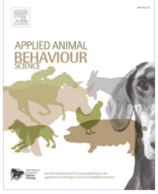
Applied Animal Behaviour Science 243 (2021) 105462

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim



Smart carnivores think twice: Red fox delays scavenging on conspecific carcasses to reduce parasite risk

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ARTICLE INFO

Keywords:
Cannibalism
Carnivore
Carrion
Landscape of disgust
Parasite avoidance behaviour
Parasite transmission risk

ABSTRACT

The recent SARS-CoV-2 epidemic has highlighted the need to prevent emerging and re-emerging diseases, which means that we must approach the study of diseases from a One Health perspective. The study of pathogen transmission in wildlife is challenging, but it is unquestionably key to understand how epidemiological interactions occur at the wildlife-domestic-human interface. In this context, studying parasite avoidance behaviours may provide essential insights on parasite transmission, host-parasite coevolution, and energy flow through food-webs. However, the strategies of avoiding trophically transmitted parasites in mammalian carnivores have received little scientific attention. Here, we explore the behaviour of red foxes (*Vulpes vulpes*) and other mammalian carnivores at conspecific and heterospecific carnivore carcasses using videos recorded by camera traps. We aim to determine 1) the factors influencing the probability of foxes to practice cannibalism, and 2) whether the scavenging behaviour of foxes differ when facing conspecific vs. heterospecific carcasses. We found that red foxes were generally reluctant to consume mesocarnivore carrion, especially of conspecifics. When recorded, consumption by foxes was delayed several days (heterospecific carcasses) or weeks (conspecific carcasses) after carcass detection. Other mammalian scavengers showed a similar pattern. Also, meat-borne parasite transmission from wild carnivore carcasses to domestic dogs and cats was highly unlikely. Our findings challenge the widespread assumption that cannibalistic or intra-specific scavenging is a major transmission route for *Trichinella* spp. and other meat-borne parasites, especially for the red fox. Overall, our results suggest that the feeding decisions of scavengers are probably shaped by two main contrasting forces, namely the nutritional reward provided by carrion of phylogenetically similar species and the risk of acquiring meat-borne parasites shared with these species. This study illustrates how the detailed monitoring of carnivore behaviour is essential to assess the epidemiological role of these hosts in the maintenance and dispersion of parasites of public and animal health relevance.

1. Introduction

Host-parasite interactions are pervasive in ecosystems and may strongly influence food-web structure and function (Byers, 2009; Lafferty et al., 2006, 2008; Sukhdeo, 2012). Ecological networks are frequently characterized by multi-host/multi-parasite systems, with hosts being susceptible to both species-specific and multi-host parasites (Craft et al., 2008; Morand, 2015; Petney and Andrews, 1998). Through an astonishing diversity of direct (e.g., food-borne) and indirect pathways (e.g., intermediate hosts), parasites may alter consumer-resource dynamics (Hatcher et al., 2012; Hudson et al., 2006). Exploring ecological patterns that are shaped by the continuous “arms race” between coevolving hosts and parasites (Betts et al., 2016, 2018) may contribute to our understanding of wildlife epidemiology (Pedersen and Fenton, 2007; Roche et al., 2012; Vander Wal et al., 2014) and conservation (Herrera and Nunn, 2019).

Host species exhibit a wide array of strategies to avoid, remove and control parasites (i.e., macro- and microparasites, the latter including protists, fungi, bacteria and viruses; Behringer et al., 2018), including immunological and behavioural responses (Blumstein et al., 2017). Among them, behaviour may be regarded as the animals’ first line of defence against infection (Hart, 1990, 2011). Given that detecting

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https://doi.org/10.1016/j.applanim.2021.105462
Received 16 June 2021; Received in revised form 20 September 2021; Accepted 23 September 2021

parasites is challenging, usually due to their small size, there has been selection for animals to respond to indirect signs associated with the risk of parasite transmission, regardless of actual parasite presence (Curtis, 2014; Moleón et al., 2017; Weinstein et al., 2018). In response to trophically transmitted parasites, infection risk can therefore be minimized by avoiding risky foods or feeding sites, i.e., parasite-rich environments (Buck et al., 2018; Curtis, 2014; Hart and Hart, 2018; Weinstein et al., 2018). For instance, herbivores usually avoid grazing close to faeces (Ezenwa, 2004). At a landscape scale, animals are thus forced to modify their use of space and time to reduce exposure to parasites (Weinstein et al., 2018). Hosts may perceive parasite infection risk on a "landscape of disgust", with high-risk patches that are avoided and low-risk patches that are safe (Buck et al., 2018; Weinstein et al., 2018), whose distribution and magnitude may change with time (Fritzsche and Allan, 2012). In turn, parasite avoidance behaviours may alter energy flow through food-webs (Wood and Johnson, 2015).

Despite the important ecological, evolutionary and epidemiological implications of host behaviour (Ezenwa et al., 2016; Sarabian et al., 2018; Weinstein et al., 2018), little is known about the strategies, mechanisms and consequences of trophically transmitted parasite avoidance in carnivore species. In general, carnivores seem to avoid feeding upon conspecific prey (Caro and Stoner, 2003; Fox, 1975; Palomares and Caro, 1999), especially if prey is found dead rather than killed by the consumer, as dead animals may have succumbed to a disease (Hart, 2011; Moleón et al., 2017). Thus, carrion may play a prominent role in the carnivores' landscape of disgust (Moleón and Sánchez-Zapata, 2021). Given that phylogenetically related carnivores harbour similar parasite assemblages (Huang et al., 2014), the carnivore is more prone to be infected by parasites present in the carcass if both the consumer and the carcass belong to the same species or to a phylogenetically related group of species (Hart, 2011; Moleón et al., 2017). In this case, scavengers must face a trade-off between the changing nutritive value of the carcass, which is maximum for conspecific flesh (as it supplies nutrients in proportions that are easier to assimilate than heterospecific tissues; Mayntz and Toft, 2006; Meffe and Crump, 1987), and its associated parasite risk (Moleón et al., 2017; Pfennig, 2000; Pfennig et al., 1998; Rudolf and Antonovics, 2007). Both the nutritive value and the parasite risk decrease with time (Parmenter and MacMahon, 2009; Rossi et al., 2019), but probably at different rates, which could lead carnivores to also change their foraging decisions over time. However, whether and when a scavenger decides to feed on a risky carcass while obtaining sufficient nutritional revenue are largely unresolved questions in scavenging and disease ecology.

For instance, it is widely accepted within the scientific community that scavenging, including intraspecific consumption (i.e., cannibalism), plays an important role in the transmission of meat-borne parasites in wild carnivores, especially *Trichinella* spp. (phylum Nematoda), one of the most relevant zoonoses occurring at the wildlife-domestic-human interface (Badagliacca et al., 2016; Campbell, 1988; Pozio, 2000; Pozio and Murrell, 2006). This nematode and other species such as the zoonotic protozoan *Toxoplasma gondii* (phylum Apicomplexa) are among the paradigmatic parasites that are transmitted by meat consumption. These multi-host parasites are globally distributed (Dubey, 1991; Pozio and Murrell, 2006) and have been described in numerous mammalian carnivores, including the red fox (*Vulpes vulpes*) and several mustelids and viverrids (Kirjušina et al., 2016; Lukášová et al., 2018; Oivanen et al., 2002a; Pérez-Martín et al., 2000; Sobrino et al., 2007). Intra-specific and intra-family consumption of somatic larvae in muscle could also potentially be a possible transmission route for more specific parasites, such as *Toxocara canis* in red fox and other canids (Saeed and Kapel, 2006). However, recent empirical (Moleón et al., 2017; Muñoz-Lozano et al., 2019; Olson et al., 2016; Selva et al., 2005) and modelling (Moleón et al., 2017) findings have shown that mammalian carnivores tend to avoid feeding on carrion of other carnivores, especially of conspecifics, possibly as a strategy to reduce the risk of acquiring parasites. Thus, further research on carnivore scavenging behaviour in relation to carcass identity is needed to adequately interpret, based on scientific evidence, the epidemiological factors that characterize the transmission of meat-borne parasites in the wild (Polley and Thompson, 2015; Moleón and Sánchez-Zapata, 2021). This is particularly important in the current context of emerging and re-emerging diseases of global distribution, among which there are many zoonoses that should be studied from an integrated One Health perspective (Bueno-Marí et al., 2015; Evans et al., 2020; Wong et al., 2020).

The general objective of this study is to explore meat-borne parasite avoidance strategies of carnivores, especially the red fox, at carnivore carcasses. The red fox, a ubiquitous and typically generalist carnivore (Wilson and Mittermeier, 2009), is one of the most important reservoirs involved in the sylvatic cycle of many parasites with potential zoonotic and veterinary significance (Karamon et al., 2018). Moreover, foxes are major scavengers (Mateo-Tomás et al., 2015). All of these features make the red fox a good candidate for detailed research on trophic behaviour in relation to the risk of parasite transmission (Díaz-Ruiz et al., 2013; Vercammen et al., 2002).

Specifically, we aim to answer the following main questions: 1) does the probability of foxes to practice cannibalism change with time since the conspecific carcass is available, and on which factors does this depend?; and 2) does the scavenging behaviour of foxes differ between conspecific carcasses and carcasses of other mesocarnivore species? For this purpose, we assessed the consumptive patterns of mammalian carnivore carcasses over time, including the final stages of carcass depletion, in areas with different scavenging communities and degree of anthropization. The latter will allow to control to which extent the propensity to cannibalism is influenced by environmental factors. Our general hypothesis is that the perceived risk of acquiring trophically transmitted parasites through scavenging behaviour is dependent on carcass type (conspecific vs. heterospecific to the consumer), and that carnivores will show behavioural responses to reduce exposure to parasites, including consumption avoidance and delay (Moleón and Sánchez-Zapata, 2021). Based on the results of this and previous studies on scavenging patterns of herbivore carcasses in the same study areas (see "Study areas and scavenging context"), we elaborate a conceptual model that synthesizes how the main forces that carnivores face at carrion resources, namely their nutritional value and the risk of acquiring meat-borne parasites, change over time.

2. Material and methods

2.1. Study areas and scavenging context

Fieldwork was conducted in three mountainous, Mediterranean areas of southeastern Spain: Sierras de Cazorla, Segura y Las Villas Natural Park, Sierra Espuña Regional Park, and periurban areas of Murcia city (hereafter Cazorla, Espuña and Murcia, respectively). For more information on the orography, climate and environmental characteristics of these areas, see Gonzálvez et al. (2021). In Cazorla, there is a rich representation of both obligate (i.e., vultures) and facultative vertebrate scavengers. Espuña holds a similar scavenging community, though vultures are less abundant. In Murcia, vultures are rare, and the presence of domestic carnivores (dogs *Canis lupus familiaris* and cats *Felis silvestris catus*) is more frequent than in the other study areas. The red fox is the commonest wild mammalian carnivore in the three study areas, and it is more abundant in Espuña than in Cazorla (there are no data for Murcia; see Moleón et al. (2017), Morales-Reyes et al. (2017) for more details on the study areas of Cazorla and Espuña).

The highly efficient consumption patterns of herbivore carcasses by the scavenging communities of Cazorla and Espuña have been well-documented (e.g., Arrondo et al., 2019; Moleón et al., 2017; Morales-Reyes et al., 2017). As average, wild ungulate carcass detection time by scavengers is less than one day in Cazorla and less than three days in Espuña, while carcasses are totally consumed in three days in Cazorla and eight days in Espuña, mainly by vultures (especially, in Cazorla), foxes, wild boars and dogs (Arrondo et al., 2019; Moleón et al., 2017; Morales-Reyes et al., 2017). In Cazorla, livestock carcasses in open areas are consumed even more quickly, normally within one day (Arrondo et al., 2019). These figures are within the general patterns found worldwide for herbivore carcasses (Sebastián-González et al., 2020). In contrast, mesocarnivore carcasses are rarely scavenged and may last for months (Moleón et al., 2017; Muñoz-Lozano et al., 2019), though detailed data on scavenger foraging behaviour at these carcasses and how this may change over time are lacking.

2.2. *Data collection*

We deployed 66 carcasses of red fox ("fox carcasses") and other mesocarnivore species ("other carcasses") from November 2016 to March 2018 in Cazorla (n = 27 foxes), Murcia (n = 19 foxes) and Espuña (n = 10 foxes, 4 stone martens *Martes foina*, 3 Eurasian badgers *Meles meles*, 2 common genets *Genetta genetta*, and 1 wild cat *Felis silvestris silvestris*). Carcasses of other mesocarnivores are much more difficult to obtain than fox carcasses, given that these species are scarcer than foxes; also, they are protected, so their hunting is prohibited. Thus, we focused the searching effort of other carcasses around the best-known area, namely Espuña (e.g., see Moleón et al., 2017 and references therein). All carcasses came from animals that were run over and, in the case of some foxes, shot in approved hunts. Before deployment in the study areas, carcasses were carefully eviscerated and examined in order to rule out the presence of macroscopic alterations indicating infection; in addition, all specimens were subject to diagnostic procedures to ensure that they were free from *Trichinella* spp. (artificial digestion of muscles from base of tongue, forearms and diaphragm; Gamble et al., 2000; Kapel et al., 1994), *Sarcoptes scabiei* (skin skrapping) and the most common viral diseases affecting wild and domestic carnivores (assays for antibody detection of canine distemper virus, feline coronavirus, canine and feline parvovirus, feline leukemia virus and feline immunodeficiency virus). In this study, only pathogen-free carcasses were used, and the tissue around the shot point was removed to avoid lead residues (see Gonzálvez et al., 2021).

Carcasses were frozen in plastic bags (−20 °C) and defrosted at laboratory temperature during 12–24 h before being placed in the field. Carcasses were regularly distributed throughout the study areas, with a minimum distance between neighboring carcasses of 1.5 km (Moleón et al., 2017; Gonzálvez et al., 2021). Altitude of carcass sites ranged 772–1676 in Cazorla, 433–1432 in Espuña and 125–448 in Murcia. Each site was classified as "closed area" or "open area", depending on whether tree and shrub cover in a 10 m radius around the carcass exceeded or not 50% of the surface area, respectively (Gonzálvez et al., 2021).

To obtain information about the presence of scavengers and their trophic behaviour at carcass sites, we fixed automatic cameras (Bushnell Trophy Cam and Bushnell Aggressor) to a tree or shrub trunk (50–100 cm height) at 3–4 m from the carcasses. Cameras were programmed to take a 15-second video after detection of movement (one minute-interval between consecutive videos). Batteries and memory cards were checked weekly, and cameras were removed when no carrion was left or after 10 weeks. We focused on vertebrate species that have been found to scavenge in our study areas (Sebastián-González et al., 2019). These species were grouped in three categories: red fox, other mammals and birds. For each carcass, we defined independent events as: a) consecutive videos of unequivocally different individuals of the same species or individuals of different species; b) if individual identification was not possible, consecutive videos of individuals of the same species taken more than 30 min apart; or c) non-consecutive videos of individuals of the same species (O'Brien et al., 2003; Ridout and Linkie, 2009; Gonzálvez et al., 2021). We then made a distinction between "consumption events", when we observed unequivocal carrion biting and feeding behaviour, and "non-consumption events" otherwise.

2.3. *Data analyses: weekly scavenging patterns*

First, we explored the general patterns of mesocarnivore carcass use by the studied scavenging communities. For each carcass type (fox and others) and study area, we used the images provided by the cameras to calculate, on a weekly basis, the proportion of carcasses that were consumed (i.e., with at least one consumption event) and visited but not consumed (i.e., no consumption events recorded), for all scavengers together and separately for each scavenger category. We did the same for the number of consumption and non-consumption events.

We then explored the changing probability of red foxes to scavenge fox and other mesocarnivore carcasses by calculating these ratios per week: a) consumed:non-consumed carcasses and b) consumption:non-consumption events. In addition, we determined the accumulated number of carcasses that were a) detected and b) consumed (i.e., at least one consumption event) each week by red foxes. For each carcass, we estimated carcass "detection time" as the time elapsed between carcass placement and the arrival of the first fox.

2.4. *Data analyses: determinants of carrion consumption by fox*

We used generalized linear models (GLMs) to analyse the factors influencing "time of first consumption" (only carcasses with at least one consumption event by foxes were used; n = 27) and the "ratio consumption:non-consumption events" (all carcasses detected by fox; n = 62). For each response variable, we carried out two separate analyses, according to these two different datasets: 1) all fox carcasses in the three study areas; and 2) both fox and other carcasses in Espuña only. The first analysis is mainly focused on exploring the cannibalistic behaviour of foxes, while the second one is aimed to determine if fox scavenging behaviour is influenced by carcass type (see the particular goals of this study in Introduction). Time of first consumption was estimated as the time elapsed since carcass detection by foxes until the first consumption event by foxes. The carcass was the sample unit for these analyses. The explanatory variables were study "area" (Cazorla, Espuña, Murcia; used only for the analysis of fox carcasses in the three study areas), "carcass type" (fox, other; used only for the analysis of fox and other carcasses in Espuña), "habitat" (closed, open), "year", "season" (winter: November-February; spring: March-April), "hour" of carcass placement (morning —from dawn to 12:00 h, afternoon —from 12:00 h to dusk), and carcass "detection time" by foxes (in days). Habitat, season and hour may influence scavenger foraging patterns and interspecific interactions among scavengers (e.g., Arrondo et al., 2019). For the ratio consumption:non-consumption events, we also included "scavenger presence" (presence of scavengers other than foxes) and "scavenger consumption" (at least one consumption event by a scavenger other than fox).

We then proceeded with model construction, using Gaussian error distributions and identity functions for time of first consumption and binomial error distributions and logit link functions for the ratio consumption:non-consumption events; in the latter case, we used the function cbind() in R to combine the vectors "consumption events" and "non-consumption events" in a single response variable, which avoided losing the information on the number of events, i.e., the sample size from which the ratio is estimated (Crawley, 2007). We ran univariate models with all the possible explanatory variables for each case. We did not run multivariate models due to limitations imposed by the low sample size (i.e., number of monitored carcasses). We based model selection on Akaike's Information Criterion, which allows the identification of the most parsimonious model (lowest AIC) and ranks the remaining models. We corrected the AIC value for small sample sizes (AICc). Then, we calculated delta AICc (ΔAICc) as the difference in AICc between each model and the best model in the evaluated set, considering models with $\Delta\text{AICc} < 2$ to have similar support (Burnham and Anderson, 2002). Finally, we calculated the deviance (D^2) explained by each candidate model according to this formula: D^2 = (null deviance − residual deviance) / null deviance * 100 (Burnham and Anderson, 2002). Analyses were done in R studio software v1.0.143 (R Core Team, 2018).

3. Results

3.1. *General results: the scavenging community*

A total of 1617 events of scavenger species were recorded in the three studied areas (Cazorla: 68%; Murcia: 13%; Espuña: 19%; Table S1). We detected 14 scavenger species (eight mammals and six birds). Species richness was highest in Cazorla (13 spp.) and lowest in Espuña at fox carcasses (5 spp.). Differences in species richness were mainly due to birds, with six species recorded in Cazorla and only one species in Murcia and Espuña. The red fox was the most frequently recorded scavenger species in the three study areas (59.4% of total events). Consumption events represented 15.7% of the total events recorded. Taking into account all study areas together, foxes were responsible for most consumption events (53.4% of events). Carcasses were consumed by nine species (five birds and four mammals) in Cazorla, two species in Murcia (one bird and one mammal), two species in Espuña at fox carcasses (two mammals), and two species in Espuña at other carcasses (one bird and one mammal). When focusing on those avian scavenger species that scavenge more frequently, consumption events were more frequent than non-consumption events, while the opposite was true for all mammalian scavengers (Table S1). Cannibalism represented 16.9% of the total events recorded for the red fox at fox carcasses. We did not record any consumption event by domestic carnivores (dogs and cats). General patterns of carcass use by the three scavenger categories in each study area are shown in Table 1.

3.2. *Weekly scavenging patterns*

For a given week, there were more carcasses visited but not consumed by mammalian scavengers than carcasses visited and consumed, for all areas and carcass types. This pattern was not observed for scavenging birds, especially in Cazorla, where visited carcasses were more frequently consumed than not consumed. Mammalian scavengers other than fox only consumed fox carcasses. The number of carcasses visited and consumed was highest in Cazorla and Espuña (foxes at other carcasses), and lowest in Murcia (Fig. 1a, Fig. S1). In relation to events per studied carcass, we observed a similar general pattern, with far more non-consumption events than consumption events, except for foxes at other carcasses in Espuña (Fig. 1b; Fig. S2).

The ratio between consumed and non-consumed carcasses by foxes (Fig. 2) showed a bell-shaped distribution, with maximum values (i.e., more carcasses consumed than non-consumed) from the third (in Cazorla) to the fifth (in Murcia) week in the case of fox carcasses. In the carcasses of other species, the maximum took place in the second week, i.e., two weeks earlier than the maximum recorded for fox carcasses in the same study area (Espuña). Even during the peaks, fox carcasses were more frequently left unconsumed than consumed, and only for other carcasses in Espuña the number of consumed carcasses was higher than those left unconsumed. We observed a similar general pattern for events, with peaks occurring from the third week on in the case of fox carcasses and in the second week in the case of other carcasses, i.e., several weeks earlier than the peak for fox carcasses in the same study area. While fox carcasses in Cazorla and other carcasses in Espuña began to be consumed during the first week after their deployment, the first events of consumption of fox carcasses in Espuña and Murcia began to be recorded from the second and third week, respectively. The lowest

Table 1

Scavenging patterns at carcasses of red fox and other mesocarnivores in the three study areas of southeastern Spain, according to different scavenger groups (red fox, other mammals, birds and total scavengers). Number of monitored carcasses is indicated for each study area and carcass type. Mean±SD (min.-max.) is shown for carcass detection time, time of first consumption, total events and consumption events for each scavenger group. The number of carcasses visited and consumed by each scavenger group is shown together with the percentage relative to the total carcasses monitored per area and carcass type (in parentheses). Time rounded to the nearest hour. We considered carcasses consumed as those carcasses with at least one consumption event by a given scavenger group.

Area	Carcass type	N	Scavenger group	Detection time (h)	Time of first consumption (h)	Carcasses visited	Carcasses consumed	Total events	Consumption events
Cazorla	Foxes	27	Red fox	78 ± 105 (4–395)	465 ± 371 (4–1191)	27 (100%)	17 (63.0%)	22.0 ± 13.8 (5–53)	4.3 ± 7.0 (0–27)
			Other mammals	132 ± 128 (2–530)	623 ± 213 (324–880)	26 (96.3%)	7 (25.9%)	9.6 ± 7.0 (0–24)	0.7 ± 2.0 (0–10)
			Birds	293 ± 293 (1–890)	231 ± 247 (20–791)	18 (66.7%)	10 (37.0%)	9.2 ± 11.9 (0–45)	5.5 ± 10.3 (0–37)
			Total	44 ± 58 (1–195)	372 ± 381 (4–1191)	27 (100%)	21 (77.8%)	40.7 ± 21.2 (15–85)	10.5 ± 12.6 (0–40)
Murcia	Foxes	19	Red fox	302 ± 245 (17–901)	632 ± 217 (359–932)	16 (84.2%)	6 (31.6%)	8.4 ± 8.8 (0–31)	0.8 ± 1.9 (0–7)
			Other mammals	395 ± 343 (1–981)	–	12 (63.2%)	0 (0%)	1.4 ± 1.8 (0–7)	0
			Birds	213 ± 132 (34–350)	386	3 (15.8%)	1 (5.3%)	1.2 ± 3.2 (0–13)	0.2 ± 0.7 (0–3)
			Total	271 ± 299 (1–974)	627 ± 223 (359–932)	17 (89.5%)	6 (31.6%)	11.0 ± 11.4 (0–45)	1.0 ± 2.3 (0–8)
Espuña	Foxes	10	Red fox	134 ± 104 (9–290)	601 ± 235 (267–795)	9 (90.0%)	4 (40.0%)	7.7 ± 6.2 (0–21)	0.8 ± 1.3 (0–4)
			Other mammals	234 ± 194 (33–583)	199	10 (100%)	1 (10.0%)	2.2 ± 1.6 (1–6)	0.2 ± 0.6 (0–2)
			Birds	41	–	1 (10.0%)	0 (0%)	3.8 ± 12.0 (0–38)	0
			Total	103 ± 73 (9–200)	521 ± 272 (199–795)	10 (100%)	5 (50.0%)	13.7 ± 13.5 (1–48)	1.0 ± 1.3 (0–4)
	Others	10	Red fox	222 ± 185 (4–462)	365 ± 343 (88–927)	10 (100%)	5 (50.0%)	12.9 ± 24.1 (2–81)	5.9 ± 15.6 (0–50)
			Other mammals	293 ± 267 (34–972)	–	10 (100%)	0 (0%)	3.6 ± 3.1 (1–10)	0
			Birds	502 ± 418 (257–985)	745	3 (30.0%)	1 (10.0%)	0.6 ± 1.1 (0–3)	0.2 ± 0.6 (0–2)
			Total	151 ± 153 (4–427)	429 ± 343 (88–927)	10 (100%)	6 (60.0%)	17.1 ± 23.6 (3–83)	6.1 ± 15.5 (0–50)

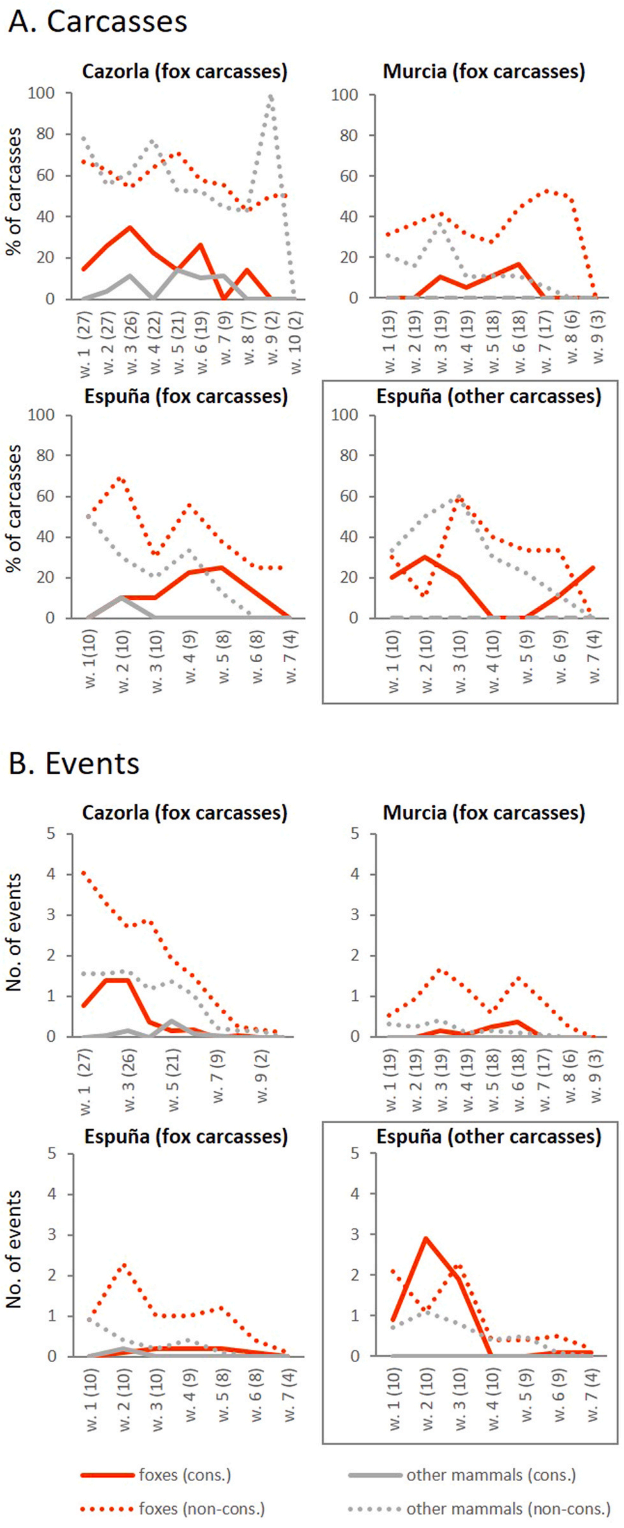

Fig. 1. Weekly variation in consumption patterns of mesocarnivore carcasses by red fox and other mammalian scavengers in three areas of southeastern Spain. A) Weekly percentage of consumed ("cons."; i.e., with at least one consumption event) and non-consumed ("non-cons."; i.e., visited, but no consumption events recorded) carcasses by red fox and other mammalian scavengers per study area and carcass type. B) Weekly number of consumption ("cons.") and non-consumption ("non-cons.") events by red fox and other mammalian scavengers per study area and carcass type. For a given week, the number of events are divided by the grand total number of carcasses studied in each study area. The number of carcasses available each week to scavengers is given in parentheses. Panels for carcasses of carnivores other than foxes are in boxes.

number of consumption events in relation to non-consumption events at fox carcasses was found in Espuña, an area where, in contrast, consumption events of other carcasses exceeded non-consumption events during the peak (Fig. 2).

Red foxes detected 94% of studied carcasses, but consumption events were recorded only in one-third to two-thirds of them (Cazorla: 63%; Murcia: 38%; Espuña, fox carcasses: 44%; Espuña, other carcasses: 50%). No other carnivore species consumed carcasses of carnivores other than fox. Foxes detected most carcasses within the first three weeks after carcass deployment. However, the stabilization of the number of carcasses consumed took longer. Within carcasses visited by foxes, the difference in the accumulated number of carcasses consumed and not consumed during the first two weeks was higher for fox carcasses compared to those of other carnivores (Fig. S3).

3.3. *Determinants of carrion consumption by fox*

Regarding fox carcasses, the time from carcass detection by foxes to the first record of consumption was mainly related to the former variable (detection time by foxes) in the three study areas, according to the GLM model with the highest D^2 (Table 2). In particular, foxes started to consume earlier carcasses that were detected later (Table 3). The ratio consumption:non-consumption events of foxes was mainly related to consumption by other scavenger species (Table 2), with a ratio more biased towards consumption events in carcasses also consumed by other scavengers (Table 3).

In relation to carcasses of fox and other carnivores in Espuña, both the time of first consumption by foxes and the ratio consumption:non-consumption events of foxes were mainly dependent on carcass type (Table 2). Foxes started to consume heterospecific carrion c. 10 days earlier as average than conspecific carcasses (Tables 1, 3; Fig. 1), and showed relatively more consumption events at other carcasses compared to conspecific ones (Table 3; Fig. 2). Specifically, as average, consumption events by foxes were c. seven times more frequent in heterospecific carcasses than in conspecific ones (Table 1). In general, according to deviance values, the models for this dataset (fox and other carcasses in Espuña) had higher explanatory capacity than the models for the dataset of fox carcasses only (Table 2).

4. Discussion

Despite being a key defensive barrier against trophically transmitted parasites (Ezenwa et al., 2016; Hart, 1990, 2011; Sarabian et al., 2018; Weinstein et al., 2018), parasite avoidance behaviours in carnivore species have received little scientific attention, especially in the context of carrion use (Moleón and Sánchez-Zapata, 2021). Here, we found that red foxes were very efficient in detecting mesocarnivore carrion, as they visited nearly all monitored carcasses. However, as expected, foxes were generally reluctant to consume them, especially those of conspecifics. In addition, consumption by foxes, when recorded, was delayed several days (heterospecific carcasses) or weeks (conspecific carcasses) after carrion detection, and time elapsed between fox carcass detection and consumption by foxes was shorter for carcasses discovered later. Other mammalian scavengers showed a similar pattern than foxes: they detected most carcasses during the first week after their deployment but we observed very few consumption events (no cannibalistic events recorded), with all consumption taking place from the second week on. The use of videos instead of photos and the longer monitoring period in this study may explain why we found more cannibalistic events here than in a previous study in two of the three study areas (Cazorla and Espuña; Moleón et al., 2017). For comparison, in these two study areas, ungulate carcasses are normally consumed within the first week

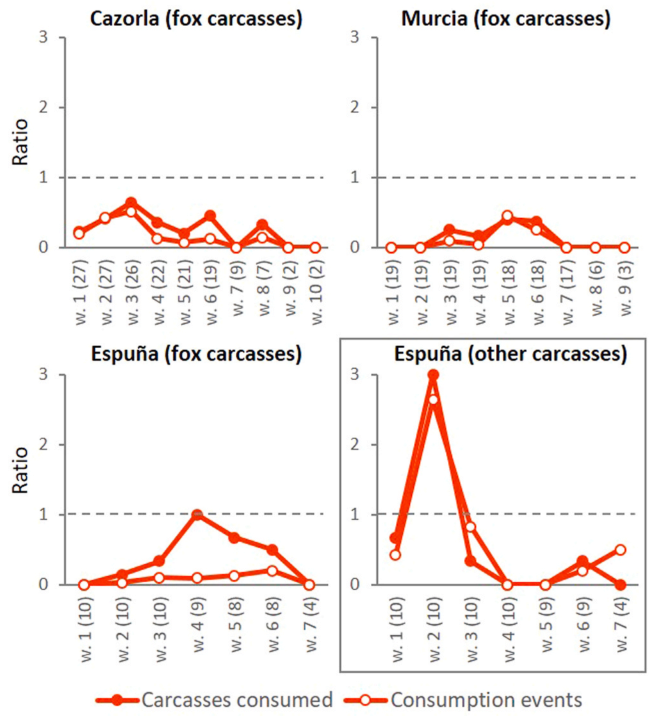

Fig. 2. Weekly variation in the ratios consumed:non-consumed carcasses and consumption:non-consumption events by the red fox per study area and carcass type. Values above and below the dashed horizontal grey line indicate, respectively, ratios biased towards consumption and non-consumption. For a given week, the number of carcasses available to scavengers is given in parentheses. Panel for carcasses of carnivores other than foxes is in the box.

Table 2
AICc-based model selection to assess the factors influencing "time of first consumption" by foxes and the "ratio consumption:non-consumption events" by foxes on conspecific carcasses in three study areas of southeastern Spain ("among areas" comparisons) and on conspecific and heterospecific carcasses in one of these study areas ("fox vs. other carcasses" comparisons). Explanatory variables include study "area", "habitat", "year", "season", "hour", "carcass type", presence of scavengers other than fox ("scav. pres."), consumption by scavengers other than fox ("scav. cons."), and carcass "detection time" by foxes (see text for details on the variables). Number of estimated parameters (k), AICc values, AICc differences (ΔAICc) with the model with the lowest AICc, and the variability of the response variable explained by the predictor (deviance, D^2) are shown. Selected models are in bold.

Response variable	Comparison	Model	k	AICc	delta-AICc	D^2
Time to first consumption	Among areas (fox carcasses)	**detection time**	**1**	**221.14**	**0**	**8.85**
		hour	**1**	**223.10**	**1.96**	**2.00**
		habitat	1	223.31	2.17	
		season	1	223.53	2.39	
		year	2	224.32	3.18	
		area	2	225.60	4.46	
	Fox vs. other carcasses	**carcass**	**1**	**79.60**	**0.00**	**21.51**
		hour	**1**	**79.68**	**0.08**	**20.85**
		detection time	**1**	**81.00**	**1.40**	**8.30**
Ratio consumption: non-consumption events	Among areas (fox carcasses)	**scav. cons.**	**1**	**323.60**	**0**	**9.42**
		season	1	328.17	4.57	
		habitat	1	331.27	7.67	
		area	2	339.87	16.27	
		detection time	1	344.95	21.35	
		scav. pres.	1	346.82	23.22	
		hour	1	348.37	24.77	
		year	2	350.35	26.75	
	Fox vs. other carcasses	**carcass**	**1**	**80.83**	**0.00**	**36.19**
		hour	1	94.07	13.24	
		detection time	1	95.98	15.15	
		scav. cons.	1	106.63	25.80	

(Arrondo et al., 2019; Moleón et al., 2017; Morales-Reyes et al., 2017; see "Study areas and scavenging context" for more details). These differences can not be explained by the different size of mesocarnivore carcasses in relation to the larger ungulate carcasses, as smaller carcasses are normally consumed earlier (Moleón et al., 2015). Overall, our results are in agreement with diet studies on red fox (Fairley, 1970; Remonti et al., 2005) and other mammalian carnivores (Caro and Stoner, 2003; Fox, 1975; Palomares and Caro, 1999) that indicate that cannibalism is very uncommon in these species, and support the hypothesis that avoidance of carrion from phylogenetically related prey is a widespread behaviour in carnivores to prevent meat-borne parasite risk (Moleón et al., 2017; though see Van Allen et al., 2017 for other taxa).

Why do foxes and other mesocarnivores not feed on carnivore carcasses, especially conspecific carrion, upon detection? Our results suggest that the foraging decisions of scavengers are probably shaped by two major contrasting forces (Fig. 3), namely the nutritional reward provided by carrion of phylogenetically similar species (Mayntz and Toft, 2006; Meffe and Crump, 1987) and the risk of acquiring meat-borne parasites shared with these species (Huang et al., 2014; Moleón et al., 2017; Pfennig, 2000; Pfennig et al., 1998; Rudolf and Antonovics, 2007). On one hand, the nutritional quality of carrion decreases with time (Parmenter and MacMahon, 2009). Thus, the most advantageous strategy for foxes would be feeding before carrion is too degraded. On the other hand, the risk of acquiring viable trophically transmitted parasites is also highest when the carcass is fresh (Fan et al., 1998; Pozio, 2016). This may force foxes to wait until the carcass reaches a "safety" parasite load threshold, which is probably more restrictive for conspecific carrion because the number of parasite species that can affect the consumer is maximum (Fig. 3). At this point, it is important to remark that the risk of parasite infection is a perceived risk related to potential rather than actual parasite presence (Curtis, 2014; Moleón et al., 2017; Weinstein et al., 2018). In this sense, many meat-borne parasites, such as *Trichinella* spp., do not provoke any external lesion or sign of disease after the establishment of the infective larvae in the musculature (Gottstein et al., 2009), and all carnivore carcasses of our study belonged to healthy animals without any macroscopic lesions. Future investigations could assess whether the presence of macroscopic lesions on carnivore carcasses may condition the trophic behaviour of scavenger species, considering, nevertheless, that external signs of infection are usually more difficult to identify for meat-borne parasites than for non-trophically transmitted parasites. Finally, within a carnivore-animal flesh context, all prey can be considered of relatively high-quality (Swift et al., 1979). Thus, the risk of acquiring meat-borne parasites is probably much more determinant than the nutritive value of the carcass when guiding foraging decisions (see Fig. 3).

At which stage of carcass decomposition this nutritional value-parasite risk trade-off favours feeding on conspecific and phylogenetically related carcasses may depend on several extrinsic and intrinsic factors to the scavenger. Regarding extrinsic factors, the infectivity of *Trichinella* spp. and other meat-borne parasites is known to be highly related to environmental conditions and the changes that occur during carrion decay (Bengis, 1997; Pozio, 2000). For instance, high humidity and low temperature favours the survival and transmission of *Trichinella* larvae (Fariña et al., 2017; Oivanen et al., 2002b; Pozio, 2016; Riva et al., 2012; Rossi et al., 2019). In cold environments, at constant low temperatures such as those reached beneath the snow, the infective capacity of *T. britovi* larvae in red fox carcasses does not show important

Table 3
Generalized linear models (GLMs) showing the relationship between "time of first consumption" by foxes and the "ratio consumption:non-consumption events" by foxes with the explanatory variables included in the selected models ("detection time": carcass detection time by foxes; "hour" of carcass placement: morning, afternoon; "carcass" type: fox, other; "scav. cons.": consumption by scavengers other than fox). The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degree of freedom of the models (df) are shown.

Response variable	Comparison	Model	Parameter	Estimate	SE	df
Time to first consumption	Among areas (fox carcasses)	detection time	Intercept	18.81	3.23	26
			detection time	-0.51	0.33	
		hour	Intercept	16.52	2.87	26
			hour (morning)	-5.32	7.45	
	Fox vs. other carcasses	carcass	Intercept	20.39	6.27	8
			carcass (other)	-11.65	8.41	
		hour	Intercept	11.90	4.45	8
			hour (morning)	18.14	13.36	
		detection time	Intercept	17.64	6.51	8
			detection time	-0.66	0.82	
Ratio consumption: non-consumption events	Among areas (fox carcasses)	scav. cons.	Intercept	-2.09	0.15	51
			scav. cons. (yes)	0.95	0.19	
	Fox vs. other carcasses	carcass	Intercept	-2.15	0.37	18
			carcass (other)	1.98	0.41	

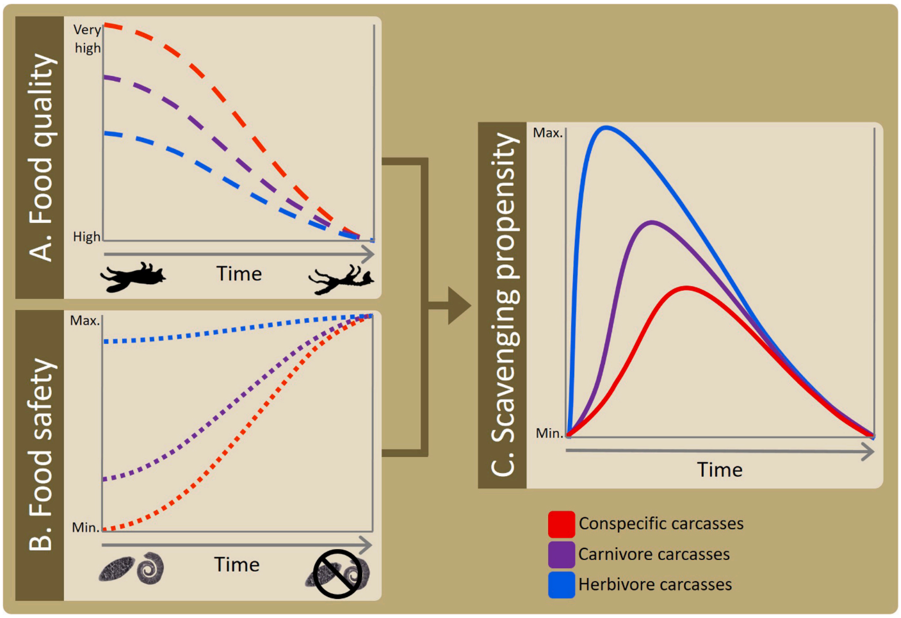

Fig. 3. Conceptual model showing how food quality and safety shape the propensity of mammalian carnivores to scavenge on carcasses of species differing in their phylogenetic distance to the consumer. A) On one hand, the nutritive value, which is maximum for conspecific carcasses, decreases with time. Note that all meat can be regarded as high- to very high-quality food for a carnivore (Swift et al., 1979). B) On the other hand, the probability of a carcass to have fewer infective stages of meat-borne parasites increases with time. In fresh carcasses, the risk for a consumer of acquiring meat-borne parasites, at least for direct life cycle parasites, is maximum when it ingests conspecific carrion, and minimum for carcasses belonging to weakly related species, with which the number of shared parasite species is lowest. Non-linearity is probably a fundamental property of all of these functions. C) These contrasting forces probably shape the observed patterns of carcass consumption (for our study areas, see this study, Arrondo et al., 2019, Moleón et al., 2017, Morales-Reyes et al., 2017, Muñoz-Lozano et al., 2019).

reductions during the first four months. However, above the snow, with more oscillating temperatures, the parasite's reproductive capacity sharply decreases after two months, and almost no viable larvae are present after three months (Rossi et al., 2019). At higher temperatures (average: 23ºC), the number of infective *T. spiralis* larvae in rat carcasses decreases severely after the first week (Oivanen et al., 2002b). In the case of decaying fox meat, the number of infective larvae of several *Trichinella* genotypes has been found to decrease rapidly during the first two weeks at 22–27 °C and 100% relative humidity (Von Köller et al., 2001). In our study areas, characterized by mild to warm temperatures and with carcasses rarely covered by snow during winter, meat-borne parasites are expected to survive only a few weeks even in the coldest season. Moreover, in these climatic conditions, flesh decomposes faster than in colder latitudes (Selva et al., 2005), with most non-scavenged carrion disappearing within the first two months due to necrophagous invertebrates, decomposers and dehydration (Muñoz-Lozano et al., 2019). In this regard, indirect infection from eating carrion insects could also affect scavenging carnivores. However, the survival period of meat-borne parasites inside insect bodies seems to be very limited. For instance, *Trichinella* larvae may survive and be infective after being ingested by maggots, though maximum survival under the most favourable environmental conditions is five days (Maroli and Pozio, 2000). Given that climate may play an important role in determining parasite survival around carcasses, further research is needed in colder areas, especially in light of the ongoing global climate change (Cizauskas et al., 2017).

All of this is consistent with our findings of low rates and delayed consumption of carnivore carrion, especially of conspecifics, and could explain why foxes practiced earlier cannibalism when they discovered the carcass at advanced stages of decomposition. The fact that the ratio between consumption and non-consumption events of foxes was higher at carcasses that were also consumed by other scavengers suggest some inter-specific facilitative process, as is typical in scavenging assemblages (Moleón et al., 2014). In particular, carrion consumption by other scavenger species could be interpreted as a signal that the carcass is safe, so foxes may have partly relied on these indirect cues to guide their foraging decisions. Alternatively, it may indicate that all scavengers rely on similar cues.

In relation to intrinsic factors, our study design (with carcasses normally separated from each other several kilometers) and occasional individual recognition of foxes (thanks to external, identifiable features observed in the images) revealed that some foxes practiced cannibalism while others rejected conspecific carcasses, which could indicate some individual variation in the way foxes confront the trade-off between the nutritional gains and the risk of acquiring parasites associated with carrion. According to state-dependent foraging theory (McNamara and Houston, 1987), hungry, young, senescent and sick individuals could be more prone to feeding on low quality food and assuming the risk of a dangerous meal (Fodrie et al., 2012; Mukherjee and Heithaus, 2013), which needs to be confirmed in future investigations.

4.1. *Epidemiological implications*

The results of this and previous studies (Moleón et al., 2017; Muñoz-Lozano et al., 2019; Olson et al., 2016; Selva et al., 2005) show that cannibalistic scavenging is a rare feeding strategy in mammalian mesocarnivores. In the case of the red fox, all mesocarnivore carcasses are risky carcasses in epidemiological terms, but the risk associated with fox carcasses is highest because of highest probability of sharing parasite species. Here, we also showed that cannibalistic scavenging, when it does occur, generally takes place after the period of maximum survival of infective stages of potential meat-borne parasites, i.e., several weeks after the carcass becomes available. Overall, this suggests that cannibalistic scavenging is an infrequent transmission route of meat-borne parasites among foxes – and possibly other wild carnivores. This challenges the widespread assumption that multi-host parasites such as *Trichinella* spp. are closely linked to intra-specific consumption, including both predation and scavenging (Badagliacca et al., 2016; Campbell, 1988; Pozio, 2000). This assumption may be partially based on the frequent presence of fox hairs in the faeces of this canid, which has traditionally been interpreted as evidence of cannibalism. However, Remonti et al. (2005) argued that undigested fox hairs found in faeces are mainly related to coat-cleaning rather than cannibalism. Thus, the transmission and maintenance of the sylvatic cycle of multi-host parasites transmitted by meat is likely to depend, more than previously thought, on transmission routes other than cannibalistic consumption of infected carrion.

Similar scavenger's behavioural patterns have recently been described at carnivore carcasses regarding non-trophically tramsitted parasites in the same study areas (Gonzálvez et al., 2021). However, the fact that contact with carnivore carcasses occurs much more frequently (Gonzálvez et al., 2021) than carrion consumption (this study) suggests that mammalian scavenger behaviour is primarily constrained by the perceived risk of acquiring meat-borne parasites.

Importantly, our findings indicate that the risk of meat-borne parasite transmission from carcasses of wild carnivore species to domestic carnivores (dogs and cats) is negligible, at least in our study areas. This was true even in the periurban study area, where the probability of dogs and cats to find a carcass is higher compared to more natural landscapes. Thus, our study suggests that carrion removal from the field, a usual management method against the spread of meat-borne parasites (e.g., Donázar et al., 2009; Probst et al., 2017), is not a justified strategy in the case of carnivore carcasses. Overall, we provide an example of how the detailed study of scavenging animals using images (especially videos) provided by camera traps at carcass sites can help to identify which behaviours and host species may represent an epidemiological risk in the wildlife-domestic-human interface, especially regarding mammalian carnivores, which are often elusive and cryptic species that are difficult to survey (Barea-Azcón et al., 2007; Balme et al., 2009). In this sense, our study provides scientific evidence towards precisely assessing the risk associated with mesocarnivore carcasses and the role that wild carnivore species may have as spreader or reservoir of meat-borne parasites, which has important implications from a One Health perspective.

4.2. *Conclusions*

Carnivore carcasses are fundamental components in the landscape of disgust for carnivores (Buck et al., 2018; Moleón and Sánchez-Zapata, 2021; Weinstein et al., 2018), and offer many emerging epidemiological, ecological, and evolutionary research opportunities (Gonzálvez et al., 2021; Moleón et al., 2017, 2020; Moleón and Sánchez-Zapata, 2021). Our findings support the view that the indirect, nonconsumptive effects of parasites may strongly influence host behaviour, with potential effects that propagate through food-webs (Buck et al., 2018; Moleón and Sánchez-Zapata, 2021; Sarabian et al., 2018). From an epidemiological context, the role of carnivore carrion in the transmission of meat-borne pathogens at the wildlife-domestic-human interface, many of which have relevant zoonotic implications (e.g., *Trichinella* spp.), seems questionable. We have also shown the advantages of detailed behavioural studies that use camera-trapping and combine different metrics to test — and challenge — widely accepted assumptions on meat-borne parasite transmission. Future research may benefit from our conceptual model, which allows making predictions on the decisions of carnivores foraging at carcasses of different nature (including different parts of carcasses, which may differ in both nutritional quality and parasite presence and abundance) and in different ecological contexts (e.g., different scavenger communities, which may influence risk perception). This conceptual model may be further expanded by adding the predation risks associated with carcasses, especially in areas with top predators that may prey upon subordinate carnivores (Allen et al., 2015; Moleón and Sánchez-Zapata, 2021). Exploring how animal species and individuals recognize and respond to cues associated with parasite risk may help in our understanding of the ecological and evolutionary relationships between carnivore hosts and their parasites, and is fundamental to efficiently manage zoonotic diseases under global change scenarios.

Funding

M.M. was supported by a research contract Ramón y Cajal from the MINECO (RYC-2015-19231). This study was partly funded by the Spanish Ministry of Economy, Industry and Competitiveness and EU ERDF funds through the project CGL2017-89905-R.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Wayne M. Getz provided critical comments to an earlier version. Gerard Valls, Judith Jiménez, Eva Cutillas and Clara Muñoz helped during the fieldwork.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2021.105462.

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