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Original Article

Surveillance for gastrointestinal, subcutaneous, and ectoparasites of invasive North American raccoons (*Procyon lotor*) in central Spain

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ABSTRACT

The American raccoon (*Procyon lotor*) is an invasive meso-carnivore which has been introduced and established in many European countries. Although the presence of the raccoon in the Iberian Peninsula was confirmed around 20 years ago, there are few data on pathogens of these animals in this region. For this work, 72 American raccoons from two subpopulations in the central region of the Iberian Peninsula were examined for selected parasites. Ectoparasite species richness (both fleas and ticks) increased during the sampling season and was highest in the Henares subpopulation and on males. Similarly, ectoparasite abundance increased during the sampling season and was highest in Henares and on adult raccoons. Four species of ticks were detected including *Rhipicephalus pusillus* (71%), followed by *R. sanguineus* sensu lato (24%), *Ixodes ventalloi* (3%), and *Dermacentor marginatus* (1.4%). Four species of fleas were detected including *Pulex irritans* (44%), *Ctenocephalides felis* (3%), *C. canis* (1.4%), and *Paraceras melis* (1.4%) infestations. A subset of raccoons ($n = 56$) was examined for intestinal parasites; low prevalence and diversity were found including *Strongyloides procyonis* (4%), *Dilepis* sp. (5%), *Plagiorchis* sp. (2%), and *Moniliformis moniliformis* (2%). Importantly, *Baylisascaris procyonis* was not found. Finally, no subcutaneous nematodes (i.e., *Dracunculus* and *Dirofilaria* spp.) were found in the 56 raccoons examined. The results of this work show that the invasive North American raccoons currently are infected with few endoparasites but are commonly infested with native ectoparasites, several of which can transmit pathogens relevant for public and veterinary health. However, the geographically distinct populations of raccoons in Spain have different introduction histories, thus additional surveillance for parasites is warranted.

1. Introduction

Invasive animal species negatively impact native ecosystems and species through direct (e.g., predation, parasitism or competence for resources) and indirect (e.g., alterations of habitat or food chains) mechanisms (Sakai et al., 2001). On a global scale, 14% of threatened vertebrate species are negatively affected by invasive species (Duenas et al., 2021). There are many explanations for the success of invasive species including absence of predators or severe climatic factors, decrease in native parasites and diseases (enemy release hypothesis), as well as human activity or natural selection of the most adaptive genotypes (Colautti et al., 2004).

The North American raccoon (*Procyon lotor*) is a mesomammal native to the American continent where it ranges from Central America to Southern Canada. Raccoons have become invasive in numerous countries, partially because of their diverse diet and use of many habitat types (Beasley et al., 2007). Raccoons can negatively affect native fauna through direct competition for food or other resources or feeding on specific type of prey, such as bird, crustacean, or other invertebrate species and cause economic losses to farmers (Vilà et al., 2006; Beasley et al., 2007; Beasley and Rhodes Jr, 2008). Finally, raccoons are hosts to numerous parasites and pathogens, many of which are zoonotic or infect

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domestic animals, thus introduction of raccoon pathogens is of significant concern (Beltrán-Beck et al., 2012; Myśliwy et al., 2022; Tedeschi et al., 2022).

The first records of raccoons in Europe date from the 1930s in Germany (Kauhala, 1996). Within the next few decades, raccoons were detected in other nearby countries in Europe (Frantz et al., 2005; Kauhala, 1996; Tedeschi et al., 2022) and recently have been documented in several northern and eastern European countries (Canova and Rossi, 2009; Ćirović and Milenković, 2003; Kauhala, 1996; Tedeschi et al., 2022). Currently, raccoons have become established in at least 27 European countries, and in central Europe, raccoon populations are growing exponentially with an population increase of 300% compared to the 1990s (Salgado, 2018; Tedeschi et al., 2022). Genetic analyses suggest that raccoons throughout Europe have arisen from a combination of multiple independent introductions from various sources and range expansion (Fischer et al., 2015; Fischer et al., 2017). The first records of the raccoon in Spain were in 2001 from Algaida (Mallorca) (Salgado, 2018). Since then, raccoons has been reported in at least 30 locations on the Iberian Peninsula (García et al., 2012). The largest raccoon population is central Spain (80% of >1000 raccoon records have been in the provinces of Madrid and Guadalajara) (García et al., 2012; Alda et al., 2013; Ceballos-Escalera et al., 2013; Salgado, 2018; Valdez, 2020). Genetic characterization of raccoons in this region showed that there are two subpopulations, each of which originated from an introduction event of raccoons along the Henares and Jarama rivers, respectively (Alda et al., 2013). Although raccoons were sporadically reported in the Community of Madrid between 2004 and 2007, it was in 2008 when the existence of a well-established population in this region was confirmed (García et al., 2012). The origin of these raccoons seems to be related to escapes and/or deliberate releases of individuals (García et al., 2012).

In their native range, raccoons are hosts for a very high diversity of ectoparasites and endoparasites, many of which are zoonotic (Otranto and Deplazes, 2019). In addition, raccoons introduced to other regions have also become infested with ectoparasites, and possibly endoparasites, native to their new region and are infected with tick- or flea-borne pathogens (Sashika et al., 2010; Sashika et al., 2011; Baba et al., 2013; Doi et al., 2018; Hildebrand et al., 2018; Doi et al., 2021; Sharifdini et al., 2021; Hildebrand et al., 2022; Myśliwy et al., 2022). Ectoparasites are a concern because raccoons could serve as additional hosts for ticks that may transmit important veterinary or human pathogens and evidence of *Ehrlichia* infection has been noted in raccoons in Madrid, Spain suggesting raccoons in Spain are hosts to ticks (Criado-Fornelio et al., 2018). There are two endoparasites of particular interest for Spain, *Baylisascaris procyonis* and *Dracunculus* sp. *Baylisascaris procyonis* is a parasite of public health concern, but this parasite can also cause disease in numerous wildlife and domestic species (Logiudice, 2003; Page, 2013; Kazacos, 2016; Sapp et al., 2016; Yabsley and Sapp, 2017; Sapp et al., 2020). The prevalence of *B. procyonis* infection in North American raccoon populations can be high (>90%). In Europe and Asia, invasive raccoons in many countries are infected with *B. procyonis*, although prevalence and distribution varies considerably at local levels (Hohmann et al., 2002; Al-Sabi et al., 2015; Kazacos, 2016; Heddergott et al., 2020; Maas et al., 2022; Frantz et al., 2021). Although *B. procyonis* has not been reported in raccoons from Spain, two captive white-headed lemurs (*Eulemur albifrons*) from Lugo, Galicia were diagnosed with baylisascarisis after being in close contact with captive raccoons (Martinez et al., 2015). Finally, raccoons in North America are common hosts for *Dracunculus insignis*, a parasite that can infest dogs and cats (Cleveland et al., 2018; Williams et al., 2018; Cleveland et al., 2020). Recently, a dog from Toledo, Spain was infected with a *Dracunculus* sp. that is most similar to *Dracunculus* sp. OPO28 (Diekmann et al., 2020). Although *Dracunculus* sp. OPO28 parasite was initially detected in a Virginia opossum (*Didelphis virginianus*), raccoons are a suspected host (Cleveland et al., 2020).

Currently there are no data on parasites of raccoons in Spain. Thus, the primary objective of this study was to evaluate invasive raccoons as hosts for parasites in the Community of Madrid in central Spain. There was a particular focus on ectoparasites, gastrointestinal parasites (specifically *B. procyonis*) and the subcutaneous parasite, *Dracunculus* sp. In addition, we analyzed the data to determine if there were differences in prevalence or abundance of parasites by sampling date, host sex or age, or by raccoon population.

2. Materials and methods

2.1. Collection of samples

Raccoons were captured using live capture cage traps as part of the raccoon population control and eradication campaign carried out by the Community of Madrid. Individuals were transferred to the Centro de Recuperación de Animales Silvestres (CRAS) Madrid-Viñuelas for humane euthanasia and sampling. From March to July 2021, 72 raccoons were captured from 11 locations in Madrid (Table 1; Fig. 1). At total of 33 raccoons were from the Henares subpopulation and 39 individuals were from the Jarama subpopulation (as defined by Alda et al. (2013)). A total of 41 males and 31 females (65 adults and seven juveniles) were sampled. Specific capture location and the approximate age and sex was recorded for each individual. All animal capture and sampling methods were approved by the Dirección General de Biodiversidad y Recursos Naturales de la Comunidad de Madrid (document verification code: 1276516383071600270582).

Each raccoon was carefully examined for ectoparasites (fleas and ticks) by slowly combing the hair and all ectoparasites found were preserved in 70% ethanol. No raccoons had lesions consistent with mange. From a subset of raccoons ($n = 56$), the animals were fully skinned and examined for subcutaneous parasites (e.g., *Dracunculus* or *Dirofilaria*) and the gastrointestinal tracts (stomach to colon) were collected and frozen until examination for helminth parasites.

2.2. Preparation and processing of samples

To examine for gastrointestinal parasites, the stomach and intestines were linearized and vigorously washed in water. The intestinal contents were washed through a 0.1 mm sieve and any retained material was preserved in 70% ethanol. The entire container was examined in small volumes under a dissecting scope.

Table 1
General information about the raccoons (*Procyon lotor*) captured in Madrid localities.

Locality	Subpopulation	No. of raccoons	Sex [1]	Age
San Fernando de Henares	Henares	19	13M, 6F	Adults
Mejorada del Campo	Henares	6	5M, 1F	Adults
Alcalá de Henares	Henares	6	4M, 2F	Adults
Los Santos de la Humosa	Henares	2	1M, 1F	Adults
Rivas-Vaciamadrid	Jarama	11	4M, 7F	Adults
Velilla de San Antonio	Jarama	9	5M, 4F	Adults
Coslada	Jarama	5	1M, 4F	2 Adults, 3 Juveniles
Madrid-Barajas	Jarama	2	2M	Adults
Alcobendas	Jarama	3	2M, 1F	1 Adult, 2 Juveniles
Fuenlabrada	Jarama	1	1M	Adult
Madrid	Jarama	8	3M, 5F	6 Adults, 2 Juveniles
Total		72	41M, 31F	65 Adults, 7 Juveniles

[1] M = males, F = females.

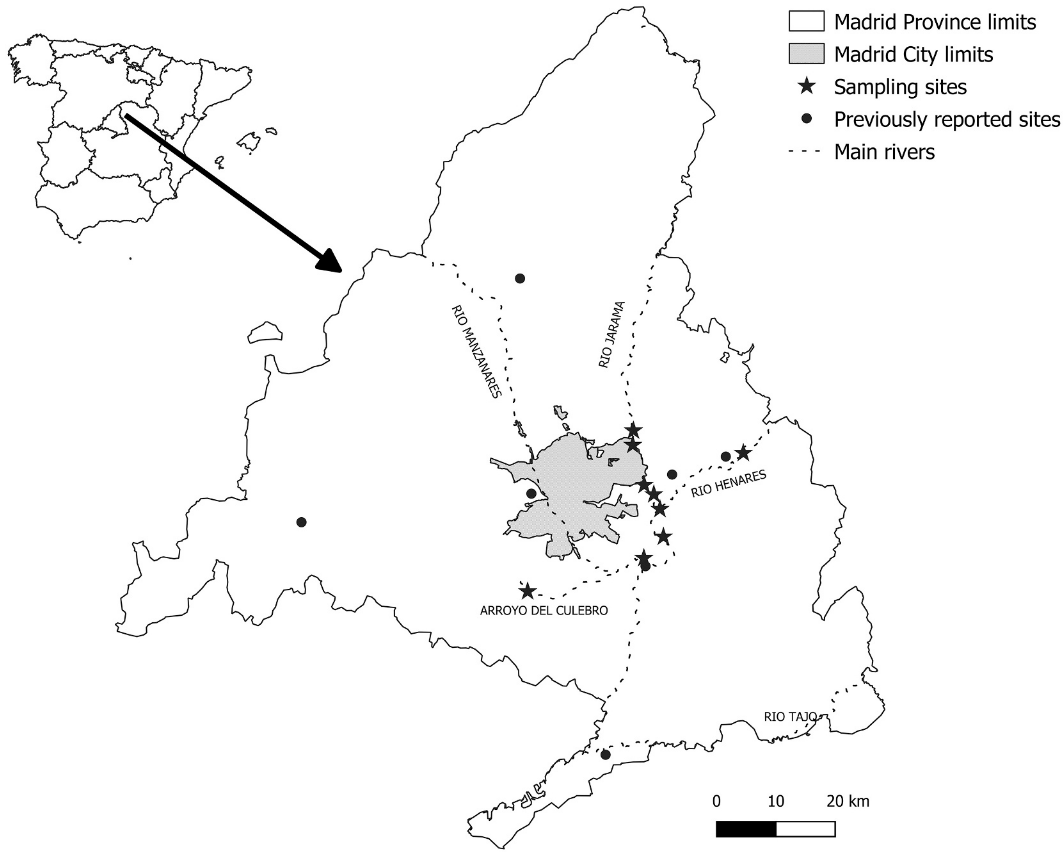

Fig. 1. Locations where raccoons (*Procyon lotor*) were captured in Madrid, Spain (stars). Also shown are areas where raccoons had previously been reported within this region (circles).

2.3. Identification of parasites

Ectoparasites were morphologically identified to species using published keys and descriptions for ectoparasites (Estrada-Peña et al., 2018a, 2018b, 2018c; Pratt, 1956; Walker et al., 2003). Endoparasites were identified to genus or species using published keys and descriptions (Van Cleave, 1923; Amin, 1987; Khalil et al., 1994; Little, 1966a; Little, 1966b; Amin et al., 2016).

2.4. Statistical analyses

The species richness for both ectoparasites and endoparasites was calculated and the prevalence, mean intensity and relative abundance values for each species were calculated as described by Margolis et al. (1982). General Linear Models (GLM) were used to examine differences between the richness, abundance and prevalence of the different parasites and sex of the individuals (male or female), age (adult or juvenile), subpopulation to which they belong (Henares or Jarama as defined by Alda et al. (2013)) and date (transformed to Julian date). For ectoparasites, overall richness and abundance were examined, while prevalences were examined separately for ticks and fleas. Statistical analyses were not conducted for endoparasites because of their low prevalence. Analysis of the data was done using the lme4 package (v1.1–26; Bates et al., 2015) in R.

Table 2
Summary of data for ectoparasites and gastrointestinal parasites collected from raccoons (*Procyon lotor*) from central Spain.

Parasite Group	Species	n	No. of infested raccoons (%)	Total No. of parasites collected	Mean intensity	Relative abundance
Ectoparasites						
Ticks	*Rhipicephalus pusillus*	72	51 (70.8)	342	6.71	4.75
	Rhipicephalus sanguineus sensu lato	72	17 (23.6)	44	2.59	0.61
	Ixodes ventalloi	72	2 (2.8)	2	1	0.03
	Dermacentor marginatus	72	1 (1.4)	1	1	0.01
Fleas	*Pulex irritans*	72	32 (44.4)	59	1.84	0.82
	Ctenocephalides canis	72	1 (1.4)	1	1	0.01
	Ctenocephalides felis	72	2 (2.8)	2	1	0.03
	Paraceras melis	72	1 (1.4)	1	1	0.01
Endoparasites						
Nematodes	*Strongyloides procyonis*	56	2 (3.6)	3	1.5	0.054
	Unidentified Nematoda	56	4 (7.4)	4	1	0.071
Trematode	*Plagiorchis* sp.	56	1 (1.8)	1	1	0.018
Cestode	*Dilepis* sp.	56	3 (5.4)	3	1	0.054
Acanthocephalan	*Moniliformis moniliformis*	56	1 (1.8)	2	2	0.036

3. Results

3.1. Ectoparasites

The only ectoparasites detected on raccoons were fleas and ticks (Table 2). Most of raccoons were infested with one or two ectoparasite species (38.9% and 37.5%, respectively), but 11.1% of raccoons were infested with three species. Tick infestation rates were higher (73.6%, 53 raccoons) compared with fleas (44.4%, 32 raccoons). Coinfection with fleas and ticks were observed for 22 raccoons (30.6%).

For ticks, *R. pusillus* (71% prevalence) was the most common tick found followed by *R. sanguineus* sensu lato (s.l.). which occurred on 24% of raccoons (Table 2). Note that the *R. sanguineus* s.l. ticks morphologically were identified as *R. turanicus* which is a species that is debated to occur in Spain (i.e., could be a unique species in the *R. sanguineus* s.l. group) (Dantas-Torres et al., 2018; Estrada-Peña et al., 2018c). Along with several other species, *R. turanicus* is part of the *R. sanguineus* complex; therefore, we have only identified these ticks to the species complex. Few individuals were infested with *Ixodes ventalloi* (2.8%) or *Dermacentor marginatus* (1.4%) (Table 2). *Pulex irritans* was the most prevalent flea species (44%) (Table 2). Three raccoons (4.2%) were infested with *Ctenocephalides* spp. and one was infested with a single *Paraceras melis* (Table 2).

Ectoparasite species richness significantly increased during the sampling season ($p = 0.0002$) (Fig. 2A). Species richness was significantly greater in the Henares subpopulation compared to the Jarama subpopulation ($p = 0.0036$) with all 8 ectoparasite species being found in Henares subpopulation (Fig. 2B, Supplemental Table 1, Supplemental Table 2). Furthermore, species richness was significantly higher in males than females ($p = 0.0186$) (Fig. 2C). No significant differences were

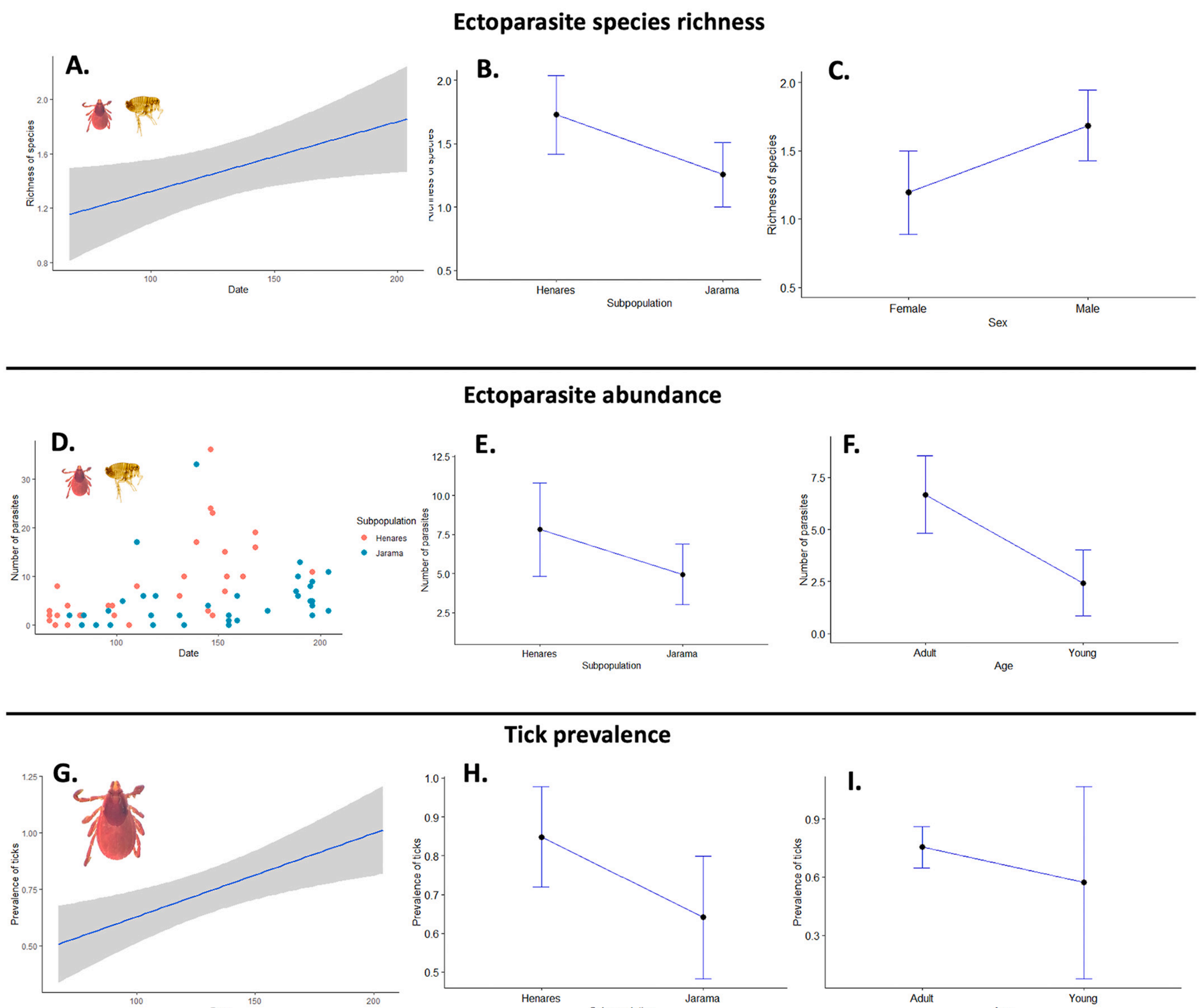

Fig. 2. A. Representation of the relationship between the ectoparasite species richness in raccoons (*Procyon lotor*) and the date. The darker zone represents the 95% confidence interval. B. Ectoparasite species richness in two subpopulations of raccoons in Madrid, Spain. C. Ectoparasite species richness in male and female raccoons. D. Representation of the relationship between the number of ectoparasites in raccoons and the date. Red points correspond to raccoons of the Henares subpopulation while blue points correspond to raccoons of the Jarama subpopulation. E. Ectoparasite abundance in adult and young raccoons. F. Ectoparasite abundance in two subpopulations of raccoons in Madrid, Spain. G. Representation of the relationship between the prevalence of tick infection in raccoons and the date. The darker zone represents the 95% confidence interval. H. Prevalence of ticks in two subpopulations of raccoons in Madrid, Spain. I. Prevalence of ticks in adult and young raccoons. Flea image from https://britishfleas.myspecies.info/file/95 and used under CC BY 4.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

found between adult and juveniles.

The abundance of ectoparasites significantly increased during the sampling season ($p = 1.21e\text{-}05$) (Supplemental Table 3; Fig. 2D). It was also higher in racoons from the Henares subpopulation ($p = 0.0185$) (Fig. 2E) and adults than in juveniles ($p = 0.0261$) (Fig. 2F). No significant differences were found between male and females (Supplemental Table 3).

Specifically for ticks, the prevalence was significantly greater in raccoons from the Henares subpopulation compared to the Jarama subpopulation ($p = 0.004$) (Supplemental Table 4; Fig. 2H). Prevalence was significantly higher for adult racoons compared to juveniles ($p = 0.0298$) (Supplemetnal Table 1, Fig. 2I). Prevalence of tick infestation increased as the season advanced ($p = 0.0006$) (Supplemental Table 4; Fig. 2G). *R. pusillus* whereas the prevalence of *R. sanguineus* s.l. increased in later months (Fig. 3). No significant relationship was found for sex (Supplemental Table 4).

For fleas, no significant differences were found for any of the studied variables (Supplemental Table 5; Fig. 3). The most comomonly detected flea, *P. irritans*, was found in all months sampled (Fig. 3).

3.2. Endoparasites

A total of 56 raccoons were examined for gastrointestinal and subcutaneous parasites. Although no stomach parasites were observed, five species of parasites were observed in the small intestine of sampled raccoons with eight raccoons (14.3%) being infected with one (14.29%) parasite and a single raccoon (1.8%) being infected with three parasite species.

Overall, the prevalence, mean intensity and relative abundance were low for all endoparasites (Table 2). A single species of nematode (*Strongyloides procyonis*), cestode (*Dilepis* sp.), acanthocephalan (*Moniliformis moniliformis)* (15.38%) and trematode (*Plagiorchis* sp.) were detected in 1–3 raccoons (Table 2). An additional four raccoons were infected with damaged nematodes that could not be identified. No subcutaneous nematodes (i.e., *Dracunculus* or *Dirofilaria* spp.) were found.

4. Discussion

4.1. Ectoparasites

Overall, four species of ticks and four species of fleas were found on raccoons. All eight species were detected on raccoons from the Henares subpopulation and this subpopulation had a higher ectoparasite richness and abundance compared to those from Jarama subpopulation.

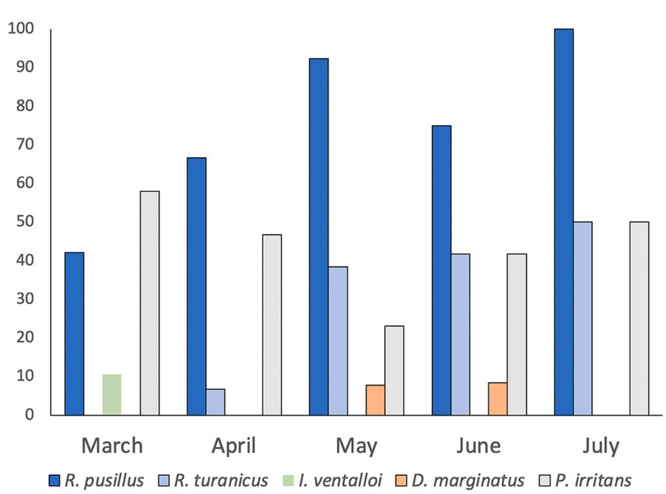

Fig. 3. Monthly prevalence of most commonly collected tick and flea species on raccoons (*Procyon lotor*) in Madrid, Spain.

Although the reason for this difference is unknown, the natural history and host diversity of ticks and fleas likely are important factors (Monello and Gompper, 2009). The Henares region includes a large city (Alcala de Henares) but is also more natural compared to the more industrialized Jarama region; therefore, raccoons would have more opportunities to encounter ectoparasites from a diversity of habitats. However, the five ectoparasite species absent from the Jarama subpopulation occurred in low prevalence (3–6%) so additional sampling may have resulted in their detection. In addition, male raccoons had a higher species richness, but not abundance. The home territory of male raccoons is generally 2–3 times larger than females and males also disperse to new territories (Hohmann et al., 2000). Both of these factors could result in greater exposure to ectoparasites. Finally, the ectoparasite richness and abundance increased throughout the sampling season, although this effect was only significant for ticks when ticks and fleas were examined separately.

4.1.1. Ticks

The four tick species that were identified on raccoons are native to the Mediterranean region (Estrada-Peña et al., 2004; Estrada-Peña et al., 2018d). Previous studies also noted that invasive raccoons were infested with tick species that were endemic to that region including in Germany (*I. hexagonus* and *I. ricinis*), Iran (*Haemaphysalis concinna*, *I. ricinus*, *R. sanguineus* and *R. turanicus*), Caucasia (specific region not specified) (*I. ricinus* and *R. turanicus*), and Japan (*H. flava*, *H. megaspinosa, H. longicornis, H. japonica*, *I. ovatus*, *I. persulcatus*, *I. pavlovskyi,* and *I. tanuki*) (Aliev and Sanderson, 1966; Lux and Priemer, 1995; Sashika et al., 2011; Doi et al., 2021; Sharifdini et al., 2021). Although this is the first study of ectoparasites on raccoons in Spain, similar high prevalences of the same ectoparasite species have been reported on other wild mammals of the Iberian Peninsula, such as red foxes (*Vulpes vulpes*), wildcats (*Felis silvestris*), Egyptian mongooses (*Herpestes ichneumon*) and European badgers (*Meles meles*) (Domínguez, 2004; Millán et al., 2007; Márquez et al., 2009; Sagarna, 2010; Domínguez-Peñafiel et al., 2011). Importantly, we did not find *I. ricinis* or any *Hyalomma* or *Haemaphysalis* species on raccoons in Spain. These ticks are associated with several important pathogens and they are found on raccoons in other regions and on wild mammals in the central region of the Iberian Peninsula, although reports from wild carnivores are rare (Estrada-Peña et al., 2004; Toledo et al., 2009; Estrada-Peña et al., 2018d; Sharifdini et al., 2021; White et al., 2021).

Many of the tick species detected on the raccoons are vectors of pathogens of veterinary and public health concern which highlights the importance of raccoons hosting these ticks. In addition, a number of *Rickettsia* and *Anaplasma* spp. have been reported in invasive raccoons in Japan, Poland and Germany (Sashika et al., 2010; Sashika et al., 2011; Baba et al., 2013; Hildebrand et al., 2018; Hildebrand et al., 2022). *Rhipicephalus pusillus* typically infests the European rabbit (*Oryctolagus cuniculus*), but it can be found in a great diversity of wild fauna, including rodents, ungulates and carnivores (Estrada-Peña et al., 2018d). It is a vector of human rickettsial pathogens such as *Rickettsia sibirica mongolitimonae, R. massiliae* and *Anaplasma* spp. (Santos-Silva, 2018; Estrada-Peña et al., 2018d; Toledo et al., 2009). *Rhipicephalus sanguinius* s.l. (often reported as *R. turanicus*) also infests a wide range of domestic and wild species, including birds and mammals (Estrada-Peña et al., 2004) and is also a suspected vector of *R. aeschlimannii* and *R. massiliae* (Toledo et al., 2009). Although *D. marginatus* was rare on raccoons in our study, this species also infest a large diversity of hosts, including carnivores, ungulates or insectivore mammals (Estrada-Peña et al., 2018d). This tick is an important vector of numerous pathogens including human pathogens such as *Rickettsia conori* (Boutonneuse fever or Mediterranean spotted fever), *R. slovaca* (TIBOLA, tick-borne lymphadenopathy), Crimean-Congo haemorrhagic fever virus, Omsk haemorrhagic fever virus, and Tick-borne encephalitis virus (Estrada-Peña et al., 2004; Estrada-Peña et al., 2018d) and animal pathogens such as *Babesia canis*, causative agent of babesiosis in domestic dogs (Estrada-

Peña et al., 2004). Other pathogens associated with this tick include *Francisella tularensis* (tularemia), *Borrelia burgdorferi* (Lyme disease) and *Anaplasma* spp. (Merino et al., 2005; Toledo et al., 2009). Finally, *I. ventalloi* was also rarely detected on raccoons. Although this tick typically infests lagomorphs, it also infests a wide diversity of wild fauna, including rodents, meso-mammals and birds (Petney et al., 2018; Estrada-Peña et al., 2018d). This tick species can also transmit pathogens such as *Rickettsia helvetica*, *Rickettsia* sp. IRS3, *Coxiella burnetii*, and Eyach and Erve viruses (Estrada-Peña et al., 2018d).

Similar to the results of ectoparasite diversity, the prevalence of tick infestation was higher in the Henares subpopulation. Furthermore, it was observed that the tick prevalence increased as the sampling season progressed. *Rhipicephalus pusillus*, the predominant species detected on the raccoons in this study, potentially drove this trend. All of the ticks detected on raccoons were adults despite careful examination for small larvae and nymphs. Ticks were found on raccoons during every month sampled (March – July) which generally agrees with published phenology data for these species. Adults of *R. pusillus* are reported to be active from February to June which agrees with our findings although we detected *R. pusillus* on 100% of raccoons sampled in July (Estrada-Peña et al., 2018d; Millán et al., 2007). Because of previous taxonomic uncertainly of *R. sanguineus* s.l. and *R. turanicus* specimens in past studies, the natural history of the tick species is generally poorly understood. In Italy, the peak adult host-seeking activity of adult ticks identified as *R. turanicus* was March to July (peak in April) which is earlier than our peak detections of *R. sanguineus* s.l. on raccoons which was May–July (Di Luca et al., 2013; Dantas-Torres et al., 2018).

4.1.2. Fleas

Three of the flea species that were found on the raccoons are cosmopolitan and infest a large diversity of vertebrate hosts. The human flea, *P. irritans,* was the predominant species on the raccoons while *C. felis* and *C. canis* were rarely collected. Although all three of these flea species occur in the native range of raccoons, they are rarely found on raccoons in North America (Durden and Richardson, 2013; Monello and Gompper, 2010; Richardson et al., 1994). The other flea species detected was *P. melis* which has historically been considered a badger-specialist species. However, it infests a wide range of vertebrate hosts, including raccoons in Germany and Caucasia (Aliev and Sanderson, 1966; Ancillotto et al., 2014; Striese et al., 2020). Interestingly, studies of invasive raccoons in Iran and Caucasia also reported infestations with *P. irritans* but surveys of raccoons in Germany and Poland did not report this flea species (Aliev and Sanderson, 1966; Lux and Priemer, 1995; Haitlinger and Łupicki, 2009; Striese et al., 2020; Sharifdini et al., 2021). Although *C. felis* was rare on raccoons in Spain, this flea species was reported from raccoons in Iran, Germany and Poland (Lux and Priemer, 1995; Haitlinger and Łupicki, 2009; Striese et al., 2020; Sharifdini et al., 2021). Interestingly, studies in Germany found a much higher diversity of fleas including *C. felis, Archaeopsylla erinaceid, Ceratophyllus sciurorum, Ctenophthalmus bisoctodentatus, Archaeopsylla erinaceid, Chaetopsylla matina,* and *P. melis*. The reason for this higher diversity compared to Spain, Poland, Caucasia, and Iran is unknown but could be due to habitat, climate, sympatric vertebrate hosts, sampling technique, among others. Similar to our results, the four flea species detected on raccoons are commonly documented on other wild mammals of the Iberian Peninsula including the red fox, the wildcat, and the European badger and *C. felis* is the predominate species found on domestic dogs (Domínguez, 2004; Gracia et al., 2008; Márquez et al., 2009; Millán et al., 2007). All four of these species are also intermediate hosts (*Dipylidium caninum*) or vectors (*Bartonella* spp., *Trypanosoma pestanai*, and *Rickettsia felis*) of pathogens of medical and veterinary concern (Márquez et al., 2009; Lledó et al., 2010; Fenton et al., 2021; Sgroi et al., 2021).

In contrast to the findings with ticks, flea infestation prevalence decreased throughout the sampling period. In general, mild temperatures and high relative humidity promote increases in flea populations (Durden and Hinkle, 2019). On the Iberian Peninsula, summers are very dry and hot which would explain a decrease in fleas during the summer. Previous studies on wild carnivores of the Iberian Peninsula also noted that fleas were more abundant in winter than in spring (Millán et al., 2007) and the peak abundance of *P. irritans* on domestic dogs was in autumn (Gálvez et al., 2017).

4.2. Endoparasites

We detected a very low prevalence and diversity of gastrointestinal parasites in raccoons from central Spain. In their native range, raccoons are infected with a high diversity of parasites and the species composition varies considerably based on geographic area and habitat. The low prevalence and diversity of parasites we detected was expected based on studies on raccoons in Asia and other regions of Europe. However, prevalence and diversity were lower than reports from invasive raccoons in Poland, Italy, and Japan (Matoba et al., 2006; Sato and Suzuki, 2006; Sato et al., 2006). It is well known that invasive species host far fewer parasite species in those areas where they have been introduced compared to their native range as some parasites may not be translocated or appropriate intermediate hosts may not be available (Torchin et al., 2003). In Spain, different raccoon populations come from different introduction events with some developing from escaped pets, escaped animals from captivity, or unknown sources. For example, the two subpopulations sampled in our current study (Jarama and Henares) are genetically distinct and are estimated to have founded by 2 (Jarama) and 4 (Henares) individuals. It is likely that populations that develop from a limited number of founders do not introduce parasites. For host-specific parasites with direct life cycles, like *S. procyonis*, the population density may be important for transmission; however, there are few data on the current population densities of raccoons from Spain and from other populations previously sampled in Europe and Asia. Alternatively, hosts may acquire new parasites in their introduced range.

Of the four gastrointestinal parasites detected in raccoons, at least one, *S. procyonis,* is known to have come from their endemic range. The prevalence we detected in Spain (4%) was lower than Poland (11%), Italy (27%), Iran (63%), and Japan (28%) (Matoba et al., 2006; Sato et al., 2006; Bartoszewicz et al., 2008; Popiołek et al., 2011; Sharifdini et al., 2020; Romeo et al., 2021). Various *Plagiorchis* species have been reported from raccoons in their native range as well as in Italy, Iran and Japan so the origin of these parasites is unknown (Matoba et al., 2006; Sato and Suzuki, 2006; Sharifdini et al., 2020; Romeo et al., 2021). *Moniliformis moniliformis* was detected in a single raccoon in Spain. A previous report of a *Moniliformis* sp. from a raccoon in the United States was considered to have been acquired from a prey item and was not a parasite of the raccoon (Kresta et al., 2009). Three raccoons were positive for a *Dilepis* sp. which could have been acquired by raccoons in Spain as they have not been reported from raccoons in North America. In Italy, a similar low prevalence (4.5%) of raccoons were positive for a *Dilepis* sp. (Romeo et al., 2021). However, Dilepididae cestodes are common parasites of birds, and rarely rodents and shrews, so these detection in raccoons could be incidental findings of prey parasites (Caira and Jensen, 2017).

The absence of two nematode parasites (*B. procyonis* and *Dracunculus* sp.) was particularly notable. The raccoon roundworm, *B. procyonis*, has been found in raccoons in numerous European countries but not all individual populations are infected (Kazacos, 2016; Maas et al., 2022; Frantz et al., 2021; Lombardo et al., 2022) Although *B. procyonis* was found in lemurs in a zoo that also housed raccoons in northwestern Spain (Martinez et al., 2015), there is currently no evidence of this parasite in free-ranging raccoons in Spain. Recently, Diekmann et al. (2020) reported the first detection of a mammalian *Dracunculus* sp. in Europe. The infected dog was from Toledo and had no travel history. We hypothesized that because this *Dracunculus* sp. was genetically similar to a parasite from North America, that raccoons may have been responsible for the introduction of this parasite in Spain. Toledo is in cnetral Spain but is ~75–125 km away from our general sampling region. No raccoons near Toledo were sampled in this study, although raccoons are known to occur there in certain parts of that region, so infections with *Dracunculus* may occur in that population. Although we did not find these two parasites, raccoon populations vary in their introduction histories; therefore, additional surveillance of other populations in Spain is warranted.

Ethical statement

No animals were specifically harmed for the purpose of this study but were used opportunistically and abided by institutional IACUCs.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.vprsr.2022.100793.

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