Title: Cardiopulmonary nematode infections in wild canids: does the key lie on host-prey-parasite evolution?

Francisco José Martínez-Rondán[a], María Rocío Ruiz de Ybáñez[a], Ana María López-Beceiro[b], Luis Eusebio Fidalgo[b], Eduardo Berriatua[a], Liron Lahat[a], Irene Sacristán[c], Álvaro Oleaga[d], Carlos Martínez-Carrasco[a,*]

[a] Department of Animal Health, Regional Campus of International Excellence "Campus Mare Nostrum", University of Murcia, Murcia, Spain.

[b] Department of Anatomy, Animal Production and Clinical Veterinary Sciences. University of Santiago de Compostela, Lugo, Spain.

[c] PhD Program in Conservation Medicine, Facultad de Ciencias de la Vida, Universidad Andres Bello, República 252, Santiago, Chile.

[d] SERPA, Sociedad de Servicios del Principado de Asturias S.A., 33203 Gijón, Asturias, Spain.

* Corresponding author: E-mail address: cmcpleit@um.es (Carlos Martínez-Carrasco)

E-mail address: Francisco José Martínez-Rondán (fjmr_aguilas@hotmail.com), María Rocío Ruiz de Ybáñez (rocio@um.es), Ana María López-Beceiro (anam.lopez.beceiro@usc.es), Luis Eusebio Fidalgo (luis.fidalgo@usc.es), Eduardo Berriatua (berriatu@um.es), Liron Lahat (lironlavet@gmail.com), Irene Sacristán (isacristan.vet@gmail.com), Álvaro Oleaga (alvaroleaga@yahoo.es), Carlos Martínez-Carrasco (cmcpleit@um.es)

ABSTRACT

Cardiopulmonary nematodes are among the most pathogenic parasites of domestic and wild canids. The aim of this study was to describe the species diversity, prevalence and infection intensity of these parasites in the Iberian wolf (*Canis lupus signatus*) and the red fox (*Vulpes vulpes*) in the northwest of the Iberian Peninsula. 257 foxes and 74 wolves were necropsied between 2008 and 2014. Four nematode species were identified: *Angiostrongylus vasorum*, *Eucoleus aerophilus*, *Crenosoma vulpis* and *Filaroides hirthi*. This last species was only found in wolves, being the first time that is cited worldwide in this wild canid. The overall parasite prevalence was significantly higher in foxes (70%) than in wolves (28%). Specifically, prevalences in foxes and wolves were, respectively, 43% and 22% for *A. vasorum*, 33% and 5% for *E. aerophilus*, and 30% and 9% for *C. vulpis*. The prevalence of *F. hirthi* was 16%. The *A. vasorum* intensity was significantly higher in foxes than in wolves. Differences between host species in the risk of infection would be associated to diverging feeding behavior, and possibly reflects a parasite-host adaptation related to host´s hunting strategies and cardiorespiratory requirements. This study revealed an association between infection and environmental factors, and highlighted a wide variation in the spatial distribution of *A. vasorum*. Our results indicate that cardiopulmonary parasites are widespread in wild canids in northwest Spain, and further agrees with other studies indicating the expansion of *A. vasorum* in Europe and, therefore, the urgent need to investigate infection in dogs in sympatric areas.

Keywords: cardiopulmonary parasites; Iberian Peninsula; Iberian wolf; red fox; Spain

1. INTRODUCTION

The Iberian wolf (*Canis lupus signatus*) and the red fox (*Vulpes vulpes*) are the only two wild canid species present in the Iberian Peninsula. There are around 2000 wolves in Spain, with the main population located in the northwest (Blanco and Cortés, 2012). In contrast, red fox can be found throughout the Iberian Peninsula (Gortázar, 2007). Both species occupy a wide variety of habitats, including anthropogenic landscapes (Blanco, 2017; Harris and Smith, 1987; Gloor et al., 2001; López-Martín, 2017).

Parasite distributions in wildlife are highly conditioned by the nature of their life-cycle. Specifically, in the case of trophic transmitted parasites of carnivores, the kind of prey affects both predator-prey and host-parasite interactions and, thus, potentially influence the dynamics and trophic web structure (Friesen and Roth, 2016). In this regard, it has been suggested that vertebrate carnivores are able to balance their nutrient intake through selective predation or feeding to obtain specific nutrients (Kohl et al., 2015; Potter et al., 2018). On the other hand, the size of the prey caught by carnivores and, consequently, the foraging strategy are influenced by the ecological niches available to them and the encounter rate with prey. In fact, large terrestrial mammalian carnivores over 21.5 kg usually prey on large-sized animals to maximize their energetic intake while minimizing their energy expenditure (Carbone et al., 1999; Carbone et al., 2007).

There are remarkable differences between the diet of the wolf and the fox; the wolf prefers to prey on domestic and wild ungulates (Llaneza et al., 2012; Torres et al., 2015; López-Martín, 2017), whereas the fox is a generalist predator with a high ecological plasticity (Dell'Arte et al., 2007) that feeds on a broad trophic spectrum, including vegetables, small prey, carrion and garbage (Díaz-Ruiz et al., 2013; López-Martín, 2017).

Cardiopulmonary nematodes are among the most important parasites of canids, specially *Angiostrongylus vasorum* and *Dirofilaria immitis*, which are highly pathogenic and emerging parasites that cause congestive heart failure, severe dyspnea and even death (Traversa et al., 2010). The impact of these and other cardiopulmonary parasites as *Crenosoma vulpis* and *Eucoleus aerophilus* on wild canids has not been analysed but, based on the evolutionary proximity of wolves, foxes and dog, we could assume a comparable pathogenicity in all species. Moreover, considering that wolves and, to a lesser extent, foxes require optimal cardiorespiratory capacity for successful predatory activity, it is reasonable to infer that

cardiopulmonary parasites could have a significant impact on the species survival and especially on individuals with high parasite loads and co-infections. The trend so far has been to study cardiopulmonary nematodes in wolves and foxes separately, without considering that both species share habitats and are susceptible to the same parasites. For all these reasons, the objective of this study was to describe the cardiopulmonary parasites of wolves and foxes in the northwestern Iberian Peninsula, discussing the epidemiological role that each of these wild canids have in the natural nidality of these parasites.

2. MATERIAL AND METHODS

The study was performed on Iberian wolves and red foxes from the regions of Asturias and Galicia (northwest Spain), covering an area of approximately 11000 km^2 and 30000 km^2, respectively. Galicia includes the provinces of A Coruña, Lugo, Ourense and Pontevedra (Fig. 1). Climate is predominantly oceanic with average annual rainfall and temperature ranging 960-1688 mm and 11.4-13.3°C (Castillo-Rodríguez et al., 2006; Valenzuela et al., 2018). The study was performed in 257 red foxes hunted in January and February 2008 in municipalities of A Coruña (34), Lugo (156) and Pontevedra (67), in the context of official hunting tournaments, and 74 Iberian wolves from Asturias (40)A Coruña (18), Lugo (8), Ourense (1) and Pontevedra (7), mostly shot in officially authorized hunts between 2009 and 2014, and some found dead due to road traffic accidents.

Animals were necropsied, and the trachea, lungs and heart were removed and stored frozen at -20°C until examined for parasites. To this effect, following defrosting, the heart chambers and its great vessels were carefully dissected, washed and filtered through a 62 µm mesh sieve. Trachea, bronchial tree and pulmonary blood vessels were longitudinally opened and observed under a stereomicroscope to collect parasites. Subsequently, in order to remove nematodes that may have remained in the bronchi and of smaller diameter vessels, the lungs were washed through a sieve and the retained material was examined under a stereomicroscope. Finally, to ensure that no nematode was left undetected, pulmonary parenchyma was enzymatically digested in pepsin and chlorhydric acid, according to Martínez-Rondán et al. (2017).

Nematodes were cleared with lactophenol and identified according to Georgi (1979), Butterworth and Beverley-Burton (1980), Costa et al. (2003) and Popiolek et al. (2009). Prevalence (percentage of infected

105 animals), parasite intensity (number of parasites in infected animals) and species richness (number of
106 species in infected animals) were calculated (Bush et al., 1997) and Yate´s-corrected chi-square test and the
107 non-parametric Kruskal-Wallis test were used to compare proportions and medians, respectively. Mixed
108 logistic regression models were developed to investigate the relationship between infection with a
109 particular parasite species (outcome variable) and host species (fox or wolf), adjusted for sex, age and
110 environmental variables of the area were animals were collected, and including municipality as a random
111 effect to allow for spatial clustering of infection (Agresti, 2013). Environmental variables, included the
112 human population density, average annual temperature and average annual rainfall, were categorized prior
113 to inclusion in the model. Parameters were estimated using the maximum likelihood method, p-values
114 were calculated with the chi-squared test and significance was considered at the 5% ($p<0.05$) level for a
115 two-tailed test. Analyses were carried out using R 3.4.3 software (R core Team, 2018).

116 **3. RESULTS**

117 Four nematode species were identified: *Angiostrongylus vasorum*, *Eucoleus aerophilus*, *Crenosoma vulpis*
118 and *Filaroides hirthi* (Table 1). Parasite prevalence (95% CI) was 70% (65-76) in foxes and 28% (18-39) in
119 wolves ($p<0.05$). The percentage of foxes infected with one, two or three nematode species were 54%
120 (98/181), 40% (73/181) and 6% (10/181), respectively. These same prevalences for wolves were 62%
121 (13/21), 24% (5/21), and 5% (1/21), and 10% (2/21) of wolves were infected with the four nematode
122 species.

123 The parasite distribution in infected foxes and wolves was widely variable and positively skewed, with most
124 animals having low parasite burdens. Foxes had the largest number of *A. vasorum*, *C. vulpis* and *E.*
125 *aerophilus*, and median *A. vasorum* and *C. vulpis* intensity were higher ($p<0.05$) and marginally higher (p-
126 value=0.06), respectively, in this host species compared to wolves. It was not possible to estimate the
127 median intensity of *F. hirthi*, because most nematodes were fragmented or damaged after the enzymatic
128 digestion of the pulmonary parenchyma required to detect this small nematode species.

129 The prevalence and median intensity of *A. vasorum*, *C. vulpis* and *E. aerophilus* in wolves and foxes varied
130 according to some of the environmental variables, but they did not follow an increasing or decreasing trend

with any of the variables analyzed except for *E. aerophilus* prevalence in foxes, which decreased with increasing annual rainfall (Tables 2 and 3).

The logistic regression models confirmed the significantly higher risk of foxes being infected with cardiopulmonary parasites compared to wolves, and the association between *A. vasorum* infection and areas with medium human population density, *C. vulpis* and juvenile hosts, and *E. aerophilus* and low temperature and precipitation ($p<0.05$). Moreover, *A. vasorum* models revealed additional, unexplained variation in the risk of infection between municipalities, highlighting the strong spatial aggregation of this parasite species.

4. DISCUSSION

Angiostrongylus vasorum has been described in canids worldwide (Spratt, 2015). However, until a few decades ago, its geographical distribution in Europe was localized to a few endemic foci (Morgan et al., 2009). The study confirms that *A. vasorum* is endemic in northwest Spain with higher prevalence in foxes (43%) than elsewhere in the Iberian Peninsula (16-36%) (Gortázar et al., 1998; Segovia et al., 2004; Mañas et al., 2005; Eira et al., 2006; Gerrikagoitia et al., 2010). Likewise, prevalence of this species in wolves (22%) was higher than in previous surveys in northwest Spain (2-5%) (Torres et al., 2000; Segovia et al., 2001; Segovia et al., 2007; Garrido-Castañé et al., 2015). The sensitivity of detection of *A. vasorum* in foxes by dissection of the heart and pulmonary arteries is estimated at 84% (Houpin et al., 2016). We additionally used enzymatic digestion of lung parenchyma to reduce the number of false-negative cases. It is likely that the prevalence of *A. vasorum* was underestimated in other studies in which enzymatic digestion was not used.

The prevalence of *A. vasorum* was higher in foxes than in wolves, coinciding in general terms with the literature mentioned above. This result reflects dietary differences between species, with foxes feeding more on intermediate and paratenic hosts of this parasite than wolves, including a wide variety of gastropod species (Ferdushy and Hasan, 2010), and frogs and birds (Bolt et al., 1993; Elsheikhaet al., 2014; Mozzer and Lima, 2015), respectively. Moreover, the similar prevalence and *A. vasorum* intensity in juvenile and adult foxes indicates that these intermediate and paratenic hosts are food sources for foxes throughout their life, and that the host´s immune response tolerates or is unable to eliminate this parasite;

158 this finding is in agreement with Gillis-Germitsch et al. (2017), who showed that previously exposed adult
159 foxes can be reinfected and suffer persistent infections. However, the fact that a substantial number of
160 wolves were also infected with *A. vasorum* emphasizes the potentially important epidemiological role of
161 wolves in maintaining its life cycle. In contrast to foxes, *A. vasorum* prevalence and median intensity was
162 higher in juvenile compared to adult wolves, supporting that gastropods and paratenic hosts of *A. vasorum*
163 constitute part of the diet of juveniles during the developmental period until they become accomplished
164 adult hunters of large prey (MacNulty et al., 2012; Zimmermann et al., 2015). It is important to point out,
165 moreover, that carnivores modify their nutrient intake through selective predation or feeding in order to
166 obtain a balanced diet (Kohl et al., 2015). This could partly explain that 19% of adult wolves were
167 parasitized by *A. vasorum*; that is, although adults usually hunt large animals, they also eat smaller prey.
168 The geographic distribution of *A. vasorum* is characterized by stable foci of high prevalence (Morgan et al.,
169 2009), mostly in areas with mild and wet climates, as is our study area, since the invertebrate hosts are
170 highly sensitive to temperature and moisture (Jeffery et al., 2004; Ferdushy and Hasan, 2010). In Europe,
171 the distribution of *A. vasorum* has increased in recent decades, probably due to the fox's expansion (Van
172 Doorn et al. 2009; Al-Sabi et al. 2013, Al-Sabi et al. 2014). Although the pathogenicity of *A. vasorum* has
173 been described in foxes (Morgan et al., 2008) and wolves (Eleni et al., 2014; De Liberato et al., 2017), the
174 impact on the wider population is unknown. Also, the role of foxes and wolves in the epidemiology of
175 infection in dogs living in close-by areas is also discussed (McCarthy et al., 2016; Schug et al., 2018, Lange et
176 al., 2018). Although few studies compared *A. vasorum* prevalence in synanthropic wild and domestic
177 canids, a wide molecular study of strains from dogs and foxes revealed no evidence of genetic segregation
178 suggesting a common transmission cycle (Jefferies et al., 2010). In our study, prevalence was highest in
179 rural areas with medium human density, as well as the highest intensities in foxes. We hypothesize that, in
180 these rural areas, there are probably more dogs that are allowed to roam freely and, therefore, have the
181 possibility of ingesting intermediate hosts, playing a summative role in the local *A. vasorum* life cycle
182 involving domestic and wild canids.
183 *Crenosoma vulpis* has been described in canids from temperate regions worldwide (Shimalov and Shimalov,
184 2000; Latrofa et al., 2015; Figueiredo et al., 2016; Maksimov et al., 2017), including the Iberian Peninsula, in

185 both foxes (Gortázar et al., 1998; Segovia et al., 2004; Mañas et al., 2005; Eira et al., 2006; Garrido-Castañé
186 et al., 2015) and wolves (Segovia et al., 2007). Like *A. vasorum*, gastropods are the intermediate hosts of
187 this nematode species (Jeffery et al., 2004). The higher *C. vulpis* prevalence in foxes compared to wolves
188 indicates than this host species plays a more prominent role than wolves in the epidemiological dynamics
189 of this parasite. Similar to what has been argued in *A. vasorum*, this result suggests that both canids prey on
190 gastropods, but more notably in foxes (Colella et al., 2016; Lange et al., 2018). *C. vulpis* was more prevalent
191 in juvenile foxes than in adults, and was only found in juvenile wolves. This could be due to differences in
192 trophic behavior and a more effective immune response in adults (Jeffery et al., 2004; Davidson et al.,
193 2006; Hodžić et al., 2016). Notwithstanding this, some adult foxes had a high parasite burden which,
194 although not fatal, would reduce the host's respiratory capacity significantly (Traversa et al., 2010).

195 *Eucoleus aerophilus* has been reported in wild and domestic canids (Torres et al., 2000; Morgan et al., 2008;
196 Conboy, 2009; Traversa et al., 2009; Di Cesare et al., 2014). The prevalence in foxes was similar to those
197 reported in other Iberian areas (Gortázar et al., 1998; Segovia et al., 2004; Mañas et al., 2005), contrasting
198 with the low prevalence described by other authors (Eira et al., 2006; Martínez-Carrasco et al., 2007). High
199 prevalences (65-84%) have been described in foxes in other European countries (Davidson et al., 2006;
200 Saeed et al., 2006; Lalošević et al., 2013; Al-Sabi et al., 2014; Hodžić et al., 2016; Schug et al., 2018). In our
201 study, *E. aerophilus* was the least prevalent cardiopulmonary nematode in wolves; in other European
202 countries, the prevalence in wolves (8-36%) is usually lower than that described in foxes (Shimalov and
203 Shimalov, 2000; Popiołek et al., 2007; Bagrade et al., 2009; Varodi et al., 2017). As with *C. vulpis*, the
204 prevalence of *E. aerophilus* was related to altitude, annual temperature and annual rainfall. This parasite
205 has a direct life cycle, and earthworms can act as paratenic hosts (Anderson, 2000), yet there is limited
206 information on other ecological and epidemiological aspects of *E. aerophilus* infection that could help
207 interpret these associations.

208 *Filaroides* spp. has been sporadically described in dogs in Europe (Caro-Vadillo et al., 2005; Cervone et al.,
209 2018) and rarely in wild canids (Magi et al., 2015). Sanchis-Monsonís et al. (2013) detected *F. hirthi* in 2% of
210 foxes in southeast Spain. Here we report the first *F. hirthi* infection in wolves worldwide. The rare detection
211 of this parasite in wild canids could be partly due to the fact that *F. hirthi* is a very small, fragile nematode

212 located in the bronchioles and alveoli and, consequently, difficult to detect by direct examination. The
213 absence or low prevalence of *F. hirthi* in wild canids in general should be evaluated with care, as the
214 presence of this parasite in these host species may be underestimated. We have been able to detect *F.*
215 *hirthi* because the lung parenchyma of each animal was enzymatically digested, which increases the
216 probability of detection, as has been proven in dogs (Bahnemann and Bauer, 1994). This finding highlights
217 the potential role of wolves in the maintenance of the parasite´s transmission in nature. Dogs are infected
218 by ingestion of infectious larvae present in saliva (Anderson, 2000). In the case of *Filaroides osleri*, maternal
219 cleanliness is assumed to be an important transmission route in the dog, while regurgitation of food by
220 parents to feed pups may also be an important form of transmission in wild canids (Polley and Creighton,
221 1977; Clayton and Lindsay, 1979; Dunsmore and Spratt, 1979). In addition, it has been suggested that
222 infection in dogs is possible by coprophagy of fresh faeces (Georgi et al., 1979). Since *F. hirthi* and *F. osleri*
223 belong to the same genus, it is assumable that the transmission is similar in both parasites and, therefore,
224 the social behavior of the wolf could explain the intraspecific transmission of *F. hirthi*. Further
225 epidemiological studies are needed to better understand the risk factors associated with *F. hirthi*
226 transmission and to assess the role of the wolf as a reservoir of this parasite, as well as the degree of
227 overlap between the domestic and sylvatic epidemiological cycles.

228 Finally, *Dirofilaria immitis* was not detected in our study, but this was somewhat not surprising, since the
229 northwest Spain is considered an area of low risk of transmission, given that climatic conditions are not
230 ideal for the mosquito vector (Simón et al., 2014). *D. immitis* has been previously detected in Iberian wolves
231 (Segovia et al*.,* 2001) and foxes (Gortázar et al., 1994; Gortázar et al., 1998; Mañas et al., 2005; Eira et al.,
232 2006) in other parts of the Iberian Peninsula, and also in other European areas (Georgieva et al., 2001;
233 Pascucci et al., 2007; Magi et al., 2008; Kirkova et al., 2011; Penezić et al., 2014).

234 **5. Conclusions**

235 Northwest Spain is highly endemic for *A. vasorum*, *C. vulpis* and *E. aerophilus*, and prevalence and infection
236 intensity is significantly greater in foxes than in wolves. Differences between host species are probably
237 related to differences in trophic behavior (Buck et al., 2018), with foxes of all ages and juvenile wolves
238 feeding on intermediate and paratenic hosts of the first two nematode species, and adult wolves more on

larger prey which not participate of the life cycle of these parasites. We hypothesized that this is an adaptive host-parasite response, so the highest infection risk occurs in the wild canid species (fox) that requires less cardiorespiratory effort to hunt their usual prey (Brose, 2010; Sand et al., 2016). In other words, cardiopulmonary nematodes, although adapted to several host species, have managed to link their life cycle to a type of prey more likely to be consumed by the smaller predator (fox). This prevents the cardiorespiratory capacity of a large predator, located at the top of the trophic chain (mainly adult wolves), to be compromised, which has meant the adoption of a trophic strategy by the wolf that reduces the risk of infection.

6. Conflict of interest statement

The authors declare that they have no conflict of interest.

7. Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

8. Acknowledgements

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. The study was carried out with the permission of the Dirección Xeral de Conservación da Natureza de la Consellería de Medio Ambiente, Ordenación do Territorio e Vivienda (Xunta de Galicia, Spain) and Consejería de Agroganadería y Recursos Autóctonos de Caza y Pesca (Gobierno del Principado de Asturias, Spain). We acknowledge the support provided by both institutions and by the Galician Hunting Federation in obtaining samples.

9. References

Agresti, A., 2013. Categorical Data Analysis, third ed. John Wiley & Sons, Hoboken, New Jersey.

Al-Sabi, M.N.S., Willesen, J., Koch, J., Espersen, M.C., Johansson, A., Kapel, C.M.O., 2013. A coprological investigation of gastrointestinal and cardiopulmonary parasites in hunting dogs in Denmark. Vet. Parasitol. 196, 366-372.

264 Al-Sabi, M.N.S, Halasa, T., Kapel, C., 2014. Infections with cardiopulmonary and intestinal helminths and
265 sarcoptic mange in red foxes from two different localities in Denmark. Acta Parasitol. 59 (1), 98-107.
266 Anderson, R.C., 2000. Nematode parasites of vertebrates. Their development and transmission, second ed.
267 CABI Publishing, Wallingford, Oxon.
268 Bagrade, G., Kirjušina, M., Vismanis, K., Ozoliņš, J., 2009. Helminth parasites of the wolf *Canis lupus* from
269 Latvia. J. Helminthol. 83 (1), 63-68.
270 Bahnemann, R., Bauer, C., 1994. Lungworm infection in a beagle colony: *Filaroides hirthi*, a common but not
271 well-known companion. Exp. Toxicol. Pathol. 46 (1), 55-62.
272 Blanco, J.C. 1995. Ganado y grandes carnívoros. Quercus. 107, 12-15.
273 Blanco, J.C., 2001. El hábitat del lobo: la importancia de los aspectos ecológicos y socioeconómicos, in:
274 Camprodon, J., Plana, E. (Eds.), Conservación de la biodiversidad y gestión forestal. Su aplicación a la fauna
275 vertebrada. Ed. Universitat de Barcelona, Barcelona, pp. 415-432.
276 Blanco, J.C., 2017. Lobo - *Canis lupus*, in: Salvador, A., Barja, I. (Eds.), Enciclopedia virtual de los vertebrados
277 españoles. Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org/
278 Blanco, J.C., Cortés, Y., 2012. Surveying wolves without snow: a critical review of the methods used in
279 Spain. HYSTRIS. 23 (1), 35-48.
280 Bolt, G., Monrad, J., Frandsen, F., Henriksen, P., Dietz, H.H., 1993. The common frog (*Rana temporaria*) as a
281 potential paratenic and intermediate host for *Angiostrongylus vasorum*. Parasitol. Res. 79 (5), 428-430.
282 Bourdeau, P., 1993. Canine *Angiostrongylus vasorum* infestation. Rec. Med. Vet. 169, 401-407.
283 Bowman, D.D., Atkins, C.E., 2009. Heartworm biology, treatment, and control. Vet. Clin. North Am. Small
284 Anim. Pract. 39 (6), 1127–1158.
285 Bridger, K.E., Baggs, E.M., Finney-Crawley, J., 2009. Endoparasites of the coyote (*Canis latrans*), a recent
286 migrant to insular Newfoundland. J. Wildl. Dis. 45, 1221-1226.
287 Brose, U., 2010. Body-mass constraints on foraging behaviour determine population and food-web
288 dynamics. Funct. Ecol. 24, 28-34.

289 Bruzinskaite-Schmidhalter, R., Sarkunas, M., Malakauskas, A., Mathis, A., Torgerson, P.R., Deplazes, P.,
290 2012. Helminths of red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania.
291 Parasitology. 139, 120-127.

292 Buck, J.C., Weinstein, S.B., Young, H.S., 2018. Ecological and evolutionary consequences of parasite
293 avoidance. Trends Ecol. Evol. 33 (8), 619-632.

294 Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own term:
295 Margolis et al. revisited. J. Parasitol. 83 (4), 575-583.

296 Butterworth, E.W., Beverley-Burton, M., 1980. The taxonomy of *Capillaria* spp (Nematoda: Trichuroidea) in
297 carnivorous mammals from Ontario, Canada. Syst. Parasitol. 1 (3), 211-236.

298 Cancrini, G., Gabrielli, S., 2007. Vectors of *Dirofilaria* nematodes, biology, behaviour and host/parasite
299 relationships, in: Genchi, C., Rinaldi, L., Cringoli, G. (Eds), *Dirofilaria immitis* and *D. repens* in dog and cat
300 and human infections. Rolando Editore, Naples, pp. 47-58.

301 Capelli, G., Frangipane di Regalbono, A., Simonato, G., Cassini, R., Cazzin, S., Cancrini, G., Otranto, D.,
302 Pietrobelli, M., 2013. Risk of canine and human exposure to *Dirofilaria immitis* infected mosquitoes in
303 endemic areas of Italy. Parasit. Vectors. 6, 60.

304 Caro-Vadillo, A., Martínez-Merlo, E., García-Real, I., Fermín-Rodríguez, M.L., Mateo, P., 2005. Verminous
305 pneumonia due to *Filaroides hirthi* in a Scottish terrier in Spain. Vet. Rec. 157, 586-589.

306 Castillo-Rodríguez, F., Martínez Cortizas, A., Blanco Chao, R., 2006. O clima de Galicia, in: Naranjo L., Pérez-
307 Muñuzuri, V. (Eds), A Variabilidade natural do clima en Galicia. Consellería de Medio Ambiente e
308 Desenvolvemento Sostible (Xunta de Galicia) y Fundación Caixa Galicia, Santiago de Compostela, pp. 19-91.

309 Carbone, C., Mace, G.M., Roberts, S.C., Macdonald, D.W., 1999. Energetic constraints on the diet of
310 terrestrial carnivores. Nature. 402, 286-288.

311 Carbone, C., Teacher, A., Rowcliffe, J.M., 2007. The costs of carnivory. PLoS Biol. 5, 363-368.

312 Cervone, M., Giannelli, A., Rosenberg, D., Perrucci, S., Otranto, D., 2018. Filaroidosis infection in an
313 immunocompetent adult dog from France. Helminthologia. 55 (1), 77-83.

314 Clayton, H.M., Lindsay, F.E., 1979. *Filaroides osleri* infection in the dog. J. Small Anim. Pract. 20, 773-782.

315 Colella, V., Mutafchiev, Y., Cavalera, M.A., Giannelli, A., Lia, R.P., Dantas-Torres, F., Otranto, D., 2016.
316 Development of *Crenosoma vulpis* in the common garden snail *Cornu aspersum*: implications for
317 epidemiological studies. Parasit Vectors. 9: 208.

318 Conboy, G., 2009. Helminth parasites of the canine and feline respiratory tract. Vet. Clin. North Am. Small
319 Anim. Pract. 39 (6), 1109-1126.

320 Costa, J.O., De Araujo Costa, H.M., Guimaraes, M.P., 2003. Redescription of *Angiostrongylus vasorum*
321 (Baillet, 1866) and systematic revision of species assigned to the genera *Angiostrongylus* Kamensky, 1905
322 and *Angiocaulus* Schulz, 1951. Rev. Med. Vet. 154 (1), 9-16.

323 Davidson, R.K., Gjerde, B., Vikøren, T., Lillehaug, A., Handeland, K., 2006. Prevalence of *Trichinella* larvae
324 and extra-intestinal nematodes in Norwegian red foxes (*Vulpes vulpes*). Vet. Parasitol. 136, 307-316.

325 De Liberato, C., Grifoni, G., Lorenzetti, R., Meoli, R., Cocumelli, C., Mastromattei, A., Scholl, F., Rombolà, P.,
326 Calderini, P., Bruni, G., Eleni, C., 2017. *Angiostrongylus vasorum* in wolves in Italy: prevalence and
327 pathological findings. Parasit. Vectors. 10 (1), 386.

328 Dell'Arte, G.L., Laaksonen, T., Norrdahl, K., Korpimäki, E., 2007. Variation in the diet composition of a
329 generalist predator, the red fox, in relation to season and density of main prey. Acta oecol. 31, 276-281.

330 Di Cesare, A., Otranto, D., Latrofa, M.S., Veronesi, F., Perrucci, S., Lalošević, D., Gherman, C.M., Traversa, D.,
331 2014. Genetic variability of *Eucoleus aerophilus* from domestic and wild hosts. Res. Vet. Sci. 96, 512-515.

332 Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, J.L., López-Martín, J.M., Ferreira, C., Ferreras, P., 2013.
333 Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes vulpes* in the Iberian
334 Peninsula. Mammal Rev. 43 (1), 59-70.

335 Dunsmore, J.D., Spratt, D.M., 1979. The life history of *Filaroides osleri* in wild and domestic canids in
336 Australia. Vet. Parasitol. 5, 275-286.

337 Eira, C., Vingada, J., Torres, J., Miquel, J., 2006. The Helminth Community of the Red Fox, *Vulpes Vulpes*, in
338 Dunas de Mira (Portugal) and its effect on host condition. Wildl. Biol. Pract. 2, 26-36.

339 Eleni, C., De Liberato, C., Azam, D., Morgan, E. R., Traversa, D., 2014. *Angiostrongylus vasorum* in wolves in
340 Italy. Int. J. Parasitol. Parasites Wildl. 3 (1), 12-14.

341 Elsheikha, H.M., Holmes, S.A., Wright, I., Morgan, E.R., Lacher, D.W., 2014. Recent advances in the
342 epidemiology, clinical and diagnostic features, and control of canine cardio-pulmonary angiostrongylosis.
343 Vet. Res. 45, 92.

344 Ferdushy, T., Hasan, M.T., 2010. *Angiostrongylus vasorum*: The “French Heartworm”. Parasitol. Res. 107 (4),
345 765-771.

346 Figueiredo, A., Oliveira, L., Madeira de Carvalho, L., Fonseca, C., Torres, R.T., 2016. Parasite species of the
347 endangered Iberian wolf (*Canis lupus signatus*) and a sympatric widespread carnivore. Int. J. Parasitol.
348 Parasites Wildl. 5 (2), 164-167.

349 Friesen, O.C., Roth, J.D., 2016. Alternative prey use affects helminth parasite infections in grey wolves. J.
350 Animal Ecol. 85 (5), 1265-1274.

351 Garrido-Castañé, I., Ortuño, A., Marco, I., Castellà, J., 2015. Cardiopulmonary helminths in foxes from the
352 Pyrenees. Acta Parasitol. 60, 712-715.

353 Georgi, J.R., 1979. Differential Characters of *Filaroides milksi* Whitlock, 1956 and *Filaroides hirthi* Georgi and
354 Anderson, 1975. Proc. Helminthol. Soc. Wash. 46 (1), 142-145.

355 Georgi, J.R., Georgi, M.E., Fahnenstock, G.R., Theodorides, V.J., 1979. Transmission and control of *Filaroides*
356 *hirthi* lungworm infection in dogs. Am. J. Vet. Res. 40, 829-831.

357 Georgieva, D., Kirkova, Z., Ivanov, A., 2001. A study on the incidence and diagnostics of dirofilariosis
358 (Heartworm disease) in carnivores. Bulg. J. Vet. Med. 4, 231-237.

359 Gerrikagoitia, X., Barral, M., Juste, R.A., 2010. *Angiostrongylus* species in wild carnivores in the Iberian
360 Peninsula. Vet. Parasitol. 174 (1-2), 175-180.

361 Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P., Breitenmoser, U., 2001. The rise of urban fox populations
362 in Switzerland. Mamm. Biol. 66, 155-164.

363 Gortázar, C., 2007. *Vulpes vulpes*. Zorro, in: Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), Atlas y Libro Rojo de
364 los Mamíferos Terrestres de España. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, pp.
365 277-279.

366 Gortázar, C., Castillo, J.A., Lucientes, J., Blanco, J.C., Arriolabengoa, A., Calvete, C., 1994. Factors affecting
367 *Dirofilaria immitis* prevalence in red foxes in northeastern Spain. J. Wildl. Dis. 30, 545-547.
368 Gortázar, C., Villafuerte, R., Lucientes, J., Fernández-de-Luco, D., 1998. Habitat related differences in
369 helminth parasites of red foxes in the Ebro valley. Vet. Parasitol. 80 (1), 75-81.
370 Gillis-Germitsch, N., Kapel, C.M.O., Thamsborg, S.M., Deplazes, P., Schnyder, M., 2017. Host-specific
371 response to *Angiostrongylus vasorum* infection in red foxes (*Vulpes vulpes*): implications for parasite
372 epidemiology. Parasitology. 144, 1144-1153.
373 Harris, S., Smith, G.C., 1987. Demography of two urban fox (*Vulpes vulpes*) populations. J. Appl. Ecol. 24, 75-
374 86.
375 Hecker, N., Sharma, V., Hiller, M., 2019. Convergent gene losses illuminate metabolic and physiological
376 changes in herbivores and carnivores. Proc. Natl. Acad. Sci. U.S.A. 116 (8), 3036-3041.
377 Helm, J.R., Morgan, E. R., Jackson, M.W., Wotton, P., Bell, R., 2010. Canine angiostrongylosis: An emerging
378 disease in Europe. J. Vet. Emerg. Crit. Care. 20 (1), 98-109.
379 Houpin, E., McCarthy, G., Ferrand, M., De Waal, T., O'Neill, E.J., Zintl, A., 2016. Comparison of three
380 methods for the detection of *Angiostrongylus vasorum* in the final host. Vet. Parasitol. 220, 54-58.
381 Hodžić, A., Alić, A., Klebić, I., Kadrić, M., Brianti, E., Duscher, G.G., 2016. Red fox (*Vulpes vulpes*) as a
382 potential reservoir host of cardiorespiratory parasites in Bosnia and Herzegovina. Vet. Parasitol. 223, 63-70.
383 Jefferies, R., Shaw, S.E., Willesen, J., Viney, M.E., Morgan, E.R., 2010. Elucidating the spread of the emerging
384 canid nematode *Angiostrongylus vasorum* between Palaearctic and Nearctic ecozones. Infect. Genet. Evol.
385 10, 561-568.
386 Jeffery, R. A., Lankester, M. W., McGrath, M. J., Whitney, H. G., 2004. *Angiostrongylus vasorum* and
387 *Crenosoma vulpis* in red foxes (*Vulpes vulpes*) in Newfoundland, Canada. Can. J. Zool. 82 (1), 66-74.
388 Kohl, K., Coogan, S., Raubenheimer, D., 2015. Do wild carnivores forage for prey or for nutrients? Bioessays.
389 37 (6), 701-709.
390 Kunkel, K.E., Pletscher, D.H., Boyd, D.K., Ream, R.R., Fairchild, M.W., 2004. Factors correlated with foraging
391 behavior of wolves in and near Glacier National Park, Montana. J. Wildl. Manage. 68 (1), 167-178.

392 Lalošević, D., Lalošević, V., Klem, I., Stanojev-Jovanović, D., Pozio, E., 2008. Pulmonary capillariasis miming
393 bronchial carcinoma. Am. J. Trop. Med. Hyg. 78 (1), 14-16.
394 Lalošević, V., Lalošević, D., Capo, I., Simin, V., Galfi, A., Traversa, D., 2013. High infection rate of zoonotic
395 *Eucoleus aerophilus* infection in foxes from Serbia. Parasite. 20, 3.
396 Lange, M., Penagos-Tabares, F., Hirzmann, J., Failing, K., Schaper, R., Van Bourgonie, Y.R., Backeljau, T.,
397 Hermosilla, C., Taubert, A., 2018. Prevalence of *Angiostrongylus vasorum*, *Aelurostrongylus abstrusus* and
398 *Crenosoma vulpis* larvae in native slug populations in Germany. Vet. Parasitol. 254, 120-130.
399 Latrofa, M. S., Lia, R.P., Giannelli, A., Colella, V., Santoro, M., D'Alessio, N., Campbell, B.E., Parisi, A., Dantas-
400 Torres, F., Mutafchiev, Y., Veneziano, V., Otranto, D., 2015. *Crenosoma vulpis* in wild and domestic
401 carnivores from Italy: a morphological and molecular study. Parasitol. Res. 114 (10), 3611-3617.
402 Llaneza, L., 1999. Hábitos alimenticios del lobo en la cordillera Cantábrica. Quercus. 157, 16-19.
403 Llaneza, L., López-Bao, J.V., Sazatornil, V., 2012. Insights into wolf presence in human-dominated
404 landscapes: the relative role of food availability, humans and landscape attributes. Divers. Distrib. 18, 459-
405 469.
406 López-Martín, J.M., 2017. Zorro – *Vulpes vulpes*, in: Salvador, A., Barja, I. (Eds.), Enciclopedia Virtual de los
407 Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.
408 http://www.vertebradosibericos.org/
409 Lurati, L., Deplazes, P., Hegglin, D., Schnyder, M., 2015. Seroepidemiological survey and spatial analysis of
410 the occurrence of *Angiostrongylus vasorum* in Swiss dogs in relation to biogeographic aspects. Vet.
411 Parasitol. 212 (3-4), 219-226.
412 MacNulty, D.R., Smith, D.W., Mech, L.D., Vucetich, J.A., Packer, C., 2012. Nonlinear effects of group size on
413 the success of wolves hunting elk. Behav. Ecol. 23, 75-82.
414 Magi, M., Calderini, P., Gabrielli, S., Dell'Omodarme, M., Macchioni, F., Prati, M.C., Cancrini, G., 2008.
415 *Vulpes vulpes*: a possible wild reservoir forzoonotic filariae. Vector Borne Zoonotic Dis. 8, 249-252.
416 Magi, M., Guardone, L., Prati, M., Mignone, W., Macchioni, F., 2015. Extraintestinal nematodes of the red
417 fox *Vulpes vulpes* in north-west Italy. J. Helminthol. 89 (4), 506-511.

418 Maksimov, P., Hermosilla, C., Taubert, A., Staubach, C., Sauter-Louis, C., Conraths, F.J., Vrhovec, M.G.,
419 Pantchev, N., 2017. GIS-supported epidemiological analysis on canine *Angiostrongylus vasorum* and
420 *Crenosoma vulpis* infections in Germany. Parasit. Vectors. 10 (1): 108.

421 Mañas, S., Ferrer, D., Castellà, J., López-Martín, J.M., 2005. Cardiopulmonary helminth parasites of red
422 foxes (*Vulpes vulpes*) in Catalonia, northeastern Spain. Vet. J. 169 (1), 118-120.

423 Martínez-Carrasco, C., Ruíz de Ybáñez, M.R., Sagariminaga, L., Garijo, M.M., Moreno, F., Acosta, I.,
424 Hernández, S., Alonso, F.D., 2007. Parasites of the red fox (*Vulpes vulpes* Linnaeus, 1758) in Murcia,
425 southeast Spain. Rev. Med. Vet. 158, 331-335.

426 Martínez-Rondán, F.J., Ruiz de Ybáñez, M.R., Tizzani, P., López-Beceiro, A.M., Fidalgo, L.E., Martínez-
427 Carrasco, C., 2017. The American mink (*Neovison vison*) is a competent host for native European parasites.
428 Vet. Parasitol. 247, 93-99.

429 McCarthy, G., Ferrand, M., De Waal, T., Zintl, A., McGrath, G., Byrne, W., O'neill, E.J., 2016. Geographical
430 distribution of *Angiostrongylus vasorum* in foxes (*Vulpes vulpes*) in the Republic of Ireland. Parasitology.
431 143, 588-593.

432 Morchón, R., Carretón, E., González-Miguel, J., Mellado-Hernández, I., 2012. Heartworm disease (*Dirofilaria*
433 *immitis*) and their vectors in Europe - new distribution trends. Front. Physiol. 3, 1-11.

434 Morgan, E.R., Jefferies, R., Krajewski, M., Ward, P., Shaw, S.E., 2009. Canine pulmonary angiostrongylosis:
435 The influence of climate on parasite distribution. Parasitol. Int. 58 (4), 406-410.

436 Morgan, E.R., Tomlinson, A., Hunter, S., Nichols, T., Roberts, E., Fox, M.T., Taylor, M.A., 2008.
437 *Angiostrongylus vasorum* and *Eucoleus aerophilus* in foxes (*Vulpes vulpes*) in Great Britain. Vet. Parasitol.
438 154 (1-2), 48-57.

439 Mozzer, L.R., Lima, W.S., 2015. *Gallus gallus domesticus*: paratenic host of *Angiostrongylus vasorum*. Vet
440 Parasitol. 207, 81-84.

441 Otranto, D., Cantacessi, C., Dantas-Torres, F., Brianti, E., Pfeffer, M., Genchi, C., Guberti, V., Capelli, G.,
442 Deplazes, P., 2015. The role of wild canids and felids in spreading parasites to dogs and cats in Europe. Part
443 II: Helminths and arthropods. Vet. Parasitol. 213 (1-2), 24-37.

444 Pascucci, I., Fico, R., D'Angelo, A.R., Serini, S., Cammà, C., 2007. First notification in Italy of cardiopulmonary
445 filariosis (heartworm disease) in a wolf (*Canis lupus*). Vet Ital. 43 (4), 843-850.
446 Penezić, A., Selaković, S., Pavlović, I. Ćirović, D., 2014. First findings and prevalence of adult heartworms
447 (*Dirofilaria immitis*) in wild carnivores from Serbia. Parasitol. Res. 113 (9), 3281-3285.
448 Polley, L., Creighton, S.R., 1977. Experimental direct transmission of the lungworm *Filaroides osleri* in dogs.
449 Vet. Rec. 100, 136-137.
450 Popiolek, M., Jarnecki, H., Luczynski, T., 2009. A record of *Crenosoma vulpis* (Rudolphi, 1819) (Nematoda,
451 Crenosomatidae) from the Eurasian badger (*Meles meles* L.) from Poland. Wiad. Parazytol. 55 (4), 437-439.
452 Popiołek, M., Szczęsna, J., Nowak, S., Mysłajek, R., 2007. Helminth infections in faecal samples of wolves
453 *Canis lupus* L. from the western Beskidy Mountains in southern Poland. J. Helminthol. 81 (4), 339-344.
454 Potter, T.I., Stannard, H.J., Greenville, A.C., Dickman, C.R., 2018. Understanding selective predation: Are
455 energy and nutrients important?. PLoS One. 13 (8): e0201300.
456 R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical
457 Computing. Vienna, Austria. URL. http://www.R-project.org/.
458 Reig, S., de la Cuesta, L., Palacios, F., 1985. The impact of human activities on the food habits of red fox and
459 wolf in Old Castille, Spain. Rev. Ecol.-Terre Vie. 40 (2), 151-155.
460 Saeed, I., Maddox-Hyttel, C., Monrad, J., Kapel, C.M., 2006. Helminths of red foxes (*Vulpes vulpes*) in
461 Denmark. Vet. Parasitol. 139, 168-179.
462 Sanchis-Monsonís, G., Tizzani, P., Sánchez-Isarria, M.A., García, I., Lizana, V., Chitimia,l., Martínez-Carrasco,
463 C., 2013. Aspectos epidemiológicos de los nematodos cardio-respiratorios del zorro rojo (*Vulpes vulpes*) en
464 la Comunidad Valenciana (S.E. España). XVIII Congreso de la Sociedad Española de Parasitología.
465 Sand, H., Eklund, A., Zimmermann, B., Wikenros, C., Wabakken, P., 2016. Prey selection of Scandinavian
466 wolves: single large or several small?. PLoS One. 11 (12): e0168062.
467 Sarmento, P., Cruz, J., Eira, C., Fonseca, C., 2009. Evaluation of camera trapping for estimating red fox
468 abundance. J. Wildl. Manage. 73 (7), 1207-1212.

469 Schug, K., Krämer, F., Schaper, R., Hirzmann, J., Failing, K., Hermosilla, C., Taubert, A., 2018. Prevalence
470 survey on lungworm (*Angiostrongylus vasorum*, *Crenosoma vulpis*, *Eucoleus aerophilus*) infections of wild
471 red foxes (*Vulpes vulpes*) in Central Germany. Parasit. Vectors. 11, 85.

472 Schweiger, A., Ammann, R.W., Candinas, D., Clavien, P.A., Eckert, J., Gottstein, B., Halkic, N., Muellhaupt, B.,
473 Prinz, B.M., Reichen, J., Tarr, P.E., Torgerson, P.R., Deplazes, P., 2007. Human alveolar echinococcosis after
474 fox population increase, Switzerland. Emerg. Infect. Dis. 13 (6), 878-882.

475 Segovia, J. M., Torres, J., Miquel, J., Llaneza, L., Feliu, C., 2001. Helminths in the wolf, *Canis lupus*, from
476 north-western Spain. J. Helminthol. 75 (2), 183-192.

477 Segovia, J. M., Torres, J., Miquel, J., Sospedra, E., Guerrero, R., Feliu, C., 2007. Analysis of helminth
478 communities of the pine marten, *Martes martes*, in Spain: Mainland and insular data. Acta Parasitol. 52 (2),
479 156-164.

480 Segovia, J., Miquel, J., Torres, J., Feliu, C., 2007. Role of satellite species in helminth communities of the
481 Iberian wolf (*Canis lupus signatus* Cabrera, 1907). Res. Rev. Parasitol. 67 (1-4), 79-86.

482 Segovia, J.M., Torres, J., Miquel, J., 2004. Helminth parasites of the red fox (*Vulpes vulpes* L. 1758) in the
483 Iberian Peninsula: an ecological study. Acta Parasitol. 49 (1), 67-79.

484 Shimalov, V.V., Shimalov, V.T., 2000. Helminth fauna of the wolf (*Canis lupus* Linnaeus, 1758) in Belorussian
485 Polesie. Parasitol. Res. 86 (2), 163-164.

486 Simón, L., Afonin, A., López-Díez, L.I., González-Miguel, J., Morchón, R., Carretón, E., Montoya-Alonso, J.A.,
487 Kartashev, V., Simón, F., 2014. Geo-environmental model for the prediction of potential transmission risk of
488 *Dirofilaria* in an area with dry climate and extensive irrigated crops. The case of Spain. Vet. Parasitol. 200
489 (3-4), 257-264.

490 Spratt, D.M., 2015. Species of *Angiostrongylus* (Nematoda: Metastrongyloidea) in wildlife: A review. Int. J.
491 Parasitol. Parasites Wildl. 4 (2), 178-189.

492 Szczesna, J., Popiołek, M., Schmidt, K., Kowalczyk, R., 2008. Coprological study on helminth fauna in
493 Eurasian lynx (*Lynx lynx*) from the Białowieza primeval Forest in eastern Poland. J. Parasitol. 94 (4), 981-984.

494 Torres, J., Miquel, J., Fournier, P., Fournier-Chambrillon, C., Liberge, M., Fons, R., Feliu, C., 2008. Helminth
495 communities of the autochthonous mustelids *Mustela lutreola* and *M. putorius* and the introduced *Mustela*
496 *vison* in south-western France. J. Helminthol. 82 (4), 349-355.

497 Torres, J., Segovia, J.M., Miquel, J., Feliu, C., Llaneza, L., Petrucci-Fonseca, F., 2000. Helmintofauna del lobo
498 ibérico (*Canis lupus signatus* Cabrera, 1907). Aspectos potencialmente útiles en mastozoología. Galemys.
499 12, 1-11.

500 Torres, R.T., Silva, N., Brotas, G., Fonseca, C., 2015. To eat or not to eat? The diet of the endangered Iberian
501 wolf (*Canis lupus signatus*) in a human-dominated landscape in central Portugal. PloS One. 10 (6),
502 e0129379.

503 Traversa, D., Di Cesare, A., Conboy, G., 2010. Canine and feline cardiopulmonary parasitic nematodes in
504 Europe: Emerging and underestimated. Parasit. Vectors. 3: 62.

505 Traversa, D., Di Cesare, A., Milillo, P., Iorio, R., Otranto, D., 2009. Infection by *Eucoleus aerophilus* in dogs
506 and cats: Is another extra-intestinal parasitic nematode of pets emerging in Italy?. Res. Vet. Sci. 87 (2), 270-
507 272.

508 Valenzuela, P., Iglesias, M., Domínguez-Cuesta, M.J., Mora García, M.A., 2018. Meteorological patterns
509 linked to landslide triggering in Asturias (NW Spain): A preliminary analysis. Geosciences. 8, 18.

510 Van Doorn D.C.K., Van de Sande A.H., Nijsse E.R., Eysker M., Ploeger H.W., 2009. Autochthonous
511 *Angiostrongylus vasorum* infection in dogs in the Netherlands. Vet. Parasitol., 162, 163-166.

512 Varodi, E.I., Malega, A.M., Kuzmin, Y.I., Kornyushin, V.V., 2017. Helminths of wild predatory mammals of
513 ukraine. Nematodese. Vestn. Zool. 51(3), 187-202.

514 Verocai, G.G., Schock, D,M, Lejeune, M., Warren, A.L. Duignan, P.J., Kutz, S.J., 2013. *Oslerus osleri*
515 (Metastrongyloidea; Filaroididae) in Gray Wolves (*Canis lupus*) from Banff National Park, Alberta, Canada. J.
516 Wildl. Dis. 49 (2), 422-426.

517 Webster, P., Monrad, J., Kapel, C.M.O., Kristensen, A.T., Jensen, A.L., Thamsborg, S.M, 2017. The effect of
518 host age and inoculation dose on infection dynamics of *Angiostrongylus vasorum* in red foxes (*Vulpes*
519 *vulpes*). Parasit. Vectors. 201710:4.

520 Yao, C., O'Toole, D., Driscoll, M., McFarland, W., Fox, J., Cornish, T., Jolley, W., 2011. *Filaroides osleri*
521 (*Oslerus osleri*): Two case reports and a review of canid infections in North America. Vet. Parasitol. 179,
522 123-129.
523 Zimmermann, B., Sand, H., Wabakken, P., Liberg, O.P., Andreassen, H.P., 2015. Predator-dependent
524 functional response in wolves: from food limitation to surplus killing. J. Anim. Ecol. 84 (1), 102-112.
525
526
527
528
529
530
531
532
533
534
535
536
537
538
539
540
541