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Carnivore carcasses are avoided by carnivores

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Abstract

1. Ecologists have traditionally focused on herbivore carcasses as study models in scavenging research. However, some observations of scavengers avoiding feeding on carnivore carrion suggest that different types of carrion may lead to differential pressures. Untested assumptions about carrion produced at different trophic levels could therefore lead ecologists to overlook important evolutionary processes and their ecological consequences.

2. Our general goal was to investigate the use of mammalian carnivore carrion by vertebrate scavengers. In particular, we aimed to test the hypothesis that carnivore carcasses are avoided by other carnivores, especially at the intraspecific level, most likely to reduce exposure to parasitism.

3. We take a three-pronged approach to study this principle by: (i) providing data from field experiments, (ii) carrying out evolutionary simulations of carnivore scavenging strategies under risks of parasitic infection, and (iii) conducting a literature-review to test two predictions regarding parasite life-history strategies.

4. First, our field experiments showed that the mean number of species observed feeding at carcasses and the percentage of consumed carrion biomass were substantially higher at herbivore carcasses than at carnivore carcasses. This occurred even though the number of scavenger species visiting carcasses and the time needed by scavengers to detect carcasses were similar between both types of carcasses. In addition, we did not observe cannibalism. Second, our evolutionary simulations demonstrated that a risk of parasite transmission leads to the evolution of scavengers with generally low cannibalistic tendencies, and that the emergence of cannibalism-avoidance behaviour depends strongly on assumptions about parasite-based mortality rates. Third, our literature review indicated that parasite species potentially able to follow a carnivore–carnivore indirect cycle, as well as those transmitted via meat consumption, are rare in our study system.

5. Our findings support the existence of a novel coevolutionary relation between carnivores and their parasites, and suggest that carnivore and herbivore carcasses play very different roles in food webs and ecosystems.

KEYWORDS
agent-based model, cannibalism, carrion, disease risk, evolution of host-parasite interactions, food webs, genetic algorithm, indirect interactions, scavenger

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1 | INTRODUCTION

"Dog does not eat dog" is a commonplace expression that dates back to ancient Rome (*Canis caninam non est*; Cantera Ortiz de Urbina, 2005) and alludes to conflict avoidance among "professional guild" members. This expression may have originated from empirical observations (Houde, 2007) regarding an aversion of carnivores to feed upon the carcasses of other carnivores (Olson, Beasley & Rhodes, 2016; Selva, Jedrzejewska, Jedrzejewski & Wajrak, 2005). This aversive behaviour has been largely ignored by ecologists, likely because they have focused on herbivore carcasses as study models in scavenging research (DeVault, Rhodes & Shivik, 2003; Mateo-Tomás et al., 2015; Moleón et al., 2014; Wilson & Wolkovich, 2011). Recent advances in scavenging ecology reveal that herbivore carrion consumption plays a key role in food webs (Getz, 2011; Moleón, Sánchez-Zapata, Selva, Donázar & Owen-Smith, 2014; Wilson & Wolkovich, 2011), with ramifications for the study of evolution, biodiversity conservation and human wellbeing (Moleón & Sánchez-Zapata, 2015; Moleón et al., 2014). Through failure to separate out carrion produced at different trophic levels (but see Getz, 2011), ecologists have largely overlooked important evolutionary processes and their ecological consequences.

Carnivores have been documented to consume other carnivores, both conspecifically (i.e. cannibalistically) and heterospecifically, within the contexts of predation and scavenging. Cannibalism is rare (Elgar & Crespi, 1992) despite the increasing nutrient balance efficiency of consuming phylogenetically similar prey (Meffe & Crump, 1987). The risk of being infected by parasites adapted to specific species guilds (Pfennig, Ho & Hoffman, 1998; Polis, 1981; Rudolf & Antonovics, 2007) may be a strong selective force against carnivores eating carnivores (Bolker et al., 2008). For example, kuru, a prion neural disease in humans, is facilitated through ritualized cannibalism (Collinge, 2001). Beyond cannibalism, although interspecific killing is frequent among mammalian carnivores (Caro & Stoner, 2003; Donadio & Buskirk, 2006; Linnell & Strand, 2000; Palomares & Caro, 1999; Ritchie & Johnson, 2009), kills are often left uneaten, especially when food is abundant (Caro & Stoner, 2003; Lourenço, Penteriani, Rabaça & Korpimäki, 2014; Palomares & Caro, 1999). In these cases, interspecific killing may be a mechanism for relaxing competition (e.g. for food and space; Lourenço et al., 2014). Why killed carnivores are not consumed, however, remains largely speculative and, to our knowledge, reducing the risk of parasite transmission has not been explicitly considered as an explanation. Some authors have found that wild predators (e.g. leopards *Panthera pardus*) prey upon domestic carnivores (e.g. dogs *Canis lupus familiaris* and cats *Felis silvestris catus*) in human-dominated landscapes. This could be explained by the scarcity of wild prey and the fact that livestock are actively guarded or are in predator-proof enclosures (Athreya, Odden, Linnell, Krishnaswami & Karanth, 2016). The contributions of dead carnivores to these predators' diets are unknown.

An investigation of how scavengers exploit carnivore carrion should provide important insights into scavenging ecology, disease ecology and epidemiology, evolution of consumer-resource and host-parasite interactions, as well as animal and human behaviour. If feeding on carnivore carrion is or, in the evolutionary past, has been a costly strategy for scavengers (because of high parasite load), then carnivore carrion-avoidance behaviour should have evolved to minimize this risk. In this case we expect scavengers to prefer herbivore to carnivore carrion. Also, if carnivores evolved to avoid consuming carnivore carrion, then parasites transmitted by meat consumption should have an adaptive, coevolved response.

Here we use a three-pronged approach to explore if and why mammalian carnivores (i.e. meat-eating mammals) may be avoiding intraguild scavenging, including intraspecific consumption. First, we combine field observations and experimental methods to compare the consumption patterns of carnivore vs. herbivore carrion. Second, we use an agent-based model embedded within a genetic algorithm framework (Getz, Salter, Lyons & Sippl-Swezey, 2015) to assess conditions under which we might expect carnivore carrion-avoidance behaviour to evolve in scavenger communities. Third, we conducted a literature review to test two predictions derived from this hypothesis: (i) parasites with carnivore–carnivore indirect cycle (i.e. more than one host carnivore species are needed to complete the life cycle) should be rare and (ii) meat ingestion from carnivore to carnivore (i.e. intraguild feeding) should not be a common transmission strategy for current parasites. We focused on macroparasites that have as their main mode of transmission the ingestion of parasite-ridden flesh. Macroparasites invoke a T-helper-2 (Th2) response in the immune systems of their mammalian hosts while microparasites invoke a T-helper-1 (Th1) response (Cizauskas et al., 2014; Jolles, Ezenwa, Etienne, Turner & Olff, 2008). Since Th2 cytokines down-regulate Th1 cytokines, evolving to have a more effective immunological response to macroparasites might come at the expense of effective responses to viral and intracellular bacterial parasites. Thus, evolution of a behavioural response to macroparasites may be more effective than an immunological response that may increase vulnerability to intracellular pathogens. For this reason, our analyses, review and discussion pertain only to the problem of macroparasite avoidance. Evolutionary considerations of the immune system itself is a much more complex issue, particularly because the Th1 and Th2 immune system cell lines are both derived from the same hematopoietic stem cell line and are thus competing systems within any given host.

2 | MATERIALS AND METHODS

2.1 | Carrion monitoring: Whole carcasses

Field procedures were carried out during winter seasons in two regions of south-eastern Spain, one without (Espuña) and one with vultures (Cazorla; see Appendix S1). In Espuña, we monitored 20 herbivore (Barbary sheep *Ammotragus lervia*) carcasses from December to March 2005 and 2006, and 37 carnivore (27 red foxes *Vulpes vulpes*, four stone martens *Martes foina*, three cats *Felis silvestris*, two Eurasian badgers *Meles meles* and one common genet *Genetta genetta*) carcasses from January to April 2015 and 2016. In Cazorla, we monitored 23 herbivore (12 fallow deer *Dama dama*, six red deer *Cervus elaphus* and five mouflons *Ovis gmelini*) carcasses from

February to March 2008 and nine red fox carcasses in February 2016. All herbivore carcasses had estimated weights according to sex and age (Sánchez-Zapata & Eguía, 2007; Sebastián-González et al., 2016), and came from in situ culling and big game hunting. Barbary sheep carcasses were partially skinned and had their heads removed (Figure S1), while fallow deer, red deer and mouflon carcasses were intact. Fox carcasses were obtained from hunting states of the Region of Murcia where this species is legally hunted for population control, while other carnivore carcasses came from recent road kills in the same region. Prior to carcass placement, we eviscerated (to minimize the risk of pathogen transmission) and froze (−20°C) carnivores in individual plastic bags. In cases of shooting, we removed the area adjacent to the shot to prevent the exposure of scavengers to lead (Figure S1). Moreover, muscle samples from all carnivore carcasses were examined using a digestion method to discard the presence of *Trichinella* spp. larvae (Gamble et al., 2000). The elapsed time between carnivore death and freezing was 8–18 hr. To allow for defrosting, carnivore carcasses were taken out of the freezer for 8–12 hr prior to placement in the field. Defrosted carcasses were weighed (precision: ±50 g) and distributed throughout the study areas, with a minimum distance between simultaneous (i.e. placed within 2 weeks) neighbour carcasses of >1 km with some exceptions due to access limitations (always, >600 m; in these cases, carcasses were placed in different catchments).

The consumption of carcasses was monitored using camera-traps (Bushnell Trail Scout and Bushnell Trophy Cam) with cameras placed 5–10 m from the carcasses and programmed to take photos every 2 min (herbivore carcasses) and 1 min (carnivore carcasses) provided they detected movement. Carnivore carcasses were fixed to rocks or trunks using a wire camouflaged with soil and vegetation to avoid carcasses being moved away from the camera focus by the scavengers. Cameras were checked every 2–7 days to change batteries and memory cards as needed, and collected once the carcasses were completely consumed (herbivore carcasses, 1–2 weeks) or mummified (carnivore carcasses, 5–9 weeks). We considered complete carcass consumption if only bones and skin remained (see Blázquez, Sánchez-Zapata, Botella, Carrete & Eguía, 2009; Moleón, Sánchez-Zapata, Sebastián-González & Owen-Smith, 2015; Sebastián-González et al., 2016 for more details). At this final stage, fox carcasses processed in 2015 were again weighed.

We calculated the following variables from camera-trap pictures and visual inspections during visits to the carcass sites: "richness *a*" (number of scavenger species visiting the carcass), "richness *b*" (number of scavenger species consuming the carcass), "detection time" (time elapsed since the carcass was available until the arrival of the first scavenger), "consumption time" (time elapsed since the carcass was available until it was completely consumed), "consumption rate" (carrion biomass consumed by the scavengers divided by carcass consumption time) and "consumed biomass" (percentage of the carcass consumed by the scavengers, excluding the content of the digestive system in the case of herbivores; Moleón et al., 2015). We considered the digestive content to be 10% of the total herbivore carcass weight (Selva, 2004).

We performed generalized linear mixed model (GLMM) analyses (Zuur, Leno, Walker, Saveliev & Smith, 2009) to evaluate statistically the dependence of "richness *a*", "richness *b*", "detection time" (log-transformed) and "consumed biomass" on carcass type (herbivore and carnivore) and study area (Espuña and Cazorla) as fixed factors and sampling year and carcass identity as random factors. "Consumption time" and "consumption rate" were not compared because carnivore carcasses were hardly consumed by vertebrate scavengers (see Results section). In our analyses, we first constructed a full model with all the explanatory variables and interactions among them. We then constructed a set of alternative models with different combinations of the random structure (including a "null model", i.e. without random term), while maintaining the fixed structure unchanged. Finally, we selected the model with the most appropriate random structure. We used Gaussian error distributions and identity link functions (using the R functions *glm* and *lmer*) for richness *a*, detection time and consumed biomass, and Poisson error distributions and log link functions (using the functions *glm* and *glmer* in the R package LME4; Bates, Maechler, Bolker & Walker, 2013) for richness *b* because these models performed better in terms of normality and homocedasticity of residuals. After selecting the most appropriate random structure, we selected the model with the most appropriate fixed structure. For this, we explored the complete set of alternative models using the function *dredge* in the R package MuMIn (Barton, 2013). Model selection was based on the Akaike's Information Criterion (AIC$_c$), and we considered models with Δ-AIC$_c$ < 2 to have similar support (Burnham & Anderson, 2002). We estimated the performance of each candidate model by means of marginal R^2, which measures how much variability in the response variable is explained by the fixed term of the model (Nakagawa & Schielzeth, 2013), using the function *r.squared*GLMM (package MuMIn; Barton, 2013). Analyses were performed using R 3.0.2 (R Core Team, 2013).

2.2 | Carrion monitoring: Experiment

We performed an experiment to ascertain if carcass "external" characteristics, such as treatment (e.g. frozen or not; skinned/open vs. intact carcasses), size and other morphological features, were determinant for scavengers to discriminate between carcass types, while controlling for microhabitat conditions. During March and April 2015, we placed portions of the thoracic area and proximal section of extremities, without skin and with similar sizes (Barbary sheep portions: 410–950 g; red fox portions: 300–950 g), of both Barbary sheep and red fox carcasses in Espuña. This allowed for the external appearance of carrion portions to be similar between species (Figure S1). We used 10 experimental units; each consisting of one Barbary sheep portion and one fox portion (i.e. 20 portions in total) separated ca. 50 m from each other and placed in similar habitats within units. These units were placed near the studied whole carcass sites, 1–7 weeks after placing fox carcasses. Portions of both species, obtained from frozen carcasses, were taken out of freezers 2–5 hr before placement in the field. We fixed specimen portions to rocks or trunks of trees as specified above. We used different latex gloves for manipulating every portion to prevent odour transmission among them. After 1 week, we

recorded if the portions were consumed or not. We used GLMMs to relate the "consumption" of each portion (yes/no) with portion type (herbivore and carnivore) and initial portion weight as fixed factors, and experimental unit as random factor. Model construction and selection was done as indicated above, with the exception that we used binomial distributions and logit link functions.

In order to obtain some data on the scavenger species that visited the portions, we monitored the consumption of six portions with camera-traps (one picture every minute if cameras detected movement): three Barbary sheep portions and three fox portions in five experimental units (i.e. we used one camera in four units and two cameras in one unit). We also noted indirect signs of recent presence of vertebrate scavengers in a radius of 10 m around all portions.

2.3 | Carnivore-scavenging behaviour model

We built an evolutionary ecology model to explore conditions under which carnivores may evolve carnivore carrion-avoidance behaviour, based on the idea that debilitating or life-threatening parasites, such as an imagined highly pathogenic canine-specific variant of some strains of *Toxoplasma gondii* (see Discussion section), may invade a carnivore population in which individuals eat carnivore carcasses. Our model focused on the processes of carrion selection, starvation as a function of relatively low carrion intake rates under scavenger competition for resources, and possible parasite transmission that results in death-inducing disease when feeding on carnivore carrion. We then computed evolved carnivore-scavenging behaviour in terms of parameter values associated with these processes.

The model was coded in the Nova Platform (Getz et al., 2015). The model included an ecological component embedded in a genetic algorithm, as described in Getz, Salter and Sippl-Swezey (2015). The ecological component ran over T_E = 200 time periods and the evolutionary component over T_G (300 generations for implicit parasite model, 400 for explicit parasite model). For computational efficiency, the model runs as a semelparous process (all individuals reproduce at time T_E and then die, with their progeny comprising the next generation). For a carnivore that has an average generation time of 4 years (e.g. maturity of 2 years, maximum longevity of around a decade but a survivorship and reproductive schedule that produces a 4-year generation time) an ecological cycle of 200 time periods suggest that a unit of time within the model is roughly equivalent to 1 week. The epochal time T_G was selected to ensure that the evolutionary processes approached some stable structure (monomorphic or polymorphic behavioural guild), where the process itself depends on our choice of mutation rates and the parameters of a simulated annealing process (Getz et al., 2015; Kirkpatrick, Gelatt & Vecchi, 1983) that is included to ensure that the evolutionary processes does not get trapped early on in one part of the parameter space.

The details of the model (i.e. presentation of the mathematical equations used) are provided in the Appendix S2 (see Appendix S3 for the script used). The model is based on each individual carnivore being in one of four (initial simulation) or five (dynamic parasite simulation) idealized states (numerical designation in parenthesis): dead and removed (0), alive and healthy (1), alive and infected (2; dynamic parasite population runs only), a carcass from a healthy individual that died from starvation (3), a carcass from an infected individual that died from diseases (4; states 3 and 4 are the same for the initial runs, but not the dynamic parasite population runs). The focal processes in the model are rates at which states 1 and 2 transition to state 3 and 4, respectively, during each time step. We assume that individuals can only be in states 3 and 4 for one time period and then transition to state 0. Individuals remain in state 0 for the duration of the simulation. Only individuals in states 1 and 2 can reproduce.

To introduce a very simple notion of space into the model, we envisioned individuals as evenly spaced nodes on the circumference of a circle. Each individual was then assigned a node (i.e. node i for agent A_i) and an "interactive neighbourhood" by including a designated number of agents to the left and right of its node (cf. Appendix S2; Figure S2). During each period of ecological time, zero or more herbivore carcasses are assigned to each node, using a Poisson distribution with mean value h. Additionally, carnivore carcasses become available as neighbouring agents die either from starvation or from eating infected carcasses, based on a Bernoulli probability of dying the previous time interval.

To keep things simple, each agent A_i has a parameter value C_i that determines, in the context of a single carnivore species interpretation of model results, the propensity to which these agents practice cannibalism (i.e. forage on carnivore carcasses): thus C_i = 0 implies A_i is not cannibalistic, C_i = 1 implies A_i has no carcass type preference, while an intermediate C_i implies an intermediate preference for herbivore over carnivore carrion, implemented as follows. We assumed that the probability of agent A_i getting infected when eating carrion is a stochastic threshold function (with threshold parameter ρ) of its preference for eating conspecific carrion (e.g. C). This infection probability function depends on the relative number of carcasses that are from carnivores vs. herbivores, normalized by the degree to which agent A_i has to compete with other carnivore carcass-eating agents in N_i. Additionally, we assume that the probability of agent A_i (healthy or infected) dying from starvation depends on a stochastic threshold function (with threshold parameter γ) that depends on the normalized (divided by number of competitors for the carcass) availability of carcasses to agent A_i in neighbourhood N_i, accounting for the fact that individuals with increasing values $C_i > 0$ have an increasing carcass availability to them (cf. Appendix S2). In each ecological time step, a new set of carcasses is assigned to each node i (irrespective of the state of the agent at that node) according to a Poisson process with parameter h (i.e. h is the expected number of carcasses at each node).

At the end of each ecological run (i.e. the end of the within-generation dynamics), the fittest individuals are those still alive that have consumed the most carrion biomass over the T_E simulation period. Only the fittest agents (top half of the surviving agents) reproduce, creating at least two progeny each that inherit the C value of their parent, with perturbations to this value driving the evolutionary process. This is essentially a clonal reproduction process with mutation that is at the extreme end of sexual reproduction with assortative mating (see Getz et al., 2015 for further discussion on this point). For

the first generation, the values C_i are assigned randomly on the interval $[0, 1]$, but by generation T_G, either all individuals had virtually the same C_i values (variation due to mutation rates), or belonged to one of a few scavenging phenotypes, where the latter is characterized by a group of individuals clustering around one of several characteristic values of C (cf. Getz et al., 2015).

In an initial set of runs, we assumed constant background parasite prevalence (implicit parasite model) and explored the model parameter space to analyse the range of evolutionary outcomes. Once optimal parameter threshold values were found (γ, ρ mentioned above, carcass distribution parameter h and a rate of herbivore carcass allocation), we executed a second set of simulations in which parasite prevalence increases with the death rate of carnivores from eating parasite infected carrion (explicit parasite model). We achieved this by assuming that the proportion q_0 of scavengers infected at the start of each generation increases in a dispensatory fashion relative to the total number of individuals infected in each generation (see Appendix S2 for details). At each subsequent time period in the ecological component of the simulations, individuals reduced their propensity to forage on carnivore carrion, which, consequently, decreased their probability of eating parasite-infected carrion. The scavengers that became infected by eating such carrion were then subject to a probability μ of dying from disease in each of the subsequent ecological time periods until time T_E.

2.4 | Parasites of mammalian scavengers

We conducted an extensive literature search of the main cardiorespiratory, digestive and systemic parasites (Phyla Nematoda, Platyhelminthes and Acanthocephala, and Kingdom Protista) of the most frequent mammalian scavengers involved in this study: red fox, domestic dog (*C. lupus familiaris*), stone marten and wild boar (*Sus scrofa*). We restricted the search to studies performed in the Iberian Peninsula (Spain and Portugal). For each parasite taxon, we recorded its life cycle (direct: if a single host species is needed to complete the life cycle; indirect: if more than one host species are needed to complete the life cycle), definitive hosts, intermediate and paratenic hosts (only considered in the case of indirect cycle parasites), and transmission routes (through meat/viscera consumption vs. other, i.e. contact with feces, urine, saliva and other corporal fluids, as well as transplacental or lactogenic transmission). In the case of transmission via meat/viscera consumption, we differentiated parasites based on infecting the definitive host through the consumption of intermediate/paratenic hosts vs. intermediate/paratenic/definitive hosts.

3 | RESULTS

3.1 | Carrion consumption patterns

As part of our empirical whole carcass field study, we obtained 2,259 photographs of scavengers at herbivore carcasses (68.46 ± 55.52 pictures/carcass) and 821 at carnivore carcasses (17.85 ± 43.61 pictures/carcass). Overall (Table 1, Figure 1a), there were more scavenger species visiting carcasses in Cazorla than in Espuña. Within Espuña, we detected more species in herbivore carcasses compared to carnivore carcasses, although differences were due to avian scavengers rather than mammalian scavengers. The most frequently recorded scavenger species in both study areas were red fox, stone marten, wild boar, golden eagle (*Aquila chrysaetos*), common raven (*Corvus corax*) and Eurasian jay (*Garrulus glandarius*), with griffon vulture (*Gyps fulvus*) and carrion crow (*Corvus corone*) also being frequent in Cazorla (Table S1). The mean number of species that were observed feeding at carcasses was substantially higher at herbivore carcasses than at carnivore carcasses and slightly higher in Cazorla than in Espuña, especially at carnivore carcasses (Table 1, Figure 1a). All the scavengers detected at herbivore carcasses, and most avian scavengers detected at carnivore carcasses, were observed feeding on carrion (when it was not possible to determine from the photographs whether jays consumed small pieces of carrion or only invertebrates present at the carcass, we conservatively assumed that they were scavenging). In contrast, most mammals recorded at carnivore carcasses avoided consuming them; only red fox ($n = 2$ carcasses) and wild boar ($n = 1$ carcass) were feeding on carnivore carcasses (Table S1), and always on carcasses belonging to different species (stone marten and Eurasian badger in the case of red fox and stone marten in the case of wild boar). Thus, no cannibalism was observed in our study. The average time needed by scavengers to detect carcasses was notably lower in Cazorla than in Espuña (partly due to rapid carcass detection by vultures), and slightly lower at herbivore carcasses compared to carnivore carcasses (Table 1, Figure 1a). The percentage of consumed biomass was much higher for herbivore carcasses than for carnivore carcasses, especially in Espuña (Table 1, Figure 1a). Herbivore carcasses were completely consumed in ca. 3 and 8 days on average in Cazorla and Espuña, respectively (Table 1). In contrast, few scavengers were observed consuming carnivore carcasses before they became dehydrated (Table 1): only 23.9% of carnivore carcasses were totally ($n = 5$ carcasses, i.e. the three red foxes visited by griffon vultures plus one badger and one marten) or partially ($n = 6$ carcasses) consumed by vertebrate

TABLE 1 Scavenger richness (richness *a*: scavengers present; richness *b*: scavengers feeding) and scavenging efficiency (detection time, consumption time, consumption rate and consumed biomass) of herbivore and carnivore carcasses in the study area

| Carcass type	Study area	N	Richness *a*	Richness *b*	Detection time (hr)	Consumption time (hr)	Consumption rate (kg/hr)	Consumed biomass (%)
Herbivore	Espuña	20	2.36 ± 1.26 (7)	2.36 ± 1.26 (7)	64.00 ± 52.46	198.20 ± 109.95	0.31 ± 0.17	81.47 ± 9.31
	Cazorla	23	3.04 ± 1.46 (6)	3.04 ± 1.46 (6)	18.40 ± 16.16	66.35 ± 70.27	1.60 ± 2.89	91.10 ± 9.18
Carnivore	Espuña	37	1.78 ± 0.95 (4)	0.22 ± 0.48 (2)	88.45 ± 70.48	–	–	6.81 ± 23.49
	Cazorla	9	3.11 ± 1.45 (6)	1.00 ± 1.32 (3)	19.56 ± 18.02	–	–	34.44 ± 49.27
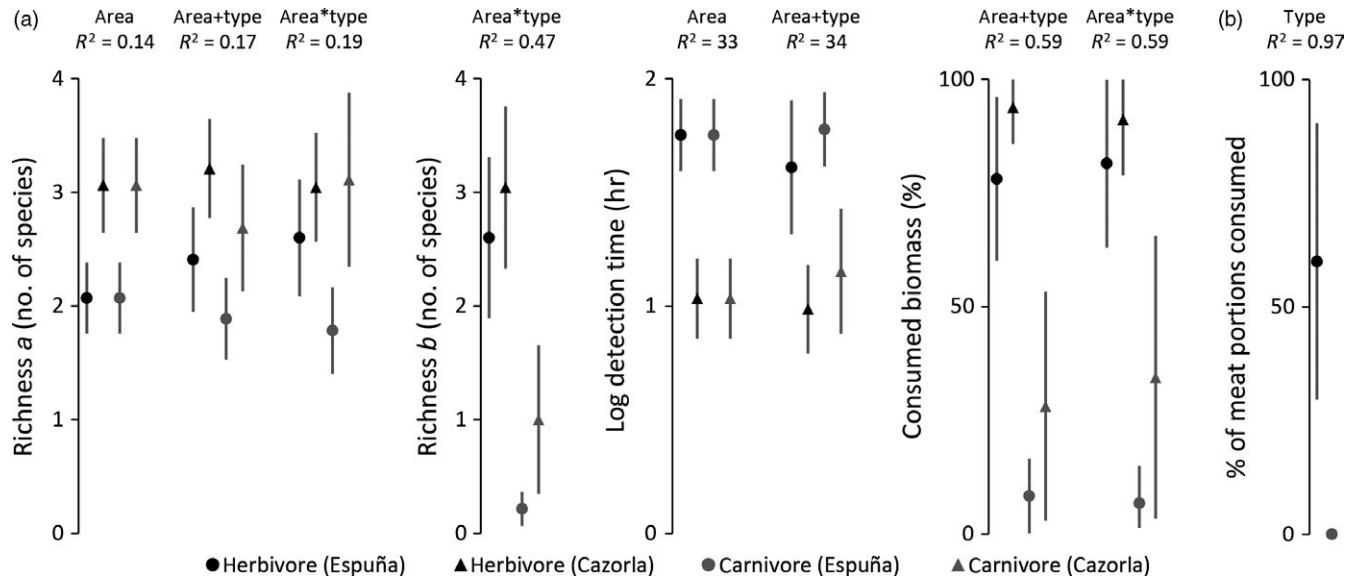
FIGURE 1 Results of the ungulate and mammalian carnivore carcass monitoring scheme (a) and the field experiment involving meat portions of herbivore (Barbary sheep) and carnivore (red fox) carcasses (b). (a) Predicted values (mean ± 95% CI) of parameters of the selected generalized linear mixed models (GLMMs) were used to explain the richness of vertebrate scavenging species that visited the carcass ("richness *a*"), the richness of vertebrate scavenging species that consumed the carcass ("richness *b*"), the time elapsed between carcass placement and the first visit of a vertebrate scavenger ("detection time") and the percentage of carrion biomass scavenged ("consumed biomass"). (b) Predicted values (mean ± 95%CI) of parameters of the selected GLMMs used to explain the percentage of meat portions of herbivore and carnivore carcasses that were consumed after a week. For each case, the variables included in the model (no random terms were selected in any case) and pseudo R^2 (Nakagawa & Schielzeth, 2013) are shown
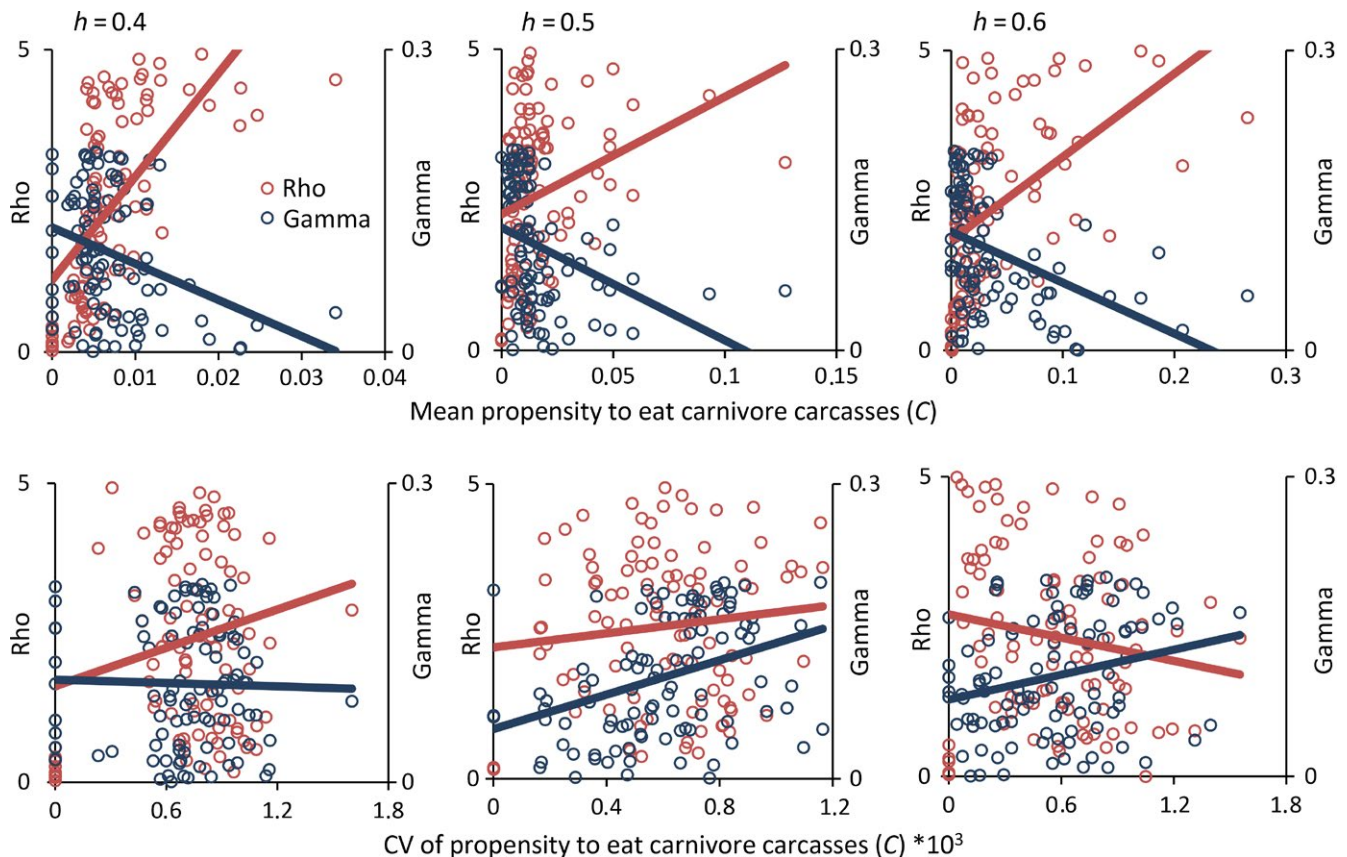

FIGURE 2 Relationship between the mean value and coefficient of variation (CV) of *C* (probability of consuming carnivore carcasses) and parameters γ (gamma; a proxy of fitness) and ρ (rho; a proxy of the risk associated to carnivore carcasses) after 300 evolutionary generations. Results of the carnivore scavenging model with implicit parasitism are shown for three different values of *h* (mean number of herbivore carcasses per site per iteration)
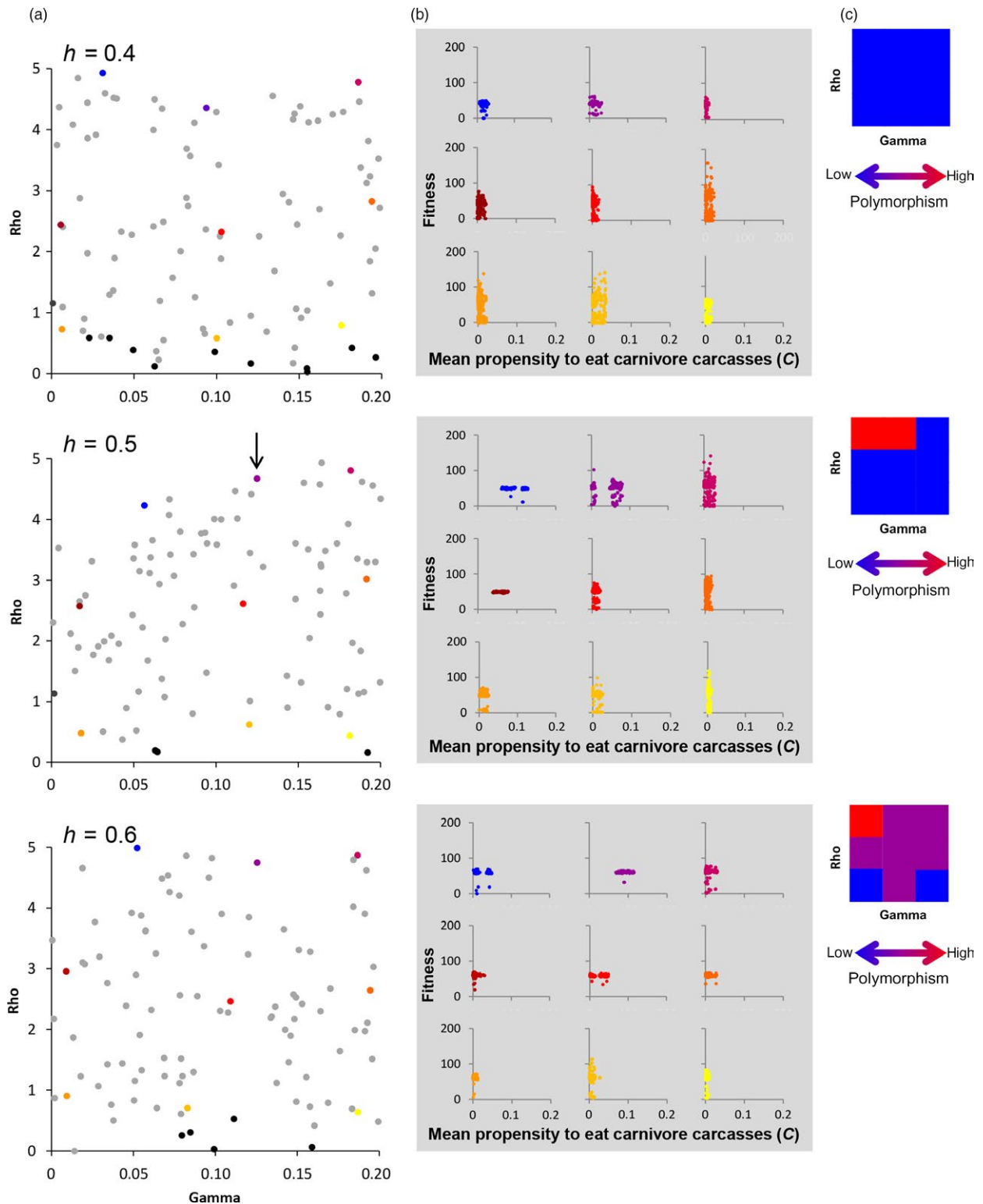
FIGURE 3 Relationship between a polymorphism in *C* and parameters γ and ρ after 300 evolutionary generations. Results of the carnivore scavenging model with implicit parasitism are shown for three different values of *h*. (a) Space defined by a uniform distribution of 100 values of γ (range 0–0.2) and ρ (range 0–5). Points represent populations (black points: populations experiencing extinction before the end of the evolutionary run; colored points: populations represented in the examples of grey panels) and black arrow indicates the population used for the multi-run represented in Figure S5. (b) An example of a model/simulation run is shown for nine different scenarios based on high, medium and low values of γ and ρ. Here, each point represents one individual after the evolutionary run. The fitness values plotted here are either the amount of carrion consumed over the total ecological period or, in the case of individuals dying, the amount of carrion consumed prior to death. (c) A qualitative interpretation of the relative probability of polymorphism (red: high; purple: moderate; blue: low) for each scenario of the space defined by γ and ρ

TABLE 2 Multi-run (10 runs) output of the model under the explicit parasite scenario after 400 evolutionary generations for two different starvation threshold parameter levels: relatively low risk (parameter set: $\gamma = 0.1$, $\rho = 4.5$, $h = 0.5$, $q_0 = 0.05$, $q_1 = 1$, $K_q = 100$) and relatively high risk of starvation (parameter set: $\gamma = 0.25$, other parameters as above), according to different parasite-based mortality rates (m)

Risk of starvation	$m = 0.001$	$m = 0.003$	$m = 0.01$	$m = 0.03$	$m = 0.1$	Implicit
Low						
C (mean; 10^{-3})	847 ± 119	810 ± 148	312 ± 415	31 ± 34	60 ± 72	18 ± 12
C (CV)	0.1 ± 0.2	0.1 ± 0.1	0.3 ± 0.3	0.3 ± 0.3	0.2 ± 0.2	0.5 ± 0.4
Died from starvation	34 ± 8	25 ± 5	3 ± 2	0.2 ± 0.4	0.3 ± 0.5	28 ± 10
Died from parasites	2 ± 2	11 ± 4	201 ± 13	355 ± 6	340 ± 120	1 ± 1
High						
C (mean; 10^{-3})	936 ± 59	825 ± 304	655 ± 372	59 ± 107	15 ± 14	9 ± 7
C (CV)	0.01 ± 0.01	0.01 ± 0.005	0.06 ± 0.14	0.36 ± 0.34	0.36 ± 0.36	0.65 ± 0.31
Died from starvation	175 ± 10	166 ± 12	25 ± 6	6 ± 3	2 ± 2	181 ± 9
Died from parasites	2 ± 2	10 ± 4	208 ± 14	358 ± 7	376 ± 5	4 ± 3

scavengers. R^2 of selected models was high in general, especially for richness b and consumed biomass (Figure 1a). Mean red fox carcass biomass loss during the study period in 2015 was 3.76 kg (mean initial weight: 4.70 ± 0.83 kg; mean final weight: 0.94 ± 0.28 kg); i.e. 80% of mean initial weight of fox carcasses was uneaten by vertebrates and then available to invertebrate scavengers and decomposers.

In our field experiments involving trimmed portions of carcasses, all red fox portions remained untouched after a week. In contrast, 60% of Barbary sheep portions disappeared within 1 week (Figure 1b). R^2 of the selected model, namely the one with portion type as the only explanatory factor, was high (Figure 1b). Cameras indicated that one fox portion was visited by stone marten and European badger, while the other two fox portions monitored with cameras were visited by wild boar. For its part, one Barbary sheep portion was consumed by red fox, Eurasian jay and northern goshawk (*Accipiter gentilis*), while the other two cameras (corresponding to two untouched portions) failed. The loss of two Barbary sheep portions which were not monitored with cameras was attributed in one case to a wild boar, on the basis of finding recent wild-boar tracks at the site, and in the other case to a large bird, on the basis of finding white down feathers adhering to the wire that held the carcass portion at the site.

3.2 | Carnivore-scavenging behaviour model

Our first set of evolutionary simulations, which only included an implicit risk of parasite transmission, clearly demonstrates, as depicted in the six panels of Figure 2, that a risk of parasite transmission leads to the evolution of scavengers with generally low cannibalistic tendencies. Depending on parameter values, evolved behaviour ranged from a willingness to eat on average around 30% of encountered conspecific carrion to complete avoidance as: (i) herbivore carcasses become more scarce (h dropping from 0.6 to 0.4), (ii) the starvation risk rose (γ rose from 0 to 0.2), and (iii) the probability of contracting disease and dying rose when eating carnivore carrion

(ρ dropped from 5 to 0). In most cases, individuals evolved to have similar scavenging strategies (all had similar values of C; Figure S3), though sometimes polymorphic behaviour at a group level (some individuals were more cannibalistic than others) evolved (Figure 3 and Figure S3). Polymorphism emerged more frequently as γ and h rose and ρ dropped (e.g. top centre panel in Figure 3b in which one group of individuals evolved to avoid cannibalism almost entirely, since their C values were all close to 0, while a second group participated in cannibalism around 6%–8% of the time, because their C values were clustered around 0.07; also see panels depicting results of runs 3, 4, 10, 13, 17, 19 and 20 in Figure S4).

Our second set of evolutionary simulations included explicit disease dynamics within, as well as across, generations. These models showed that the emergence of cannibalism-avoidance behaviour depends strongly on assumptions about parasite-based mortality rates. For example, when we set the herbivore carcass abundance parameter to $h = 0.5$, the risk of getting infected when eating infected carnivore carcasses to $\rho = 4.5$, and parasite-induced mortality to relatively low values (i.e. $m = 0.001$, $m = 0.003$), scavengers indulge in cannibalism >80% of the time, as depicted in Table 2. This level dropped to around 65% (high starvation risk case) and 30% (low starvation risk case) when mortality rates increase to $m = 0.01$. Further increases in mortality from eating infected carrion cause cannibalism to drop well below 10%. Unlike the results from the implicit parasite transmission model, however, populations mostly evolved to be monomorphic with respect to the amount of cannibalism tolerated in the group as a whole (cf. Figure S5), though a few polymorphic situations still emerged, especially for low starvation and mortality risk cases (e.g. see runs 2 and 3 in Figure S5 for the case $\gamma = 0.1$, $m = 0.003$).

3.3 | Parasites of mammalian scavengers

In our literature review, we recorded 79 different taxa belonging to 56 genera of cardiorespiratory, digestive and systemic parasites of red fox, domestic dog, stone marten and wild boar in the Iberian Peninsula.

More than half of these taxa exhibit indirect cycle (i.e. more than one host species needed for individuals to complete their cycle), either as unique (54%) or alternative (c. 4%; Table 3) strategy. However, only three parasite species could potentially follow a carnivore–carnivore indirect cycle: *T. gondii*, *Neospora caninum* and *Echinococcus granulosus*. These three species infect many mammals and birds as intermediate hosts, while their definitive hosts are felids (*T. gondii*) and canids (*N. caninum* and *E. granulosus*; Table S2). Carnivore–carnivore indirect cycles, however, have rarely been described for these parasites (Cordero del Campillo, Castañón-Ordóñez & Reguera-Feo, 1994; Sobrino et al., 2008).

Regarding the type of transmission, most of the revised parasite taxa (80%) are not meat-transmitted. Among those that are transmitted via consumption of meat of intermediate/paratenic hosts (16%), intermediate and paratenic hosts were always animals other than mammalian carnivores. Only three parasite taxa (c. 4%), which affect all the carnivore species here considered, can also be transmitted via consumption of definitive hosts (Table 3). One of them, *Trichinella* spp. (*T. spiralis* and *T. britovi* in the Iberian Peninsula), is a parasite of auto-heteroxenous cycle whose host can be a wide variety of mammal species. The other species, *T. gondii* and *N. caninum*, can have either direct or indirect cycle, with felids and canids as definitive hosts (respectively) and many mammals and birds as intermediate hosts (Table S2; Almería et al., 2007; Donahoe, Lindsay, Krockenberger, Phalen & Šlapeta, 2015; Gauss et al., 2005). These are the only three taxa that could be transmitted among carnivores through scavenging (including cannibalism), although no such cases have been accurately documented to date.

4 | DISCUSSION

In our empirical studies, we found contrasting scavenging patterns between herbivore and carnivore carcasses: unlike herbivore carrion, which was readily consumed by vertebrate scavengers (as found for other ecosystems world-wide; DeVault et al., 2003; Mateo-Tomás et al., 2015), mammalian scavengers avoided feeding on carnivore carrion, especially of conspecifics. According to the behaviour observed in both our whole carcasses and meat portions experiment, the results support a deliberate avoidance behaviour rather than differences in carrion detection time and encounter rates, which were similar between both types of carcasses in both study areas. Our findings agree with those of Selva et al. (2005) in a Polish temperate forest, and Olson et al. (2016) in an agricultural area of USA, suggesting that carnivore carrion-avoidance behaviour may be widespread in ecosystems. Indeed, our model simulation results strongly support this suggestion.

Our simulation demonstrates that whenever intraguild scavenging carries a mortality risk from pathogens transmitted while eating the carrion then intraguild scavenging cannot be an evolutionarily stable strategy. Rather our model clearly demonstrates that carnivore carrion-avoidance behaviour may well be driven by disease induced mortality (or reduced fecundity, which was not included in our model)

TABLE 3 Main cardiorespiratory, digestive and systemic parasites of red fox (*Vv*), domestic dog (*Clf*), stone marten (*Mf*) and wild boar (*Ss*) in the Iberian Peninsula. For each carnivore species, we show the total number of parasite taxa according to their life cycle (1 = direct, 2 = indirect, 3 = both), their hosts (definitive host, DH: 1 = *Vulpes vulpes* and *Canis lupus* ssp., 2 = *Canis lupus familiaris*, 3 = *Felis silvestris*, 4 = *Sus scrofa*, 5 = Mustelidae, 6 = many mammalian species, 7 = human; intermediate host, IH: 0 = none, 1 = invertebrate, 2 = lagomorph/rodent, 3 = ungulate, 4 = Suidae, 5 = mammal/bird, 6 = amphibian/reptile/fish; paratenic host, PH: 0 = none, 1 = invertebrate, 2 = rodent/bird/reptile/fish) and their type of transmission (0 = other than meat consumption, 1 = consumption of meat of intermediate/paratenic hosts, 2 = consumption of meat of intermediate/paratenic/definitive hosts; extracted from Table S2). Values within parentheses represent percentages relative to the total taxa per carnivore species (life cycle, PH and transmission) and the taxa of indirect cycle, i.e. categories 2 and 3 of life cycle (DH and IH). Note that the total (bottom row) excludes redundant taxa/genera

	Taxa	Gen.	Life cycle			DH			IH								PH			Transmission		
			1	2	3	1	2	3	0	1	2	3	4	5	6	7	0	1	2	0	1	2
Vv, Clf	40	31	12 (30.0)	26 (65.0)	2 (5.0)	26ᵃ (92.8)	1 (3.6)	10ᵃ (35.7)	0	14 (50.0)	3 (10.7)	4 (14.3)	0	2 (7.1)	5 (17.9)	0	30 (75.0)	1 (2.5)	9 (22.5)	28 (70.0)	9 (22.5)	3 (7.5)
Mf	23	19	13 (56.5)	8 (34.8)	2 (8.7)	0	1 (10.0)	0	0	4 (40.0)	0	2 (20.0)	0	2 (20.0)	2 (20.0)	8 (80.0)	20 (87.0)	1 (4.3)	2 (8.7)	17 (73.9)	3 (13.0)	3 (13.0)
Ss	24	23	12 (50.0)	9 (37.5)	3 (12.5)	1 (8.3)	1 (8.3)	0	0	6 (50.0)	1 (8.3)	0	5 (41.7)	3 (25.0)	0	1 (8.3)	23 (95.8)	1 (4.2)	0	20 (83.3)	1 (4.2)	3 (12.5)
Total	79	56	33 (41.8)	43 (54.4)	3 (3.8)	26 (56.5)	1 (2.2)	5 (10.9)	0	24 (52.2)	4 (8.7)	6 (13.0)	5 (10.9)	3 (6.5)	7 (15.2)	8 (17.4)	65 (82.3)	3 (3.8)	11 (13.9)	63 (79.7)	13 (16.5)	3 (3.8)

ᵃDH is *Vulpes vulpes*/*Canis lupus* ssp. only (n = 17), *Felis silvestris* only (n = 1) or both (n = 9).

associated with the transmission of parasites among phylogenetically similar species. As reviewed by other authors (Huang, Bininda-Emonds, Stephens, Gittleman & Altizer, 2014; Stephens et al., 2016), the proportion of shared parasite species among carnivores is higher as the phylogenetic affinity of the latter increases. Conspecific scavenging was only supported in our model when the pathogenicity of parasites was low and a concomitant risk of starvation existed due to insufficient availability of herbivore carcasses. Moreover, the explicit inclusion of parasites in our second model reduced the probability of generating polymorphism regarding the probability of consuming carnivore carrion, thereby providing additional evidence that intraguild scavenging is not an evolutionarily stable strategy.

How might intraguild scavenging be avoided when carcasses have been reduced to bits of meat and bone? Many animals use chemical cues to detect and avoid infected conspecifics, thus minimizing the risk of infection (Kavaliers, Choleris, Agmo & Pfaff, 2007; Kiesecker, Skelly, Beard & Preisser, 1999). Interpretation of chemical substances also helps some species to discriminate between pathogenic and non-pathogenic prey (Pradel et al., 2007). Thus, mammalian carnivores might well have evolved to olfactory discrimination between "risk" (carnivore) and "non-risk" (herbivore) carrion, which in turn could result in the scavenging behaviour that we both observed and modelled. The critical role of parasites in shaping ecosystems through behavioural responses in their hosts has often been highlighted
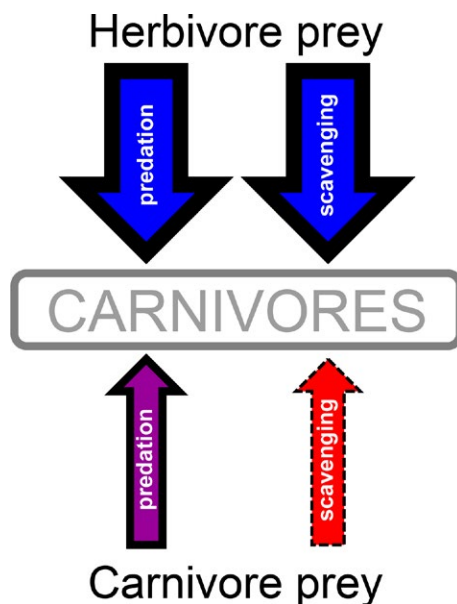

FIGURE 4 Conceptual model showing the flux of herbivore and carnivore biomass to carnivores via predation or scavenging. Arrow colour indicates relative risk of disease transmission (blue: low risk; purple: moderate risk; red: high risk), arrow width is proportional to the relative availability of each prey type in nature (high for herbivores and low for carnivores) and arrow line width is proportional to the proportion of carcasses that are killed or found by a carnivore and consumed by such carnivore. We assume that the probability of a carnivore being a disease carrier is higher when it is found dead rather than alive (Hart, 1990)

(Thomas, Poulin, de Meeûs, Guégan & Renaud, 1999). Parasites are able to affect community structure, trophic relationships and energy flow within food webs (Lafferty, Dobson & Kuris, 2006; Thompson, Mouritsen & Poulin, 2005). In this study, we have shown that parasites can also modulate the passage of biomass in scavenging communities, therefore expanding the ecological and evolutionary role of parasites to an important consumer-resource pathway (DeVault et al., 2003; Getz, 2011; Wilson & Wolkovich, 2011).

The parasite-avoidance hypothesis is also supported by the characteristics of current parasite assemblages of the studied carnivores. As predicted, we found that cardiorespiratory, digestive and systemic parasites with carnivore–carnivore indirect cycle are very rare (if any), and very few parasites could be transmitted by meat consumption from carnivore to carnivore. In contrast, parasites with intermediate hosts other than carnivores are common, and many of these parasites are transmitted by consumption of meat (Table 3 and Table S2). Overall, our study suggests a novel coevolutionary relation between scavenging carnivores and their parasites (Anderson & May, 1982). From a non-evolutionary perspective, the observed behaviour would be hard to explain (see Appendix S4). However, the generality of our results should be tested in other systems with different scavenger and parasite guilds, especially in cases where carnivores include high proportions of other carnivores in their diets. For instance, arctic foxes (*Alopex lagopus*) and polar bears (*Ursus maritimus*) that usually predate and scavenge other carnivores such as seals have elevated antibody levels to deal with protozoan parasites such as *T. gondii* (Oksanen et al., 2009; Prestrud et al., 2007).

Carnivore carrion-avoidance behaviour may have important ecological consequences. For example, an absence of vertebrate scavengers on carnivore carcasses dramatically increases the amount of carrion biomass available, as well as its temporal availability, to invertebrates and micro-organisms. In fact, we frequently observed arthropods at carnivore carcasses. For instance, although most of the biomass was consumed by dipteran larvae, a well-structured successional community comprising a total of 19 insect families was observed in the whole carcasses (authors' unpublished data). In the case of red fox portions, during inspections we recorded beetles (100% of portions), flies (90%), ants (40%) and centipedes (10%; the portions of Barbary sheep that remained unconsumed also had beetles, flies and ants). This prolonged resource availability may be critical for some invertebrates to complete their life cycle. This is the case, for example, of some fly species that need 11 days for completing their cycle (Figueroa, Flores & Rodríguez, 2007). Further research could determine the existence of scavenging invertebrates and decomposers specialized in carnivore carcasses. In addition, these scavenging invertebrates could be a food resource for many vertebrates. In our study, we detected 11 species (three mammals, seven birds and one reptile) apparently feeding on invertebrates of different life stages. Thus, for these vertebrates, carnivore carcasses could act as indirect food sources. Finally, differences in scavenging patterns on carnivore and herbivore carcasses could have an effect on other ecological processes such as those involved in nutrient input to soils and associated vegetation responses (Turner et al., 2014).

5 | CONCLUSIONS

Our study provides (i) empirical evidence that mammalian carnivores avoid the consumption of carnivore carcasses, especially at the intraspecific level, (ii) a modelling framework that supports field data indicating that the risk of disease transmission might have driven the aversion to consume carnivore carcasses, and (iii) a review of carnivore parasites that further shows a coevolutionary link reinforcing the parasite-avoidance hypothesis. We suggest that carnivore and herbivore carcasses play sufficiently different roles in food webs to make the distinction between them essential in the study of ecosystems. Compared to herbivore carrion, rate of biomass re-distribution of carnivore carrion is much lower, the diversity of carrion consumers is biased towards much smaller organisms and the community of consumers is more complex—with indirect trophic interactions probably being a common feature. This differential role, which should be taken into account when modelling biomass fluxes in food webs, would be primarily mediated by the relative risk of parasite transmission and the relative abundance of each type of carcass (Figure 4). While herbivore carcasses are comparatively abundant in terms of biomass and very low risk in terms of the transmission of parasites specializing on carnivores, carnivore carcasses are relatively scarce and represent a much higher risk of parasite transmission (Huang et al., 2014), particularly in the case of carcasses of animals found dead rather than predated (Hart, 1990). Minimizing the infection risk while maximizing biomass intake may have driven the differential consumption process observed between herbivore and carnivore carcasses.

AUTHORS' CONTRIBUTIONS

M.M., C.M.C. and J.A.S.Z. developed the core idea and designed the study. M.M., C.M.C., C.M.L. and J.A.S.Z. conducted the fieldwork and prepared the database. M.M. analysed field data. O.C.M. and W.M.G. developed the simulations, and M.M., O.C.M. and W.M.G. analysed output data. C.M.C. performed the literature review on parasites, and M.M. analysed the resulting information. M.M. and W.M.G. wrote the initial draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

The carnivore-scavenging behaviour model is available as a Nova (.nva) file in the Supporting Information. Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qn8d9 (Moleón et al., 2017).

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