

Biogeographical region and host trophic level determine carnivore endoparasite richness in the Iberian Peninsula

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SUMMARY

We address the question of whether host and/or environmental factors might affect endoparasite richness and distribution, using carnivores as a model. We reviewed studies published in international peer-reviewed journals (34 areas in the Iberian Peninsula), describing parasite prevalence and richness in carnivores, and collected information on site location, host biology, climate and detected taxa (Helminths, Protozoa and *Mycobacterium* spp.). Three hypotheses were tested (i) host based, (ii) environmentally based, and (iii) hybrid (combination of environmental and host). Multicollinearity reduced candidate variable number for modelling to 5: host weight, phylogenetic independent contrasts (host weight), mean annual temperature, host trophic level and biogeographical region. General Linear Mixed Modelling was used and the best model was a hybrid model that included biogeographical region and host trophic level. Results revealed that endoparasite richness is higher in Mediterranean areas, especially for the top predators. We suggest that the detected parasites may benefit from mild environmental conditions that occur in southern regions. Top predators have larger home ranges and are likely to be subjected to cascading effects throughout the food web, resulting in more infestation opportunities and potentially higher endoparasite richness. This study suggests that richness may be more affected by historical and regional processes (including climate) than by host ecological processes.

Key words: host-parasite associations, endoparasite richness, Carnivora, Helminths, Protozoa, *Mycobacterium*, Iberian Peninsula.

INTRODUCTION

Parasite prevalence and diversity patterns are highly influenced by environmental factors, such as climate and land cover, and their interplay with ecological factors such as host and parasite identity, interactions, routes of transmission, host spatial distribution and movement patterns and changes over time (Rogers and Randolph, 2003; Patz *et al.* 2004; Jones *et al.* 2008). Due to this complex and dynamic net of interactions, early warning systems and management of zoonotic parasitic diseases require an exhaustive knowledge of zoonoses' origins and spatial patterns at relevant local and regional scales. Among parasites, endoparasites assume particular relevance since they have the potential to profoundly influence and regulate the structure and stability of natural communities (Hudson *et al.* 1998), especially those of their hosts. Regulation can be carried out by both micro- (e.g. *Borrelia* spp. – Murray *et al.* 1999) and macroparasites (e.g. helminths – Spratt, 1990).

Parasite richness and infection are inherently spatial processes, however, biogeographical approaches to the study of parasite richness, distribution and relationship with host populations at intermediate scales (e.g. nationwide) are still needed. The available studies at this scale are often restricted to a single host species (e.g. helminths and Eurasian badgers *Meles meles* Linnaeus, 1758 – Torres *et al.* 2001, or red foxes *Vulpes vulpes* L., 1758 – Barbosa *et al.* 2005).

The level of host colonization depends on the parasite infra-communities and their characteristics (life cycle, niche utilization, mean species diversity, number of high density species), host characteristics (digestive tract type and diet, probability and patterns of colonization by parasites) and the external environment (e.g. temperature and precipitation) (Pence, 1990; Lindenfors *et al.* 2007). Some studies have focused on the ecological processes responsible for differences in parasite community richness (i.e. number of parasite species) (e.g. Bush *et al.* 1990; Lindenfors *et al.* 2007). The analysis of more than 7000 carnivore-parasite species pairs described by Lindenfors *et al.* (2007) found that higher host body mass, population density, geographical range size, distance from the equator and home-range area

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influence positively parasite species richness. Further, other studies have pointed out the positive correlation of host population density (Nunn *et al.* 2003), basal metabolic rate (Morand and Harvey, 2000), diet (Watve and Sukumar, 1995) and longevity (Torres *et al.* 2006), and the negative correlation of latitude (Nunn *et al.* 2005), gregariousness and predatory pressure (i.e. trophic level) (Watve and Sukumar, 1995) with parasite diversity. The above-mentioned species-specific studies focused on Iberian carnivores (Torres *et al.* 2001; Barbosa *et al.* 2005) highlighted the importance of the biogeographical region characteristics (namely the predator diet in the area, local patterns of temperature and mean rainfall, and animal and plant biocenosis structure – Torres *et al.* 2001), distance to urban centres, predator densities, and water availability (e.g. lower soil permeability) on parasite diversity.

Moreover, parasite adaptive evolution may also contribute to this diversity and it has been shown that there is a high degree of evolutionary association between parasites and hosts (Poulin, 1995). For instance, in the Iberian Peninsula the Lyme borreliosis group of tick-borne spirochetes presents various patterns and levels of host specialization, with some being associated with birds (e.g. *Borrelia valaisiana* and *B. garinii*) and others with rodents (e.g. *B. afzelii*) (Vitorino *et al.* 2008) and carnivores (e.g. *B. burgdorferi*) (Doby *et al.* 1991).

External environmental factors alone may determine parasite survival and population dynamics even before the effect of host condition is evident. For example, several landscape-related factors, such as the presence of human infrastructures (e.g. dams and irrigation schemes), climatic (e.g. water temperature), physical (e.g. water velocity) and chemical (e.g. water pH) variables, have been identified as determining features in the transmission of *Schistosoma* species in Africa, since they constrain the distribution of an intermediate host (water snails) of those parasites (Brooker, 2007). Temperatures and moisture/precipitation also influence the development and survival of helminth infective stages (Kates, 1965), and therefore may promote or restrain parasite transmission. Moreover, heterogeneity of environmental conditions has been suggested to affect parasite community composition by one of the few biogeographical studies of parasite richness (Torres *et al.* 2006).

The above examples suggest that parasite richness may be driven by one of two alternative factors: (1) hosts bio-ecological features or (2) the external environment context in which parasite populations exist; or their combined effect. With the aim of contributing to the topic of multispecies analysis at intermediate geographical scales, we tested hypotheses on the importance of host and/or environmental factors upon endoparasite richness and distribution in the Iberian Peninsula, using

carnivores as models. Carnivores are a good model to study endoparasite richness, since they often have large home ranges and distribution areas, encompassing different landscape units (Macdonald and Kays, 2005), they generally have a broad prey spectrum (Macdonald and Kays, 2005), which increases the probability of infection by parasites, and they are hosts to a wide variety of parasites, with high interspecific variation. Reviews by Campillo *et al.* (1994) and Torres *et al.* (2006), describing the hosts of Iberian helminths and protozoans, show that the number of endoparasites varies between 37 (for the red fox) or 25 (common genet, *Genetta genetta* L., 1758), and 3 (otter, *Lutra lutra* L., 1758) or 4 (stoat, *Mustela erminea* L., 1758). More specifically, we wanted to understand whether the richness of carnivore-infesting endoparasites was related to (1) the bio-ecological characteristics of the hosts (e.g. geographical range, body mass, longevity, diet, predatory pressure/trophic level, gregariousness), (2) the climate patterns of the region (e.g. temperature, precipitation – Kates, 1965) or (3) a combination of both (Hybrid model). Given the complexity of hosts-parasites, parasites-parasites and parasites-environment interactions, which vary among host and parasite species, we hypothesize that, due to the high bioclimatic heterogeneity (EEA, 2008) and carnivore niche specializations (e.g. Iberian lynx *Lynx pardinus* Temminck, 1827 – Ferrer and Negro, 2004) found within Iberia, parasite species richness will depend upon the interaction between climate and host characteristics.

MATERIALS AND METHODS

Data collection

We reviewed published studies in international peer-reviewed scientific journals focused on parasitology and zoology, describing parasite prevalence (e.g. abundance of individual parasite species) and richness in carnivores (Table 1). We restricted our search to the Iberian Peninsula (Fig. 1), and only studies describing the specific location of the data (e.g. latitude, longitude, valley, protected area, etc.) were considered. For each study, we gathered information on the number and identity of endoparasite species (Acanthocephala, Cestoda, Digenea, Nematoda, Trematoda, Protozoa and *Mycobacterium* spp.), host bio-ecological features, site location and climate characteristics of the region. Although relevant, information on parasite prevalence (i.e. proportion of individuals in a population that are infected) could not be considered because it was not mentioned in all the studies we reviewed. Therefore, only absence/presence data were recorded for each parasitic species.

For each study we recorded the carnivore(s) species. In addition, we also reviewed the literature

Table 1. Sources of data on carnivore parasites in Iberia

Reference	Study area	Carnivore host	Common name of host
Aranaz <i>et al.</i> (2004)	Doñana National Park (SW Spain)	<i>Lynx pardinus</i> Temminck, 1827	Iberian lynx
Briones <i>et al.</i> (2000)	Doñana National Park (SW Spain)	<i>Lynx pardinus</i>	Iberian lynx
Criado-Fornelio <i>et al.</i> (2000)	Guadalajara (Central Spain)	<i>Vulpes vulpes</i> Linnaeus, 1758	Red fox
Domínguez and Torre (2002)	Burgos (N Spain)	<i>Canis lupus</i> Linnaeus, 1758	Iberian wolf
Eira <i>et al.</i> (2006)	Dunas de Mira (Central West Portugal)	<i>Vulpes vulpes</i>	Red fox
Ferreira <i>et al.</i> (1991)	P.N. Montesinho (NE Portugal)	<i>Vulpes vulpes</i>	Red fox
Gortázar <i>et al.</i> (1998)	Central Ebro Valley (NE Spain)	<i>Vulpes vulpes</i>	Red fox
Mañas <i>et al.</i> (2005)	Catalonia (NE Spain)	<i>Vulpes vulpes</i>	Red fox
Martín-Atance <i>et al.</i> (2005)	Doñana National Park (SW Spain)	<i>Vulpes vulpes</i>	Red fox
Martínez-Carrasco <i>et al.</i> (2007)	Altiplano region (North of Murcia, Spain)	<i>Vulpes vulpes</i>	Red fox
Millán and Casanova (2007)	Southern Andalusia (SW Spain)	<i>Herpestes ichneumon</i> Linnaeus, 1758; <i>Genetta genetta</i> Linnaeus, 1758	Egyptian mongoose; common genet
Millán <i>et al.</i> (2004)	Basque Country (NE Spain)	<i>Meles meles</i> Linnaeus, 1758	Eurasian badger
Petrucci-Fonseca (1990)	Northern Portugal	<i>Canis lupus</i>	Iberian wolf
Ribas <i>et al.</i> (2009)	P. N. Montseny (NE Spain)	<i>Genetta genetta</i>	Common genet
Rosalino <i>et al.</i> (2006)	Grândola Mountain (SW Portugal)	<i>Meles meles</i>	Eurasian badger
Santos-Reis (1989)	Samarra (Central Portugal)	<i>Mustela nivalis</i> Linnaeus, 1766	Least weasel
Segovia <i>et al.</i> (2007)	Cantabrian Mountains (NW Spain); Pyrenean Mountains (NE Spain); Minorca island (Spain); Majorca island (Spain)	<i>Martes martes</i> Linnaeus, 1758	Pine marten
Silva 2010	P. N. Peneda-Gerês (NW Portugal)	<i>Canis lupus</i> ; <i>Vulpes vulpes</i>	Iberian wolf
Torres <i>et al.</i> (2006)	Barcelona and Girona	<i>Neovison vison</i> Schreber, 1777	American mink
Vicent <i>et al.</i> (2004)	Doñana National Park (SW Spain)	<i>Lynx pardinus</i>	Iberian lynx

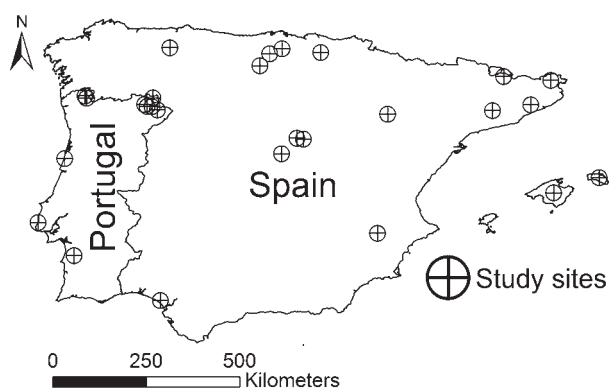


Fig. 1. Location of the reviewed studies used in our analysis.

to gather information on the host species: weight and geographical range (Palomo and Gisbert, 2002), longevity in the wild (<http://www.demogr.mpg.de/>),

trophic level (small, meso or top predator), type of diet (generalist, specialist), and life strategies (solitary, gregarious) (e.g. Palomo and Gisbert, 2002).

Study area location was described as the easting (x) and northing (y) coordinate in lat/long. When not explicitly reported, approximate location was estimated using the area's geographical description within a Geographical Information System (GIS). We also recorded sample sizes, which corresponded to the number of faeces, guts or individuals analysed in the reviewed studies.

Finally, we used a GIS in ArcGIS 9.3 (ESRI, California, USA) to collect climatic and biogeographical data for each study location. The mean annual temperature and mean annual precipitation for the sites were determined using data available at the WorldClim – Global Climate Data database (<http://www.worldclim.org/>). Data were downloaded in the

Table 2. Candidate variables assumed to influence parasitic burden of carnivores in Iberia (PIC – Phylogenetic Independent Contrasts)

	Variable	Acronym	Type
Dependent	Residuals of endoparasites diversity	Res_Div_sp	Covariate
Independent	Host weight (g)	H_weight	Covariate
	Host longevity (year)	H_longev	Covariate
	PIC (Host weight)	PIC_H_weight	Covariate
	PIC (Host longevity)	PIC_H_longiv	Covariate
	Mean annual precipitation (mm)	M_Precip	Covariate
	Mean annual temperature (°C)	M_Temp	Covariate
	Trophic level	Troph_level	Factor (Top; mesopredator)
	Diet	Diet	Factors (Specialist; Specialist)
	Geographical range in the Iberian Peninsula (IP)	Geo_range	Factors (5 categories: <20% of IP; 20%–40%; 40%–60%; 60%–80%; 80%–100%)
	Biogeographical region	Bio_region	Factors (2 categories: Atlantic and Mediterranean)
Random factor	Life strategies	Life	Factor (Gregarious; solitary)
	Host species	SP	Factor
	Study area region	Reg	Factor

format of global climate layers (climate grids) with a spatial resolution of 2.5 arc min ($\sim 5 \text{ km}^2$). These layers represent the mean monthly temperature and mean total early precipitation values, restricted to the period 1950–2000 (see data details in Hijmans *et al.* 2005). Data regarding biogeographical regions were downloaded from the European Environment Agency database (EEA, 2008; <http://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-2008>) and overlapped with the studies' geographical locations (Table 2). Although 3 bioclimatic regions are found in the Iberian Peninsula (Alpine, Atlantic and Mediterranean), the studies analysed here fell in either the Atlantic or the Mediterranean regions. A single exception was 1 study in the Alpine region whose location neighboured the Atlantic region limits and that, therefore, was included in the latter region (also because the climatic characteristics of the Alpine and Atlantic regions are more alike than with the Mediterranean region).

Data analysis

Since the reviewed studies presented a high variation in sample size, and this parameter influences the number of species detected (Soetaert and Heip, 1990; Poulin, 1998), we calculated the residual of parasite species richness from a linear regression on the studies sample size (Lindenfors *et al.* 2007). The remaining used variables are listed in Table 2.

All the following analyses were performed using R software, version 2.11.0 (R Development Core Team 2008) and the specified packages. We assessed the data for spatial autocorrelation by calculating Moran's I index ("ape – Analyses of Phylogenetics and Evolution" package – Paradis *et al.* 2004). Spatial autocorrelation, which is intrinsic to most biological data, implies the violation of the assumption of

independence, resulting in possible pseudoreplication (Legendre, 1993; Carl and Kühn, 2007). Due to the significant results, we opted to define geographical areas for each study, according to their proximity, and use this variable (Reg) as a random factor in the subsequent models. Data overdispersion was not tested since residuals showed a distribution not significantly different from normal (K-S = 1.092, $P = 0.184$).

Since bio-physical variables are often correlated (i.e. their variations assume similar patterns), it is important to test for multicollinearity between variables in order to exclude those highly correlated and be able to separate the effects of 2 (or more) variables on a response variable (Tabachnick and Fidell, 1996). Thus, we tested the correlation between continuous variables using the Spearman's rank correlation coefficient (rs), the Kendall's Tau (T) for ordinal variables, and Cramer's V when at least one of the variables was nominal (Siegel and Castellan, 1988). From those variable pairs that presented significant correlations ($P < 0.05$), we selected the one with a higher correlation with the response variable.

To test whether host characteristics, environmental patterns or a combination of both influence carnivore endoparasite richness (as defined above) (see Table 2 for variable description), we used a General Linear Mixed Model (GLMM) with a Gaussian distribution and an identity link function (Zuur *et al.* 2009). The use of a Gaussian distribution function was supported because the data had a tendency to normality. We created a set of 18 models, aggregated into 3 categories: (i) host model (host weight and trophic level), (ii) environmental model (temperature and biogeographical region), and (iii) hybrid models (combination of environmental and host features, including a full model with all

variables). Furthermore, since several of the reviewed studies concerned the same species, this could be introducing a bias towards the causal characteristics of the more represented species. To deal with this bias and to account for the effects of host phylogenetic relationships we also included the host species (SP) as a random effect. We also controlled for the confounding effect of phylogeny by considering the phylogenetic independent contrasts (PICs) of the variables host weight and host longevity. PHYLOCOM 4.1 (Webb *et al.* 2008) was used to compute PICs from a phylogeny of host sequences (Oliveira *et al.* 2010) of the nuclear gene IRBP (interphotoreceptor retinoid-binding protein). The phylogeny was estimated using maximum likelihood in TREEFINDER (Jobb *et al.* 2004). A phylogeny of host sequences (Fernandes *et al.* 2008) of the mitochondrial gene *cytb* (cytochrome *b*) was also estimated, but the IRBP tree topology more faithfully represented the carnivore consensus phylogeny from Flynn *et al.* (2005). The correlation between PICs for both variables calculated from the IRBP phylogeny was tested so that, if significant, the variable with the higher correlation with the dependent variable could be retained for modelling.

The GLMM was built using the 'lme4 – Linear mixed-effects models using Eigen and S4 classes' package for R (Bates and Maechler, 2010).

We used an information criterion model selection procedure to detect which was the most parsimonious model to explain the measured variability in carnivore endoparasite standardized richness. We used an extension of the Akaike's information criterion for small samples (AICc), as this index includes a bias-adjustment for small sample sizes. AICc should be used if the ratio between the number of cases (*n*) and number of parameters (*K*) is less than 40 (Burnham and Anderson, 2002, 2004). The best models were assumed to be those with the lowest AICc value. We also calculated the difference in AICc between each pair of models (ΔAICc), which corresponds to the difference between the AICc of the *i*th model and the minimum AICc value. This metric allows determination of how good the *i*th model is as an approximation to the expected best model. We considered best models to be those with $\Delta\text{AICc} < 2$ (Burnham and Anderson, 2002, 2004). Finally, we also calculated the Akaike weights (w_i) to obtain each model's probability of being the best model for the data (Burnham and Anderson, 2004).

RESULTS

We reviewed 20 studies, corresponding to a total of 34 different study areas, widely distributed within the Iberian Peninsula (Fig. 1 and Table 1). These sites showed a non-significant spatial autocorrelation (Moran $I = 0.076$, $P = 0.236$). Being conservative, and although no significant autocorrelation was

detected, we included the study location as a random effect to account for possible bias associated with this factor in the models.

We detected that several explanatory variables presented multicollinearity. From the original set of candidate variables that could be influencing endoparasite richness, only 5 were used for the subsequent modelling procedure: host weight, PIC host weight, mean annual temperature, trophic level and biogeographical region (Table 2).

The most parsimonious model to describe the richness of endoparasites in carnivore species was a hybrid model where biogeographical region and carnivore trophic level were included (Tables 3 and 4). This model had the lowest ΔAICc , highest support (highest w_i , reaching almost 0.74), and showed a negative effect of biogeographical region 2 (Mediterranean) and of host trophic level (top predator) on residuals of parasite species richness (i.e. these 2 variables reduce the residuals and thus influence positively parasite diversity in hosts).

DISCUSSION

Our study revealed that the richness of endoparasites in Iberia is higher in the Mediterranean biogeographical region, and when host species correspond to top predators (e.g. wolf, *Canis lupus*, and Iberian lynx). The distribution and success of endoparasite infection is usually associated with the environment, heterogeneity in parasite burden among individuals, age and genetic specificities of hosts, and polyparasitism (Hotez *et al.* 2008).

Among the environmental promoters of endoparasite colonization success, climate seems to be crucial (Brooker, 2007). The Mediterranean biogeographical region, which showed a positive effect on carnivores' endoparasite richness, is characterized by moderate and mild temperatures, except in the summer when it is hot and dry (Blondel and Aronson, 1999; Condé and Richard, 2002). In this region, unpredictable diurnal temperatures and wind fluctuations occur, and infrequent floods and prolonged droughts are also characteristic (Condé and Richard, 2002).

Most of the detected endoparasites were helminths (Acantocephala, Cestoda, Digenea, Nematoda and Trematoda), and several environmental factors have been identified as necessary conditions for the development and survival of these parasites outside the final hosts: moderate temperatures, adequate moisture, and protection from freezing, desiccation and direct sunlight (Kates, 1965). Even some of the Protozoa detected in the reviewed studies have dispersal benefits from mild environments (Schuster and Visvesvara, 2004), such as those found in the Mediterranean region of the Iberian Peninsula throughout most of the year. Genera like *Isospora*, *Sarcocystis* or *Cryptosporidium*, whose oocysts are present in the faecal matter prior to

Table 3. Summary of fitted models Information Criteria (AICc – Akaike's Information Criterion; Δ AICc – difference to the lowest AICc value; wi – Akaike weights), that corresponded to the 3 tested hypotheses: endoparasite infection depends upon hosts, environment or a combination of both

(The best candidate model is identified in bold and grey. (H_weight – host weight, PIC_H_weight – phylogenetically independent contrasts of the variable H_weight, Troph_level – host trophic level, M_temp – mean annual temperature, Bio_region – biogeographical region).)

Models	AICc	Δ AICc	AICcwi
Full Model	204.42	18.09	< 0.001
Intersect	197.93	11.42	< 0.001
Host Model			
H_weight + Troph_level	203.03	16.07	< 0.001
PIC_H_weight + Troph_level	215.03	28.70	< 0.001
Environmental Model			
M_temp + Bio_region	193.33	7.00	0.022
Hybrid Models			
M_temp + Troph_level	194.33	8.00	0.014
H_weight + Bio_region	202.43	16.01	< 0.001
PIC_H_weight + Bio_region	213.13	26.8	< 0.001
Bio_region + Troph_level	186.33	0	0.739
H_weight + M_temp	211.33	25.00	< 0.001
PIC_H_weight + M_temp	221.63	35.3	< 0.001
H_weight + Bio_region + Troph_level	201.63	15.30	< 0.001
PIC_H_weight + Bio_region + Troph_level	208.43	22.10	< 0.001
M_temp + Bio_region + Troph_level	188.73	2.40	0.222
H_weight + M_temp + Troph_level	210.03	23.70	< 0.001
PIC_H_weight + M_temp + Troph_level	217.03	30.7	< 0.001
H_weight + M_temp + Bio_region	205.03	18.70	< 0.001
PIC_H_weight + M_temp + Bio_region	215.53	29.20	< 0.001

Table 4. Estimated coefficients and standard error for the variables of the best model

(β , estimated coefficients; Bio-region (2) – Mediterranean, Troph_level (2) – top predator.)

Best model	β	S.E.
Intercept	5.745	1.862
Bio-region (2)	-3.961	1.533
Troph_level (2)	-3.933	1.248

infecting vectors (e.g. insects – Graczyk *et al.* 2005), are sensitive to freezing and desiccation, although freezing is more limiting to survival (Robertson *et al.* 1992).

Thus, most endoparasites, prior to infecting their hosts, survive better in environments with mild temperatures and some humidity (e.g. Christensen *et al.* 1980). Mediterranean regions of Iberia may suffer severe summer droughts, but most of the year the climate is mild, which may favour parasite survival outside hosts (in contrast with the Atlantic and Alpine regions, in which winters are rigorous, with temperatures often dropping below 0 °C).

Although most life cycles of endoparasites take place inside hosts, which act as a protective barrier against deleterious environmental conditions (e.g. associated with latitude – Willig *et al.* 2003), some of

the most crucial phases associated with dispersal or host changing take place outside hosts' bodies (Piekarski, 1962; Graczyk *et al.* 2005). In such occasions parasites are sensitive to adverse environmental factors and benefit from mild conditions (e.g. soil-transmitted helminths are constrained by surface temperature, soil type and rainfall – Hotez, 2008). Therefore, carnivores living under Iberian Mediterranean climate, with high temperatures in the summer and mild winters, are more prone to have a higher richness of parasites than their counterparts inhabiting Atlantic-type areas.

Our results also indicate that the highest level of endoparasite richness is at the top predator level. This is likely because these species have larger home ranges (Nowak, 2005) and thus are likely to encounter more opportunities of infestation and a higher number of endoparasite species than carnivores with smaller home ranges. Moreover, endoparasite infection has been reported to have cascading effects throughout the food web, due to bottom-up (number of species of parasites that top-predators encounter) and/or top-down (the area that the top predator covers and its interactions with other species) effects. It has been shown that there is an increase in the richness of endoparasites in upper levels of the trophic chain (Chen *et al.* 2008). Evidence exists that parasites frequently adapt to host predation by parasitizing the predator (Dobson *et al.* 2006). For example, many

of the endoparasites infect hosts by ingestion, and therefore host diet and trophic level should influence, at least partially, the number of species to which a host will be exposed (Poulin, 1995). This mechanism is particularly important in heteroxenic parasites (i.e. with complex life cycles), whose stages occupy several different positions in the trophic web, leading to complex long-loops in interactions (Dobson *et al.* 2006).

Our results, however, do not match previous findings on Iberian carnivore endoparasite richness. The helminthological study of Torres *et al.* (2006) showed that the number of parasite species in each carnivore species was positively affected by host body mass, density and distribution and, marginally, by host longevity. Although we tested similar ecological and environmental parameters, we believe that the differences found may be related to the parasite taxa included in each study. In our study we also considered Protozoa and *Mycobacterium*, both having substantially different requirements from those of helminths (Baker, 1969). Also at variance with the results of Torres *et al.* (2006), the review by Watve and Sukumar (1995) showed that host body weight, home range, population density, gregariousness, and diet did not affect parasite loads. This lack of consistency in results may suggest that parasite species richness is more affected by historical (e.g. phylogenetic determinants – Bush *et al.* 1990) and regional processes (including climate) than by host ecological processes. However, the factors that drive parasite richness may vary regionally, since several parameters may interact upon this community, with the relative contribution of each one depending on their interplay (Poulin, 2004).

Finally, it is important to mention that our review is limited to already published research and some of the carnivore species inhabiting Iberia were hence not considered in the analysis (e.g. stoats, polecats *Mustela putorius* L., 1758, stone martens *Martes foina* Erxleben, 1777). How the inclusion of these mesocarnivores would affect the results is unknown, but the present study has the value of highlighting that the factors that influence parasite richness vary, and that this variation may be dependent on the host and parasite groups considered, as well as on the environmental characteristics of the study areas.

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