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

Irene Castañeda, Diane Zarzoso-Lacoste, Elsa Bonnaud

1   **Feeding behaviour of red fox and domestic cat populations in suburban areas in**

2   **the south of Paris**

3   Irene Castañeda[1,2], Diane Zarzoso-Lacoste[2,3], Elsa Bonnaud[2]

4   [1]Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Sorbonne

5   Universités, MNHN, CNRS, UPMC, 43 rue Buffon, CP51, 75005, Paris, France.

6   [2]Ecologie Systématique Evolution, Univ. Paris-Sud, CNRS, AgroParisTech, Université

7   Paris-Saclay, 91400, Orsay, France

8   [3]Unité "Ecologie et Dynamique des Systèmes Anthropisés" (UMR7058 CNRS),

9   Université de Picardie Jules Verne, 1 rue des Louvels, 80037 Amiens Cedex 1, France

10

11   Corresponding author:

12   Irene Castañeda

13   Ecologie, Systématique et Evolution, UMR CNRS 8079, Université Paris-Sud, F-91405

14   Orsay Cedex, France

15   Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Sorbonne

16   Universités, MNHN, CNRS, UPMC, 43 rue Buffon, CP51, 75005, Paris, France

17   irene.castanedagonz@gmail.com

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.

Introduction

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

Among medium-sized carnivores, the red fox (*Vulpes vulpes*) is one of the most widespread species (Schipper et al. 2008), while the domestic cat (*Felis silvestris catus*) is one of the most popular pets worldwide. Out of 18.83 million pets in France, 11.4 million are cats. Moreover, the generalist trophic behaviour of red foxes and domestic cats makes them successful species in human-dominated landscapes (Bateman and Fleming 2012). Red fox diets in urban areas are mostly characterized by the presence of anthropogenic food refuse (Harris 1981; Doncaster et al. 1990; Contesse et al. 2004; Hegglin et al. 2007; Meckstroth et al. 2007), while in rural areas, they are more diversified with mammals and birds (Goldyn et al. 2003), mammals, invertebrates, and fruits (Ghoshal et al. 2016), or invertebrates and fruits (Dell'Arte et al. 2005) as the principal food categories. Like red foxes, domestic cats living in urban areas consume 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 km^2 and comprises three main habitat types: open areas (lawns

93   and meadows), wooded areas (composed of 16% *Fraxinus* sp., 14% *Acer platanoïde*,

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   km^2 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   (- 20ºC) 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 *Octolasium 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
$$(i) \; no. \, chaetae \; in \; scat = \frac{no. \, chaetae \; \times \; total \; scat \; weight \; (dry)}{weigth \; of \; analysed \; sample \; (0.0025 \; gr)}$$

179

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

181

182
$$(iii) \, prey_{MNI} = \frac{no. \, of \; segments}{no. \, of \; segments \; in \; one \; earthworm}$$

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 $$(iv)\ prey_{IBS} =\ small\ prey_i\ MM\ \times small\ prey_i\ MNI$$

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 $$(v)\ prey_{IBS} = \frac{MIB - \sum_{i}^{n}(small\ prey_i\ MM\ \times\ small\ prey_i\ MNI)}{RIB_j}$$

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

214

215 $$(vi)\ RIB_j = \frac{(large\ prey_j\ biomass\ \times\ large\ prey_j\ number)}{\sum_{1}^{n}(large\ prey_j\ biomass\ \times\ large\ prey_j\ number)}$$

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: diet ~ predator + study site * season. Secondly, we fitted one GLM for each

223 predator species using the following formula: predator diet ~ study site * 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 prey$_{MNI}$ 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

Discussion

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

Red fox and domestic cat diets

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

The trophic index based on the minimum number of ingested individuals (prey$_{MNI}$)
revealed that earthworms were the most abundantly consumed prey in red fox diet. This
result is in good agreement with other studies once refuse is removed from red fox diet
(MacDonald 1980; Harris 1981; Doncaster et al. 1990; Reynolds and Aebischer 1991;
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

455   kindly reviewed this manuscript. We also thank all the students who participated in the

456   field and laboratory work.

457 **References**

458 Bang P, Dahlström P (1975) Huellas y Señales de los Animales de Europa, Omega,

459   Barcelona.

460 Bateman PW, Fleming PA (2012) Big city life: Carnivores in urban environments. J

461   Zool 287:1–23. doi: 10.1111/j.1469-7998.2011.00887.x

462 Bienert F, De Danieli S, Miquel C, et al (2012) Tracking earthworm communities from

463   soil DNA. Mol Ecol 21:2017–2030. doi: 10.1111/j.1365-294X.2011.05407.x

464 Blancher P (2013) Estimated number of birds killed by house cats (Felis catus) in

465   Canada. Avian Conserv Ecol 8:3. doi: 10.5751/ACE-00557-080203

466 Bonnaud E, Bourgeois K, Vidal E, et al (2007) Feeding Ecology of a Feral Cat

467   Population on a Small Mediterranean Island. J Mammal 88:1074–1081. doi:

468   10.1644/06-MAMM-A-031R2.1

469 Boyer S, Wratten SD, Holyoake A, et al (2013) Using Next-Generation Sequencing to

470   Analyse the Diet of a Highly Endangered Land Snail (Powelliphanta augusta)

471   Feeding on Endemic Earthworms. PLoS One 8:1–8. doi:

472   10.1371/journal.pone.0075962

473 Bradshaw JWS, Goodwin D, Legrand-Defrétin V, Nott HMR (1996) Food selection by

474   the domestic cat, an obligate carnivore. Comp Biochem Physiol - A Physiol

475   114:205–209. doi: 10.1016/0300-9629(95)02133-7

476 Brickner-Braun I, Geffen E, Yom-Tov Y (2007) The domestic cat as a predator of

477   Israeli wildlife. Isr J Ecol Evol 53:129–142. doi: 10.1560/IJEE.53.2.129

478 Caceres M De, Legendre P (2009) Associations between species and groups of sites:

479   indices and statistical inference. Ecology 90:3566–3574. doi: 10.1890/08-1823.1

480 Catling PC (1988) Similarities and contrasts in the diets of foxes, Vulpes vulpes, and

481   Cats, Felis catus, relative to fluctuating prey populations and drought. Aust Wildl

482   Res 15:307–17

483   Contesse P, Hegglin D, Gloor S, et al (2004) The diet of urban foxes (Vulpes vulpes)

484   and the availability of anthropogenic food in the city of Zurich, Switzerland.

485   Mamm Biol 69:81–95. doi: 10.1078/1616-5047-00123

486   Crooks K, Soulé M (1999) Mesopredator release and avifaunal extinctions in a

487   fragmented system. Nature 400:563–566. doi: 10.1038/23028

488   Crooks KR (2002) Relative Sensitivites of Mammalian Carnivores to Habitat

489   Fragmentation. Conserv Biol 16:488–502. doi: 10.1046/j.1523-1739.2002.00386.x

490   Dauphiné N, Cooper RJ (2009) Impacts of free-ranging domestic cats (Felis catus) on

491   birds in the United States: a review of recent research with conservation and

492   management recommendations. Proc Fourth Int Partners Flight Conf Tundra to

493   Trop 205–219

494   Dell'Arte GL, Leonardi G, Dell'Arte GL, et al (2005) Effects of habitat composition on

495   the use of resources by the red fox in a semi arid environment of North Africa.

496   Acta Oecologica 28:77–85. doi: 10.1016/j.actao.2004.12.003

497   Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, et al (2013) Biogeographical

498   patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the

499   Iberian Peninsula. Mamm Rev 43:59–70. doi: 10.1111/j.1365-2907.2011.00206.x

500   Doherty TS, Davis RA, van Etten EJB, et al (2015) A continental-scale analysis of feral

501   cat diet in Australia. J Biogeogr 42:964–975. doi: 10.1111/jbi.12469

502   Doncaster CP, Dickman CR, Macdonald DW (1990) Feeding ecology of red foxes in

503   the city of Oxford, England. J Mammal 71:188–194. doi: 10.2307/1382166

504   Drygala F, Werner U, Zoller H (2014) Diet composition of the invasive raccoon dog

505   (Nyctereutes procyonoides) and the native red fox (Vulpes vulpes) in north-east

506   Germany. Hystrix 24:190–194. doi: 10.4404/hystrix-24.2-8867

507   Fleming PA, Bateman PW (2018) Novel predation opportunities in anthropogenic

508   landscapes. Anim Behav 138:145–155. doi: 10.1016/j.anbehav.2018.02.011

509   Flockhart DTT, Norris DR, Coe JB (2016) Predicting free-roaming cat population

510   densities in urban areas. Anim Conserv 19:472–483. doi: 10.1111/acv.12264

511   Flux JEC (2007) Seventeen years of predation by one suburban cat in New Zealand.

512   New Zeal J Zool 34:289–296. doi: 10.1080/03014220709510087

513   Galan M, Pons J-B, Tournayre O, et al (2018) Metabarcoding for the parallel

514   identification of several hundred predators and their preys: application to bat

515   species diet analysis. Mol Ecol Resour 18:474–489. doi:

516   10.1017/CBO9781107415324.004

517   Ghoshal A, Bhatnagar YV, Mishra C, Suryawanshi K (2016) Response of the red fox to

518   expansion of human habitation in the Trans-Himalayan mountains. Eur J Wildl Res

519   62:131–136. doi: 10.1007/s10344-015-0967-8

520   Glen AS, Pennay M, Dickman CR, et al (2011) Diets of sympatric native and

521   introduced carnivores in the Barrington Tops, eastern Australia. Austral Ecol

522   36:290–296. doi: 10.1111/j.1442-9993.2010.02149.x

523   Goldyn B, Hromada M, Surmacki A, Tryjanowski P (2003) Habitat use and diet of red

524   fox Vulpes vulpes in an agricultural landscape in Poland. Z jagdwiss 49:191–200

525   Gordon JK, Matthaei C, Van Heezik Y (2010) Belled collars reduce catch of domestic

526   cats in New Zealand by half. Wildl Res 37:372–378. doi: 10.1071/WR09127

527   Hansson L (1988) The domestic cat as a possible modifier of vole dynamics. Mammalia

528   52:159–164. doi: 10.1515/mamm.1988.52.2.159

529   Harris S (1981) The food of suburban foxes (Vulpes vulpes), with species reference to

530   London. Mamm Rev 11:151–168

531   Hegglin D, Bontadina F, Contesse P, et al (2007) Plasticity of predation behaviour as a

532   putative driving force for parasite life-cycle dynamics: The case of urban foxes and

533   Echinococcus multilocularis tapeworm. Funct Ecol 21:552–560. doi:

534   10.1111/j.1365-2435.2007.01257.x

535   Herrera CM (1989) Frugivory and Seed Dispersal by Carnivorous Mammals, and

536   Associated Fruit Characteristics, in Undisturbed Mediterranean Habitats. Oikos

537   55:250. doi: 10.2307/3565429

538   Jackson WB (1951) Food habits of Baltimore, Maryland, cats in relation to rat

539   populations. J Mammal 82:458–461

540   Jiménez J, Nuñez-Arjona JC, Mougeot F, et al (2019) Restoring apex predators can

541   reduce mesopredator abundances. Biol Conserv 238:108234. doi:

542   10.1016/j.biocon.2019.108234

543   Kays RW, Dewan AA (2004) Ecological impact of inside/outside house cats around a

544   suburban nature preserve. Anim Conserv 7:1–11. doi:

545   10.1017/S1367943004001489

546   Klare U, Kamler HF, MacDonald DW (2011) A comparison and critique of different

547   scat-analysis. Mamm Rev 41:294–312. doi: 10.1111/j.1365-2907.2011.00183.x

548   Krauze-Gryz D, Gryz J, Goszczyński J (2012) Predation by domestic cats in rural areas

549   of central Poland: An assessment based on two methods. J Zool 288:260–266. doi:

550   10.1111/j.1469-7998.2012.00950.x

551   Lin YK, Batzli GO (1995) Predation on Voles: An Experimental Approach. J Mammal

552   76:1003–1012

553   Loss SR, Will T, Marra PP (2013) The impact of free-ranging domestic cats on wildlife

554   of the United States. Nat Commun 4:1396. doi: 10.1038/ncomms2380

555   MacDonald DW (1980) The Red Fox, Vulpes vulpes, as a predator upon earthworms,

556   Lumbricus terrestris. Z Tierpsychol 52:171–200

557   Matías L, Zamora R, Mendoza I, Hódar JA (2010) Seed Dispersal Patterns by Large

558   Frugivorous Mammals in a Degraded Mosaic Landscape. Restor Ecol 18:619–627.

559   doi: 10.1111/j.1526-100X.2008.00475.x

560   McKinney ML (2008) Effects of urbanization on species richness: A review of plants

561   and animals. Urban Ecosyst 11:161–176. doi: 10.1007/s11252-007-0045-4

562   Meckstroth AM, Miles AK, Chandra S (2007) Diets of Introduced Predators Using

563   Stable Isotopes and Stomach Contents. J Wildl Manage 71:2387. doi:

564   10.2193/2005-527

565   Medina FM, Bonnaud E, Vidal E, et al (2011) A global review of the impacts of

566   invasive cats on island endangered vertebrates. Glob Chang Biol 17:3403–3510.

567   doi: 10.1111/j.1365-2486.2011.02464.x

568   Molsher R, Newsome AE, Newsome TM, Dickman CR (2017) Mesopredator

569   management: Effects of red fox control on the abundance, diet and use of space by

570   feral cats. PLoS One 12:1–15. doi: 10.1371/journal.pone.0168460

571   Morgan SA., Hansen CM, Ross JG, et al (2009) Urban cat (Felis catus) movement and

572   predation activity associated with a wetland reserve in New Zealand. Wildl Res

573   36:574–580. doi: 10.1071/WR09023

574   Myhrvold NP, Baldridge E, Chan B, et al (2015) An amniote life-history database to

575   perform comparative analyses with birds, mammals, and reptiles. Ecology

576   96:3109–000. doi: 10.1890/15-0846R.1

577   Oksanen AJ, Blanchet FG, Kindt R, et al (2018) Package ' vegan '

578   Paltridge R (2002) The diets of cats, foxes and dingoes in relation to prey availability in

579   the Tanami Desert, Northern Territory. Wildl Res 29:389–403. doi:

580   10.1071/WR00010

581   Pansu J, De Danieli S, Puissant J, et al (2015) Landscape-scale distribution patterns of

582   earthworms inferred from soil DNA. Soil Biol Biochem 83:100–105. doi:

583   10.1016/j.soilbio.2015.01.004

584 Pompanon F, Deagle BE, Symondson WOC, et al (2012) Who is eating what: Diet

585   assessment using next generation sequencing. Mol Ecol 21:1931–1950. doi:

586   10.1111/j.1365-294X.2011.05403.x

587 Reynolds JC, Aebischer NJ (1991a) Comparison and Quantification of Carnivore Diet

588   by Fecal Analysis - A Critique, with Recommendations, Based on A Study of the

589   Fox Vulpes-Vulpes. Mamm Rev 21:97–122. doi: 10.1111/j.1365-

590   2907.1991.tb00113.x

591 Reynolds JC, Aebischer NJ (1991b) Comparison and quantification of carnivore diet by

592   faecal analysis: a critique, with recommendations, based on a study of the Fox

593   VUlpes vulpes. Mamm Rev 21:97–122

594 Ripple WJ, Wirsing AJ, Wilmers CC, Letnic M (2013) Widespread mesopredator

595   effects after wolf extirpation. Biol Conserv 160:70–79. doi:

596   10.1016/j.biocon.2012.12.033

597 Risbey DA, Calver MC, Short J (1999) The impact of cats and foxes on the small

598   vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential

599   impact using diet analysis. Wildl Res 26:621–630

600 Šálek M, Drahníková L, Tkadlec E (2015) Changes in home range sizes and population

601   densities of carnivore species along the natural to urban habitat gradient. Mamm

602   Rev 45:1–14. doi: 10.1111/mam.12027

603 Santamouris M, Papanikolaou N, Livada I, et al (2001) On the impact of urban climate

604   on the energy consumption of buildings. Sol Energy 70:201–216. doi:

605   10.1016/S0038-092X(00)00095-5

606 Saunders G, White PCL, Harris S, Rayner JMV (1993) Urban foxes (Vulpes vulpes):

607   food acquisition, time and energy budgeting of a generalized predator. Symp zool

608   Soc L 65:215–234

609   Schipper J, Chanson JS, Chiozza F, et al (2008) The status of the world's land and

610   marine mammals: diversity, threat, and knowledge. Science (80-) 322:225–230.

611   doi: 10.1126/science.1165115

612   Seton ET (1925) On the Study of Scatology. J Mammal 36:47–49. doi:

613   10.1644/870.1.Key

614   Sillero C, Macdonald D, Hoffmann M (2004) Canids : Foxes, Wolves, Jackals and

615   Dogs. Status asurvey and Conservation Action Plan

616   Soulsbury CD, Iossa G, Baker PJ, Harris S (2008) Environmental variation at the onset

617   of independent foraging affects full-grown body mass in the red fox. 2411–2418.

618   doi: 10.1098/rspb.2008.0705

619   Széles GL, Purger JJ, Molnár T, Lanszki J (2018) Comparative analysis of the diet of

620   feral and house cats and wildcat in Europe. Mammal Res 63:43–53. doi:

621   10.1007/s13364-017-0341-1

622   Thomas RL, Fellowes MDE, Baker PJ (2012) Spatio-Temporal Variation in Predation

623   by Urban Domestic Cats (Felis catus) and the Acceptability of Possible

624   Management Actions in the UK. 7:20–23. doi: 10.1371/journal.pone.0049369

625   Tschanz B, Hegglin D, Gloor S, Bontadina F (2011) Hunters and non-hunters: Skewed

626   predation rate by domestic cats in a rural village. Eur J Wildl Res 57:597–602. doi:

627   10.1007/s10344-010-0470-1

628   United Naions, Department of Economic and Social Affairs PD (2019) World

629   Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420)

630   van Heezik Y, Smyth A, Adams A, Gordon J (2010) Do domestic cats impose an

631   unsustainable harvest on urban bird populations? Biol Conserv 143:121–130. doi:

632   10.1016/j.biocon.2009.09.013

633   Vlasseva A, Chassovnikarova T, Atanassov N (2017) Autumn-winter diet and food

634   niche overlap between red fox (Vulpes vulpes L., 1758) and golden Jackal (Canis

635   aureus L., 1758) in two Regions in Bulgaria. Acta Zool Bulg 69:217–220

636   Wang Y, Naumann U, Eddelbuettel D, et al (2016) Statistical methods for analysing

637   multivariate abundance data. Package 'mvabund'. R Proj. Stat. Comput. Vienna,

638   Austria

639   Woinarski JCZ, South SL, Drummond P, et al (2017) The diet of the feral cat (Felis

640   catus), red fox (Vulpes vulpes) and dog (Canis familiaris) over a three-year period

641   at Witchelina Reserve, in arid South Australia. Aust Mammal 40:204–213. doi:

642   10.1071/AM17033

643   Woods M, Mcdonald RA, Phen STE, et al (2003) Predation of wildlife by domestic cats

644   Felis catus in Great Britain. Mamm Rev 33:174–188. doi: DOI 10.1046/j.1365-

645   2907.2003.00017.x

646