described by other authors in natural habitats (Drygala et al. 2014;
422 Vlasseva et al. 2017; Széles et al. 2018). This result confirms that these predators hunt
423 targeted prey groups with a focus on large birds and mammals.

424 Because foxes and cats had similarly varied diets across habitat types and seasons, we
425 have confidence in the main result of a high dietary overlap despite the lack of within-
426 habitat site replication.

427 These are the first results regarding the degree of diet overlap between red foxes and
428 domestic cats within human-dominated landscapes, which are in good agreement with
429 those found in natural habitats (Paltridge 2002; Woinarski et al. 2017). In our study, in
430 summer, red fox and domestic cat diets only marginally overlapped, suggesting that they

431 can hunt a wider prey spectrum to reduce their degree of trophic overlap through niche
432 partitioning. On the contrary, diet overlaps between red foxes and domestic cats were
433 particularly high during the less productive seasons (i.e., autumn, winter, and spring)
434 when they have to share scarcer main and alternative prey (i.e., mammals, birds, and
435 earthworms). This indicates that competition between red foxes and domestic cats may
436 occur, particularly if these predators are in high abundance in city centres (Šálek et al.
437 2015; Flockhart et al. 2016) and probably more broadly in human-dominated areas.
438 However, competition for food between species is eased by their generalist behaviour.
439 In addition, these high seasonal diet overlaps between red foxes and domestic cats may
440 exacerbate their predation pressure over shared prey populations and can lead to
441 potential negative effects on shared prey population dynamics. To quantify predation
442 impacts on prey population dynamics, future studies should simultaneously monitor
443 predator diets as well as prey and predator availabilities through space and time.

444

445 **Author's contributions**

446 IC collected and analysed the data and led the writing of the manuscript. DZL
447 contributed to performing the diet descriptors. EB conceived the ideas and designed the
448 methodology. All authors contributed to the writing and gave their final approval for
449 publication.

450

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